USING LANDSCAPE SIMULATION MODELS TO HELP BALANCE CONFLICTING GOALS IN CHANGING FORESTS

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USING LANDSCAPE SIMULATION MODELS TO HELP BALANCE CONFLICTING GOALS IN CHANGING FORESTS

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EDITORIAL
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Editorial: Using Landscape Simulation Models to Help Balance Conflicting Goals in Changing Forests

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Editorial on the Research Topic

Using Landscape Simulation Models to Help Balance Conflicting Goals in Changing Forests

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Forest ecosystems have long been affected by forestry practices and climate change will have additional affects (Soja et al., 2007; Boulanger et al., 2017; Montoro Girona et al., 2018) on the distribution of tree species (Iverson and Prasad, 1998) and on natural disturbance regimes (Boulanger et al., 2014; Seidl et al., 2017; Navarro et al., 2018). As these effects will have strong economic and ecological implications, there are strong incentives to adapt forestry practices to mitigate anticipated negative effects of climate change, through for instance increasing uptake of carbon by vegetation (Lal, 2004), tree species diversification (Hof et al., 2017), and minimizing tree damage by natural disturbances (Noss, 2001; Montoro Girona et al., 2019; Lavoie et al., 2021). Such adaptations may have uncertain effects on other ecosystem services provided by forests (Noss, 2001; Hof and Hjältén, 2018). Thus, a good understanding of how forestry practices and climate change may affect forest dynamics is required if we want to safeguard the ecosystem services that forests provide and the biodiversity they host.

Landscape simulation models are useful tools to assess the effects of anthropogenic and natural disturbances as well as that of climate change on forests. They are primarily used in forestry management, but can also be valuable for other purposes (Xi et al., 2009). They provide valuable information on possibilities for increased carbon sequestration (Scheller et al., 2011), effects of bioenergy extraction (Hof et al., 2018), effectiveness of forest restoration practices (Hof and Hjältén, 2018), and biodiversity (Cadieux et al., 2019, 2020). The 13 articles collected in this research topic on "Using Landscape Simulation Models to Help Balance Conflicting Goals in Changing Forests" give an overview of current work on the use of simulation and modeling techniques to better understand the current and potential future effects of forestry practices and natural disturbances on ecosystem services provided by forests, and how to balance conflicting goals. In this spirit, Sturtevant and Fortin reviewed the recent progress in simulation and modeling techniques used to integrate the effects of disturbances across scales. Gustafson et al. enhanced the PnET-Succession of the forest landscape model LANDIS-II to allow simulation of waterlogged soils and their effects on tree growth and competition. They tested how these modifications to the model alter the water balance and its effect on tree growth and competition, while simulating species range expansion and contraction under climate change across a latitudinal gradient in Siberia.

Several articles addressed the balance between biodiversity conservation and resource extraction in forest landscapes. Biber et al. simulated forest biodiversity, carbon sequestration, and wood production for three combined climate and socio-economic scenarios in ten European forest landscapes. The projections revealed that there was generally no reduction in outcomes for biodiversity indicators with an increase in wood production and that net carbon uptake was not strongly correlated with biodiversity. Furthermore, levels of sustainable wood production varied widely across the landscapes. This demonstrates the complexity of simulating impacts of disturbances on forest ecosystem services across wide scales and stresses the need for individual studies because results cannot necessarily be transferred across time and space. Haga et al. simulated scenarios of potential conflicts between renewable energy and biodiversity conservation in a watershed in north-eastern Japan in the face of climate change. They showed that impacts of renewable energy extraction on biodiversity can be large and that careful planning is needed to balance decarbonization and biodiversity conservation. Pearman-Gillman et al. used a combination of species distribution models and landscape change models to assess how landscape change scenarios built around natural resource planning and socio-economic drivers affect wildlife distributions in the forests of New England, USA. They found that occurrence of most species declined under all scenarios, which emphasizes the importance of integrating such landscape change drivers to assess future suitability of an area for species. Mikusinski et al. assessed habitat suitability for low and high demanding forest specialist species in the network of high conservation value forests in boreal Sweden strengthened by older forests that have not been clear-felled in a long time. They showed that by adding the older forests to the existing conservation value forest network, substantial suitable area can be gained for low demanding species whilst additional habitat restoration is needed for high demanding species. Norris et al. examined the cumulative effects of multiple disturbances on future habitat for a near threatened songbird in Canada's western boreal forest by developing habitat suitability models and using simulation models to project future change in habitat availability under different management and fire regime scenarios. Their results indicate that forest management needs to adapt if we are to conserve specific birds. Micheletti et al. used a novel toolkit built in R to forecast the combined direct and indirect effects of climate pathways, including their interactions and feedbacks, on birds in Canada. They found that, especially due to direct climate effects, the amount of suitable habitat would increase in future for 73% of species assessed. They suggest that hybrid approaches using statistical models and landscape simulation tools could improve forecasts of wildlife presence. Leston et al. projected how boreal birds will respond to cumulative effects of harvest plans, natural disturbances, conservation strategies, and energy-sector development in Alberta, Canada. They evidenced that harvest plans increased habitat for most species associated with forests older than 50 years, but that fire generally reduced the relative amount of habitat for these species. They conclude that multiple anthropogenic impacts should be considered in conservation and land use planning.

Other articles in the collection were focused on the balance between the management of several natural resources. De Jager et al. simulated the impacts of climate change and moose (*Alces alces*) browsing rates on the forests of Isle Royale National Park, USA. Their results suggest that the effects of current moose population management may not be effective in future, because moose may not be able to persist on the island any longer due to decreasing productivity of the vegetation. Robinne et al. used a conservation planning approach to compare nine scenarios of retention harvesting in a boreal mixed wood forest, Canada. Their findings allow assessments of trade-offs between timber production and conservation goals. Lundholm et al. incorporated ecosystem service indicators in a Forest Management Decision Support System (Remsoft Woodstock) that can deal with climate change and dynamic timber markets and analyzed the impact that intensified forest management will have on such indicators in the face of climate change in Ireland. The system they developed can be applied to other forest landscapes across Europe, and by stakeholders that use Remsoft Woodstock. Suárez-Muñoz et al. give a step-by-step workflow to initialize and calibrate a frequently used forest landscape model in a forest landscape in the Mediterranean mountains in Europe and thoroughly test model behavior. As such, this article may greatly benefit and guide new users of such models.

This series of papers stresses the importance of combining models and approaches to address current forest management issues under climate change to maintain ecosystem services provided by forests as well as conserve biodiversity. Despite these developments, we can conclude that we still need to (1) increase our understanding of how successional pathways will be influenced by the sequence of disturbances and drivers, (2) improve the accuracy and availability of parameters needed for models, especially regarding natural disturbances at regional scales, (3) develop new or enhance existing modeling tools to be able to simulate e.g., the impact of other natural disturbances, invasive species propagation, terrestrial and aquatic interactions, understorey vegetation, (4) integrate or augment interactions and feedback loops among ecological processes (for example, annual vegetation changes to affect annual wildfire forecasts, which in turn affect subsequent vegetation). More multidisciplinary scientific collaboration is needed at an international level to create a powerful and useful network of ecological modelers able to include these methodological challenges. Furthermore, collaboration between policymakers and the scientific community is essential to transfer and apply findings in climate change policies.

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AH, MMG, JT, and M-JF: conceptualization, writing original draft, and writing—review and editing. All authors contributed to the article and approved the submitted version.

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Scenario Analysis of Renewable Energy–Biodiversity Nexuses Using a Forest Landscape Model

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The introduction of renewable energy (RE) is essential for building a sustainable society. However, RE can cause conflicts between energy production and biodiversity conservation. This study conducted a scenario analysis to evaluate potential conflicts in the nexuses between energy and biodiversity for the Bekambeushi River watershed located in northeastern Japan. The increasing rate of pastureland abandonment resulting from a declining farmer population is a source of great uncertainty in this area. Two alternative sources of RE were selected to utilize these abandoned pasturelands, each taking a unique approach to meet targets stipulated by regional energy plans, thereby producing different ecological consequences at the landscape scale. Thirty-one RE introduction options were simulated, comprising a range of pastureland abandonment expansion speeds and ratios of solar photovoltaic (PV) plant installation to biomass energy use. These were superimposed using two IPCC representative concentration pathway (RCP) scenarios, 2.6 and 8.5, resulting in 62 scenarios that were summarized as three groups based on the RE supply–demand balance and the ecological impacts. The LANDIS-II model was used to simulate these scenarios from 2016 to 2100. The results indicate that both the rate of pastureland abandonment and the ratio of the two RE sources had a large impact on changes in tree species diversity and the habitat suitability of raptors. Abandoned pastureland converted to tree biomass energy production shifted to pioneer species-dominated forest. The plant species composition of transitional forests varied between the climate scenarios. The higher temperature of the RCP 8.5 scenario toward 2100 prevented the establishment of *Betula platyphylla* and altered tree species diversity and the habitat suitability of *Ketupa blakistoni blakistoni*. Biomass energy utilization produced less energy than the demand but increased the three ecological indicators. Solar PV systems provided more energy than the regional demand, but the tree diversity and habitat suitability indices for two raptors declined. However, an appropriate mixture of the two RE sources satisfied the regional energy demand and maintained ecological conditions. Our results suggest that land–energy planning should consider energy–biodiversity nexuses to strike a balance between decarbonization and biodiversity conservation.

Keywords: climate change, renewable energy mix, farmland abandonment, solar power generation, woody biomass energy, LANDIS-II

INTRODUCTION

Building a decarbonized society has become a key global concern (UNFCCC, 2015). Currently, 186 parties have submitted a nationally determined contribution (NDC) aimed at limiting global warming to 1.5–2°C (UNFCCC, 2019). Japan's NDC pledged to reduce CO_2 emissions by 80% by 2050 (Cabinet Office, Government of Japan, 2016). In Japan, 86.3% of greenhouse gas emissions in 2016 were CO_2 from the energy sector (Ministry of the Environment, Japan [MOE], 2019a), and the government is planning to shift to a decarbonized energy supply system (Ministry of the Environment, Japan [MOE], 2018, 2019b). However, the *Special Report on Global Warming of* 1.5°C (IPCC, 2018) suggested that the emission pathway reflecting the current NDCs will raise the global mean temperature by 3°C. Therefore, against the current situation, transformative changes in social systems are required to build a sustainable society (IPCC, 2018; IPBES, 2019).

Promoting the introduction of renewable energy (RE) plays a key role in reducing greenhouse gas emissions (IPCC, 2014), but its introduction could impose a burden on ecosystems, such as land use change during construction and maintenance during operation (Abbasi and Abbasi, 2000; Field et al., 2008; Gasparatos et al., 2017; Gibson et al., 2017). The IPBES also indicated the need for careful consideration of ecosystems when introducing RE (IPBES, 2019). The introduction of RE is related to the UN's Sustainable Development Goals (SDGs): Goal 7: Affordable and clean energy, Goal 13: Climate action, and Goal 15: Life on land (United Nations, 2015). Therefore, toward developing a post-2020 biodiversity framework, RE utilization constructed in harmony with nature is essential for building a sustainable society.

Previous global-scale studies have demonstrated trade-offs between biodiversity conservation and climate change mitigation, including the introduction of RE (de Vries et al., 2007; Santangeli et al., 2016a; Palomo et al., 2019). Santangeli et al. (2016b) identified the overlap of biodiversity conservation areas with high potential for crop, solar photovoltaic (PV), and wind energy production to identify areas that have a low impact on biodiversity. Harper et al. (2018) pointed out that the land use conversions of carbon-rich forests for energy crop production to mitigate climate change would reduce the total amount of carbon fixation by coupling an integrated assessment model (IAM) and a dynamic global vegetation model or DGVM. Ohashi et al. (2019) predicted changes in the habitats of 8,428 species using a species distribution model based on future land use under Shared Socioeconomic Pathways (SSPs) scenarios reflecting climate change mitigation measures calculated using an IAM and stated that habitat reduction due to climate change is greater than land use conversion under mitigation measures.

Local-scale studies have also indicated potential conflicts between the introduction of RE and biodiversity (Kienast et al., 2017). Tarr et al. (2017) calculated the future habitat suitability of 16 wildlife species under biomass energy harvesting scenarios using a spatially explicit state-and-transition model. Tarr et al. (2017) stated that bioenergy policies will cause trade-offs between species that require different ecological niches. Hori et al. (2016) and Hori et al. (2019) optimized the RE mix at a local scale by focusing on solar, hydro, wind, geothermal, and biomass resources and visualized trade-offs six indicators: the proportion of developed RE, economic balance between initial installation costs and returns from RE production, decrease in CO_2 emissions, circulation rate of biomass resource in a region, RE diversity, and area of potentially impacted ecosystem. Moore-O'Leary et al. (2017) described relationships between land, energy, and ecosystems as nexuses that invoke such trade-offs. The types and amount of RE sources are spatially distributed heterogeneously (Pogson et al., 2013), and the environmental impacts of RE utilization differ among RE sources (Abbasi and Abbasi, 2000; Gibson et al., 2017). Therefore, climate change mitigation plans need to be developed considering the nexuses between local RE resources and biodiversity conservation.

Quantitative models can effectively evaluate the impact of RE on ecosystems (Laranjeiro et al., 2018; Raoux et al., 2018). Future climate change will also affect local ecosystem conditions and alter the supply potentials of various ecosystem services (Cantarello et al., 2017). Most studies dealing with conflicts between the introduction of RE and biodiversity have only focused on changes in land use and land cover classes as state spaces of the Markov process (Costanza et al., 2015; Duden et al., 2017; Tarr et al., 2017). However, process-based models that simulate the climate change response of vegetation will provide robust and informative scientific suggestions (Gustafson et al., 2015; Keane et al., 2015) for maintaining future energy–biodiversity nexuses to local stakeholders.

A FLM is a process-based dynamic simulation model of vegetation succession at a landscape scale under future climate change (Xi et al., 2009; Shifley et al., 2017). Previous studies have applied FLMs to quantify the effects of human and natural disturbances, such as vegetation change caused by economic growth (Ward et al., 2005; Thompson et al., 2016; Duveneck and Thompson, 2019) and from a shrinking society (Haga et al., 2018; Sil et al., 2019). FLMs have also been used to simulate the impacts of aboveground and deadwood biomass harvesting for fuels on ecosystem services and the quality of wildlife habitats (see, for example, Creutzburg et al., 2016; Thompson et al., 2016; Hof et al., 2018).

Future social scenario narratives in the fields of both climate change and biodiversity and ecosystem services do not specify ecosystem management activities under decarbonization requirements at local scales (Millennium Ecosystem Assessment [MA], 2005; O'Neill et al., 2014). Therefore, the purpose of this study was to explore future scenarios that strike a balance between the introduction of RE and biodiversity conservation under changing climate and societal conditions using a process-based forest landscape model (FLM). The specific objectives were to (1) simulate ecosystem impacts and expected energy supply under mixed RE energy installation scenarios, (2) identify the RE–biodiversity nexuses in a local basin, and (3) explore the scenarios to meet both RE utilization and biodiversity conservation.

MATERIALS AND METHODS

We simulated vegetation succession under different land use scenarios and evaluated energy supply potential, ecosystem services, and ecological impacts using an FLM.

Study Area Description

The Bekambeushi River watershed in northeastern Japan, where RE introduction plans, such as woody biomass (Akkeshi town, 2018a) and a solar PV plant (Nikkei XTECH, 2018), are underway, was selected as the case study area (**Figure 1A**). The total area of the watershed is 700 km^2, with a small difference in elevation (maximum elevation = 141 m) (**Figure 1B**; Geosptial Information Authority of Japan [GSI], 2019). The forest and pastureland soils consist of Andosols (Obara et al., 2016). The current monthly mean air temperature ranges from −8 to 20°C and annual precipitation is 1200 mm (Esgf-CoG, 2017). In particular, changes in temperature are concerned, with the mean air temperature increase 1.4–5.0°C by 2100 under RCP scenarios (Esgf-CoG, 2017). Forests and pasture lands cover 70 and 20% of the watershed, respectively (**Figure 1C**; Biodiversity Center of Japan, 2017). The Bekambeushi River wetland was listed in the Ramsar Convention in 1993 (Akkeshi town, 2019a). In the national forest in the northern areas, the dominant species is *Larix kaempferi* (Lamb.) Carrière. In the private forest in the southern areas, the dominant species are Sakhalin fir [*Abies sachalinensis* (F. Schmid)] Mast.] and a mixed forest of Sakhalin fir and Japanese oak (*Quercus crispula* Blume). In this study area, deer browsing damages to agriculture and forestry are the major natural disturbances, and local government are working to capture them (Akkeshi town, 2018c).

The main industries are fisheries and aquaculture in Akkeshi Bay, Lake Akkeshi, and the offshore area; forestry in the national and private forests; and dairy farming (Akkeshi town, 2018b), but the rapid decline in primary industries is of major concern in the region. The total residential population in the watershed was 8,604 in 2010 and is projected to be 4,980 by 2050 (National Land Numerical Information [NLNI], 2017). The area of the clear-cutting and thinning of larch and Sakhalin fir for timber and pulp production has declined in recent years (Hokkaido Prefecture, 2019). The region's administrative documents reflect concern that the abandonment of pastureland will increase because of the declining population (Akkeshi town, 2019b). This decline is a baseline trend in Japan (National Institute of Population and Social Security Research [NIPSSR], 2018; Saito et al., 2018), especially in rural areas (Matsui et al., 2019).

Model Description

In this study, the LANDIS-II model, version 7.0 (Scheller et al., 2007), a widely applied FLM, was used to simulate the ecological impact of the introduction of RE. LANDIS-II is a modeling platform comprising a suite of extensions to simulate various establishment, growth, and disturbance processes. This modeling platform currently attempts to integrate growth and material cycles by referring to mechanistic models, such as the CENTURY soil organic matter model and PnET-II to expand its applicability to robust climate change impact assessment (Scheller et al., 2011; de Bruijn et al., 2014). The model computes vegetation succession at landscape scales by representing landscapes as grid cells. The state of vegetation in each grid cell is represented as a species–age cohort.

The Net Ecosystem Carbon and Nitrogen (NECN) Succession version 6.3 (Scheller et al., 2011), was used to simulate vegetation dynamics under climate change. The extension computes cohort establishment and biomass growth as functions of the environmental condition. The probability of establishment for each grid cell for each species is defined by a function of the minimum January temperature, soil and water, growing degree days (GDD), and light availability. The biomass growth is calculated as the balance between monthly net primary productivity (NPP) and mortality. The monthly NPP was computed by multiplying the monthly maximum NPP by the environmental limits in a grid cell: monthly mean temperature, plant-available soil N, the water and light availability, and density effects. Species and functional group parameters were determined in reference to Haga et al. (2018) and the default value of the CENTURY soil organic matter model (see **Supplementary Material 1**). We calibrated the NECN succession extension by comparing the simulated and observed aboveground biomass (AGB) growth and litterfall (see **Supplementary Material 2**).

Settings for the Introduction of Renewable Energy Scenarios

In a shrinking society, there are great uncertainties around the presence of unused land and how to use it (Shoyama et al., 2018). Therefore, we designed 31 scenarios of land use and RE introduction from 2016 to 2100 comprising varied speeds of pastureland abandonment expansion and ratios of solar PV plant installation to biomass energy use (**Table 1**). First, six scenarios for pastureland abandonment expansion speed were set (**Table 1**). The lowest speed scenario was 0 ha year^{-1}, maintaining all pastureland to 2100. In the highest speed scenario, we assumed that pastureland would be abandoned at the same speed of population decline. Therefore, the area of abandoned pastureland increased to 42% of the current pastureland in 2050 according to

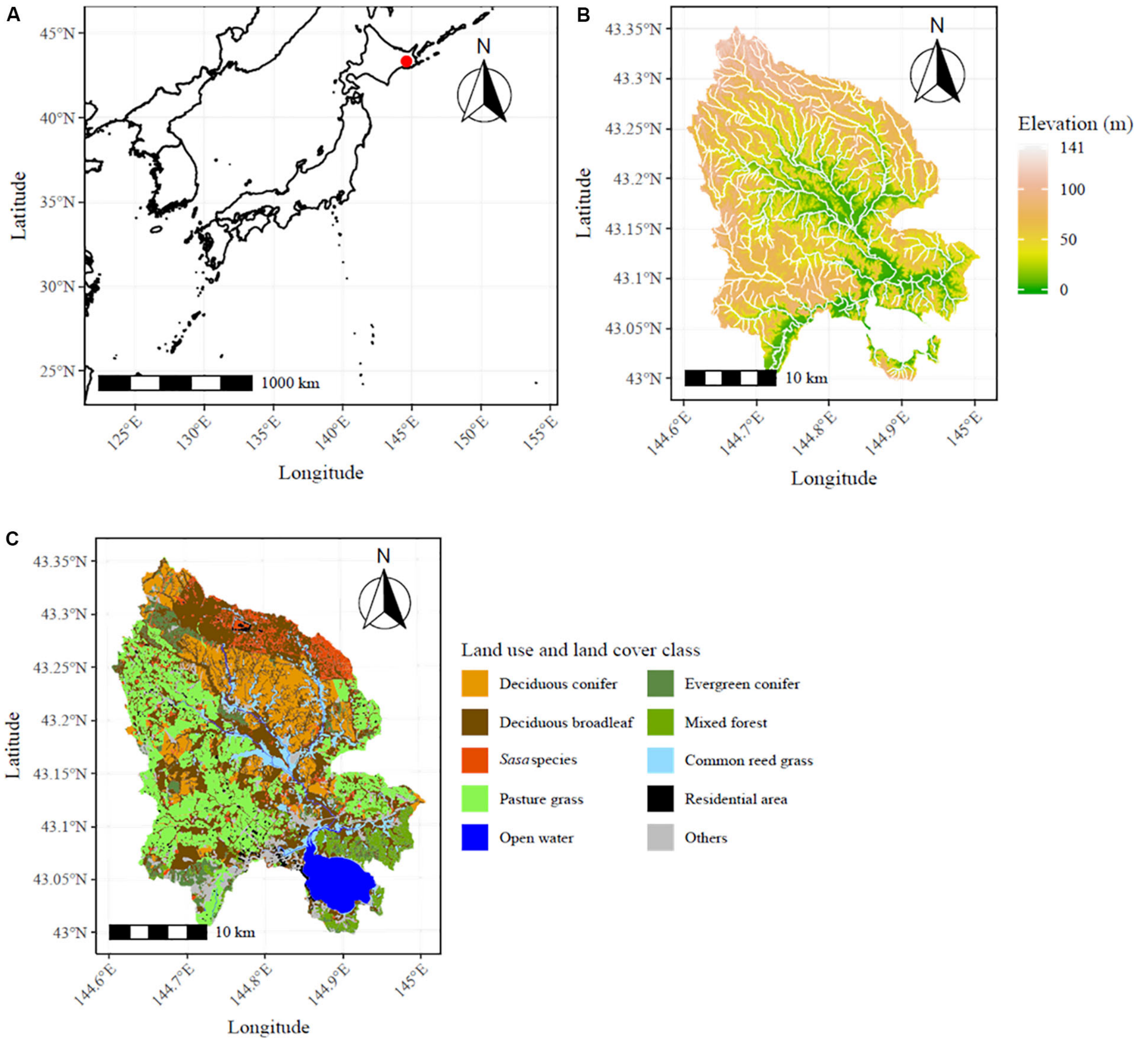

FIGURE 1 | Description of the study area. **(A)** The location of the Bekambeushi River watershed (red dot), **(B)** the digital elevation model and distribution of rivers (white lines), and **(C)** the vegetation distribution.

a population decline of 58%. The other four scenarios were set at equal intervals between 0 and 223 ha year^{-1} (**Table 1**).

For each pastureland abandonment scenario, the locations of the abandoned pastureland were determined using a *Manageability* index that considered the multiple socio-geographical conditions of each grid cell. The index assumes that a grid cell with a lower population in the nearest residential area, a farther the distance to the residential area and the nearest road, a larger slope, higher elevation, and the smaller the pastureland patch area, the lower the *Manageability* (Haga et al., 2018; Kobayashi and Nakamura, 2018). Pastureland grid cells with lower *Manageability* were abandoned first. *Manageability* was calculated as follows:

$$Manageability_i = \frac{pop_i}{distToResi_i} \times \frac{1}{distToRoad_i} \times \frac{1}{meaSlope_i} \times \frac{1}{meaElev_i} \times patchArea_i \qquad (1)$$

where $Manageability_i$ is the manageability of grid cell i; pop_i; and $distToResi_i$ are the population and the distance to the nearest residential grid cell in 2050 from the grid cell i (m), respectively (National Land Numerical Information [NLNI], 2017); and $distToRoad_i$is the distance to the nearest road from the grid cell i (m). $meaSlope_i$ and $meaElev_i$ denote the mean slope (degree) and elevation (m) of grid cell$i$, respectively. $patchArea_i$ is the area of the pastureland patch in which the grid cell i belongs (m^2).

The following two types of abandoned pastureland were excluded from any RE introduction: abandoned pastureland (1) within 300 m of a river or (2) with a wetland history. The former was to conserve riparian forest, which is an ecologically and culturally important ecosystem (Nakaoka et al., 2018), and the latter was because the pastureland has the potential to become wetland (Morimoto et al., 2017). Wetland history was identified using a 1920s historical topographical map (Kaneko et al., 2008).

TABLE 1 | Pastureland management and renewable energy introduction scenarios.

	Scenarios
Annual pastureland abandonment expansion speed (ha $year^{-1}$)	A0: All pastureland will be managed
	A45: 45 ha $year^{-1}$
	A89: 89 ha $year^{-1}$
	A134: 134 ha $year^{-1}$
	A178: 178 ha $year^{-1}$
	A223: 223 ha $year^{-1}$
Solar photovoltaic (PV) plant installation and biomass energy use mix	S0.0: No solar PV plant installation
	S0.2: 20% of abandoned pastureland used for solar PV plant installation
	S0.4: 40%
	S0.6: 60%
	S0.8: 80%
	S1.0: 100%

Abandoned pastureland was categorized as two types of land use according to the distance to the nearest forest for each year: land for producing solar energy and land for obtaining woody biomass energy. This allocation was based on the development policy that solar PV plants are initially installed on abandoned pastureland far away from forests to minimize impacts on wildlife, with the balance of the abandoned pastureland used for biomass energy production. Six ratios were used to represent the mixture of solar PV plants and woody biomass energy scenarios (**Table 1**).

The AGB of all tree species in the abandoned pastureland used for biomass energy production was harvested. Under the current climate condition, Japanese white birch (*Betula platyphylla* Sukaczev var. japonica) is the representative regional pioneer species expected to establish on the abandoned pastureland. Therefore, we clear-cut all the tree species in the abandoned pastureland for biomass energy production where it contained 25-year-old Japanese white birch, the maximum growth period. No species were planted after the clear-cutting because natural regeneration was expected. On the abandoned pastureland used for solar PV plants, all the grass and tree species were removed every year for the maintenance of the solar PV panels.

Simulation Settings Common for All Scenarios

The NECN succession extension requires spatially explicit initial conditions for both the age and AGB for each plant species. We created an initial tree species distribution at 100 m resolution. Plant species distribution was obtained from a vegetation map that recorded community names (Biodiversity Center of Japan, 2017). The dominant plant communities, which cover 95% of the watershed, were selected for the simulation (**Supplementary Table 4**), and seven tree species and two grass species were selected as a result (**Table 2**). The initial age and AGB were set according to the forest registers of the national, prefectural, and private forests (Hokkaido Prefecture, 2017a,b; Ministry of Agriculture Forestry and Fisheries [MAFF], 2017).

TABLE 2 | List of simulated species.

Common names	**Scientific names**
Japanese white birch	*Betula platyphylla* Sukaczev var. japonica (Miq.) H. Hara
Japanese ash	*Fraxinus mandshurica* Rupr.
Japanese oak	*Quercus crispula* Blume
Japanese elm	*Ulmus davidiana* Planch. var. japonica (Rehder) Nakai
Japanese alder	*Alnus japonica* (Thunb.) Steud.
Larch	*Larix kaempferi* (Lamb.) Carrière
Sakhalin fir	*Abies sachalinensis* (F. Schmidt) Mast.
Pasture grass	–
Sasa species	–

Soil organic matter (SOM) content, soil depth and properties related to soil carbon and water dynamics were determined uniformly for each forest and pasture from the literature (Hokkaido National Agricultural Experiment Station, 1983). The decomposition rates of SOM were set according to the calibration criteria proposed in the previous study (Lucash et al., 2019).

The Biomass Harvest extension, version 4.3, was used to apply the same forest management practice to all scenarios referring to the regional standard plan (Akkeshi town, 2017; Hokkaido Prefecture, 2017c; **Supplementary Table 4**). The target species were larch, Sakhalin fir, and Japanese oak. In the timber production forest, the target species were clear-cut and replanted. In the conservation area, such as the riparian forest, selective cutting and planting of the target species were conducted. Thinning was applied to cohorts that reached the thinning age used as standard practice in this area (Akkeshi town, 2017; Hokkaido Prefecture, 2017c).

Representative concentration pathway (RCP) 2.6 and 8.5 scenarios (IPCC, 2013) calculated by the MRI-CGCM3 model (Esgf-CoG, 2017) were selected as the climate data to evaluate uncertainty corresponding to climate change. To correct for bias between the MRI-CGCM3 data and the observations, monthly mean temperature and monthly precipitation offsets were determined by comparing data from the model and the Ota Meteorological Observatory (Japan Meteorological Agency, 2018; **Supplementary Table 5**). In total, 62 simulations, a combination of the 31 RE introduction scenarios and the two climate scenarios were conducted from 2016 to 2100.

Evaluation Indicators

Renewable energy production and three ecological indicators were evaluated as follows using the simulated land use and land cover (LULC) changes, AGB, and harvested biomass. R, version 3.6.3 (R Core Team, 2019) was used for the analysis.

Renewable Energy Supply

The amount of RE supply was estimated as heat energy. First, the heat energy obtained by burning the woody biomass (TJ $year^{-1}$) was calculated (Tatebayashi et al., 2015) by assuming that all harvested AGB (oven-dry kg biomass $year^{-1}$) obtained from the abandoned pastureland and forest thinning was used for pellets. The moisture content, yield rate, and lower calorific value were set to 10, 80%, and 16.0 MJ kg^{-1} (Japan Wood Pellet Association, 2017). Harvested biomass is storable, so a 5 years moving average was used to evaluate the expected amount of heat energy per year.

Second, the amount of the electrical energy generated by the solar PV plants was calculated by multiplying the total area of the solar PV plants per year (m^2) with a basic unit of annual power generation. We used 61.58 kWh m^{-2} year^{-1} as the basic unit, as used in a previous RE estimation procedure (Ministry of the Environment, Japan [MOE], 2010). This generated electrical energy was then converted to heat energy (TJ year^{-1}) by multiplying with a conversion unit of 3.6×10^6.

Ecological Impacts

Three ecological indicators were evaluated: plant species diversity and two habitat suitability indices (HSI), the mountain hawk-eagle (*Spizaetus nipalensis orientalis*) and the Blakiston's fish owl (*Ketupa blakistoni blakistoni*).

The Shannon–Wiener diversity indices for the plant species were calculated using the simulated AGB for each grid cell. Abandoned pastureland converted to solar PV plants was regarded as a zero diversity index. Abandoned pastureland with a wetland history was also set to zero because the land was excluded from the LANDIS-II simulation.

We calculated the habitat suitability indices for the mountain hawk-eagle and the Blakiston's fish owl, which have different ecological niches, as representative species affected by the land use changes. The mountain hawk-eagle is a raptorial bird, 70–80 cm in length, that lives in steeply sloping mountain forests (Ministry of the Environment, Japan [MOE], 2012). The eagle uses mature forests and forest edges to prey on small to medium reptiles, birds, and mammals living in the forest (Ministry of the Environment, Japan [MOE], 2012). A habitat suitability index for the mountain hawk-eagle was calculated with a 1 km resolution using the following (Itoh et al., 2012):

$$\log \frac{p_s}{1 - p_s} = -12.7853 + 0.0018 \times X_1 + 0.0987 \times X_2 + 0.1071 \times X_3 + 0.0879 \times X_4 + 0.0851 \times X_5 + 0.0001 \times X_6 \qquad (2)$$

where p_s is the habitat suitability index for the mountain hawk-eagle for each 1 km grid cell; X_1 and X_2 are the mean elevation (m) and slope (degree) of the grid cell, respectively; X_3 is the occupancy of the broadleaf forest and mixed forest area of the grid cell; X_4 is the occupancy of the plantation *Cryptomeria japonica* (L.f.) D. Don and *Chamaecyparis obtusa* (Siebold et Zucc.) Endl. of the grid cell; X_5 is the occupancy of open area suitable for foraging activities in the grid cell; and X_6 is the length of forest edge (m) between the open area and forests in the grid cell. For X_3, if the AGB of the broadleaf species occupy more than 30% of the total AGB for each 1 km grid, the grid was identified as broadleaf and mixed forest. X_4 was set to zero for all grids because these tree species are not distributed in the study area. Pastureland, grassland, and wetland were regarded as open areas for X_5 and X_6. A previous study reported that solar PV plants contribute to increases in the populations of small grassland birds (Kitazawa et al., 2019). However, because there is concern that the feeding behavior of raptors could be hindered by solar PV plants (Walston et al., 2016), we excluded the solar PV plants.

The Blakiston's fish owl is a nocturnal raptor with a total length of ~70 cm. In 2018, the owls were only living in Hokkaido, Japan, and are classified as a critically endangered species (Ministry of the Environment, Japan [MOE], 2019c). This owl preys mainly on fish and amphibians and normally nests in tree cavities in riparian forests (Yoshii et al., 2018), however, successful cases of nesting in artificially installed nest boxes have been confirmed (Takenaka, 2018). Therefore, habitat suitability for the Blakiston's fish owl was calculated for each grid with a 4 km resolution using the following (Yoshii et al., 2018):

$$\log \frac{p_k}{1 - p_k} = -23.36 + 9.32 \times 10^{-3} \times Y_1 + 5.026 \times log\left(Y_2 + 1\right) - 0.326 \times \left\{log\left(Y_2 + 1\right)\right\}^2 \qquad (3)$$

where $p_k$is the habitat suitability index for the owl for each 4 km grid cell, Y_1 is the total area (m^2) of riparian natural forest within 300 m of rivers (National Land Numerical Information [NLNI], 2009) for each grid cell, and Y_2 is the total length (m) of rivers for each grid cell. The current species composition in natural forests in this region is *Abies sachalinensis*, *Abies sachalinensis-Quercus crispula*, *Ulmus davidiana*, *Alnus japonica*, and *Alnus japonica-Fraxinus mandshurica* communities (Biodiversity Center of Japan, 2017). If riparian forests within 300 m of rivers consisted of these species and had not been either clear-cut or planted, we categorized them as natural forests. Regular maintenance activities for solar PV systems near riparian forests may diminish the breeding success of the owl; therefore, we excluded riparian natural forests within 300 m of solar PV plants in the calculation (Takenaka, 2018).

Finally, 62 scenarios were summarized into three groups by referring to the balance between the mean RE production from 2090 to 2100 and the total energy demand of the area in 2010. We evaluated the relative ecological impacts of land use change, RE introduction, and climate change for each scenario by comparing mean values from 2090 to 2100 for the three ecological indicators.

RESULTS

Changes in LULC and Aboveground Biomass

In the A0 scenario, which maintains all pastureland, the changes in both LULC and AGB differed between the RCP scenarios (**Figure 2**). However, Japanese white birch forest shifted to the other broadleaf forests regardless of the RCP scenario, but this trend was accelerated in the RCP 8.5 scenario (**Figure 2A**). The birch forest declined from 137 to 26 km^2 in 2100 and shifted to Japanese alder after 2050 in the RCP 8.5 scenario (**Figure 2A** and **Supplementary Table 6**). The total changes, including both an increase and a decrease in area, were the highest among the pioneer species, such as the Japanese birch and Japanese alder, and the target forestry species, such as larch and Sakhalin fir (**Figure 2A**; total change in **Supplementary Table 6**). These two pioneer species and the larch forest shifted to the other

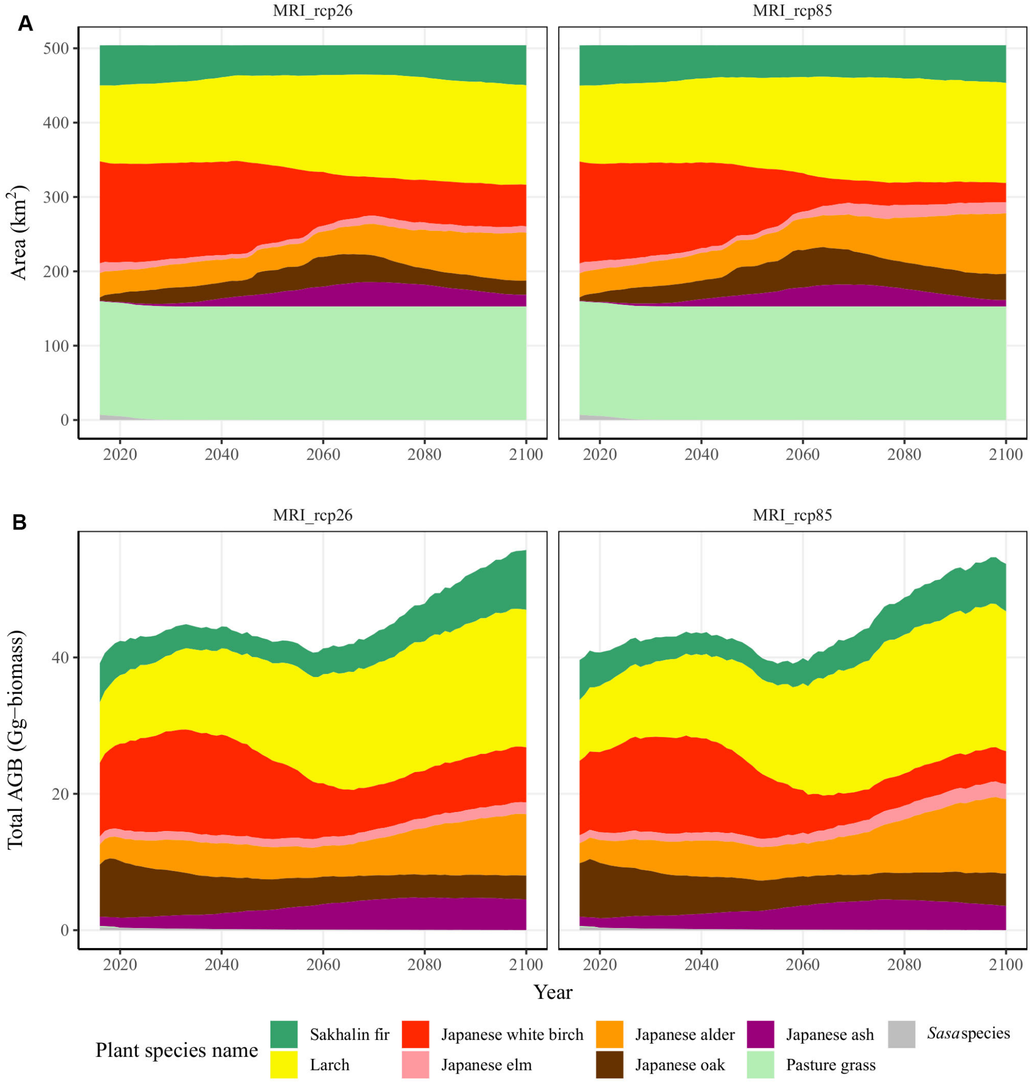

FIGURE 2 | Changes in the **(A)** land use and land cover and **(B)** the total aboveground biomass (AGB) for the scenario with no pastureland abandonment expansion (A0) for two climate scenarios (left = IPCC RCP 2.6 and right = IPCC RCP 8.5). The colors indicate the nine plant species simulated in this study.

species (net change in **Supplementary Table 6**). The total area of Sakhalin fir forest was maintained (**Supplementary Table 6**). With an increasing area of alder forest, the total AGB within the watershed reached 55.8 and 53.7 Gg biomass in the RCP 2.6 and 8.5 scenarios, respectively (**Figure 2B**). In the RCP 8.5 scenario, the AGB of Sakhalin fir, Japanese alder, and Japanese ash declined by 20–40%, and the AGB of Japanese white birch and Japanese oak increased by 22–36% (**Figure 2B**).

In the RE introduction scenarios, the abandoned pastureland was shifted to broadleaf forests and wetlands or converted to solar PV plants (**Supplementary Figures 7A,B**). In the 1920s, 8% of the pastureland was wetland, and these converted pasturelands were returned to wetlands after being abandoned. In the abandoned pastureland converted to tree biomass energy production, pioneer species, such as Japanese white birch and Japanese alder, were established. Like the changes in the forests, the AGB of alder increased toward 2100 in the RCP 8.5 scenario (**Supplementary Figures 7A,B**). In the riparian forest, especially, the total AGB increased up to 3 and 5 Gg biomass with increasing Japanese alder in the RCP 2.6 and 8.5 scenarios, respectively. In the abandoned pastureland used for tree biomass energy production, Japanese white birch declined in the RCP 8.5 scenario, and thus, the total AGB in 2100 was 15 and 13 Gg biomass in the RCP 2.6 and 8.5 scenarios, respectively.

The distribution of Japanese white birch and Japanese alder in Japan ranges between 958–2,598 and 1,066–2,842 degrees in annual GDD, respectively (5°C base threshold). The Japanese alder is thus distributed in a warmer environment than the Japanese white birch (Forestry Agency of Japan, 2019; National Land Numerical Information [NLNI], 2012). The Japanese white birch is the representative pioneer plant species in this region under the current climate (Resco de Dios et al., 2005). In the RCP

2.6 scenario, the Japanese white birch successfully established on abandoned pastureland until 2100 because the temperature changes were relatively small (**Figure 2** and **Supplementary Figures 5, 9**). However, only the Japanese alder had the potential to establish because the mean annual temperature rose by 5°C in 2100 in the RCP 8.5 scenario compared with the current climate (**Figure 2** and **Supplementary Figures 5, 9**).

Ecological Impacts

Figure 3 shows the trends of the three ecological indicators and the RE supply for each scenario.

In the no pastureland abandonment scenario (A0), selective cutting and planting of broadleaf species increased the Shannon–Wiener diversity index, increasing the mean value within the watershed from 0.04 to 0.08 toward 2100 (**Figure 3**). After 2060, the diversity index decreased due to the increased occupancy of Japanese alder. The same trend was observed for the A45–A223 scenarios. In the faster pastureland-abandonment expansion speed scenarios, the diversity index linearly increased with the expansion of secondary forest established on the abandoned pastureland. The introduction of solar PV plants decreased the diversity index compared with the same expansion speed scenarios. In the RCP 8.5 scenario, higher temperatures increased the AGB of Japanese alder, and the diversity index was lower than for the RCP 2.6 scenario.

Without pastureland abandonment, the habitat suitability index for the mountain hawk-eagle increased toward 2030 and then decreased to 0.03 by the end of this century because the area of broadleaf forest and mixed forest decreased due to the increase in larch and Sakhalin fir biomass (**Figure 3** and **Supplementary Figure 8**). In the scenarios that used abandoned pastureland to supply only woody biomass (S0.0), the HSI_s increased with increasing pastureland abandonment expansion speed. The A223-S0.0 scenario resulted in the highest HSI (0.04) among the RE introduction scenarios in 2100. The HSI decreased with the introduction of solar PV plants compared with scenarios with the same abandonment rate, and the difference in index values between the RCP scenarios was the smallest among the ecological indicators (**Figure 3**).

The mean of the HSI for the Blakiston's fish owl (i.e., HSI_k) increased from 0.07 to 0.12 toward 2100 in the A0 scenario (**Figure 3**). In the A45–A223 scenarios, the riparian forest area increased with the expansion of pastureland abandonment and the mean value increased (**Figure 3**). The higher temperature of the RCP 8.5 scenario increased the AGB of Japanese alder, categorized as natural forest, within 300 m of rivers (**Supplementary Figure 7B**). The mean HSI value for the owl thus increased, especially, in the RCP 8.5 scenario, however, the greater introduction of solar PV plants increased the area of riparian forests adjacent to the solar panels (**Supplementary Figure 8**), decreasing the index value (**Figure 3**).

Renewable Energy Production

The total RE supply in 2100 varied from 3.6×10^{-1} PJ in the A0 scenario to 1.3×10 PJ in the A223-S1.0 scenario (**Figure 3** and **Supplementary Table 10**). Tree biomass harvesting from abandoned pastureland emerged around 2040. The amount of harvested AGB fluctuated yearly because the spatial distribution of AGB from abandoned pastureland was affected by seed dispersal from surrounding forests. The amount of energy provided by solar PV plants increased in proportion to the expansion of abandoned pastureland.

Features of the 62 Scenarios

The total energy demand in this watershed was 1.3 PJ in 2010 (Hori et al., 2016). As shown in **Figure 3**, RE introduction scenarios had the potential to supply 28–998% of the regional energy demand. The 62 scenarios were thus classified into three scenarios: scenario 1, where energy production was less than the energy demand ($N = 14$); scenario 2, where RE production satisfied the energy demand and was less than five times the demand ($N = 29$); and scenario 3, where RE production satisfied the energy demand and was more than five times the RE demand ($N = 19$) (**Figure 4** and **Supplementary Table 10**).

Group 1 included the scenarios where the solar PV mixture rate was zero (S0.0) and the A45-S0.2 scenario where the area of abandoned pastureland was small and the number of installed solar PV plants was low (**Figure 4** and **Supplementary Table 10**). The amount of RE supply ranged from 3.6×10^{-1} PJ in the A0-S0.0 scenario to 1.3 PJ in the A45-S0.2 scenario (**Figure 3**). In group 1, all three ecological indicators around 2100 were higher than for the A0 scenario (**Figure 4**). In group 2, scenarios with a lower solar PV plant fraction (S0.2) maintained the three ecological indicators, whereas the higher fraction (S0.4-1.0) diminished the HSI of the mountain hawk-eagle (**Figure 4** and **Supplementary Table 10**). The habitat suitability of the Blakiston's fish owl also declined with increasing solar PV plant fraction but was higher than that of the A0 scenario (**Figure 4** and **Supplementary Table 10**). In group 3, the solar PV plant fractions for all scenarios were greater than 60% (**Figure 4**). The HSI for the mountain hawk-eagle was lower than for the A0 scenario in all scenarios in group 3 (**Figure 4**). Scenarios that relied on only solar PV plants demonstrated a greater decline in the HSI for the Blakiston's fish owl than for the A0 scenario (**Supplementary Table 10**).

DISCUSSION

This study simulated a vegetation succession by considering multiple disturbances, climate change, pastureland abandonment, and two types of RE introduction and visualized the impact on plant species diversity and the habitat suitability of two raptorial birds. The following sections identify the nexuses among these disturbances and the vegetation and wildlife habitat quality and discuss the ecosystem management required to strike a balance between RE introduction and biodiversity conservation.

Climate–Vegetation–Habitat Quality Nexus on Abandoned Pasturelands

The differences in both the establishment probability and seed dispersal ability of the two pioneer species affected the

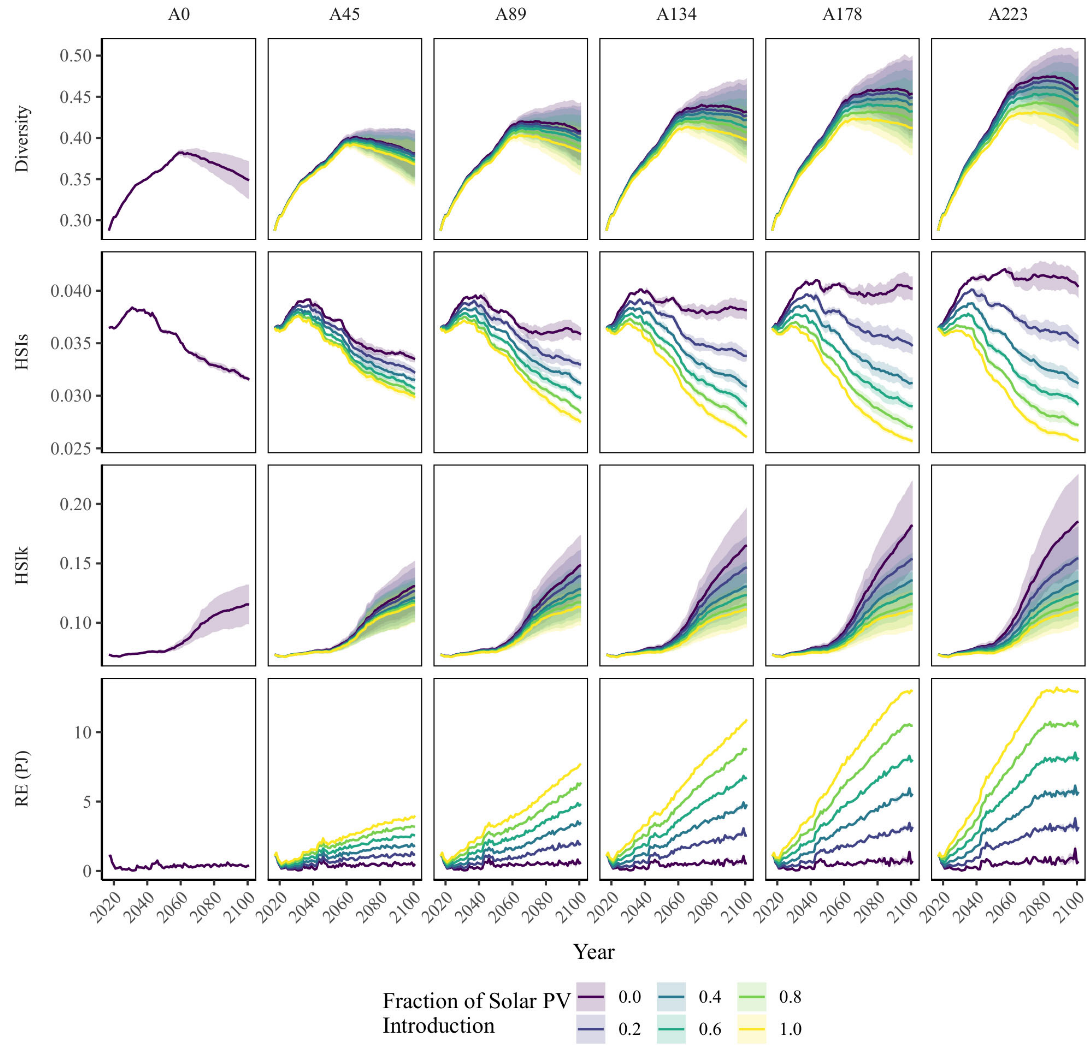

FIGURE 3 | IPCC RCP 2.6 and 8.5 scenarios for the three ecological indicators and renewable energy (RE) production potential from 2016 to 2100 for the 62 scenarios. Each line represents the mean between the two RCP scenarios, and the difference between the scenarios is represented by shading. A0–A223 represent the pastureland abandonment expansion speed, and the colors indicate the solar PV plant fraction (**Table 1**). Diversity = Shannon–Wiener diversity index, HSI$_S$ = habitat suitability index for the mountain hawk-eagle (*Spizaetus nipalensis orientalis*), HSI$_K$ = habitat suitability index for Blakiston's fish owl (*Ketupa blakistoni blakistoni*), and RE = the total renewable energy supply from tree biomass utilization and solar PV plants.

total AGB of Japanese alder from 2050 as the difference in temperatures between the two climatic scenarios became larger (**Supplementary Figure 5**) and created trade-offs between the plant species diversity indices, the HSI for the Blakiston's fish owl, and the total biomass of the abandoned pastureland (**Figure 2**). On the abandoned pasturelands converted for biomass energy production, the Japanese alder biomass also increased in the RCP 8.5 scenario, but the total biomass was lower than for the RCP 2.6 scenario (**Supplementary Figure 7A**). In these abandoned pasturelands, it became harder for seeds supplied by the Japanese birch that had been distributed near the pasturelands to establish, resulting in a decrease in total biomass (**Supplementary Figure 7A**). Previous studies have estimated the potential habitat of broadleaf tree species in eastern Asia under future climate change using species distribution models (see, for example, Tanaka et al., 2012; Nakao et al., 2013). To understand nexus among climate change and biodiversity, our results further demonstrate the need to model climate change impacts on multiple species dynamics considering species traits, distribution ability, and spatial distributions of plant species at finer scales.

Previous studies have shown that the effects of climate change become more significant and uncertain toward the end of this century (Lucash et al., 2019; Ohashi et al., 2019), and our results are also consistent with this finding (**Figure 3**). Moreover, pioneer species dynamics were dominant in this study, suggesting the need for longer-term simulations beyond 2100. Although governments and international organizations often develop future social scenario narratives for toward 2030 or

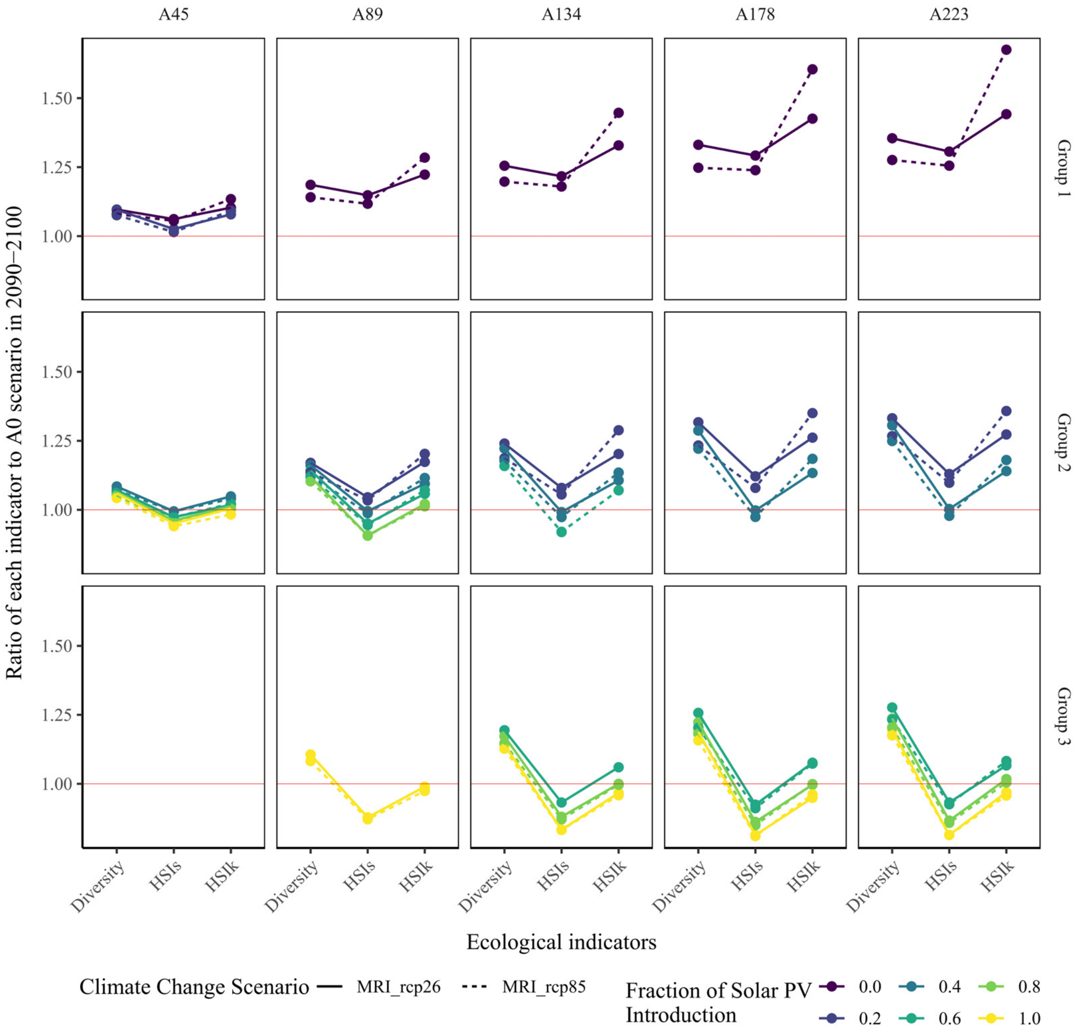

FIGURE 4 | Ratio of each ecological indicator to the no pastureland abandonment scenario (A0) from 2090 to 2100 by pastureland abandonment expansion speed and level of renewable energy production. The red line indicates the same indicator value as the A0 scenario. Values over 1.0 indicate that the ecological indicators are better than the A0 scenario. Three scenario groups were identified based on the balance between renewable energy (RE) supply and demand: group 1, where energy production is less than energy demand; group 2, where RE production satisfies the energy demand and is less than five times the demand; and group 3, where RE production satisfies the energy demand and is more than five times the RE demand. Diversity = Shannon–Wiener diversity index, HSI_S = habitat suitability index for the mountain hawk-eagle (*Spizaetus nipalensis orientalis*), HSI_K = habitat suitability index for Blakiston's fish owl (*Ketupa blakistoni blakistoni*). A0–A223 represents the pastureland abandonment expansion speed, and the colors indicate the solar PV plant fraction (**Table 1**).

2050 (United Nations, 2015; Predicting and Assessing Natural Capital and Ecosystem Services [PANCES], 2016; IPBES, 2020), our work implies that longer-term future vision and ecosystem management plans are required for pre-emptive actions.

Pastureland Abandonment–Renewable Energy–Raptorial Bird Habitat Nexus

Pastureland abandonment led to the expansion of mixed forests of broadleaf and conifer at landscape scales and, thus, increased the diversity and habitat suitability of the two raptorial birds (**Figure 3**). However, the decrease in the area of managed pastureland caused the loss of open areas and forest edge, which are used by the mountain hawk-eagle. For this reason, the HSI for the mountain hawk-eagle diminished or remained the same after 2030 (**Figure 3** and **Supplementary Figure 8**). In particular, the change of pastureland to solar PV plants reduced the open area and length of forest edge suitable for foraging environments (**Supplementary Figure 8**). As societies shrink, local managers need to select important pasturelands and maintain a mosaic of different ecosystems on them to conserve biodiversity hotspots.

Solar PV plants were located away from forests and more than 300 m from riversides to conserve the foraging environment of the mountain hawk-eagle and the nesting sites of the Blakiston's fish owl. Therefore, in scenarios with the small fractions of solar PV plants, the three ecological indicators were improved compared with the A0 scenario, which maintained the current land use (**Figure 4**). These indicators were improved because the contribution of transitional forests on abandoned pastureland exceeded the ecological impacts associated with solar PV installation at the landscape scale. Our results suggest that a better understanding of the nexus between pastureland abandonment, the introduction of multiple RE sources, and raptorial bird habitat would enable land managers to design local RE energy implementations to mitigate ecological impacts.

Renewable Energy–Biodiversity Nexus

By integrating the previous studies on RE mixes, spatially explicit ecological impact assessment, and process-based landscape modeling, this study has explored scenarios to meet both RE utilization and biodiversity conservation on an energy demand basis that is of interest to local stakeholders. Scenario 1 converted 80–100% of abandoned pastureland into biomass energy production, supplied 28–80% of the current regional energy demand, and improved the three ecosystem indicators. The residential population in the watershed is estimated to decrease to 4,118 by 2050 (48% of 2010) (National Land Numerical Information [NLNI], 2017). Considering that the energy demand will decrease from the current level as the population declines, group 1 could fulfill the regional energy demand, however, depending only on biomass energy would result in annual energy supply fluctuations (**Figure 3**). Therefore, mixing with other RE, as in the scenario of A45-S0.2, is recommended. In group 3, where the energy production far exceeded the current demand, more than 60% of abandoned pasture was converted to solar PV plant installation (**Figure 4**). The habitat suitability indices for the two raptorial birds, especially the mountain hawk-eagle, diminished compared with the A0 scenario, which maintained the current land use (**Figure 4**). In contrast, group 2, where the energy production and the current demand were almost of the same order, promotes the mixed use of solar PV plants and biomass energy. Group 2 produced more energy than the local demand and has the potential to supply energy to surrounding areas under a shrinking society. Concurrently, this mixed use of the two RE sources minimized the impact on the two habitat suitability indices (**Figure 4**). Therefore, both (1) combining multiple renewable energy sources and (2) arranging the spatial distribution of solar PV plant installations to avoid habitat degradation are essential for the production of sufficient energy while suppressing the impact on the ecosystem, as in groups 1 and 2. A participatory approach supported by scientific evidence can be effective in developing local future energy visions (Belmonte et al., 2015; Hori et al., 2019). Because our approach explicitly addresses not only ecological status but also energy supply potentials, it is useful for designing desirable future visions with different stakeholders to explore future visions that satisfy RE utilization and biodiversity conservation.

CONCLUSION AND FUTURE PERSPECTIVES

We identified nexuses between climate, vegetation, the habitat of the two raptorial bird species, and energy and successfully explored three future scenario groups: group 1 that improved plant species diversity and the habitat of the two raptorial bird species with less energy production than the current regional demand, group 2 that supplied sufficient energy production from the mixed use of woody biomass and solar PV systems while minimizing impacts on the three ecological indicators, and group 3 that resulted in high dependency on solar PV systems and the diminished habitat of the two raptorial bird species. Our quantitative modeling provides scientific information about energy–biodiversity nexuses for local stakeholder meetings, which contribute to developing land use and energy strategies.

To promote the use of quantitative forest landscape modeling to other areas, such as the Asia Pacific region, a reliable species parameter database is required for robust simulations. Our study suggests that the need for such a dataset is required, especially, for pioneer species. Currently, large accumulated datasets of traits (e.g., TRY, 2020) and occurrence maps of plant species (see, for example, GBIF, 2020; Tanaka and Matsui, 2007; Forestry Agency of Japan, 2019; Ministry of the Environment, Japan [MOE], 2020; Long Term Ecological Research [LTER], 2020) enable us to systematically prepare the standard parameters required for forest landscape simulation models. These standard datasets facilitate forest model intercomparison practice (Erickson and Strigul, 2019) and reduce uncertainties when simulating the vegetation dynamics of region-specific tree species under climate change.

Our results underestimate the effects of natural disturbance regimes, such as deer browsing and windthrow. In Japan, *Sasa* species play a key role in regeneration dynamics by preventing the establishment of other plant species. Because the vegetation map and forest registers used in this study lack detailed spatial distribution information of *Sasa* species, it is necessary to estimate its initial density from the overstory tree density (Tatsumi and Owari, 2013). Climate change and deer browsing affect the survival of *Sasa* species (Yokoyama and Shibata, 1998; Tsuyama et al., 2011, 2012). More frequent windthrow events and post-windthrow management under future climate will affect species composition and carbon dynamics (Lucash et al., 2019; Morimoto et al., 2019; Hotta et al., 2020). Therefore, integrative modeling of the nexus between (1) natural disturbances at a broader scale, (2) the distribution of *Sasa* species, and (3) regeneration dynamics under future climate change is a fundamental future perspective.

Recently, SSPs scenarios (O'Neill et al., 2014) have been developed in the climate change domain, and research is progressing to downscale global-scale scenarios to national scales (Frame et al., 2018; Guo et al., 2019; Chen et al., 2020). IPBES is also developing a Nature Futures Framework as a unified future scenario from the aspect of biodiversity conservation (PBL, 2018; IPBES, 2020). Local scenario analysis is thus expected to couple seamlessly with socio-economic conditions provided by such external scenarios. Through the modeling of the nexus between SDG goals 13 (Climate action) and 15 (Life on land), to which forest landscape modeling can contribute, nexus structures are expected to be identified for people, the planet, prosperity, peace, and partnership in collaboration with other research fields.

DATA AVAILABILITY STATEMENT

Input data and analysis scripts have deposited in our GitHub repository: https://github.com/hagachi/Project-RE-biodiversity-nexus-2020. The species parameters and calibration procedure can be found in the **Supplementary Material**. Redistribution of the forest registers, which were used for initializing landscapes, are restricted by the Forest Management Bureau of Hokkaido Prefecture. Requests to access the datasets should be directed to the bureau: https://www.rinya.maff.go.jp/hokkaido/keikaku/map/map.html (in Japanese).

AUTHOR CONTRIBUTIONS

CH, MM, TMt, and TMc contributed the conception, design, and analysis. WH, TI, and JM organized the vegetation and environmental dataset. CH, TI, and HS contributed the localization of forest landscape model. MN arranged the field survey. SH and OS provided the ideas and discussion for the design scenarios. CH and MM wrote the first draft of the manuscript. All authors contributed to the revision of the manuscript. CH and TMt finalized the submitted manuscript with input from all the authors.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00155/full#supplementary-material

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Drivers and Consequences of Alternative Landscape Futures on Wildlife Distributions in New England, United States

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In an era of rapid climate and land transformation, it is increasingly important to understand how future changes impact natural systems. Scenario studies can offer the structure and perspective needed to understand the impacts of change and help inform management and conservation decisions. We implemented a scenario-based approach to assess how two high impact drivers of landscape change influence the distributions of managed wildlife species (n = 10) in the New England region of the northeastern United States. We used expert derived species distribution models (SDMs) and scenarios developed by the New England Landscape Futures Project (NELFP) to estimate how species distributions change under various trajectories (n = 5) of landscape change. The NELFP scenarios were built around two primary drivers – Socio-Economic Connectedness (SEC) and Natural Resource Planning and Innovation (NRPI) – and provide plausible alternatives for how the New England region may change over 50 years (2010–2060). Our models generally resulted in species occurrence and richness declines by 2060. The majority of species (7 of 10) experienced declines in regional occurrence for all NELFP scenarios, and one species experienced a projected increase in mean regional occurrence for all scenarios. Our results indicate that the NRPI and SEC drivers strongly influenced projected distribution changes compared to baseline projections. NRPI had a greater impact on distribution change for five species (coyote, moose, striped skunk, white-tailed deer, and wild turkey), while SEC had a greater impact on four species (American black bear, bobcat, raccoon, and red fox); one species (gray fox) was equally influenced by both NRPI and SEC. These results emphasize the importance of integrating both natural resource planning and socio-economic factors when addressing issues of distribution change and offer insights that can inform proactive management and conservation planning.

Keywords: climate change, land use change, New England, occurrence probability, scenarios, species distribution models (SDMs), species richness, wildlife

INTRODUCTION

Humans are a dominant driver of landscape change (Vitousek et al., 1997; Díaz et al., 2019). Historical alterations in land use, primarily the conversion of undisturbed forest to other forms of land use like agriculture and urban development, have resulted in the modification of landscapes at a global scale (Foley et al., 2005; Díaz et al., 2019). The rate of landscape modification is accelerating as human-dominated land use continues to expand worldwide (Klein Goldewijk et al., 2011; Seto et al., 2012). More than 30% of the world's land area is already under some degree of development and over 70% of the all forests are in close proximity (<1 km) to a non-forest edge (Foley et al., 2005; Haddad et al., 2015). With less than 15% of the world's terrestrial land under protection, natural ecosystems are highly susceptible to modification (UNEP-WCMC and IUCN, 2016).

Natural ecosystems are also exposed to the escalating pressures of shifting climatic conditions due to human activities (Walther et al., 2002; IPCC, 2014). With a global temperature increase of ca. 1°C over the past century and rates of warming nearly doubling over the latter quarter of the century, natural landscapes are subject to climate-induced changes at accelerating rates (IPCC, 2014; Hayhoe et al., 2018). The last three decades alone experienced global surface temperatures that were warmer than any preceding decade since 1850 and collectively represent the warmest 30-year period in the past 1,500 years (IPCC, 2014; Hayhoe et al., 2018).

Land use and climatic shifts can have substantial impacts on wildlife globally (Root et al., 2003; Thomas et al., 2004; Chen et al., 2011; Díaz et al., 2019). Changes in land use and climate can alter the quality and distribution of habitat (e.g., shifting the composition, structure, and configuration of plant communities), availability of food, prevalence of parasites and diseases, and frequency and intensity of physiological stress from heat or drought (Rustad et al., 2012; Díaz et al., 2019). While these changes can have considerable consequences for wildlife, information gaps and uncertainty around climate and land use trajectories currently limit our understanding of how future changes may impact wildlife species.

In the New England region of the northeastern United States (US), which covers six states and nearly 200,000 km^2, the recent and historic effects of climatic change and land use are evident for some species. For example, Canada lynx (*Lynx canadensis*) has experienced a distribution shift toward higher latitude and elevation in response to landscape change and warming conditions (Laliberte and Ripple, 2004; Koen et al., 2014). Similarly, warming climate conditions have benefited parasites like winter tick (*Dermacentor albipictus*) that have impacted moose (*Alces alces*) populations by reducing fitness and causing periodic epizootics (>50% die-offs) in some regions (Murray et al., 2006; Jones et al., 2019). With the continued pressures of human population expansion, urban development and sprawl, and warming climate trends, New England's natural landscapes are expected to experience rapid modification over the next half-century (White et al., 2009; Olofsson et al., 2016; Thompson et al., 2017; Dupigny-Giroux et al., 2018; Duveneck and Thompson, 2019).

Rapidly changing environments present considerable management challenges for federal and state agencies charged with maintaining viable wildlife populations. Across the New England region, wildlife management largely occurs at the state-level, and is characterized by different strategies for different species, which creates challenges for broader-scale conservation planning (Aycrigg et al., 2016; McBride et al., 2017). Scenario-based planning offers an approach to better understand the larger-scale impacts of change that can lead to more effective and proactive decision-making for species (Carpenter and Folke, 2006; Thompson et al., 2016). In New England, studies have been initiated to improve understanding and anticipate future trajectories of land-use and natural infrastructure (McBride et al., 2017; McGarigal et al., 2017; Thompson et al., 2017; Duveneck and Thompson, 2019). For example, the Designing Sustainable Landscapes project developed a Landscape Change, Assessment and Design model to simulate current trends scenarios for landscape change in the northeastern US and assess the associated ecological impacts (McGarigal et al., 2017).

Another study, the New England Landscape Futures Project (NELFP), developed five scenarios that simulate different landscape futures for the New England region. Led by the Harvard Forest Long-Term Ecological Research program and the Scenarios, Services, and Society Research Coordination Network, this study simulated future conditions based on recent trends (Thompson et al., 2017; Duveneck and Thompson, 2019), and four alternative scenarios of landscape change (Thompson et al., 2019). The alternative scenarios were built around two uncertain, yet highly influential drivers of landscape change: Natural Resource Planning and Innovation (NRPI) and Socio-Economic Connectedness (SEC; McBride et al., 2017; Thompson et al., 2019). The NRPI driver provides the extent to which the government and private sector invest in proactive land-use planning, ecosystem services, and technological advances for resource use, primarily land, energy, and water. The SEC driver provides the extent of local or global connectivity in population migration, culture, economic markets, trade policy, goods and services, and climate policy. These drivers form the basis for the four alternative scenarios to the continuation of recent trends (i.e., the "Business-As-Usual" scenario): "Connected Communities," "Yankee Cosmopolitan," "Go It Alone," and "Growing Global." The NELFP scenarios were collaboratively designed by stakeholders, simulation modelers, and researchers throughout New England and provide plausible trajectories of landscape change that incorporate informed simulations of climate, development, and agriculture, as well as forest structure and composition. However, wildlife species have not been assessed in the context of these scenarios.

Given the recent rates of landscape change in the New England region, combined with extensive evidence that changing climate, human expansion, and land transformation can have negative consequences for many wildlife species, decision-makers are faced with two crucial and unresolved questions: (1) How will changing climate and landscape conditions impact the future viability and distribution of the region's wildlife species? (2) How do social drivers, such as NRPI or SEC, influence species distribution change in a future New England landscape? With uncertainty around natural resource planning, innovation and socio-economic factors, we need a systematic approach that addresses these questions and advances our understanding of the complex, dynamic systems that affect wildlife. Approaching these questions proactively may (1) lead to more efficient, cost effective and sustainable conservation and management practices, (2) improve the state of biodiversity and natural systems, and (3) help protect iconic species and the benefits they offer to humans and society (Güneralp et al., 2013). By considering forecasted shifts in species distributions, wildlife agencies can plan for long-term conservation at multiple spatial and temporal scales.

We addressed these questions by evaluating how climate change and different trajectories of land-use may influence a group of commonly managed wildlife species in the New England region. We used expert-derived species distribution models (SDMs) developed by Pearman-Gillman et al. (2020) and the NELFP scenarios to: (1) estimate and map the future distributions of 10 focal wildlife species under five alternative scenarios, and assess regional species richness patterns, (2) quantify changes in species distributions under each scenario, and (3) compare distribution change across scenarios to quantify the impacts of SEC and NRPI, and identify the drivers with the greatest potential influence on individual and multi-species change.

MATERIALS AND METHODS

Study Area

The study area encompassed the six New England states (Connecticut, Rhode Island, Massachusetts, Vermont, New Hampshire, and Maine) in the northeastern US (**Figure 1**). The region spans 186,458 km^2 with topography ranging from coastal plains to mountain peaks reaching nearly 2,000 m above sea level. Climatic conditions vary by season and geographic location throughout the region. Long-term climate records indicate an average annual precipitation of 104 cm (range: 79–255 cm) and a mean regional temperature ranging from 6°C (January) to 19°C (July) (Huntington et al., 2009).

The New England region supports a growing human population (14,845,063 in 2019) with three-quarters of the population concentrated in the regions major metropolitan areas (U.S. Census Bureau, 2019). The uneven distribution of people contributes to regional variability in land use patterns and intensities with large population centers in the south and more rural undeveloped landscapes in the north. Currently, approximately 80% of the region is covered by forest (Foster et al., 2010). Forested regions are ecologically diverse with areas dominated by northern hardwood, spruce-fir, oak-hickory, and pitch pine forest types (Brooks et al., 1992; Duveneck et al., 2015). Development (9.3%), agriculture (5.9%), and water (12.3%) also cover large portions of the New England landscape (Homer et al., 2015).

Focal Species

We focused our analysis on harvested wildlife species (n = 10) that occur widely throughout the region. This group includes nine mammals: American black bear (*Ursus americanus*), Bobcat (*Lynx rufus*), Coyote (*Canis latrans*), Gray fox (*Urocyon cinereoargenteus*), Moose (*Alces alces*), Raccoon (*Procyon lotor*), Red fox (*Vulpes vulpes*), Striped skunk (*Mephitis mephitis*), and White-tailed deer (*Odocoileus virginianus*); and one bird species: Wild turkey (*Meleagris gallopavo*). We selected these species because they are largely the emphasis of wildlife management at the state-level. Game species are important economically and culturally as they are harvested and often sought by wildlife watchers. Several of these species also exert large ecological effects on ecosystems, such as moose and deer (Jones et al., 1994; Pastor et al., 1998; Horsley et al., 2003).

Objective 1 – Map Species Future Distributions

Distribution Models

We used SDMs developed by Pearman-Gillman et al. (2020) to estimate and map distributions of the focal species. SDMs are often developed using presence-only data (e.g., animal locations) and relate environmental conditions to a measure of occurrence. For example, programs such as Maxent and BIOCLIM use presence-only data to model occurrence and map distribution across a landscape (Phillips et al., 2006; Franklin, 2010; Booth et al., 2014). Here, we used an alternative method that developed models from probability of occurrence data obtained through expert elicitation techniques, as outlined by James et al. (2010). Expert opinion based models have been used to estimate occupancy and map distribution for a variety of species and contexts (e.g., Pearce et al., 2001; Yamada et al., 2003; Mouton et al., 2009; Murray et al., 2009; Aylward et al., 2018). Developing SDMs from expert opinion data (occurrence estimates) can help overcome some of the limitations of presence-only modeling approaches, and yield models that capture the influence of climate and land use on regional wildlife dynamics (e.g., Pearce et al., 2001; Murray et al., 2008). For details about the expert elicitation model development for this study, see Pearman-Gillman et al. (2020). Briefly, we used the online survey tool, AMSurvey[1], to elicit expert opinion data on the probability of occurrence of each focal species throughout the New England region. We then used mixed-model methods and stepwise model selection (Zar, 1999; Burnham and Anderson, 2002; Bates et al., 2014) to develop a model for each species that predicted probability of occurrence as a function of landscape and climate variables (**Table 1**). Models included random effects that accounted for expert-to-expert variation in responses, and fixed effects that were identified in the literature, selected by experts, or were highly correlated with perceived occurrence (**Tables 2**, **3**). Validation tests using independent data indicated that the models performed well at predicting species occurrence across the New England region (Pearman-Gillman et al., 2020).

Scenario Simulations

To estimate species distributions under projected conditions, we applied each SDM to the Recent Trends scenario and the four NELFP scenarios (McBride et al., 2017; Thompson et al., 2019), each defined by their degree of Natural Resource Planning and

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[1] https://code.usgs.gov/vtcfwru/amsurvey

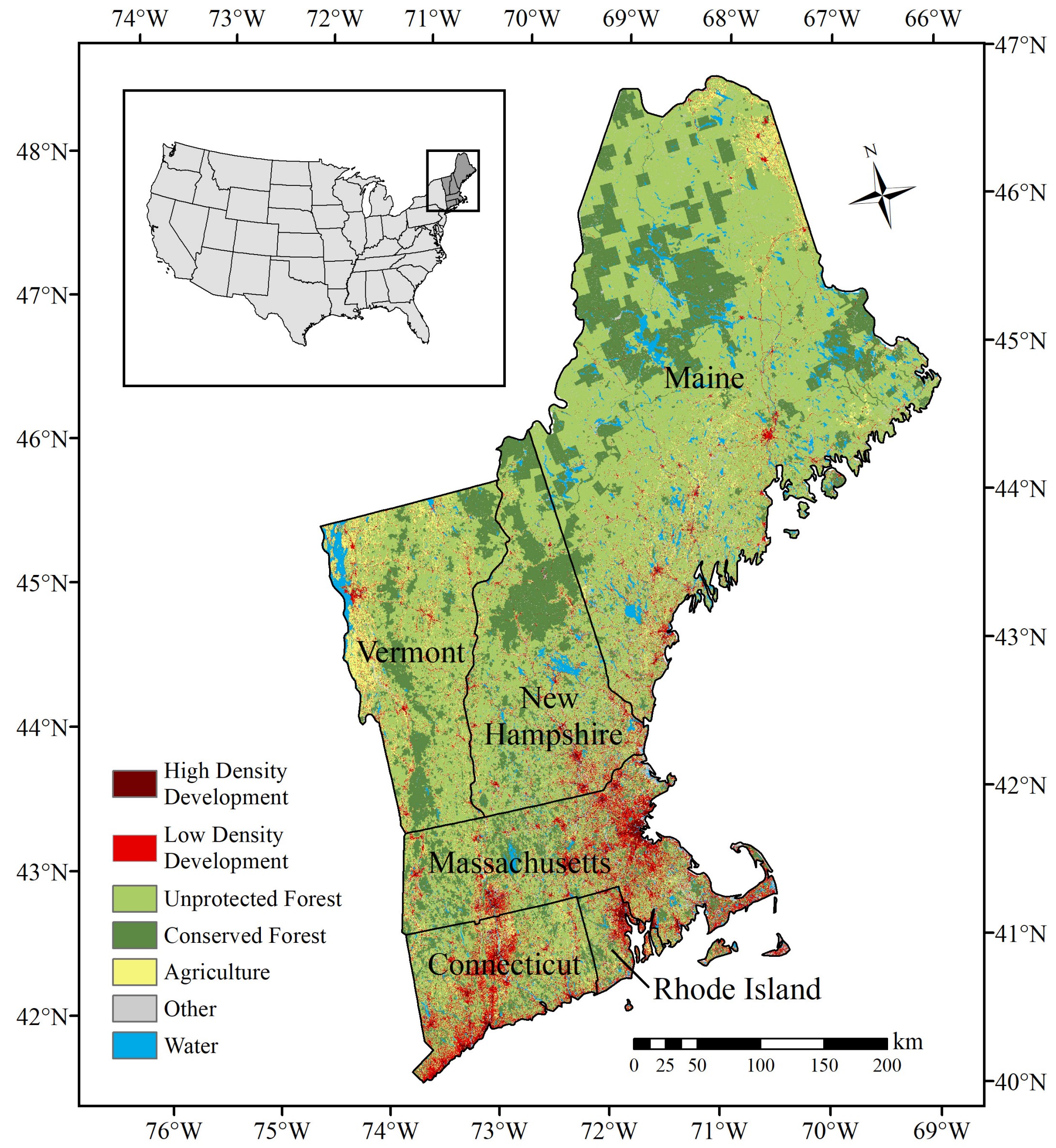

FIGURE 1 | Map of the study region located in the northeastern United States. The study region included the six New England states: Connecticut, Maine, Massachusetts, New Hampshire, Rhode Island, and Vermont.

Innovation (NRPI) and Socio-Economic Connectedness (SEC). For details about the NELFP scenario development process, detailed scenario descriptions, and scenario figures, see McBride et al. (2017) and Thompson et al. (2019). A summary of each scenario is described below:

(1) ***Recent Trends (Business-As-Usual).*** This scenario represents a baseline projection extended from the region's contemporary circumstances. It depicts the linear continuation of New England's recent trends in the rate and spatial patterns of landscape change. This scenario offers a baseline for evaluating the other scenarios of change.

(2) ***Connected Communities (High NRPI and Local SEC).*** In this scenario, the New England population has slowly increased over the past 50 years and communities are coping with climate change by anchoring in place, making local culture and the protection of local resources important government and community priorities. Concerns about global unrest and the environmental impacts of global trade led New England communities toward a more community-focused lifestyle. Strengthened local relations and advances in local green energy contribute to more self-reliant communities. Heightened community interest and public policies protected wildlands, strengthened local economies and fueled growing local markets (primarily local food, wood, and recreation).

TABLE 1 | Species distribution models (SDMs) used to map distributions for 10 wildlife species and estimate changes in distribution across the New England region of the northeastern United States.

Species	Model formula
American black bear	Mean ∼ prop_mature_forest + prop_all_roads + prop_forest_5k + mean_annual_precip_mm_5k + prop_fagugran_5k + (1 | State) + (1 | Expert) + (1 | Site)
Bobcat	Mean ∼ prop_developed + prop_forest_edge + prop_agriculture + (1 | Expert) + (1 | Site)
Coyote	Mean ∼ prop_waterbodies + prop_forest_edge + prop_major_roads_3k + prop_wetland_3k + prop_agriculture + (1 | Expert) + (1 | Site)
Gray fox	Mean ∼ prop_forest_edge + prop_agriculture_3k + mean_DEM_km + (1 | State) + (1 | Expert) + (1 | Site)
Moose	Mean ∼ prop_young_forest + prop_developed + prop_shrubland + mean_fall_tmax_degC + prop_forest_5k + (1 | Expert) + (1 | Site)
Raccoon	Mean ∼ prop_agriculture_500m + prop_mature_forest_500m + mean_DEM_km_500m + prop_oak_500m + prop_developed_500m + (1 | Expert) + (1 | Site)
Red fox	Mean ∼ prop_agriculture + prop_high_dev + mean_winter_precip_mm_3k + prop_shrubland_3k + (1 | Expert) + (1 | Site)
Striped skunk	Mean ∼ mean_DEM_km_500m + prop_mature_forest_500m + prop_agriculture_500m + prop_forest_edge_500m + (1 | Expert) + (1 | Site)
White-tailed deer	Mean ∼ prop_agriculture + prop_high_dev + prop_mature_forest + prop_hemlock_tamarack_cedar_3k + (1 | EcoRegion) + (1 | Expert) + (1 | Site)
Wild turkey	Mean ∼ prop_decid_forest + prop_forest_edge + prop_riparian + prop_grassland_3k + (1 | EcoRegion) + (1 | Expert) + (1 | Site)

Models were developed using expert-opinion data and generalized linear mixed modeling. Models include random-effects, noted in parentheses, and scaled fixed-effect variables. See ***Table 2*** *for descriptions of model variables. For details on model development and parameter estimates, see Pearman-Gillman et al. (2020).*

(3) ***Yankee Cosmopolitan (High NRPI and Global SEC).*** This scenario describes a future in which New England remains relatively resilient to climate change, has become a leader in research and technology, and subsequently experienced substantial population growth. The region's population has largely grown due to an influx of international migrants seeking areas less vulnerable to the effects of climate change (e.g., heat, drought, sea-level rise). As a world leader in biotech and engineering, New England has a large demand for a skilled labor work force and established itself as a major center of economic and population growth within the U.S. Most development has occurred in urban areas with sprawl occurring as populations grow faster than the infrastructure can support. In a globally connected world, the region relies on imports for most food products. With a global shift toward sustainability, New England has invested in land protection, ecosystem services, and its carbon storing forests.

(4) ***Growing Global (Low NRPI and Global SEC).*** In this scenario, New England has remained relatively sheltered from the effects of climate change and has become a desirable location for migrants seeking more environmentally stable areas. This has led to population and development increases that have outpaced local planning efforts and contributed to city sprawl, haphazard expansion of development, poor transportation infrastructure and inefficient energy use. Underprepared government entities have struggled to support the region's growing population leading to higher levels of privatized municipal services, limited natural resource planning and sharp declines in land protection. With trade barriers lifted, global trade has amplified and the U.S. has experienced a surge in the production and export of commodity crops. Increased agriculture, development and growing biofuel markets have increased the degradation and conversion of New England's forested land. Globalization and increased transportation demands have strengthened a global reliance on conventional and cheap energy sources (fossil fuels). With little innovation and no global commitment to climate action, the world remains divided on issues of climate change and renewable energy.

(5) ***Go It Alone (Low NRPI and Local SEC).*** This scenario describes a New England with fairly low economic opportunity, population growth, and land development. A lack of global economic connectivity, tightened national borders, and reductions in national budgets have limited the nation's ability to deal with unemployment, demographic change, and climate resilience. Global efforts at climate adaptation have failed and conventional energy sources still dominate. In New England, the lack of regulation decreased natural resources protection, technological innovation and availability of goods and municipal services. With reduced access to global energy markets, failure to launch new energy development projects and the degradation of conventional energy infrastructure, the price of energy has continued to rise. Increased energy and export expenses have reduced timber harvesting and commercial agriculture contributing to economic collapse. New residential developments lack appropriate planning and most public authorities lack the funds to maintain critical infrastructure such as roads and sewers. High energy costs, poor infrastructure planning and failure to fund climate change adaption has left communities isolated and heavily reliant on local resources. Poor planning and extractive use have significantly degraded the region's ecosystem services and considerably decreased quality of life.

Each scenario narrative was translated into spatial patterns of change using methods described by Thompson et al. (2017, 2019) and Duveneck and Thompson (2019). Briefly, these simulations were developed in two stages: first using a spatially explicit cellular land change model, Dinamica Environment for Geoprocessing Objects (Dinamica EGO 2.4.1; Soares-Filho et al., 2009) and second using a forest landscape succession model, LANDIS-II v6.2 (Scheller et al., 2007). Dinamica was used to simulate 50 years (2010–2060) of forest loss, land-use change, and land protection relative to the underlying narrative of each

TABLE 2 | Variables and associated spatial (raster) layers used in the development of wildlife species distribution models and maps across the New England region of the northeastern United States.

						Source	
Variable	**Category**	**Covariate name**	**Description**	**Measurement**	**Scale(s)**	**Current**	**Future scenarios**
Annual Precipitation	Climate	mean_annual_precip_mm	Average annual precipitation during the years 2010–2012.	Meters	5k	Stoner et al., 2013; Duveneck and Thompson, 2019	Stoner et al., 2013; Duveneck and Thompson, 2019
Average Daily High Temperature (Fall)	Climate	mean_fall_tmax_degC	Average daily high temperature observed during the months of September, October, and November during 2010–2012.	Degrees Celsius	1k	Stoner et al., 2013; Duveneck and Thompson, 2017	Stoner et al., 2013; Duveneck and Thompson, 2019
Total Winter Precipitation	Climate	mean_winter_precip_mm	Average cumulative winter (December–February) precipitation during the years 2010–2012. This measure includes all types of precipitation, not just snowfall.	Meters	3k	Stoner et al., 2013; Duveneck and Thompson, 2017	Stoner et al., 2013; Duveneck and Thompson, 2019
American Beech	Forest Composition	prop_fagugran	Forested land that is occupied by American beech (*Fagus grandifolia*).	Proportion	5k	Duveneck et al., 2015	Duveneck and Thompson, 2019; Duveneck et al., 2019
Hemlock-Tamarack-Cedar Forest	Forest Composition	prop_hemlock_tamarack_cedar	Forested land where AGB (above ground biomass) is dominated by eastern hemlock (*Tsuga canadensis*), native tamarack (*Larix laricina*), and northern white cedar (*Thuja occidentalis*).	Proportion	3k	Duveneck and Thompson, 2019	Duveneck and Thompson, 2019; Duveneck et al., 2019
Mature Forest	Forest Composition	prop_mature_forest	Forested land that is classified by tree cohorts between 40 and 100 years old.	Proportion	500 m, 1k	Duveneck and Thompson, 2017	Duveneck and Thompson, 2019; Duveneck et al., 2019
Oak Forest	Forest Composition	prop_oak	Forested land where AGB is dominated by white oak (*Quercus alba*), scarlet oak (*Q. coccinea*), chestnut oak (*Q. prinus*), northern red oak (*Q. rubra*), and black oak (*Q. velutina*).	Proportion	500 m	Duveneck and Thompson, 2019	Duveneck and Thompson, 2019; Duveneck et al., 2019
Young Forest	Forest Composition	prop_young_forest	Forested land that is classified by tree cohorts between 20 and 39 years old.	Proportion	1k	Duveneck and Thompson, 2019	Duveneck and Thompson, 2019; Duveneck et al., 2019
Agriculture	Land Cover	prop_agriculture	Area where land cover is classified as pasture, hay, and cultivated crops.	Proportion	500 m, 1k, 3k	National Land Cover Database (NLCD 2011; U.S. Geological Survey, 2014)	Thompson et al., 2019
Deciduous Forest	Land Cover	prop_decid_forest	Area where land cover is classified as deciduous forest.	Proportion	1k	NLCD 2011	Duveneck and Thompson, 2019; Duveneck et al., 2019
Developed	Land Cover	prop_developed	Area where land cover is classified as developed open space, low intensity, medium intensity, and high intensity development.	Proportion	500 m, 1k	NLCD 2011	Thompson et al., 2019
Highly Developed	Land Cover	prop_high_dev	Area where land cover is classified as medium or high intensity development.	Proportion	1k	NLCD 2011	Thompson et al., 2019
Forest	Land Cover	prop_forest	Area where land cover is classified as deciduous, evergreen, and mixed forest.	Proportion	5k	NLCD 2011	Thompson et al., 2019

(Continued)

TABLE 2 | Continued

						Source	
Variable	**Category**	**Covariate name**	**Description**	**Measurement**	**Scale(s)**	**Current**	**Future scenarios**
Forest Edge	Land Cover	prop_forest_edge	Area classified as forest that is within 300 m of non-forest land cover.	Proportion	500m, 1k	NLCD 2011	Thompson et al., 2019
Grassland	Land Cover	prop_grassland	Area where land cover is classified as grassland, herbacous, pasture, or hay.	Proportion	3k	NLCD 2011	Thompson et al., 2019
Major Roads	Land Cover	prop_major_roads	Area where land cover is classified as a major road (controlled access highways, secondary highways, or major connecting roads and ramps).	Proportion	3k	National Transportation Database (NTD 2016; U.S. Geological Survey, 2016)	NTD 2016
Roads	Land Cover	prop_all_roads	Area where land cover is classified as major roads (controlled access highways, secondary highways, or major connecting roads, ramps) or local roads (local roads, 4WD roads, private driveways).	Proportion	1k	NTD 2016	NTD 2016
Riparian	Land Cover	prop_riparian	Area where vegetation is classified as riparian.	Proportion	1k	LANDFIRE 2012 (U.S. Department of the Interior and U.S. Geological Survey, 2012)	LANDFIRE 2012; Thompson et al., 2019
Shrubland	Land Cover	prop_shrubland	Area where land cover is classified as shrub/scrub.	Proportion	1k, 3k	NLCD 2011	NLCD 2011; Thompson et al., 2019
Water	Land Cover	prop_waterbodies	Area occupied by waterbodies; lakes, ponds, reservoirs, estuaries, swamps, and marshes.	Proportion	1k	NLCD 2011	Thompson et al., 2019
Wetland	Land Cover	prop_wetland	Area classified as woody wetlands or emergent herbaceous wetlands.	Proportion	3k	NLCD 2011	NLCD 2011; Thompson et al., 2019
State	Random Effect	State	Area classified by USA state boundaries.	–	–	MassGIS, 2018	MassGIS, 2018
Eco-Region	Random Effect	EcoRegion	Area classified by terrestrial Eco Regions.	–	–	The Nature Conservancy, 2009	The Nature Conservancy, 2009
Elevation	Topography	mean_DEM_km	Height above sea level.	Kilometers	500 m, 1k	Digital Elevation Model (DEM, 2017; U.S. Geological Survey, 2017)	DEM 2017

A total of 22 fixed-effect variables and 4 random-effect variables were included in map development. The fixed-effects included 3 climate variables, 5 forest composition variables, 13 land cover variables, and 1 topographic variable. The random-effects included 2 variables (site and expert) that were included in all models and 2 candidate variables (state and eco-region). Fixed-effect variables were included at the site scale (1 km) or a generalized home range scale (500 m, 3 km, or 5 km). Spatial layers were developed for current (2010) conditions and five future (2060) scenarios: Recent Trends, Community Connectedness, Yankee Cosmopolitan, Go It Alone, and Growing Global.

NELFP scenario. This process produced scenario specific land cover spatial layers (30 × 30 m) for forest, agriculture, high density development, and low density development (Thompson et al., 2017, 2019). Using these land cover spatial layers, a LANDIS-II forest simulation was run on all forest pixels for each scenario from 2010 to 2060 to simulate the growth, dispersal, and mortality of 32 individual tree species (Duveneck and Thompson, 2019). Climate change was incorporated into each scenario using climate projections (i.e., monthly maximum temperature, minimum temperature, and precipitation) based on the assumptions of the Representative Concentration Pathway (RCP) 8.5 emission scenario (IPCC, 2013) as simulated by to the Hadley Global Environment Model v.2-Earth System (HADGE) Global Circulation Model (GCM). This climate future includes an increase in temperature and slight increase in precipitation in New England by 2060. Much larger changes in climate are expected beyond 2060 (IPCC, 2014). Indeed, the effects of climate in these simulations were largely outweighed by the effects of land use (Duveneck and Thompson, 2019). The LANDIS-II simulations included changes in forest composition relative to a warming climate, development, and harvest patterns for the Recent Trends (RT) scenario (Duveneck and Thompson, 2019) and each alternative NELFP scenario. The resulting above-ground biomass layers by tree species were used for modeling wildlife distributions (see below). Additional spatial layers utilized came from the HADGE GCM simulated climate data, Dinamica land cover outputs, and recent conditions land cover data (see **Table 2**).

Mapping Projected Species Distributions

We applied the SDMs to the simulated spatial layers generated for each NELFP scenario (**Table 2**) to map the future distributions of each species in New England. Species distribution maps were generated for each scenario by (1) multiplying the scenario's covariate rasters by the corresponding SDM coefficients for a given species, then (2) summing the resulting raster layers to obtain logit scores for every pixel, and (3) transforming the logits to create a raster of occurrence probabilities. This process generated species-specific distribution maps for each scenario ($n = 5$). We also created species richness maps by stacking the 10 individual species rasters and summing the values in each pixel to generate an index of species richness for each future scenario (Sauer et al., 2013). Richness values could potentially vary from 0 (no species present) to 10 (all species present). We developed distribution maps and species richness maps using the raster package (Hijmans, 2016) in the statistical computing software, R (R Core Team, 2019).

Objective 2 – Quantify Scenario-Specific Distribution Change

Scenario-specific distribution maps were compared against current distribution maps to estimate shifts (i.e., recession or expansion) in regional distributions. We compared each species' current distribution (Pearman-Gillman et al., 2020) to each scenario's projected distribution. Current distribution map pixels were subtracted from superimposed projected distribution map pixels to calculate values of projected change. Pixels with negative distribution change values represented locations of declining species occurrence and pixels with positive values represented locations of increasing occurrence.

Objective 3 – Compare the Impacts of NRPI and SEC on Wildlife Species

Isolating Driver Impacts

Each NELFP scenario was built around two directional drivers of land use change: NRPI (high or low) and SEC (global or local). For each species, we combined (averaged) distribution change information across scenarios with a common directional driver, marginalizing the influence of the second driver. For example, to obtain a distribution shift under the High NRPI driver, we averaged the two High NRPI scenarios (Yankee Cosmopolitan and Connected Communities), marginalizing over the directional SEC drivers. As a second example, to obtain a distribution shift for each species under the Local SEC driver, we averaged the two Local SEC scenarios (Go It Alone and Connected Communities), marginalizing over the directional NRPI drivers. We used this process to provide comparative baselines for NELFP's two primary drivers of land use change. Next, we subtracted the RT values from the isolated driver maps to account for forecasted baseline changes over the 50-year period, effectively removing the external factors of change that were not a product of shifts produced by the NRPI or SEC drivers. The resulting maps depict the potential influence of each driver on species occurrence and identify areas where species benefited from high or low investment in innovation and natural resources, or were most vulnerable to globalized or localized growth.

Quantify and Compare Drivers

We calculated descriptive statistics (minimum, maximum, mean, standard deviation, and quartiles) across each isolated driver landscape to quantify the effect each driver had on species occurrence. This provided comparable statistics and allowed us to assess how and to what degree the NRPI and SEC drivers are expected to impact wildlife in the future. As a final comparison, we calculated the absolute difference that NRPI and SEC had on species occurrence (i.e., the difference between high and low NRPI and global and local SEC). This allowed for quantitative comparisons between the two primary drivers of change and indicated which driver may have a greater impact on the focal wildlife species.

RESULTS

Objective 1 and 2 – Future Distributions and Projected Distribution Change

The projected distribution maps varied among species and the five scenarios. For all species but one (red fox), average regional occurrence likelihoods were projected to decline under nearly all scenarios by 2060 (see **Supplementary Figure S1**, for individual species maps). The locations and overall extent of distribution decline varied among species and scenarios. Generally, focal species distributions shifted away from areas of potential development expansion (largely in the southern New England states), and remained relatively stable in the northern and central regions of New England where less development was projected and timber harvest, forest management, and agriculture were largely driving landscape change (**Supplementary Figure S1**).

Projected declines in species occurrence probabilities were accompanied by declines in focal species richness. A regional average focal species richness (μ_s) of 7.16 was estimated for the New England landscape in 2010 representing current conditions (**Figure 2A**). All future scenarios at 2060 projected lower focal species richness than was estimated for current conditions (**Figures 2B–F**). Of the future scenarios, average regional focal species richness was lowest under the Yankee Cosmopolitan (YC; $\mu_s = 6.44$, a 10.1% decline) and RT ($\mu_s = 6.54$, an 8.7% decline) scenarios (**Figure 2**). The Growing Global (GG) scenario had the highest average regional focal species richness ($\mu_s = 6.84$, a 4.4% decline), followed by Go It Alone (GA; $\mu_s = 6.72$, a 6.2% decline) and Connected Communities (CC; $\mu_s = 6.64$, a 7.2% decline; **Figure 2**).

TABLE 3 | Species-specific summary statistics for the two primary scenario drivers, Natural Resource Planning and Innovation (NRPI, High or Low) and Socio-Economic Connectedness (SEC, Global or Local).

Species	Driver	Minimum	Maximum	Mean	Standard deviation	Quartiles		
						25%	50%	75%
American black bear	High NRPI	−0.2541	0.2022	0.0014	0.0188	−0.0038	0.0000	0.0050
	Low NRPI	−0.3682	0.2404	0.0022	0.0356	−0.0036	0.0014	0.0129
	Local SEC	−0.1938	0.2917	0.0239	0.0347	0.0014	0.0091	0.0365
	Global SEC	−0.4977	0.1491	−0.0203	0.0448	−0.0258	−0.0040	0.0005
Bobcat	High NRPI	−0.3666	0.4959	0.0042	0.0178	0.0000	0.0000	0.0078
	Low NRPI	−0.3837	0.5928	0.0021	0.0511	−0.0190	0.0031	0.0321
	Local SEC	−0.4404	0.4942	0.0103	0.0229	0.0000	0.0013	0.0159
	Global SEC	−0.3837	0.5937	−0.0041	0.0634	−0.0253	0.0047	0.0339
Coyote	High NRPI	−0.5286	0.3179	0.0003	0.0110	−0.0007	0.0000	0.0011
	Low NRPI	−0.2935	0.3748	0.0052	0.0285	−0.0076	0.0009	0.0163
	Local SEC	−0.5286	0.3256	0.0019	0.0128	0.0000	0.0000	0.0030
	Global SEC	−0.2935	0.3699	0.0035	0.0322	−0.0083	0.0014	0.0172
Gray fox	High NRPI	−0.8065	0.5664	0.0046	0.0337	−0.0023	0.0000	0.0097
	Low NRPI	−0.5491	0.6442	0.0606	0.1442	−0.0358	0.0127	0.1776
	Local SEC	−0.8074	0.5714	0.0081	0.0433	0.0000	0.0004	0.0185
	Global SEC	−0.5505	0.6441	0.0571	0.1521	−0.0427	0.0162	0.1817
Moose	High NRPI	−0.9338	0.3746	−0.0035	0.0606	−0.0055	0.0013	0.0186
	Low NRPI	−0.9375	0.7802	0.1465	0.1529	0.0110	0.0992	0.2442
	Local SEC	−0.9343	0.6268	0.1088	0.1080	0.0120	0.0795	0.1823
	Global SEC	−0.9371	0.5295	0.0342	0.0915	−0.0025	0.0047	0.0767
Raccoon	High NRPI	−0.4653	0.2528	−0.0003	0.0150	−0.0060	0.0000	0.0062
	Low NRPI	−0.3289	0.2935	0.0108	0.0223	−0.0001	0.0072	0.0221
	Local SEC	−0.2937	0.2193	−0.0016	0.0170	−0.0094	−0.0006	0.0063
	Global SEC	−0.4657	0.2588	0.0121	0.0212	0.0002	0.0090	0.0229
Red fox	High NRPI	−0.3401	0.5809	0.0001	0.0075	−0.0001	0.0000	0.0012
	Low NRPI	−0.3123	0.5809	0.0009	0.0166	−0.0005	0.0000	0.0063
	Local SEC	−0.3023	0.5809	−0.0004	0.0064	−0.0001	0.0000	0.0008
	Global SEC	−0.3401	0.5809	0.0014	0.0188	−0.0005	0.0000	0.0072
Striped skunk	High NRPI	−0.3073	0.4228	0.0014	0.0133	−0.0027	0.0008	0.0065
	Low NRPI	−0.3477	0.3436	0.0196	0.0288	0.0001	0.0113	0.0338
	Local SEC	−0.3073	0.3076	0.0018	0.0160	−0.0024	0.0021	0.0090
	Global SEC	−0.3438	0.3787	0.0191	0.0282	0.0000	0.0114	0.0337
White-tailed deer	High NRPI	−0.5648	0.7546	−0.0058	0.0278	−0.0079	−0.0013	0.0034
	Low NRPI	−0.5312	0.8336	−0.0320	0.0532	−0.0391	−0.0182	−0.0038
	Local SEC	−0.4179	0.8509	−0.0164	0.0253	−0.0258	−0.0126	−0.0022
	Global SEC	−0.5797	0.7501	−0.0214	0.0590	−0.0176	−0.0042	0.0033
Wild turkey	High NRPI	−0.5709	0.4309	0.0016	0.0218	−0.0094	0.0008	0.0120
	Low NRPI	−0.3772	0.5091	0.0302	0.0776	−0.0224	0.0098	0.0786
	Local SEC	−0.6073	0.4148	0.0080	0.0284	−0.0048	0.0079	0.0231
	Global SEC	−0.3779	0.4952	0.0237	0.0792	−0.0308	0.0043	0.0749

All statistics were calculated from distribution change maps that were averaged across scenarios with like drivers and then adjusted by each species Recent Trends (RT) baseline. Values reflect the driver's isolated impact on regional occurrence relative to the RT baseline.

For individual species, the greatest distribution declines across scenarios were projected for American black bear, gray fox, moose, and wild turkey (**Figure 3**). Considerably lower levels of decline were observed for bobcat, raccoon, and striped skunk, and minimal declines in mean regional occurrence were projected for coyote and white-tailed deer (**Figure 3**). An increase in regional occurrence was projected for red fox across all scenarios (**Figure 3G**).

Objective 3 – Impacts of NRPI and SEC on Wildlife Species

Eight of the focal species (American black bear, bobcat, coyote, gray fox, moose, raccoon, striped skunk, and wild turkey) simulated distribution declines under the RT scenario and all four of the driver-specific assessments (**Figure 4A**). For white-tailed deer, distribution increased slightly under RT and

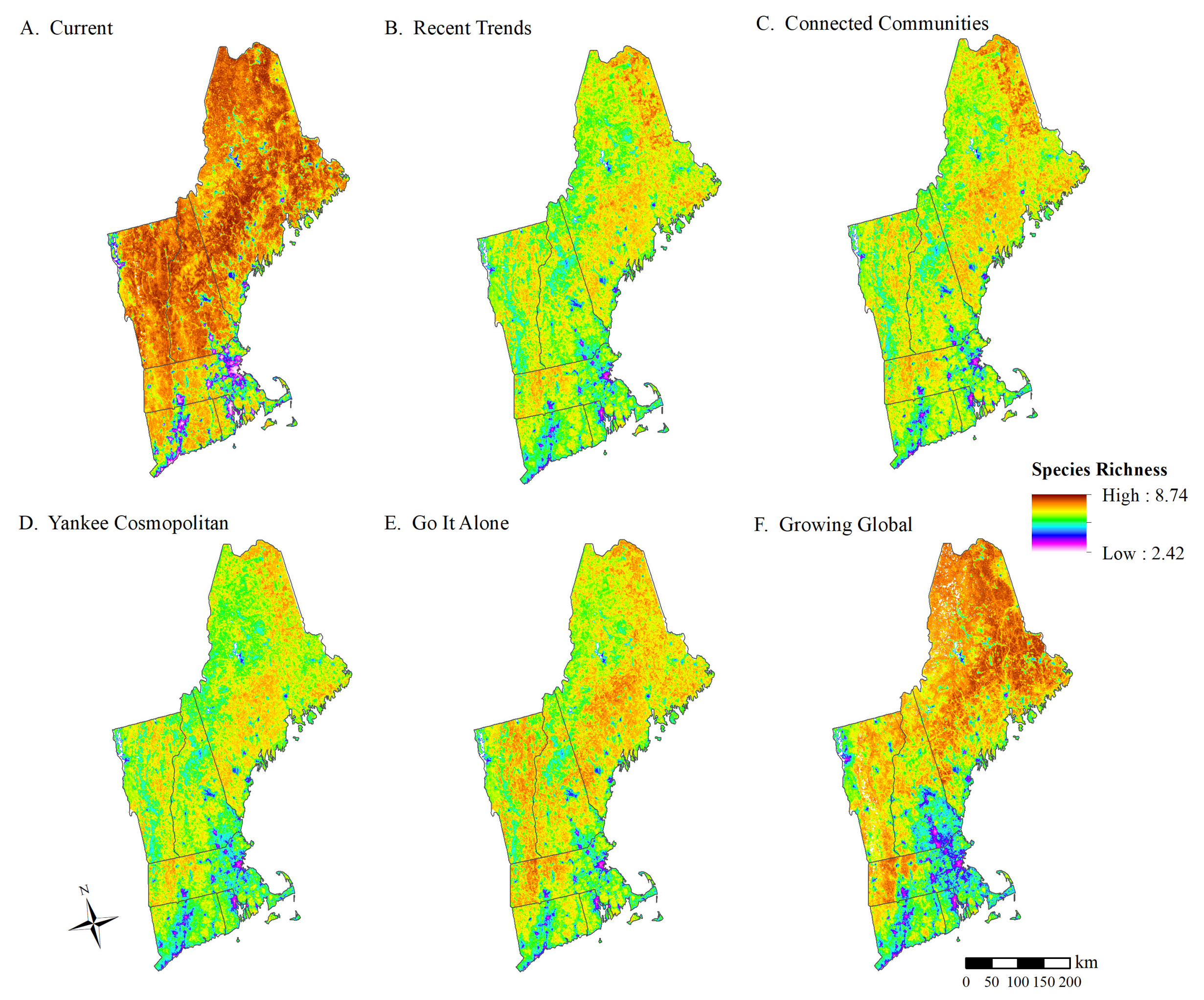

FIGURE 2 | Focal wildlife species richness across New England as projected by **(A)** current (2010) conditions, and each of the NELFP scenarios at year 2060: **(B)** Recent Trends, **(C)** Connected Communities, **(D)** Yankee Cosmopolitan, **(E)** Go It Alone, and **(F)** Growing Global.

declined under the four driver-specific assessments (although declines were generally lower than the declines for other species), and red fox distribution increased under all simulations (**Figure 4A**). Generally, the driver-specific simulations projected higher regional occurrence for the focal species than the 2060 RT simulations (**Figure 4B**).

SEC had a greater impact on distribution change than NRPI for four species, including American black bear, bobcat, raccoon and red fox (**Table 4**). For ***American black bear***, Local SEC was the only driver that simulated higher regional occurrence than the 2060 RT projection, while both High NRPI and Low NRPI drivers led to distribution loss similar to the RT baseline. Of the directional drivers, Local SEC simulated the highest regional occurrence for American black bear, while Global SEC simulated the lowest regional occurrence (**Table 3**, **Figure 4B**, and see **Supplementary Figure S2**, for species-specific maps of driver isolated distribution change). For ***bobcat***, Local SEC simulated the highest regional occurrence while Global SEC simulated the lowest regional occurrence. Both High NRPI and Low NRPI drivers led to distribution loss similar to the 2060 RT projection, and Global SEC was the only driver that projected lower regional occurrence than the RT baseline (**Table 3**, **Figure 4B**, and **Supplementary Figure S2**). The Global SEC driver simulated the highest regional occurrence for ***raccoon***, while Local SEC simulated the lowest regional occurrence. Both High NRPI and Local SEC simulated slightly lower regional occurrence than the 2060 RT projection, and Low NRPI and Global SEC projected higher regional occurrence for raccoon than RT (**Table 3**, **Figure 4B**, and **Supplementary Figure S2**). For ***red fox***, all four drivers led to distribution gain similar to the 2060 RT projection. Global SEC simulated the highest regional occurrence for red fox, while Local SEC was the only driver that simulated lower regional occurrence than the RT baseline (**Table 3**, **Figure 4B**, and **Supplementary Figure S2**).

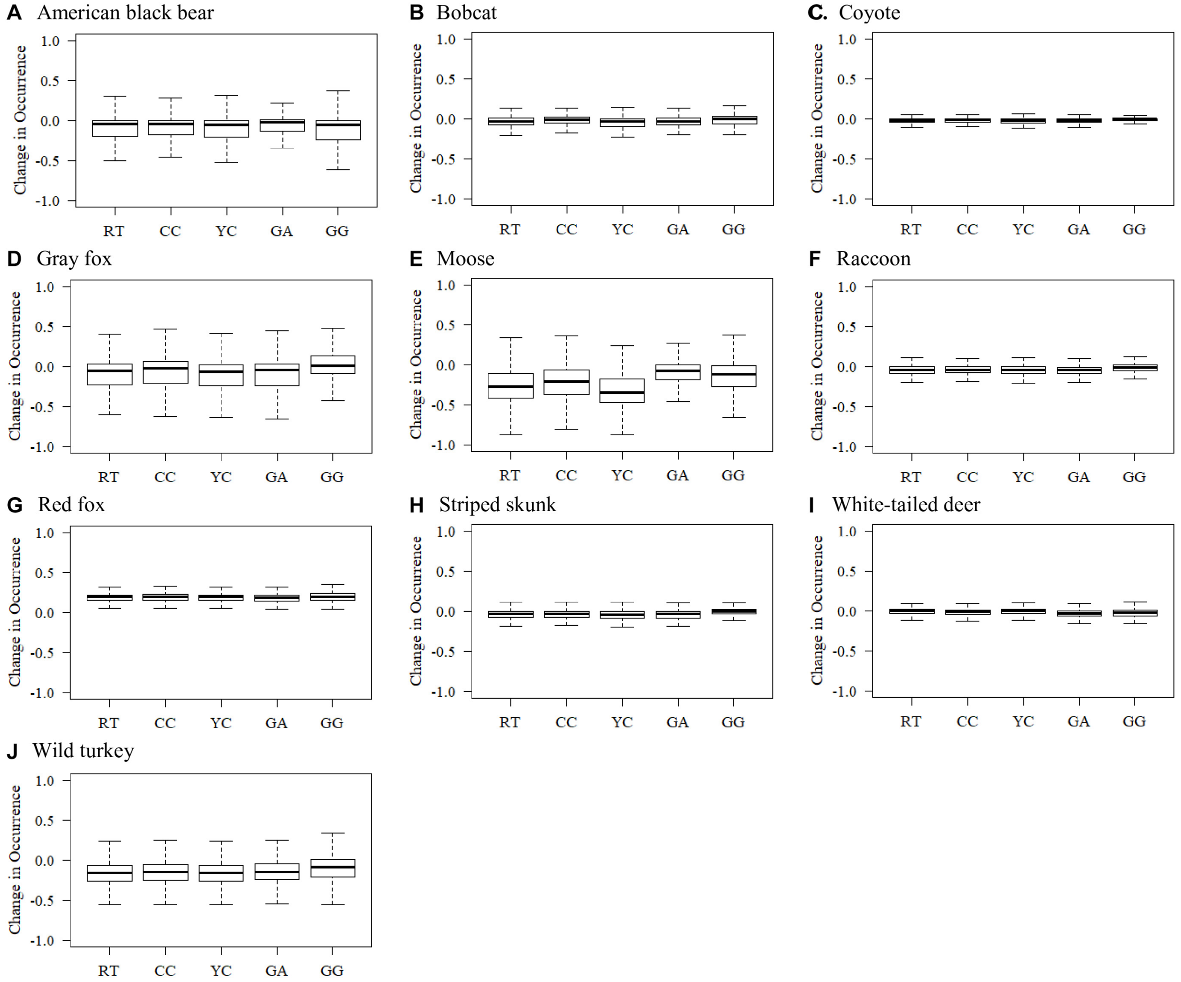

FIGURE 3 | Boxplots displaying estimated changes in species occurrence likelihoods throughout the New England region of the northeastern United States. Changes in occurrence were projected for 10 wildlife species **(A–J)** by comparing species recent (2010) distribution against the year 2060 distribution projections for each NELFP scenario: Recent Trends (RT), Connected Communities (CC), Yankee Cosmopolitan (YC), Go It Alone (GA), and Growing Global (GG).

NRPI had a greater impact on distribution change than SEC for five species, including coyote, moose, striped skunk, white-tailed deer, and wild turkey (**Table 4**). For ***coyote***, the Low NRPI driver simulated the highest regional occurrence and the High NRPI driver simulated the lowest regional occurrence (**Table 3**, **Figure 4B**, and **Supplementary Figure S2**). Low NRPI simulated the highest regional occurrence for ***moose***, while High NRPI simulated the lowest regional occurrence. High NRPI was also the only driver that simulated lower regional occurrence for moose than the 2060 RT projection, and Local SEC simulated considerably higher mean regional occurrence than expected under RT (**Table 3**, **Figure 4B**, and **Supplementary Figure S2**). For ***striped skunk***, Low NRPI simulated the highest regional occurrence; Global SEC driver had a similar impact as Low NRPI, leading to higher mean regional occurrence than expected under RT (**Table 3**, **Figure 4B**, and **Supplementary Figure S2**). For ***white-tailed deer***, Low NRPI simulated the lowest regional occurrence and had the largest impact on distribution change, while High NRPI had the smallest impact on distribution change (**Table 3**, **Figure 4B**, and **Supplementary Figure S2**). Low NRPI simulated the highest regional occurrence for ***wild turkey***, and both Low NRPI and Global SEC projected higher regional occurrence than High NRPI and Local SEC (**Table 3**, **Figure 4B**, and **Supplementary Figure S2**).

For one species, gray fox, SEC and NRPI had an equal influence on distribution change (**Table 4**). Of the directional drivers, Low NRPI simulated the highest regional occurrence for ***gray fox*** (**Table 3**, **Figure 4B**, and **Supplementary Figure S2**). Low NRPI and Global SEC also projected considerably higher regional occurrence than High NRPI and Local SEC (**Figure 4B**).

Generally, Low NRPI and Global SEC were the most influential directional drivers of distribution change (**Figure 5**). Low NRPI had the largest impact on regional distribution change for six of the species (coyote, gray fox, moose, striped skunk, white-tailed deer, and wild turkey), while Global SEC had the largest impact for two species (raccoon and red fox) and

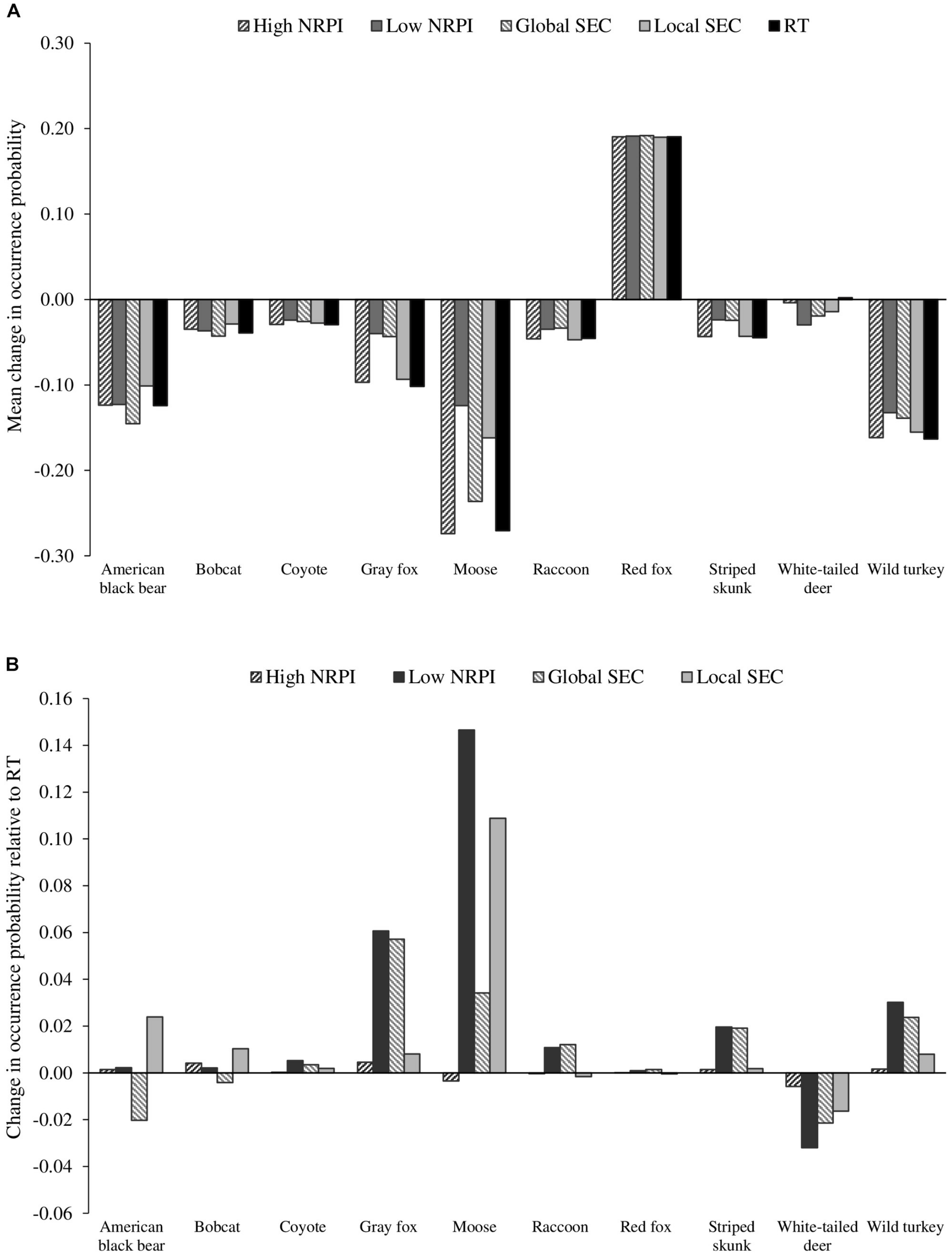

FIGURE 4 | Bar graphs showing the overall impact of drivers on mean regional change in species probability of occurrence **(A)** and drivers isolated impact on occurrence likelihood after RT adjustment **(B)**. For **(A)**, values represent mean distribution change calculated from species probability of occurrence maps averaged across scenarios with like drivers. For **(B)**, values indicate difference from the RT baseline associated with each isolated driver (i.e., High NRPI, Low NRPI, Global SEC, and Local SEC).

had a relatively large influence on distribution change for the remainder of the focal group. Of the four drivers, High NRPI had the smallest impact on distribution change for nearly all species, and Local SEC had a large impact for a few species but was otherwise less influential than the Low NRPI and Global SEC drivers (**Figure 5**). When comparing the difference between High

TABLE 4 | Driver comparison statistics showing absolute difference between regional average occurrence for High vs. Low NRPI (Natural Resource Planning and Innovation) and Local vs. Global SEC (Socio-Economic Connectedness).

Species	NRPI Effect	SEC Effect
American black bear	0.0008	0.0493
Bobcat	0.0021	0.0144
Coyote	0.0049	0.0016
Gray fox	0.0655	0.0655
Moose	0.1500	0.0746
Raccoon	0.0111	0.0137
Red fox	0.0008	0.0018
Striped skunk	0.0182	0.0173
White-tailed deer	0.0261	0.0061
Wild turkey	0.0251	0.0115

Values provide a quantified comparison between the NRPI and SEC drivers and indicate which driver has a greater impact on distribution change on a species-by-species basis.

vs. Low NRPI and Local vs. Global SEC, we found a nearly 50/50 split in the focal group for which the primary driver had a greater impact on distribution change (**Table 4**).

DISCUSSION

The New England region is a large landscape that covers six US states and includes some of the largest expanses of hardwood forest and metropolitan areas in the country. Climate change and the pace of urban development has increased substantially in recent years, and the impacts of these changes on wildlife are largely unknown (Seto et al., 2012; Hayhoe et al., 2018). Our analysis suggests that a continuation of current trends will result in declines in the distribution of harvested species, which are important ecologically, socially, and economically in the region (U.S. Department of the Interior et al., 2016). For example, in Vermont, hunting, trapping, and shooting are important activities to residents, major contributors to the state's economy, and are largely focused on species that exert strong ecological impacts on forest ecosystems like moose, deer, and bear (Pastor et al., 1998; Horsley et al., 2003; U.S. Department of the Interior et al., 2016; U.S. Bureau of Economic Analysis, 2019).

Species distributions are predicted to decline for most of the focal species if current climate and land use trends continue. The RT scenario – which simulated climate trends following the RCP 8.5 emission scenario and a continuation of recent trends in land use – resulted in 4.36% less forest cover by 2060 (Duveneck and Thompson, 2019) due to increases in development and agricultural land cover (37% and <5% more, respectively; Thompson et al., 2019). Under this scenario, eight of the ten focal species demonstrated a decrease in regional occurrence. Red fox and white-tailed deer were the only species that experienced an increase in regional occurrence (29.6 and 0.5%, respectively). The red fox is the widest ranging member of the Carnivora order and is capable of living in a variety of environments, including deserts, forests, tundra, and urban environments largely due to its physiology and behavioral plasticity (Voigt, 1987; Tesky, 1995; Lariviere and Pasitschniak-Arts, 1996). Similarly, white-tailed deer often occur at the interface between natural and developed areas and occupy a variety of habitat types (Swihart et al., 1993). Increases in these species distributions probably reflects their ability to adapt to the current trends of environmental change.

Among the species expected to decline if recent trends continue, four showed low to moderate declines in regional occurrence, including bobcat, coyote, raccoon, and striped skunk (ranging between a 3.0 and 6.6% decline by 2060). By comparison, American black bear, gray fox, moose, and wild turkey experienced relatively large reductions in distribution and average regional occurrence (ranging between 15.7 and 51.7% decline). These species are generally more sensitive to development and climate shifts, which may explain the projected negative impacts on distribution (Renecker and Hudson, 1986; Roberts and Porter, 1998; Rustad et al., 2012; COSEWIC, 2015; Evans, 2016; Lavoie et al., 2017; Environment and Climate Change Canada, 2018; Johnson et al., 2018). High levels of decline are concerning, especially for moose and gray fox, which have been identified as Species of Greatest Conservation Need by one or more of the New England states (Maine Dept. of Inland Fisheries and Wildlife, 2015; Massachusetts Division of Fisheries and Wildlife, 2015; New Hampshire Fish and Game Department, 2015; Rhode Island Department of Environmental Management Division on Fish and Wildlife, 2015; Vermont Fish and Wildlife Department, 2015). Additional assessments have also indicated recent population and distribution declines for moose in New England (Wattles and DeStefano, 2011; Timmermann and Rodgers, 2017) and many other regions in North America (Murray et al., 2006; Lenarz et al., 2010; Broders et al., 2012).

The RT scenario presents one plausible future, but we also explored the effects of other alternative futures on wildlife. The NELFP scenarios provided a set of alternative futures, influenced by climate change, yet based mainly on two social drivers of land use change – NRPI and SEC. These scenarios accounted for future climate impacts and allowed us to assess how patterns of wildlife occurrence and species richness were influenced by different drivers and trajectories of land use change. Of the four alternative scenarios, Growing Global (GG), Go It Alone (GA), and Connected Communities (CC) all led to higher species richness then RT; Yankee Cosmopolitan (YC) led to lower richness. Similarly, our assessment of the social drivers of change indicated that a low investment in NRPI and a global approach to SEC were most influential on distribution change and species richness.

In terms of land cover change, a low investment in NRPI led to increased rates of timber harvest in the NELFP scenarios. The GA and GG scenarios were built around the Low NRPI driver and simulated the highest timber harvest rates of all the scenarios (i.e., 135 and 110% increase in harvest rate compared to RT, respectively) and the highest species richness of all the scenarios. Timber harvest can benefit some species, including some in the focal group (Monthey, 1984; Hunter and Schmiegelow, 2011) by generating important habitats (e.g., early succession forest) and increasing heterogeneity in forest structure and composition (Hansen et al., 1991; Hunter and Schmiegelow, 2011). Moose,

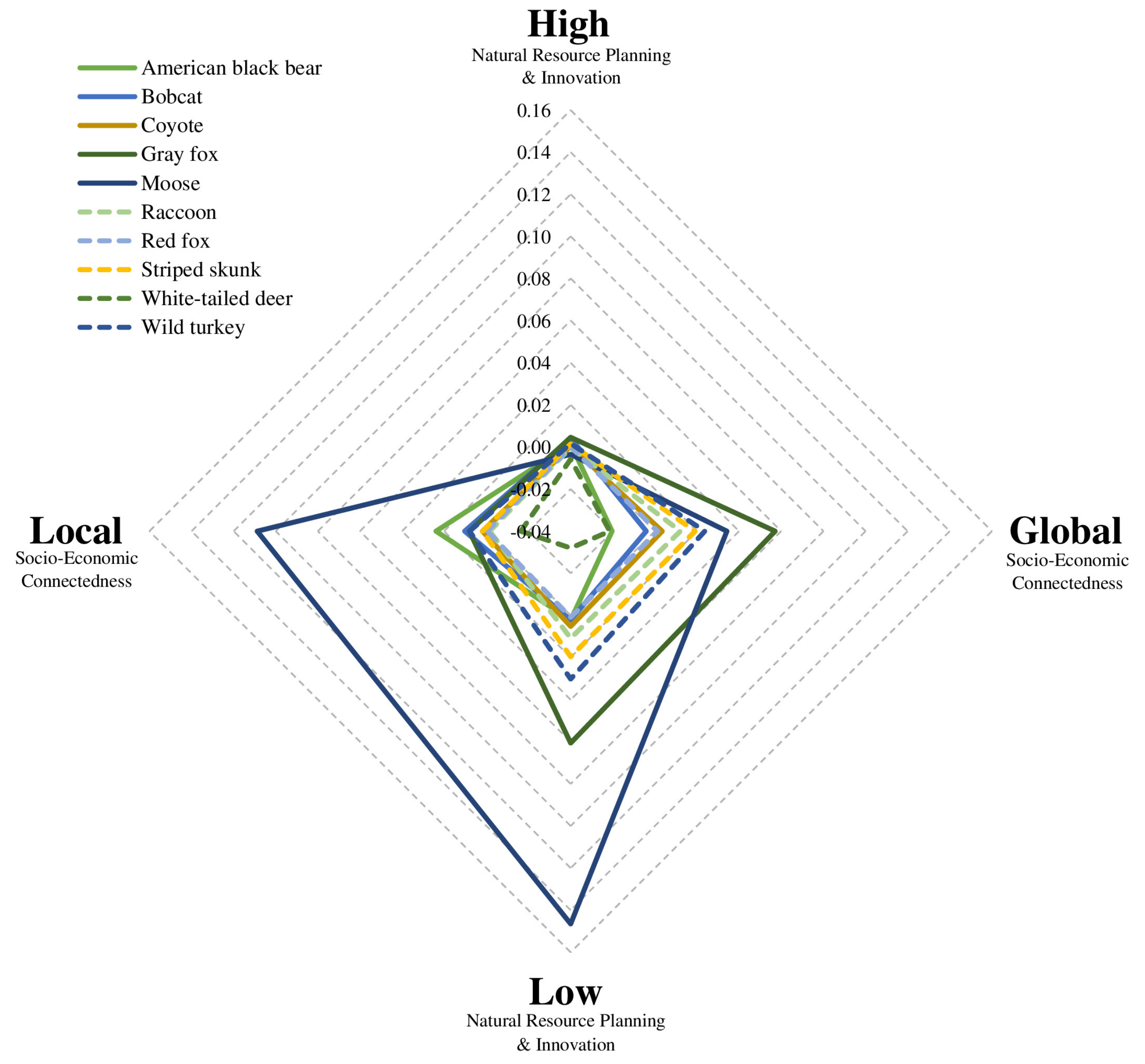

FIGURE 5 | Radar plot showing species-specific (*n* = 10) distribution changes associated with each directional driver – i.e., high or low Natural Resource Planning and Innovation (NRPI), and global or local Socio-Economic Connectedness (SEC). The NRPI and SEC axes display how each driver impacted distribution change (i.e., change in mean regional occurrence likelihood) in the New England region of the northeastern United States between 2010 and 2060. All values were derived from species distribution models and provide a measure of how each driver shifted species regional occurrence likelihood relative to the occurrence likelihood simulated for Recent Trends. The overlay of all species shows driver associated trends within the focal group.

gray fox, and wild turkey are all species that appear to benefit from increased forest heterogeneity driven by Low NRPI. For example, moose distribution was greatest under the GA and GG scenarios; probably because these scenarios resulted in high levels of timber harvest and larger amounts of young forest, which benefit moose (Monthey, 1984; Innes, 2010; Wattles and DeStefano, 2011). However, it is important to recognize that a continuation of Low NRPI actions and disregard for both innovation and more extensive natural resource planning activities will probably have less favorable long-term consequences for many other wildlife species. Climate impacts on forest composition may also have greater long-term consequences for wildlife. For this analysis we simulated climate and land use change 50 years into the future, however, the effects of climate change on forest composition are projected to increase dramatically beyond 50 years (Duveneck and Thompson, 2017; Janowiak et al., 2018). With larger shifts occurring in the second half of the 21st century, wildlife species may experience less favorable conditions over time.

Economic development activities like urban expansion and the conversion of forest to agriculture can also have considerable impacts on species richness by reducing the availability and quality of habitat in the region (Murphy and Romanuk, 2014; Newbold et al., 2015). In the NELFP simulations, the CC and GA scenarios were built around the Local SEC driver and led to lower rates of development (i.e., 75 and 25% decrease in development rate, respectively) and higher species richness than the RT projection. By comparison, the GG and YC scenarios were built around the Global SEC driver and simulated high rates of development (i.e., 180 and 40% increase in development rate compared to RT, respectively). These two scenarios resulted in the highest (GG) and lowest (YC) species richness, showing that increased development rates can negatively influence species occurrence, but may not directly translate to lower richness. Rather, other factors including the pattern and intensity of development may be more influential than rate alone. Both Global and Local SEC drivers altered development patterns and subsequently influenced distribution change – drawing attention to the considerable influence that social and economic factors can have on natural systems and emphasizing the importance of including these factors in regional planning efforts.

The scenario assessments provide measures of the response of multiple wildlife species to future natural, social, and economic changes in New England. The results provide species information that can aid in landscape decision-making around management and conservation problems (Peterson et al., 2003). For a given problem, decision-makers can set objectives, then use the models to assess the consequences associated with each scenario, evaluate trade-offs among scenarios, and identify the trajectory that most successfully meets their objectives. As a simple example, a group interested in maximizing black bear populations in New England could compare occurrence probabilities across the scenarios to evaluate the trade-offs of each type of future scenario; in this case, choosing the GA scenario may be best as it projects the highest regional occurrence for black bear. Information about the GA scenario could then be used to help guide policy and management actions.

The scenarios could also be used in more complex decision-making problems that account for trade-offs across multiple objectives and multiple spatial and temporal scales. For example, the state of Vermont has set a goal of meeting 90% of the state's energy needs through renewable sources (e.g., solar, wind, forest-derived bioenergy) by the year 2050 (Vermont Department of Public Service, 2016). Considering this objective, Vermont may change following a trajectory similar to the CC scenario – in which advances in local green energy support a more self-reliant community – or the GA scenario – in which poor planning and extractive use significantly degrades the region's ecosystem services. However, the state also has objectives related to the sustainability of harvested species, other natural resources, and climate change. Decision-making frameworks following principles of Structured Decision Making (Gregory et al., 2012) could be used to evaluate possible impacts of climate change and the trade-offs of each future scenario on renewable energy production, and the sustainability of harvested species and other natural resources, which can inform policy actions.

Our assessments of landscape change on wildlife species accounted for several social, ecological, and economic factors based on information from models, expert opinion, and consensus from a consortium of scientists, managers, and community members (i.e., the Scenarios, Services, and Society Research Coordination Network that developed the NELFP scenarios). However, any future scenario projections involve uncertainties. Uncertainty in the SDM parameters has been estimated, which provides a measure of confidence in the occurrence estimates. Other factors not considered in the modeling process, such as species interactions or variable trajectories of climate change, may impact distribution patterns and induce additional uncertainty in the outcome for species (Royle and Dorazio, 2008). For example, coyotes are dominant competitors and have been shown to shape the distribution of other sympatric carnivore species (Johnson et al., 1996; Fedriani et al., 2000); changes in their occurrence over time may have impacts on red foxes and gray foxes through competition (Johnson et al., 1996; Fedriani et al., 2000; Levi and Wilmers, 2012), and even game birds like wild turkey through altered predation risk (Guthrey, 1995). Accounting for the behavioral and ecological complexities of species interactions is challenging, and would require additional (and currently unavailable) data to be integrated into future scenario modeling. Future climate conditions are also largely uncertain and species future distributions may vary considerably under different trajectories of climate change. Here, we simulated future climate conditions based on a single high emissions scenario to aide interpretability and offer distribution projections that account for both climate and land-use change. Considering additional climate scenarios and climate-related factors could provide further insight on species future distribution patterns.

We also used probability of occurrence at a 30 m pixel level as a measure for evaluating the effects of landscape change on a species. Occurrence probability reflects habitat quality, which we assumed also relates to the number of individuals, an important measure for harvest management (e.g., setting harvest quotas or bag limits). A positive relationship between occupancy probability and abundance has been shown for several wildlife species (Blackburn et al., 2006; Zuckerberg et al., 2009). However, this relationship is not always consistent and linear (Blackburn et al., 2006). For example, recent trends suggest that gray foxes are expanding in range in the northeastern US and eastern Canada (COSEWIC, 2015; Environment and Climate Change Canada, 2018). However, our projection for gray fox shows a decline in occurrence under the RT scenario. Here, it is important to distinguish range expansion from population growth and increased species occurrence – while the range of gray fox may be expanding, localized shifts in habitat can lead to lower abundance. It is also important to recognize that current trends may not continue into the future. While current conditions appear to facilitate range expansion for gray fox, changes to New England's climate and land use may decrease gray fox occurrence in the future. Brown et al. (2018) also showed that small declines in regional occurrence probability of bird species in New England can result in large declines in the actual number of territories that a region can support. This is an important consideration, as seemingly small changes in occurrence probability may translate to much larger shifts in a species actual abundance.

Resilience of wildlife communities to change is a conservation priority for the New England region (Anderson et al., 2016). Our study focused on harvested wildlife species and provides a foundation for evaluating areas of high and low resilience under regimes of change for this group of ecologically, socially, and economically important species. Many resilience studies have focused on identifying resilient areas for broader biodiversity using focal taxa (e.g., birds) or groups (e.g., rare species). For example, Anderson et al. (2014) estimated resilience to climate change in northeastern North America using locations of rare species populations and representative natural communities as measures of biodiversity. Our study complements this and other assessments in the region (e.g., Staying Connected Initiative; Smith et al., 2012) by providing fine-scale information on harvested wildlife species that have been largely excluded in regional analyses.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available through the FEMC Data Archive and can be found at https://www.uvm.edu/femc/data/archive/project/wildlife_future_scenarios/dataset.

AUTHOR CONTRIBUTIONS

SP-G and TD contributed to the concept and design of the project. SP-G conducted the analyses and drafted the manuscript. MD provided the forest change simulations. All authors participated in revising and editing the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00164/full#supplementary-material

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Evaluating the Impact of Future Global Climate Change and Bioeconomy Scenarios on Ecosystem Services Using a Strategic Forest Management Decision Support System

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Sustainable Forest Management (SFM) has become an important pillar of modern forest management, and one way to evaluate the sustainability of forestry is to assess long-term supply of ecosystem services (ESs) indicators. The concept of sustainability also has come to include adapting to climate change and the associated dynamic timber markets. This study aims to: (1) incorporate several ESs indicators in a Forest Management Decision Support System (FMDSS) that can deal with climate change and dynamic timber markets; and (2) analyse the impact that intensified forest management, resulting from global change scenarios that represent different levels of climate change mitigation efforts, will have on forest ES indicators in the west of Ireland. A linear programming model that optimized Net Present Value (NPV) from mill-gate sales was previously developed in Remsoft Woodstock, a DSS framework used for strategic forest planning around the world. This Woodstock model was modified to include the effects of global scenarios that include climate change and dynamic timber prices. This model was further developed to include indicators for five ESs (carbon storage in the forest as well as in harvested wood products and carbon substitution, windthrow risk, biodiversity, water quality, and cultural values), to assess the impacts of these global scenarios on the forest landscape and the sustainability of forest management. The ES indicator values were mainly linked to forest age, forest type, and yield tables, and their inclusion in the FMDSS had almost no impact on total model run times. Intensified forest clearfelling, as a result of increasing timber prices associated with most global scenarios, led to increased phosphor emissions to waterbodies, and reductions in windthrow risk and carbon storage. The global scenarios only resulted in minor differences in the indicator values for biodiversity and cultural values. Besides the global scenarios, recent forest policy development and the poor soil conditions in the study area impacted on the results. The developed system, with its innovative method to incorporate climate change and associated market dynamics, could be applied to other forest landscapes in Ireland and Europe, or indeed by any forest company or organization that uses Remsoft Woodstock.

Keywords: forest planning, Remsoft Woodstock, sustainable forest management, blanket peat, linear programming, afforested western peatlands

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INTRODUCTION

The concept of sustainable forestry originates from the 18th century and concerned sustainable supply of charcoal required for the mining industry (Hofer, 2009). Since then, Sustainable Forest Management (SFM) has been expanded to include economic, ecological, and social values, as defined by the United Nations Conference on Environment and Development in Rio de Janeiro in 1992 (Forest Europe, 1993; Mulloy, 1997). Compliance with SFM has become a requirement for many forests around the world, Ireland included. The concept of Ecosystem Services (ESs) was originally introduced to raise awareness about the importance of nature protection by framing biodiverse habitat destruction in terms of economic loss (Gómez-Baggethun et al., 2010). The concept has since been expanded, and ES indicators specific to each region are now utilised to assess the status of the forest and the economic, environmental and social performance of the forest industry. ESs are defined as goods and services that contribute to human well-being (Reid et al., 2005) and they often depend on assets and functions of the world's natural capital (e.g., soil, air, freshwater, minerals etc.; Turner and Daily, 2008). The Millennium Ecosystem Assessment reported that intensified natural resource management rapidly accelerated the decline of many ESs globally (Reid et al., 2005). Implementing SFM could be simplified by having a set of measurable ES indicators tied to each SFM pillar (Biber et al., 2015; Nobre et al., 2016). However, since different methodologies are often applied across the world when assessing ESs, it is questionable if ES-values can be compared between countries (Biber et al., 2015), and utilizing internationally uniform methodologies to assess ESs could result in reduced relevance for local landscape ESs (Nordström et al., 2019). Quantifying ESs makes it possible to analyse the interactions and trade-offs between them under different forest management approaches (Raudsepp-Hearne et al., 2010). This can be done using Forest Management Decision Support Systems (FMDSSs), both at a stand and landscape level, which can then be upscaled (or modelled) to analyse regional or even global level ES trade-offs.

FMDSSs have been widely used since the 1980s to make better forest management decisions as well as to forecast the future forest condition to ensure the sustainability of timber harvesting (Reynolds, 2005; Reynolds et al., 2008). FMDSSs were initially developed to ensure sustainable strategic timber yield (Nobre et al., 2016), and timber production or Net Present Value (NPV) often remains the main focus to this day (Reynolds et al., 2008; Bettinger et al., 2017). Spatial aspects of forest planning have been developed for these systems, mainly at the tactical and operational planning level (Baskent and Keles, 2005). These aspects refer to avoiding too large adjacent clearfelled areas, i.e., green-up rules (Bettinger and Zhu, 2006), minimizing harvesting and transportation costs (Nieuwenhuis and Williamson, 1993), and maintaining large areas of un-fragmented old growth and valuable biodiverse forest (Öhman and Wikström (2008). FMDSSs have been developed to analyse the impacts of forestry operations on biodiversity, carbon sequestration, water quality, the long-term changes in forest composition and structure, as well as to analyse how pest, disease, windthrow and wildfire damage will affect the forest and the resulting timber supply and other ES-values (Eriksson and Borges, 2014; Vacik and Lexer, 2014; Biber et al., 2015; Nobre et al., 2016; Marques et al., 2017). With an increasing understanding of forest ecosystems, the concept of SFM has expanded to consider, inter alia, the impacts that changing climate may have on species suitability, forest productivity, forest ESs and the resilience to pests diseases and extreme weather events (Nordström et al., 2019). Forest ecosystems are increasingly under pressure—along with accommodating SFM principles and the pressure of climate change impacts, new policies that have been introduced as a response to climate change often emphasize increased biomass production to make societies more sustainable (Lindner et al., 2010; Söderberg and Eckerberg, 2013). Research in Europe has shown that increased harvesting levels often reduce the biodiversity levels in Europe (Verkerk et al., 2011; Duncker et al., 2012; Biber et al., 2015). High levels of biodiversity and tree species diversity have been found to be closely linked to other ESs and ecosystem functions (e.g., increasing resilience to disturbances and climate change, enhanced growth in certain species mixtures, high stocks of carbon stored in living biomass), making them strong indicators of ecosystem health (Balvanera et al., 2006; Gamfeldt et al., 2013; Brockerhoff et al., 2017).

Analyzing the long-term impacts of various global development scenarios on forest management approaches and forest ESs is crucial to avoid negative outcomes and conflicts between stakeholders. The ALTERFOR project is a collaboration between 9 countries (Germany, Ireland, Italy, Lithuania, The Netherlands, Portugal, Slovakia, Sweden, and Turkey; Marques et al., 2017; Marto et al., 2018; Schwaiger et al., 2018, 2019; Mozgeris et al., 2019; Nordström et al., 2019) that investigates the suitability of FMDSSs to analyse the complex dynamic interactions between climate change, global markets, and forest management practices to assess the suitability of current and alternative forest management systems to address future challenges and provide society with an optimal mix of ESs. Standardized ES indicators have been implemented in nine different FMDSSs to allow for comparisons across European landscapes and facilitated the large-scale analysis of long-term climate change and bioeconomy impacts on the provision of forest ESs in Europe (Nordström et al., 2019). The research presented in this article focusses on aspects of the ALTERFOR project that relate to the situation in Ireland.

Early industrialism and an increased demand for agricultural land from the rapidly increasing population in the 18th and 19th century nearly exhausted all Irish forests (OCarroll, 2004). Between 1908 and 2017 the forest cover in the Republic of Ireland increased from 1.5 to 11% or 770,020 ha (OCarroll, 2004; Forest Service, 2018). Much of this afforestation was done by the Irish state between the 1950s and 1990s, and large areas of inexpensive, mountainous, marginal agricultural and blanket peat land were planted with fast growing and hardy conifer species from Western North America (Gray, 1963; Neeson, 1991; Tiernan, 2007). The nutrient poor and excessively wet blanket peat sites were afforested using a combination of plowing, drainage, and application of rock phosphatic fertiliser to ensure stand survival (Renou-Wilson and Byrne, 2015). By 2012, about one third of all Irish afforestation had occurred on blanket peat sites (Forest Service, 2013). The main species used were Sitka spruce (*Picea Sitchensis* (Bong.) Carr.) and lodgepole pine (*Pinus contorta* Douglas), which now occupy 51.1% and 9.6% of the Irish forest estate, respectively (Forest Service, 2018). Lodgepole pine was planted on the least productive sites, while Sitka spruce was generally planted on the better sites, due to its ability to reach a high Yield Class (YC, maximum mean annual volume increment for the species on the site in m^3 ha^{-1} yr^{-1}) on a wide range of sites (Renou and Farrell, 2005). Sitka spruce is still the staple income producing species in Irish forestry and conifers in are clearfelled on a 35–50-year rotation, depending on species and site productivity. Since the 1990s, nearly all afforestation has been done on private land, with a greater focus on fertile and productive sites, while adhering to higher environmental standards, including the use of mandatory buffer zones, and, recently, with increased species diversification requirements (Byrne and Legge, 2008; Forest Service, 2016, 2017). Studies on the long-term impacts of climate change on Irish forestry found that the spruce trees utilised for sawlog production will likely suffer reduced growth in the future, causing reduced revenue for forest managers (Cabrera Berned and Nieuwenhuis, 2017; Keenan et al., 2017; Lundholm et al., 2019). However, Lundholm et al. (2019) found that increased demand for wood biomass would offset the negative growth impacts of climate change on NPV, causing a net increase in future profits due to higher timber assortment prices. Forest based ESs has been evaluated previously in Ireland, but this assessment was focused on finding the biophysical provision limits of the forest landscape (Corrigan and Nieuwenhuis, 2016), in order to find an optimal balance of ESs under future policy scenarios (Corrigan and Nieuwenhuis, 2017). Although these studies involved important development in adapting FMDSS to assess ESs, they did not consider the impact of climate change on their provision levels. Thus, it is important to investigate the impacts that increased harvesting, resulting from climate change and an increased timber demand caused by mitigation efforts, might have on biodiversity and other ESs, especially if the harvesting of forest biomass is introduced.

FMDSSs can be used to model severe biotic and abiotic disturbances, including disturbances with increased frequency and/or magnitude due to climate change (Hennigar et al., 2013). Wind is the largest abiotic disturbance causing mortality in Irish forestry; mortality from windthrow is expected to increase in boreal and temperate forests due to climate change. This increase is not only the result of increased wind speeds, but also from milder winters with less frozen soil, reducing root anchorage (Saad et al., 2017), and from excessively wet soils, limiting root growth (Ray et al., 2008). However, a lack of relevant information about future disturbances means that many potentially devastating impacts are difficult to model accurately (Cunniffe et al., 2015), and using Monte Carlo simulation to model disturbances can result in highly imprecise estimates, even if long time series are available (Armstrong, 1999). Remsoft Woodstock models using optimisation (the type of FMDSS used in this study) cannot accommodate stochastic disturbances (Walters, 1993), so these types of impacts were not included in this study.

The aims of this study were: (1) incorporate several ESs indicators in a FMDSS that can deal with climate change and dynamic timber markets; and (2) analyse the impact that intensified forest management, resulting from global change scenarios that represent different levels of climate change mitigation efforts, will have on forest ES indicators in the west of Ireland.

MATERIALS AND METHODS

Case Study Area

The Barony of Moycullen was chosen as the Case Study Area (CSA); it is located around the Cloosh Valley forest and the Derrada forest, just west of Galway city, county Galway, in western Ireland (**Figure 1**). The area contains 10,230 ha of forest, including Ireland's largest continuous forest, at almost 4,600 ha. Coillte, the Irish semi-state forestry company, owns 81.1% of the forests in the CSA, with the remainder privately owned. Atlantic blanket peat soils occupy 82% of forest area, with the remainder mainly consisting of heavy wet gley soils and shallow lithosol soils. Most of the forest was established through afforestation in the 1970s and 1980s, using plowing, drainage, fertilisation and planting, and using hardy and fast-growing tree species from western North America. Sitka spruce and lodgepole pine occupy 41.0% and 29.1% of the CSA's forests, respectively, other conifers and broadleaves occupy 10.4%, and the remainder, 19.5%, is made up of open, unstocked forest area. The CSA contains one of Ireland's eight priority Freshwater Pearl Mussel (*Margaritifera margaritifera* L) catchments (Moorkens et al., 2013), and is frequented by many visitors, both locals from Galway, as well as tourists from Ireland and abroad. As blanket peat soils are often waterlogged, poor in nutrients, and allow only shallow root growth, the forests growing on them are very susceptible to windthrow. Windthrow is further exacerbated by the CSA's proximity to the Atlantic Ocean and the associated strong winds. Additionally, peatlands had to be drained prior to afforestation, causing the peat to oxidize and release CO_2. Thus, the landscape in the CSA has multiple uses and complex ES interactions are taking place, making it an interesting study object for the analysis of the long-term sustainability impacts of climate change and the associated anticipated changes in timber prices. Many of these multiple use conflicts and ES interactions are also present in afforested peatland landscapes all along the western European seaboard, thus making the results relevant for forest managers and policy makers in a wider area.

Decision Support System (DSS)

The core model for the DSS was developed in Remsoft Woodstock (Remsoft, Fredericton, Canada), a software system used worldwide for strategic forest planning and management (Walters, 1993). The model used linear programming optimisation, with an objective function that maximises NPV from mill-gate timber sales over a 100-year planning horizon, using a 5% discount rate, commonly used in Irish forestry (Tiernan, 2007; Corrigan and Nieuwenhuis, 2016;

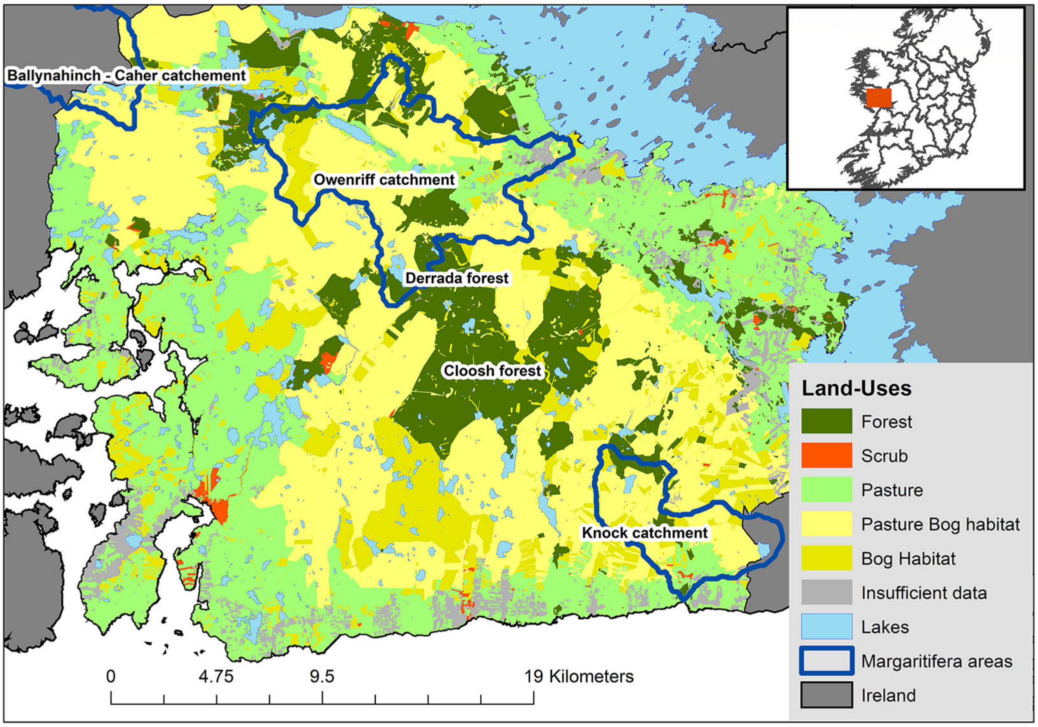

FIGURE 1 | The Barony of Moycullen CSA in County Galway, Ireland, delineated by its land-uses. Margaritifera areas are catchments with freshwater pearl mussel populations. The Cloosh Forest is the forest area at the center of the CSA, Derrada is located north of Cloosh. The Owenriff catchment contains much of the Derrada forest and is located just north of Cloosh. Source: Lundholm et al. (2019).

Teagasc, 2019). This core model was developed specifically for Irish forestry, incorporating country-specific forest management prescriptions, and to be compliant with Irish forest policy and environmental policy. The model used Irish growth and yield tables to forecast stand development and timber production, as well as the relevant costs and revenues associated with forest management actions (Lundholm et al., 2019). The core model was then expanded to include both climate change, through changes in tree species productivity, and an expanding bioeconomy, represented by dynamic wood assortment prices that reflect varying levels of mitigation efforts, for three global scenarios that were down-scaled to the national level. Since a changing climate and wood demand affect other ESs than harvest volumes and assortments, the DSS model was further expanded and customized to include indicators for five ESs: carbon storage, regulatory services, biodiversity, water quality, and cultural services. With the exception of the cultural RAFL-index, all ESs presented in this study were outputs produced by the Woodstock DSS; the cultural ES attributes were DSS outputs that were combined to produce the RAFL-index post-optimisation. The final DSS model is called the ALTERFOR model, after the research project for which is was developed.

Modelled Scenarios

Three global scenarios and a control scenario were modelled, with the global scenarios including the effect of climate change on tree growth and dynamic timber prices, based on regional and global demand for wood, affected by different levels of climate change mitigation effort. The global scenarios narratives (Forsell and Korosuo, 2016) were derived from the Global Biosphere Management Model (GLOBIOM) (Havlík et al., 2014) and were provided by the International Institute for Applied Systems Analysis. The basis for the global scenarios were combinatory analyses of the EU policy scenarios (Forsell et al., 2016) and the Representative Concentration Pathways (RCP)—Shared Socio-economic Pathways (Fricko et al., 2017), developed for the International Panel for Climate Change. Thus, GLOBIOM provided dynamic timber prices on a decennial basis and their associated climate change scenario narratives. The Irish software Climadapt (Ray et al., 2009) was used to obtain species-specific climate change impact factors which were implemented in the ALTERFOR model, bringing the global scenario narratives to the Irish level. Climadapt uses a combination of ecological site classifications, current climate, and future climate in 2080 to predict the current and future site productivity for 20 tree species used in Irish forestry, 11 of these species and species groups which were modelled in this study: alder (*Alnus glutinosa* (L.) Gaertn.), ash (*Fraxinus excelsior* L.), beech (*Fagus sylvatica* L.), birches (*Betula pubescens* Ehrh. and *Betula pendula* Roth), Japanese larch (*Larix kaempferi* (Lamb.) Carr.), lodgepole pine (*Pinus contorta* Douglas), Norway spruce (*Picea abies* (L.) H. Karst.), oaks (*Quercus robur* L. and *Quercus petraea* (Matt.)

Liebl.), Scots pine (*Pinus sylvestris* L.), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), and sycamore (*Acer pseudoplatanus* L.). The Climadapt predictions of future climate only included the average climatic factors and did not consider the increased severity of storms. The exact global scenario factors used can be found in the study by Lundholm et al. (2019), and the four modelled scenarios were:

- **BAU**—Business as usual. Control scenario with no climate change or dynamic prices implemented.
- **S1**—Reference: Temperature increase of 3.7°C by 2100, compared to pre-industrial values. Climate scenario: RCP8.5. No effort to mitigate climate change. Early increase in sawlog prices in the first 30 years, then prices remain static at 29% higher than the start year. Early increase in pulpwood price by the first 20 years, then slight decline around year 30, after which prices were mostly static at 21% higher than the start year.
- **S2**—EU Bioenergy: Temperature increase of 2.5°C by 2100, compared to pre-industrial values. Climate scenario: RCP4.5. EU effort to mitigate climate change through expanded bioeconomy. Steep increase in sawlog prices by 38% around year 60–90. Slight pulpwood price increase by 22% followed by decline all within the first 50 years, followed by static prices at 14% higher than the start year.
- **S3**—Global Bioenergy: Temperature increase of 1.5–2.0°C by 2100, compared to pre-industrial values. Climate scenario: RCP2.6. Global effort to mitigate climate change through increased bioeconomy. Steady increase in sawlog prices throughout the planning horizon to a level 42% higher than in the start year. Pulpwood prices increase by 84% over the 100-year planning horizon.

Both the climate change productivity impacts and the dynamic timber prices were converted to annual change values to avoid sharp increases and decreases between years, as those would greatly influence the model solution. The climate change productivity impacts were implemented in the DSS by scaling the growth and yield for all tree sizes, and the dynamic wood assortment prices were implemented as factors that were multiplied with the default wood assortment price.

Ecosystem Service Indicators

Carbon

The carbon ES indicator includes five categories of forest related carbon: (1) stand living carbon (above and below ground), (2) deadwood carbon (from harvesting and natural mortality), (3) carbon stored in harvested wood-products (HWP), (4) substitution of fossil fuels from using wood fiber for biofuel and in construction, and (5) carbon emissions from drained peat soil. The deadwood carbon and HWP were subjected to a decay function to represent decomposition of deadwood and degradation of HWP. The carbon ES assessment focused on the cumulative changes in total carbon stock from the start of the planning horizon (Equation 1). The absolute stock would be difficult to estimate since the historic harvest assortments and historic storage in HWP were unknown.

$$CB_i ha^{-1} = \frac{\sum \Delta Cpool_{j,i} + Psub(ff)_{total\ i} + Psub(P)_{total\ i} + (\mathbf{OSC} * peatfor_i)}{forest\ area_i} \tag{1}$$

where $CB_i ha^{-1}$ is the carbon balance per ha in year *i*, in units tons carbon ha^{-1}; $\Delta Cpool_{j,i}$ is the change in carbon for category *j* (i.e., stand living carbon, deadwood carbon, and HWP carbon), in year *i*, given in tons carbon; $Psub(ff)_{totali}$ and $Psub(P)_{totali}$ are the total carbon substitution for fossil fuels and products, respectively, in year *i*, in tons carbon; *OSC* is the organic soil carbon loss in tons carbon ha^{-1}; $peatfor_i$ is the area of drained peatland forest in year *i; forest area*$_i$ is the total area of forest, for which the carbon balance was calculated.

Stand living carbon

Stand living carbon accounts for both above and below ground stocks of carbon and was calculated based on biomass expansion factors, carbon fractions, merchantable standing volume, and root ratio, i.e., ratio of belowground biomass to aboveground biomass, in Equation (2).

$$SLC_i = BCEF_S * CF * (standvol_i * \ (1 + R)\ ) \tag{2}$$

where SLC_i is the stand living carbon, in year *i*, in tons carbon; $BCEF_S$ is the biomass conversion and expansion factor for growing stock (hence the subscript *s*) (**Supplementary Table 1**); *CF* is the carbon fraction in tons carbon (ton dry mass)$^{-1}$ (**Supplementary Table 2**); $standvol_i$ is the total merchantable stand volume in year *i*, in m^3; and *R* is the ratio of belowground biomass to aboveground biomass (**Supplementary Table 1**).

Deadwood carbon

Deadwood carbon inflow originated from both natural mortality and harvesting, recording carbon stored in logs aboveground and all belowground roots. Natural mortality was only obtained from the yield tables and therefore did not include the impacts of extreme events such as droughts, windthrow, pests and diseases. The annual inflow of deadwood went into four different stocks (aboveground and belowground stocks for both natural mortality and harvest residue deadwood carbon) that were subjected to annual decay functions. Natural mortality carbon (NMC) was calculated using Equation (3), Harvest Residue Carbon (HRC) was calculated using Equation (4).

$$inflowNMC_i = \mathrm{CF}*(\mathrm{NMvol_i} * \mathrm{D} + \mathrm{NMvol_i} * \mathrm{BCEF_S} * \mathrm{R}) \tag{3}$$

where $inflowNMC_i$is the total input of aboveground and belowground natural mortality carbon in year *i*, in tons carbon; *CF* is the carbon fraction in tons carbon (ton dry mass)$^{-1}$ (**Supplementary Table 2**); $NMvol_i$ is the natural mortality of merchantable volume in year *i*, in m^3; *D* is the density of the tree species in tons m^{-3} (**Supplementary Table 2**); $BCEF_S$ is the biomass conversion and expansion factor for growing stock

(**Supplementary Table 1**); and R is the ratio of belowground biomass to aboveground biomass (**Supplementary Table 1**).

$$\begin{aligned} inflowHRC_i = CF * (Harvvol_i * D * HF + Harvvol_i \\ * BCEF_S * R) \end{aligned} \tag{4}$$

where $inflowHRC_i$ is the total inflow of harvest residue carbon and belowground deadwood due to harvesting in year i, in tons carbon; CF is the carbon fraction in tons carbon (ton dry mass)$^{-1}$ (**Supplementary Table 2**); $Harvvol_i$ is the harvested volume in year i, in m^3; D is the density of the tree species in tons m^{-3} (**Supplementary Table 2**); HF is the harvest fraction left on sites and can be calculated from the average tree volume in m^3, based on the calculation of F in Equation (5), which is the currently used Irish industry standard; $BCEF_S$ is the biomass conversion and expansion factor for growing stock (**Supplementary Table 1**); and R is the ratio of belowground biomass to aboveground biomass (**Supplementary Table 1**).

$$F = \frac{\left(4 - (3.8 * \ln\left(avgtree\right))\right) * 0.9}{100} \tag{5}$$

If the value of $F < 0.03$, HF is given the calculated value of F, otherwise $HF = 0.03$, which only happens when the average tree volume is larger than 1.35 m^3.

The decay function was applied to all deadwood carbon pools, using Equation (6) (Bond-Lamberty and Gower, 2008).

$$DW_{ij+1} = e^{-k} * (DW_{ij} * \mathrm{FF}) + \left[\frac{\left(1 - e^{-k}\right)}{k}\right] * (Inflow_{ij} * FF) \tag{6}$$

where DW_{ij} is deadwood carbon stock in category j (i.e., NMC and HRC) in year i, in tons carbon; k is the constant for first order decay which is dependent on the product half-life given in units yr^{-1} (Equation 7); FF is the fragmentation loss factor set at 0.85 (i.e., 15% is the proportion of annually lost deadwood soil carbon due to fragmentation); and $Inflow_{ij}$is the inflow of particulate deadwood carbon from category j in year i, in tons carbon yr^{-1}.

$$\mathrm{k} = \frac{ln(\mathbf{2})}{HL} \tag{7}$$

where HL is the half-life in years for the deadwood carbon category (aboveground or belowground). Half-life for logs is 12 years (Yatskov et al., 2003; Olajuyigbe et al., 2011; Lundmark et al., 2016). Roots have a half-life of 19 years, stumps have a half-life of 14 years, and stumps make up about 30% of the total mass of stumps and roots larger than 10 cm in diameter (Olajuyigbe et al., 2011). This gives all belowground deadwood carbon a weighted mean half-life of 17.5 years. Thus, k is 0.0577 and 0.0396 for aboveground and belowground deadwood carbon pools, respectively. In the calculation, aboveground and belowground carbon were kept separate, so that of the different decay functions could be applied.

Harvested wood-products carbon

Utilisation of harvested wood and processing it into different products affects the storage of carbon outside the forest. In Ireland, HWP consist mainly of sawnwood and wood-based panels, while small amounts of the pulpwood assortment are utilised for biofuel. The inflow of carbon to each HWP category depends on tree species, log diameter, and wood allocation in each global scenario (Equation 8).

$$WInflow_{ij} = H_{productij} * PL * D * CF \tag{8}$$

where $WInflow_{ij}$ is the inflow of stored carbon in year i in HWP product category j (i.e., wood-based panels or sawnwood) given in tons carbon; $H_{productij}$is the wood allocated in year i to HWP category j, given in m^3 (Equation 9); PL is the processing loss factor, set to 0.43 for Ireland; D is the HWP category density, in tons m^{-3}(**Supplementary Table 2**); and CF is the carbon conversion factor in tons carbon (ton dry mass)$^{-1}$ (**Supplementary Table 2**).

$$H_{productij} = \sum_{h} \left[Harvvol_i * (1 - HF_i) * AF_{h,i} * \left(FsFP_{h,j}\right)\right] \tag{9}$$

where $Harvvol_i$ is the harvested volume in year i, in m^3; HF is the harvest fraction left on site (Equation 5); $AF_{h,i}$ is the assigned fraction of harvested wood removed from site that is allocated to assortment h, for each year i, AF varies by species and tree size and was derived from the yield tables; $FsFP_{h,j}$is the utilisation fraction of assortment h to HWP category j and varies between three species categories (i.e., conifers excluding lodgepole pine, lodgepole pine, and broadleaves), and by global scenario ("normal utilisation" for BAU and S1, "climate change mitigation" for S2 and S3) (**Supplementary Table 3**).

The carbon stock in each HWP category increased from the inflow of processed wood in subsequent years, but the inflow and previous year's stock was subject to decayed over time, Equation (10).

$$HWPC_{ij} = e^{-k} * HWPC_{ij-1} + \left[\frac{\left(1 - e^{-k}\right)}{k}\right] * WInflow_{ij} \tag{10}$$

where $HWPC_{ij}$ is the carbon stock in HWP category j, in year i, in units tons carbon; k is the decay constant, using 0.027726 for sawnwood and 0.019804 for wood-based panels, based on half-lives of 25 and 35 years (IPCC, 2014), respectively, calculated according to Equation (7); and $WInflow_{ij}$is the inflow of carbon to HWP category j, in year i, in tons carbon units.

Fossil fuel substitution

Utilisation of harvested wood can substitute the use of emission-heavy construction materials or fossil fuels when wood fiber is used for energy production. These were considered as one-off substitutions happening in the year of harvesting. All the substitution factors excluded forest carbon dynamics, to avoid double counting of forest carbon. Fossil fuel carbon substitution was calculated according to Equation (11), and product carbon substitution was calculated according to Eqution (13).

$$Psub(ff)_{i,j} = Harvvol_{energy(i)} * D * CF * F_{mix(j)} * DF_j \quad (11)$$

where $Psub(ff)_{i,j}$are the emission savings due to substitution of fossil fuels in year *i,* for fossil fuel category *j*, in tons carbon; $Harvvol_{energy(i)}$ is the harvested volume utilised for bioenergy in year *i*, given in m^3 (Equation 12); *D* is the species wood density in tons m^{-3} (**Supplementary Table 2**); *CF* is the carbon fraction (**Supplementary Table 2**); $F_{mix(j)}$ is the ratio of fossil fuel category *j* being replaced over the total fossil fuels being replaced, based on Ireland's fossil fuel mix of natural gas: 0.49, oil: 0.35, and coal: 0.16 (Duffy et al., 2018); and DF_i is the product substitution displacement factor for category *j*, in units ton carbon (emission ton carbon wood)$^{-1}$ (**Supplementary Table 4**). The equation used to account for burning of firewood was a modification of Equation (11), but instead of multiplying with the $F_{mix(j)}$ factor and DF_i, the estimated emission was multiplied with −1. This was done since firewood in Ireland is largely burnt in inefficient domestic stoves, resulting in immediate oxidization and a net emission, as opposed to burning wood in combined heat and power plants.

$$Harvvol_{energy(i)} = \sum_h [Harvvol_i * (1 - HF_i) * AF_{hi} * FsubE_h] \quad (12)$$

where $Harvvol_{energy(i)}$ is the harvested volume in year *i*, in m^3; *HF* is the harvest fraction left on site (Equation 5); AF_{hi} is the assigned fraction of harvested wood removed from site that is allocated to each assortment *h*, for each year *i, AF* varies by species and tree diameter and was sourced from the yield tables; $FsubE_h$ is the fraction of each wood assortment (*h*) assigned to fossil fuel energy replacement (**Supplementary Table 5**).

$$Psub(P)_{i,j} = Harvvol_{subs(i,j)} * D * CF * PL * DF_j \quad (13)$$

where $Psub(P)_{I,j}$ is the emission savings due to product category *j* in year *i,* in tons carbon; $Harvvol_{subs(I,j)}$ is the harvest volume of wood used for semi-finished substitution products for category *j*, in year *i*, given in m^3, calculated according to Equation (12), but with $FsubE_h$ replaced with $FsubP_{h,j}$, the fraction of each wood assortment (*h*) assigned to product substitution of category *j* (**Supplementary Table 5**); *D* is the species wood density in tons m^{-3} (**Supplementary Table 2**); *CF* is the carbon fraction (**Supplementary Table 2**); *PL* is the processing loss factor, set to 0.43 for Ireland; and DF_j is the product substitution displacement factor for product category *j*, in units ton carbon emission ton carbon wood^{-1} (**Supplementary Table 4**).

Soil carbon

Studies of the soil carbon balance in mineral soils are largely inconclusive on the magnitude and direction of stock changes due to forest management and forest types (IPCC, 2006). Thus, changes in mineral soil carbon stock were not included in the FMDSS and all soil carbon refers only to drained and forested organic soils, where there is significant carbon loss. The IPCC default emission factor for drained organic soils in the temperate zone is 0.61 tons C ha^{-1} yr^{-1}, with an additional loss of 0.31 tons C ha^{-1} yr^{-1} due to runoff emission from dissolved organic carbon (IPCC, 2006). These values were incorporated for all forested peatland since drainage at afforestation was a necessary practice to ensure crop survival.

Regulatory—Windthrow Risk

Regulatory ESs refers to risk management, which mainly means windthrow in Ireland. A windthrow risk model was developed for Ireland by Ní Dhubháin et al. (2009) which calculates the probability that a stand has experienced windthrow with more than 3% of stems windthrown, based on several site and stand characteristics (**Supplementary Table 6**). The windthrow risk probability was calculated for the total forest area at ≥70% windthrow risk, and fellable forest area at ≥70% windthrow risk, using the general structure of a logistic model. This model only measured the risk of windthrow having affected the stand, it did not make any prediction on the damage impact.

Biodiversity

The biodiversity ES assessment was based on measuring multiple stand structural features that contribute to improving biodiversity (Nieuwenhuis and Nordström, 2017) and some of the cultural attributes that were relevant for biodiversity assessment. These features were reported separately on a landscape level, and because they affect different aspects of biodiversity, they were not deemed equivalent, which is why no average biodiversity indicator score was calculated. These features were:

- Volume of large diameter trees, with Diameter at Breast Height (DBH) > 30 cm, > 40 cm, and > 50 cm, all in m^3 ha^{-1}.
- Volume of natural mortality logs and volume of large diameter (DBH > 30 cm) natural mortality logs, both in m^3 ha^{-1}.
- Volume of native Irish trees and broadleaves, in m^3 ha^{-1}.
- Area of buffer zones, in ha.
- Area of forest aged 61–80 and area of forest older than 80 years, in ha.
- Cultural attributes for the percentage final felling area, Hemeroby index, Shannon species diversity, and DBH evenness (**Table 1**).

Water Quality

The Source Load Apportionment Model framework, developed by Mockler et al. (2017), to measure nutrient emissions of N and P from different land-use areas in Ireland was utilised for the water quality ES indicator. The published framework, as well as unpublished work by Mockler, was implemented in the FMDSS to model long-term forestry impacts on water quality as well as background emission levels (**Supplementary Table 7**). The emission values were landscape-level average values, regardless of where in the landscape the land parcel was located, e.g., adjacent to or remote from watercourses. The FMDSS reported on emission rates both as total nutrient loads year^{-1} and average

TABLE 1 | Overview of operationalisation of indicators and attributes for all dimensions and concepts, including the specific value functions to determine upper and lower limits before averaging the score to create the RAFL-index.

Concepts	Dimensions	Attribute	Indicator (units)	Direction of attribute	Value-function
Stewardship	Sense of care/upkeep	Harvest residues	m^3/ha	–	0 m^3 = 0, ≥3 m^3 = 1, linear
Naturalness/ disturbances	Alteration/impact	Area harvested	% of forest area harvested	–	0% = 0, 5% = 1, linear
	Wilderness	Mortality volume	m^3/ha	+	0 m^3/ha = 0, 5 m^3/ha = 1, linear
	Intrusion	Hemeroby index	0 = natural, non-disturbed forest, 0.33 = close to natural, 0.66 = semi-natural, 1 = far from natural (monocultures, plantation)	–	Linear
Complexity	Diversity	Shannon index (species, standing volume)		+	0.5 = 0, 2 = 1, linear
	Variety	Evenness of tree sizes on landscape level (dbh)	0–1	+	Linear
	Spatial pattern	Stand size variation	Percent of total forest landscape occupied by largest forest stand	–	0% = 0, 5% = 1, linear
Visual scale	Openness	Mean tree number	stems/ha	–	1000 = 0, 2000 = 1, linear
	Visibility	Understory	Percent of forest stands with understory	–	Linear
Historicity/imageability	Historical richness	Mean stand age	years	+	20 year = 0, 60 year = 1, linear
	Historical continuity/place identity	Change in forest location (afforestation, deforestation)	Percent of forest area that changed location (afforestation and deforestation)	-	0% = 0, 10% = 1, linear
Ephemera	Seasonal change	Share broadleaves	Percent broadleaf volume of total	+	0% = 0, 5% = 1, linear

M. Hoogsta-Klein and G. Hengeveld (2017, personal communication to A. Lundholm, March 6, 2017).

nutrient loads ha^{-1} $year^{-1}$, for the forest and for the entire CSA, respectively.

Cultural

The Recreation Aesthetics Forest Landscape (RAFL) index was used as the cultural ESs indicator (Nieuwenhuis and Nordström, 2017). The index framework was largely based on four abstraction levels: concept—dimension—attribute—indicator, identified by Tveit et al. (2006). The concepts were based on perceived preferred forest structures to recreationalists, drawing from findings on scenic quality of landscapes (Tveit et al., 2006; Ode et al., 2008) and scenic beauty of forests (Edwards et al., 2012; Giergiczny et al., 2015). The attribute indicators were scaled to have equal impact on the RAFL index, by determining upper and lower limits of the indicator, and if they had a negative of positive impact on the index (**Table 1**). The attributes belonging to the same concept were then averaged to a concept score, and, finally, all concepts were averaged into the RAFL-index. Most attributes were determined by the forest average values from the yield tables, the Hemeroby index and understory attributes were landscape averages based on values assigned to different forest stand types, the Shannon Index and evenness of tree size on landscape level were calculated using landscape average values (Shannon, 1948; Whittaker, 1972; Mouillot and Leprêtre, 1999).

The Shannon index was calculated by multiplying the percentage merchantable volume of each species in the landscape with the natural logarithm of itself, these values were then added up and multiplied by −1 Equation (14).

$$Shannon\ index = -1 * \sum_{1}^{I} (pvol_i * \ln(pvol_i)) \tag{14}$$

where $pvol_i$ is the percentage of the merchantable volume of species i; $plnvol_i$ is the percentage of merchantable volume of species i multiplied by the natural logarithm of itself; and I is the number of forest species in the landscape at the start of the planning horizon.

The evenness of tree sizes on the landscape level was calculated by getting a percentage logarithmic estimate of each DBH class (Equation 15). These percentage logarithmic DBH class values were summed and divided by the natural logarithm of the number of diameter classes (Equation 16).

$$plnpDBHi = \left(\frac{vol_{DBH_i}}{VOL_{tot}}\right) * \ln\left(\frac{vol_{DBH_i}}{VOL_{tot}}\right) \tag{15}$$

$$DBHevenness = \frac{-1 * \sum_{1}^{I} (plnpDBHi)}{\ln(I)} \tag{16}$$

where *DBH evenness* is the evenness of tree sizes on the landscape level; I is the number of DBH classes; *plnpDBHi* is the proportion of the total volume in DBH class i multiplied by the natural logarithm of the proportion of the total volume in DBH class i; vol_{DBHi} is the volume in DBH class i; and VOL_{tot} is the total volume in the forest landscape.

RESULTS

Forest Composition and Age-Class

The main change in forest composition over the planning horizon was the replacement of Sitka spruce and other conifer stands with lodgepole pine on blanket peat sites (**Figure 2**). The area of lodgepole pine monocultures increased from around 26.0% in 2017 to 58.0, 62.2, 57.6, and 60.0% of the forest area by 2070 for BAU, S1, S2, and S3, respectively, and there was little or no change in forest composition after 2070. In the scenarios in which a smaller area was converted to lodgepole pine (i.e., BAU and S2), a larger area of non-lodgepole pine conifer stands was maintained on blanket peat. There was also a large change in total buffer zone area, which increased from 0.9% in 2017 to 5.3, 6.8, 6.4, and 6.8% of the forest area in 2070 for BAU, S1, S2, and S3, respectively (**Figure 2**). The age class distribution was largely affected by two major harvesting events around the years 2020 and 2070, which happened in all scenarios, but to a lesser degree in S3 (**Figure 3**). The area of old forest also differed between scenarios, being larger in the BAU scenario and in S2 (**Figure 3** and **Table 2**).

Carbon

Relative to the model start year, the cumulative storage of carbon increased in the first 10 years to about 25 tons of carbon ha^{-1} for all scenarios. The increase was followed by an overall slow decline for the remainder of the planning horizon for all global scenarios (**Figure 4**). In the BAU scenario 37.0 tons of carbon was stored cumulatively in the first 20 years before the overall slow decline. The overall slow decline included a small increase in cumulatively stored carbon starting around 2060, which lasted until 2087, 2078, 2087, and 2070, for the BAU, S1, S2, and S3 scenarios, respectively. The final cumulatively stored carbon was 21.1, 7.6, 9.9, and −12.1 tons carbon ha^{-1} for the BAU, S1, S2, and S3 scenarios, respectively. To visualize the impact of drained peatlands on the cumulative carbon storage, the cumulative stored carbon indicator was also reported excluding the drained peat emissions. In that case, the cumulatively stored carbon per hectare increased in all scenarios, ending at 96.5, 83.0, 85.3, and 63.3 tons ha^{-1} over the 100-year planning horizon for the BAU, S1, S2, and S3 scenarios, respectively (**Figure 4**). The cumulative carbon storage by pools fluctuated over the planning horizon and differed slightly between scenarios, but the cumulative living carbon pool increased by 60.0, 32.7, 38.1, and 6.4 tons ha^{-1} for the BAU, S1, S2, and S3 scenarios, respectively. The cumulative storage in deadwood carbon increased by 5.3, 4.7, 5.8, and 6.9 tons ha^{-1} for the BAU, S1, S2, and S3 scenarios, respectively, and the cumulative storage of carbon in HWP was 13.2, 19.1, 15.8, and 18.7 tons ha^{-1} by 2116 for the four scenarios. The total displacement and total fossil fuel substitution over the planning horizon was 21.3, 30.1, 29.3, and 34.6 tons ha^{-1} for the BAU, S1, S2, and S3 scenarios, respectively, while the total loss of carbon due to drained peatlands over the planning horizon was 75.4 tons ha^{-1} for all four scenarios.

Regulatory—Windthrow Risk

The analysis of the area of forest at high windthrow risk (≥70% probability that >3% of stems are windthrown, based on the windthrow risk model) showed a steep increase in the first decade for all scenarios, as much of the forest grew taller before being clearfelled (**Figure 5**). The scenarios started to diverge in terms of the high risk area around the year 2030 due to different harvest levels. Clearfelling was the only method to reduce the windthrow risk of a stand, and not all stands were eligible for clearfelling due to environmental regulations. The 'fellable area' with stands at high windthrow risk exhibited a similar pattern in terms of which scenarios resulted in the largest high risk area, but the total at risk area was lower (**Figure 5**). Based on the results for S3, circa 2,130 ha of non-fellable forests with a high risk of experiencing windthrow were present at the end of the planning horizon (**Figure 5**).

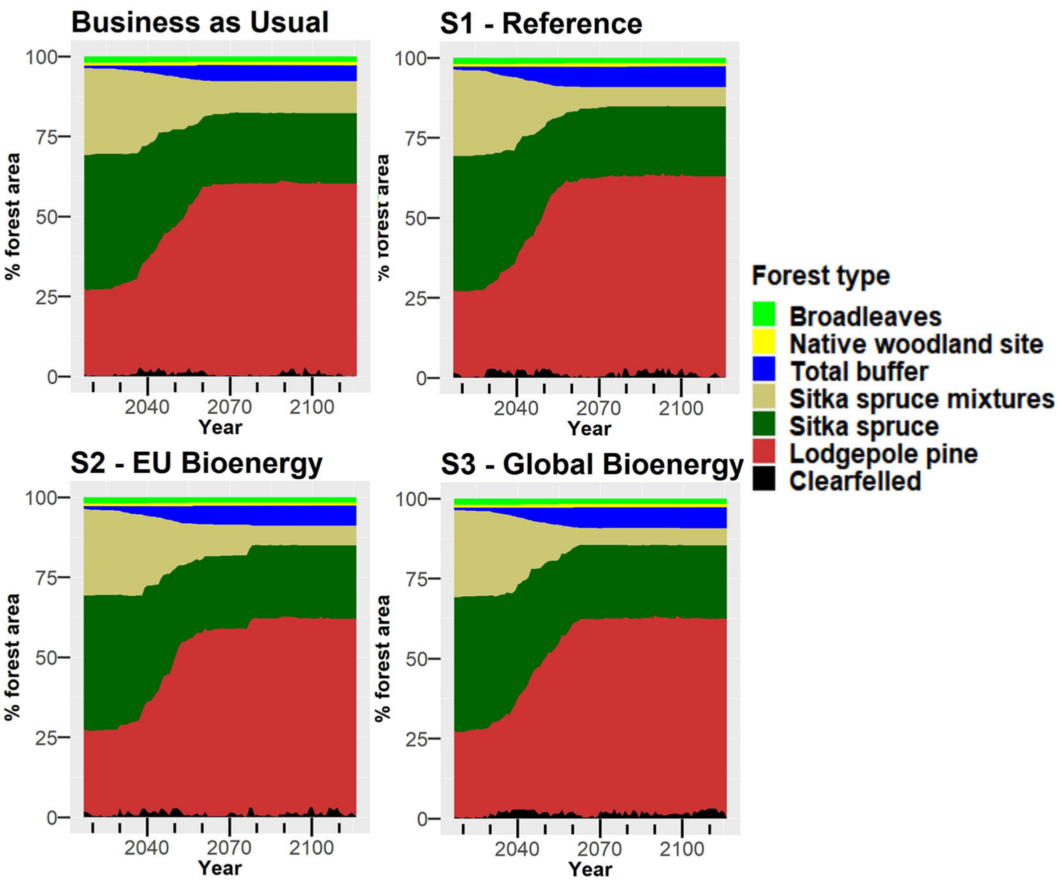

FIGURE 2 | Percentage area by forest type for the four scenarios over the planning horizon. The Broadleaves group contains managed broadleaf forests. Native Woodland Sites are mainly unmanaged native broadleaf stands retained for their high biodiversity values. Sitka spruce mixtures contain all stands dominated by non-lodgepole pine conifers (including Sitka spruce), with broadleaves and/or non-lodgepole pine conifers as secondary or tertiary species. The Sitka spruce and lodgepole pine groups refers to monoculture stands of the respective species. Source: Lundholm et al. (2019).

Biodiversity

Volume Stored in Large Diameter Trees

The volume of large diameter trees per hectare increased in all scenarios, but more so in the BAU scenario compared to the scenarios where global impacts were implemented (**Table 2**). Around 80% of the total large diameter volume was stored in trees with DBH 30–40 cm, regardless of scenario. All volume measurements (DBH $>$ 30 cm, DBH $>$ 40 cm, DBH $>$ 50 cm) increased by at least a factor of four in each scenario, and most of this increase had taken place by the planning horizon midpoint, the year 2066. The BAU scenario resulted in a greater volume per ha for trees with DBH $>$ 30 cm than the other scenarios by the end of the planning horizon, i.e., 94.31, 66.13, 75.01, and 69.49 m^3 ha^{-1} for the BAU, S1, S2, and S3 scenarios, respectively. However, at the end of the planning horizon all four scenarios produced almost an equal volume in trees with DBH $>$ 40 cm (11.03-12.81 m^3 ha^{-1}). All scenarios resulted in a volume of trees with DBH $>$ 50 cm between 2.01 and 2.18 m^3 ha^{-1} at the end of the planning horizon.

Coarse Deadwood Volume From Natural Mortality

The total volume of coarse deadwood originating from natural mortality was more than halved in all scenarios over the planning horizon (**Table 2**). Most of this total decrease had already taken place by the planning horizon midpoint, i.e., year 2066. The same was true for large diameter (DBH $>$30 cm) coarse deadwood from natural mortality, i.e., the volume per hectare decreased by more than half in all scenarios. Total deadwood volume decreased from around 3.0 m^3 ha^{-1} to 1.2–1.5 m^3 ha^{-1}, and the volume of large diameter deadwood decreased from around 1.0 m^3 ha^{-1} to around 0.3 m^3 ha^{-1}, indicating very low levels of deadwood in the forest landscape, according to the model. Almost all the natural mortality volume originated from conifers, mainly Sitka spruce and lodgepole pine.

Broadleaf Volume and Native Tree Volume

The birch (*Betula* L.) volume increased steadily in all scenarios from 0.78 m^3 ha^{-1} to around 1.45 m^3 ha^{-1} by the end of the planning horizon, due to birch being planted in buffer zones

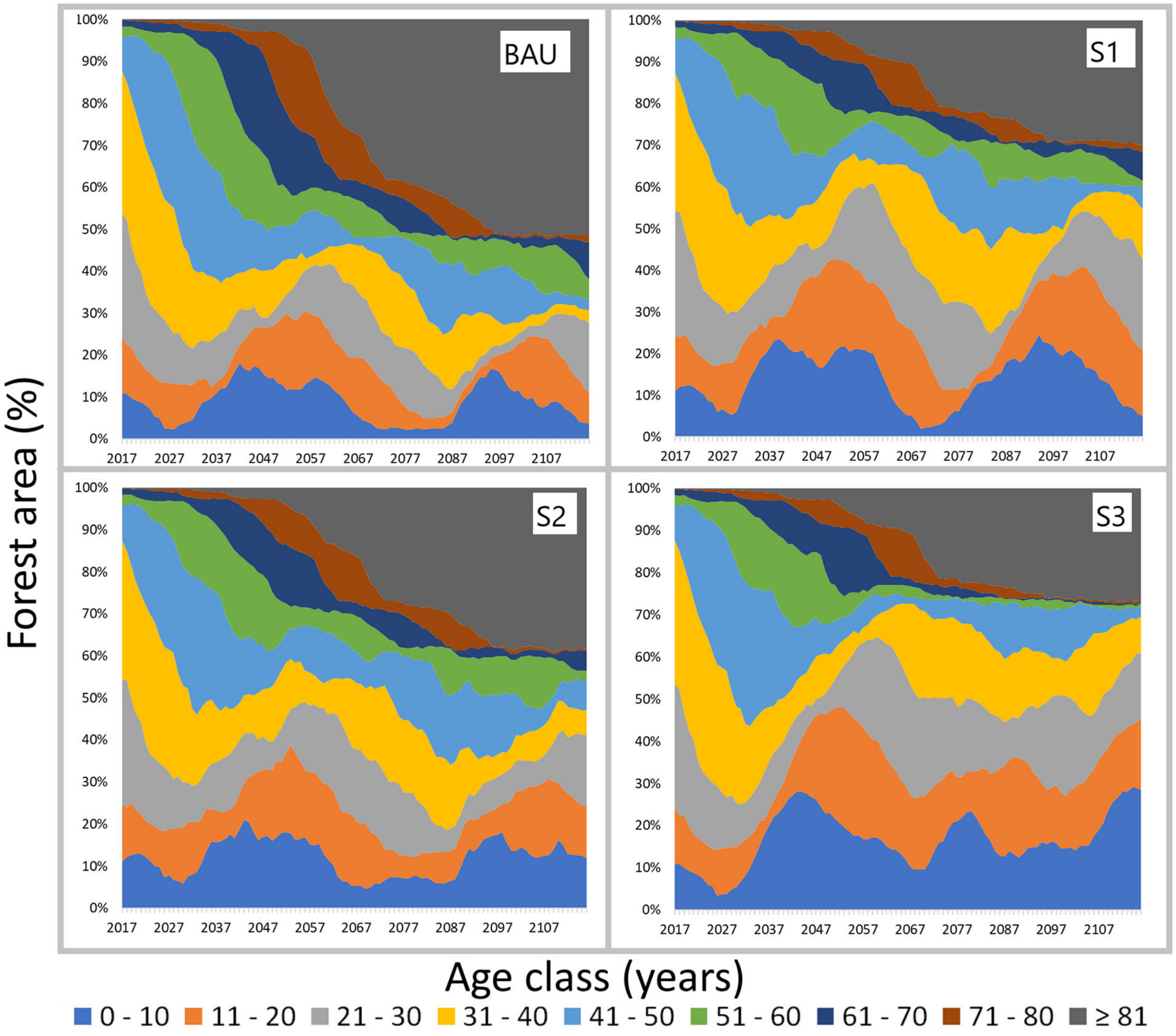

FIGURE 3 | Percent forest area by age class over the planning horizon for four scenarios.

(see section Area of Buffer Zones below). The other broadleaf species present in the forest landscape at least doubled their total volumes per hectare in all scenarios, or in the case of alder (*Alnus glutinosa* (L.) Gaertn.), quintupled it. Alder increased its volume from 0.12–0.13 m^3 ha^{-1} to 0.74–0.79 m^3 ha^{-1} due to this species being planted in buffer zones (see section Area of Buffer Zones below). The increase in volume for other broadleaf species was not the result of new planting but occurred due to existing stands growing older. However, apart from alder and birch, none of the other broadleaves ever reached more than 0.92 m^3 ha^{-1} (beech (*Fagus sylvatica* L.) in year 2116 in the S1 scenario). Compared to a combined average conifer volume of around 200 m^3 ha^{-1}, broadleaves will have a very minor presence in the forest landscape. Ireland's only native commercial conifer, Scots pine (*Pinus sylvestris* L.), had its volume reduced in all scenarios and it was never higher than 0.5 m^3 ha^{-1}.

Area of Buffer Zones

The buffer zone area increased in all scenarios, from 91 ha in 2017 to 548, 669, 625, and 670 ha in 2116 for the BAU, S1, S2, and S3 scenarios, respectively (**Table 2**). The buffer zone area peaked around the year 2060 in all scenarios and was maintained for the remainder of the planning horizon. The requirement to establish buffer zones did not exist when most of the forest stands in CSA were established and they are thus retrofitted during subsequent management actions, mainly as 10–25 m wide water setbacks, sparsely planted with birch and alder, with varying width depending on soil type and slope.

Area of Old Forests

The area of forest older than 80 years increased in all scenarios but to very different levels at the end of the planning horizon: the total area increased from 17 ha in 2017, to 4,894 ha, 2,821

TABLE 2 | Biodiversity indicators for the four scenarios, BAU, S1, S2, and S3, at three time points: 2017, 2066, and 2116.

	BAU			S1			S2			S3		
Biodiversity indicator	**2017**	**2066**	**2116**	**2017**	**2066**	**2116**	**2017**	**2066**	**2116**	**2017**	**2066**	**2116**
Volume (m^3 ha^{-1}) DBH > 30 cm	10.16	68.80	78.39	9.92	50.55	51.78	9.61	57.09	60.16	9.80	51.46	53.92
Volume (m^3 ha^{-1}) DBH > 40 cm	1.73	12.41	13.91	1.72	11.03	12.17	1.68	11.59	12.81	1.70	12.04	13.34
Volume (m^3 ha^{-1}) DBH > 50 cm	0.58	1.52	2.01	0.57	1.53	2.18	0.57	1.51	2.04	0.57	1.56	2.20
Coarse deadwood volume (m^3 ha^{-1})	3.10	1.75	1.23	2.87	2.46	1.65	2.84	2.35	1.55	3.04	1.90	1.23
Coarse deadwood volume (m^3 ha^{-1}) DBH > 30 cm	1.05	0.34	0.34	1.00	0.29	0.38	1.02	0.30	0.35	1.00	0.30	0.35
Volume share broadleaves (%)	0.96	1.24	1.31	1.05	1.46	2.00	1.06	1.37	1.54	1.01	1.65	1.90
Volume (m^3 ha^{-1}) Fagus sylvatica	0.39	0.52	0.56	0.47	0.78	0.92	0.47	0.66	0.74	0.47	0.61	0.67
Volume (m^3 ha^{-1}) Betula sp	0.78	1.03	1.49	0.78	0.97	1.50	0.78	1.01	1.50	0.78	0.94	1.43
Volume (m^3 ha^{-1}) Quercus sp	0.14	0.28	0.36	0.14	0.27	0.35	0.14	0.27	0.35	0.14	0.27	0.35
Volume (m^3 ha^{-1}) Pinus sylvestris	0.42	0.33	0.29	0.49	0.37	0.43	0.39	0.35	0.36	0.45	0.39	0.33
Volume (m^3 ha^{-1}) Fraxinus excelsior	0.23	0.66	0.79	0.22	0.57	0.63	0.21	0.61	0.70	0.22	0.62	0.73
Volume (m^3 ha^{-1}) Acer pseudoplatanus	0.03	0.07	0.08	0.02	0.06	0.07	0.03	0.07	0.07	0.03	0.07	0.08
Volume (m^3 ha^{-1}) Alnus glutinosa	0.13	0.62	0.79	0.12	0.53	0.74	0.12	0.60	0.74	0.13	0.55	0.74
Area buffer zone (ha)	91	528	548	91	667	669	91	614	625	91	667	670
Area of forest aged 61–80 years (ha)	147	1509	1002	143	1182	803	143	1351	496	143	1184	96
Area of forest older than 80 years (ha)	17	2548	4894	17	959	2821	17	1484	3613	17	967	2456
Alteration – final felling area (%)	0.35	0.99	0.75	1.08	0.83	0.73	1.32	0.84	1.68	0.32	1.32	2.17
Hemeroby index (0–1)	0.96	0.94	0.94	0.96	0.94	0.94	0.95	0.93	0.93	0.96	0.92	0.91
Shannon species diversity (0–2)	0.89	0.89	0.84	0.89	0.92	0.91	0.89	0.91	0.87	0.89	0.91	0.91
DBH evenness (0–1)	0.46	0.59	0.59	0.46	0.61	0.63	0.46	0.60	0.61	0.46	0.63	0.64

The indicators represent per hectare values for volume of large diameter trees, volume of coarse deadwood, volume of coarse deadwood with DBH > 30 cm, volume share of broadleaves (%), volume of broadleaves, volume of native tree species, and the area buffer zones (ha) and the area of old forest (ha).

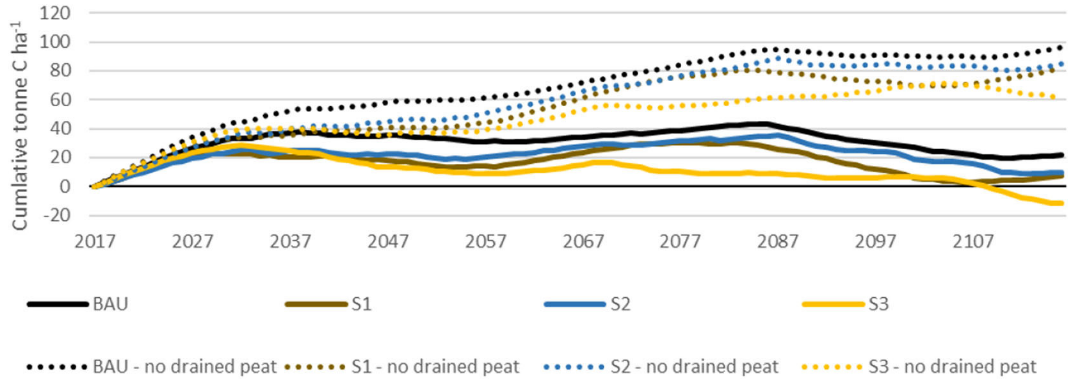

FIGURE 4 | Cumulative stored carbon by year, in tons ha^{-1}, for the four scenarios (solid lines), as well as for the four scenarios when emissions from drained peat soils are excluded (dashed lines).

ha, 3,613 ha, and 2,456 ha in 2116 for BAU, S1, S2, and S3, respectively (**Table 2**). More forest area entered this older age class in the second half of the planning horizon (i.e., year 2066–2116) than in the first half.

Cultural Attributes

Alteration, i.e., the percent of forest clearfelled, varied over time, and the cultural attribute Hemeroby index decreased in all scenarios, from 0.96 to 0.91–0.94, indicating a slightly more natural forest landscape due to the buffer zones. The Shannon species diversity index did not change much but showed a slight reduction in the BAU and S2 scenarios, but a small increase in S1 and S3, due to more broadleaf volumes in buffer zones. DBH Evenness increased more in scenarios with more clearfelling (i.e., S1 and S3), as the distribution between volume stored in small and large diameter trees became more even.

Water Quality

P emissions from a site increased in the years following a clearfell, while N emissions remained static. Thus, the total P emission loads were higher in the scenarios with greater total clearfell area. Although forest stands emitted more nutrients per hectare,

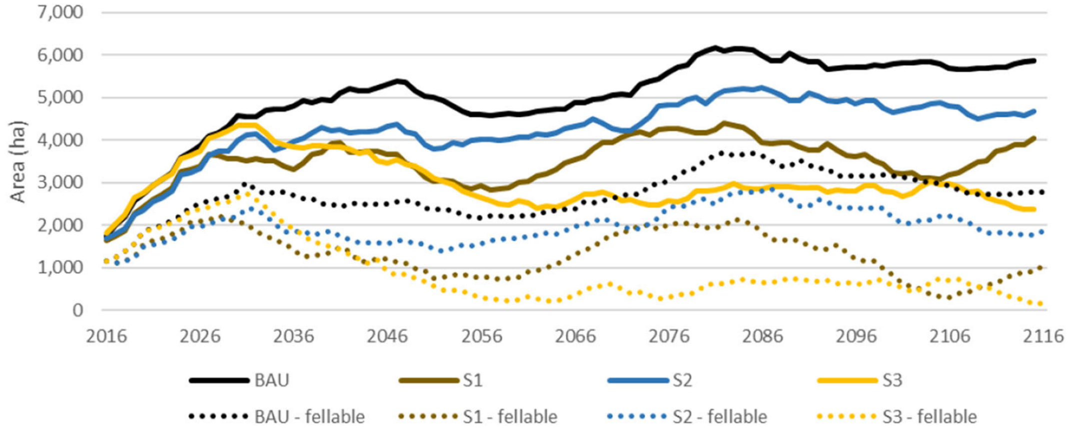

FIGURE 5 | Forest area (solid) and fellable forest area (dashed) with a critical windthrow risk over 70%, for the BAU, S1, S2, and S3 scenarios.

TABLE 3 | Emission levels for N and P, for the forest (in kg yr^{-1} ha^{-1}and kg yr^{-1}) and the entire CSA (in kg yr^{-1} ha^{-1}and kg yr^{-1}), for the BAU, S1, S2, and S3 scenarios.

Scenario	N (kg yr^{-1})				P (kg yr^{-1})			
	Forest		CSA		Forest		CSA	
	ha^{-1}	Total	ha^{-1}	Total	ha^{-1}	Total	ha^{-1}	Total
BAU	5.34	53,271.45	3.30	228,527.69	0.58	5,772.21	0.29	19,951.38
S1	5.34	53,271.45	3.30	228, 527.69	0.59	5,881.03	0.29	20,060.21
S2	5.34	53,271.45	3.30	228, 527.69	0.59	5,842.59	0.29	20,021.77
S3	5.34	53,271.45	3.30	228, 527.69	0.60	5,953.56	0.29	20,132.74

other land parcels in the landscape contributed to N and P loads in watercourses (**Table 3**). The S3 scenario resulted in the highest amount of P emissions, followed by the S1, S2, and BAU scenarios, in that order.

Cultural

All scenarios resulted in slight increases in the RAFL-index over the planning horizon, and although the index fluctuated over time, there were no large differences in the final index values between the scenarios. The RAFL-index increased from 0.50 in 2016 to 0.58, 0.58, 0.53, and 0.52 for BAU, S1, S2, and S3, respectively (**Figure 6**). The RAFL-index scores mainly changed due to a combination of changes in forest composition, clearfell areas, and the volumes of harvest residue in the forest landscape. Overall, all scenarios experienced very similar changes in forest composition but the total clearfell area differed greatly between scenarios—with respectively 61, 40, and 102% more total clearfell area in S1, S2, and S3 than in the BAU scenario.

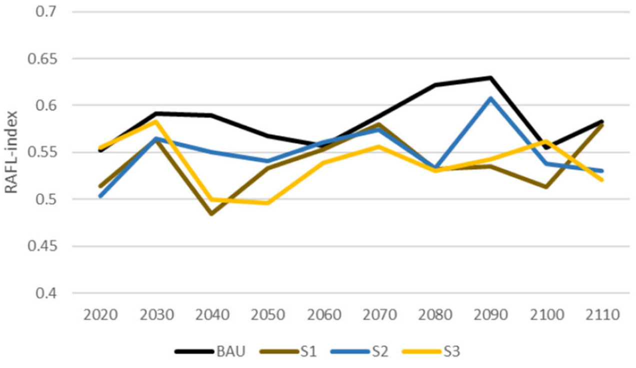

FIGURE 6 | Ten-year average RAFL-index over the planning horizon for the four scenarios.

Comparison of Ecosystem Services

The average supply of the ES indicators over the planning horizon was determined for the four modelled scenarios to evaluate and compare the levels of ESs, and to see if there were positive or negative correlations between them. Since the linear programming model operated on maximising NPV, the comparison of ES indicators was best made in relation to the NPV and clearfelling intensity in the scenarios, based on the results from a previous study (Lundholm et al., 2019), affected carbon storage, windthrow risk, broadleaf volume, P emissions, and RAFL-index (**Table 4**). The general trends were that cumulative carbon storage, windthrow risk area and RAFL-index decreased as clearfelling intensity increased, e.g., when comparing the BAU scenario with S3, a 61% increase in harvest volume resulted in 35% less carbon storage, 65% less fellable area at windthrow

TABLE 4 | Annual average ES indicator values for the four scenarios: cumulative carbon storage (tons ha^{-1}) with and without (in brackets) the impact of drained peat soils, the total area at 70% windthrow risk (ha) and the fellable area (in brackets), total broadleaf volume (m^3), average P emissions from forests (kg ha^{-1}) and average RAFL index per hectare.

Scenario	NPV	Harvest volume	Cumulative carbon storage per ha (without drained peat)	Area with Windthrow risk (fellable)	Broadleaf volume	P emission	RAFL-index
BAU	162,535	32,797	21.5 (96.2)	4,996 (2,714)	28,477	0.58	0.58
S1	231,563	45,223	7.6 (82.3)	3,471 (1,331)	32,802	0.60	0.54
S2	205,536	42,789	9.9 (84.6)	4,212 (1,944)	28,955	0.59	0.55
S3	257,089	52,773	−11.7 (63.0)	2,990 (926)	33,576	0.60	0.54

The annual NPV (€) and annual total harvest volume (m^3) from Lundholm et al. (2019) are included to put the ES indicators in the context of harvest intensity in the scenarios.

risk and a 7% lower RAFL-index. Although the scenarios that involved more harvesting had slightly higher P emissions, the absolute differences were small (3% higher P emission in S3 compared to the BAU scenario). More standing broadleaf volume was found in the scenarios with more harvesting (i.e., 15 and 17% more in S1 and S3, respectively, compared to the BAU scenario), although the actual differences were small.

DISCUSSION

This study integrated the external global factors climate change and dynamic timber prices, as well as ES indicators in a FMDSS, using an approach that modified yield tables already used in traditional forest management planning. The FMDSS Remsoft Woodstock is widely used around the world, and the modelling approach presented in this study could be integrated in the model of any forest company without requiring additional software or significant model overhauls, since the approach can simply be built into any existing Woodstock model that is oriented toward the optimisation of NPV and harvest volume. Although this model was applied to a CSA in Ireland, and locally relevant ES indicators were used, making the model results specific to the CSA and relevant to a wide group of local and national stakeholders, the basic methodology can be applied in any country or region. Of course, locally relevant ES indicators should be used wherever this approach is applied, e.g., local utilisation rates for HWP, prioritized regulatory services, relevant biodiversity indicators, etc.

External Impacts and Forest Composition

Climate change impacted on the growth rates of tree species and affected ES indicators that are based on stand volume measurements, e.g., many of biodiversity indicators and carbon, but the overall climate change impact on ES indicators was small. Determining the exact impact of external factors on ES indicators by comparing scenarios is difficult. Forest management in the scenarios differed as a response to the external factors and the largest impact on ESs was the level of clearfelling in the scenarios, which was mainly determined by the dynamic timber prices (Lundholm et al., 2019), a finding also confirmed using the same global scenario narratives in Lithuania (Mozgeris et al., 2019). Some correlations were found, where the greatest clearfell area (in the S3 scenario) resulted in more P emissions (which reduced water quality), and reductions in the area at windthrow risk, cumulative carbon storage, biodiversity indicators and RAFL-index. The opposite trend in ESs indicators was observed in the BAU scenario, which resulted in the smallest clearfell area. The results for the S1 and S2 scenarios fell somewhere between those for the BAU and S3 scenarios, both in terms of harvest level and the provision levels of the assessed ES indicators. Changes in forest composition also affected ES provision, but these changes were not only managerial responses the external factors (Dymond et al., 2016), forest policy also had a large influence. Due to certification rules and increased environmental considerations, peat sites could no longer be reforested using fertiliser. This was the reason for the landscape changing from dominated by Sitka spruce to dominated by lodgepole pine, as this is the only species that can be established on blanket peat without fertiliser (**Figure 2**). The other large change in landscape composition was the establishment of buffer zones. Stands were historically planted right up to the waterbodies, but since adopting SFM in 1996, buffer zones are being retrofitted during subsequent harvesting (DAFF, 1996). Differences in the age class distribution were due to clearfelling, which was a direct response to the external factors. Although additional afforestation, with enhanced biodiversity consideration, would be beneficial for most ES indicators, this was not a realistic option since the CSA is not suitable for afforestation (i.e., poor soils and many Natura2000 areas). Even if the land had been suitable for afforestation, studies have shown that the barriers to private landowners establishing forests are inflexibility of land management, lack of information, and the associated values and attitudes of farming and food production, rather than a lack of expected revenue (Duesberg et al., 2014a,b). Thus, increasing timber prices would have been unlikely to expand afforestation in Ireland. Furthermore, the uncertainties associated with the impacts of climate change on forestry may have a negative effect on landowners' willingness to afforest. On the other hand, potential new government policy to reduce Ireland's carbon emissions may result in the mandatory establishment of a forest area on every farm that receives subsidies.

Landscape-level management planning is the preferred and required scale for the modelling of the provision of multiple

ES indicators when both the spatial and temporal interaction between stand types and forest management actions are included, as well as to allow for the involvement of multiple stakeholders (Marto et al., 2018). The objective of this study was to analyse the potential impacts on forest ESs from climate change and dynamic timber prices, rather than finding an optimal management schedule for the future that produces the best combination of ESs possible. Therefore, linear programming was considered a useful tool, as it allowed for the optimisation of a specific ES indicator (i.e., NPV) in a forest landscape, while also evaluating the associated provision levels of other ESs.

Carbon

Large amounts of carbon were sequestered in the BAU scenario, as large forest areas grew beyond normal clearfell age, proving that set-aside is an effective method for short-term carbon sequestration (Schwaiger et al., 2019). The forests became a carbon source in the S3 scenario, due to heavy clearfelling throughout the planning horizon. The other scenarios, S1 and S2, produced sequestration levels somewhere in the middle. Carbon emissions from drained blanket peat resulted in lowering the cumulative storage of carbon by 78, 91, 88, and 119% for the BAU, S1, S2, and S3 scenarios, respectively. Additionally, the normal utilisation scenarios (BAU and S1) stored more cumulative carbon than the climate change mitigation scenarios (S2 and S3). The carbon stocks were impacted by different utilisation rates; for instance, 10% of all pulpwood was utilised for bioenergy in the BAU and S1 scenarios, while the corresponding value for the S2 and S3 scenarios was 30%. Although this higher level resulted in less carbon being stored long-term in wood-based panels, it contributed to a reduction in the use of fossil fuels for heating and energy production, reducing Ireland's high dependency on imported fossil fuels, although biomass only supplies 2.3% of Ireland's total energy needs (Dineen et al., 2016). Based on the analysis of 21 studies, Sathre and O'Connor (2010) found that displacement factors for using wood in construction varied from −2.3 to 15, with a mean on 2.1 tons carbon per ton carbon in wood. Factors that determine the actual displacement factors were mainly end-of life use, i.e., bioenergy or landfill, but also harvest and processing efficiencies. Furthermore, differences in landfill management have a large impact on released CO_2 and methane (Micales and Skog, 1997), which in some of the analyzed studies determined whether using wood products was a net sink or net source. Methodological differences mean there is a shortage of comparative studies for determining accurate carbon displacement factors, especially from utilizing wood for construction (Smyth et al., 2017). Therefore, there is some uncertainty associated with the results on fossil fuel substitution presented in this study, especially for the BAU and S1 scenarios, in which more wood in HWP was used.

Increased harvesting of biomass fuel could lead to shorter rotation periods if bioenergy species are planted, and extraction of more harvest residues, which decreases forest biodiversity (Verkerk et al., 2011; Duncker et al., 2012; Söderberg and Eckerberg, 2013). Since old-growth forests and coarse deadwood volume are important contributors to habitat provision and an indicator of forest health (Lassauce et al., 2012; Brockerhoff et al., 2017), increased biomass extraction for bioeconomy and climate change mitigation must be carefully considered against the potential trade-off of forest biodiversity. Verkerk et al. (2011) estimated that intensified bioenergy harvesting could cause a 5.5% reduction of deadwood in European forests between 2005 and 2030, whereas a business as usual scenario would increase deadwood volumes by 6.4% over the same time period. Utilizing European agricultural land for short rotation biomass crops would likely lead to increased food imports from developing countries, causing global biodiversity loss, as intensified land-use would remove species-rich habitats in the tropics (Di Fulvio et al., 2019). Alternatively to increasing bioenergy extraction, paying forest owners for creating carbon offset credits and accounting for carbon storage in HWP leads to longer rotation periods (Asante and Armstrong, 2012). However, if forest owners are also penalized for carbon emissions, there is a stronger incentive to clearfell old-growth forests to avoid natural disturbances (van Kooten, 2018), which would reduce the area of high biodiversity habitat. Thus, the trade-offs of mitigating climate change through utilizing wood products must be carefully considered, so as not to cause short-term habitat destruction and a reduction in biodiversity. Depending on how unmanaged forests will be affected by a changing climate will also determine whether it is a better climate mitigation strategy to harvest forests: will biomass growth increase as a result of more atmospheric CO_2 acting as a fertiliser of forests (Houghton et al., 2001), or will increased catastrophic windthrow events, pests and diseases, wildfire (La Porta et al., 2008), and increased decomposition rates cause these forests to become carbon sources (Bradford et al., 2014)? Cannell (1999) acknowledged that although storing carbon in living trees increases the time to find other carbon storage and mitigation solutions, it does create a problem in that the reservoir of carbon can be released in the future through catastrophic events, and it limits the future management options for those forests.

Windthrow and Modelling Risk

Although, the methodology used to assess the carbon ES was a comprehensive and science-based method, it does require a closer investigation in relation to the windthrow ES indicator. Higher carbon storage was achieved by less clearfelling rather than storing carbon in HWP, e.g., compare the cumulative carbon storage and windthrow risk area in the BAU and S3 scenarios (**Table 4**). Most of Ireland's forests are heavily production oriented and carbon stored in HWP provides a substantial positive contribution to Ireland's greenhouse gas accounting (Green et al., 2006). Other forest carbon storage calculations have also found that more carbon was stored by utilizing wood for products with long storage lives than to indefinitely store carbon in unmanaged forests (Cannell, 1999). Over time, strong wind coupled with overall increased disturbances from climate change would likely cause endemic and catastrophic windthrow, not only in unmanaged western peatland forests but also in many European forests, resulting in a loss of productivity and decaying deadwood that releases carbon, instead of large stocks of living carbon (Senf and Seidl, 2020). Thus, the BAU scenario most likely overestimated the amount of sequestered carbon stock in living biomass. Since tree height, soil type, elevation, and exposure are important factors in determining windthrow risk (Lynch, 1985; Miller, 1985; Ní Dhubháin et al., 2009), it is very unlikely that indefinite retention of coniferous blanket peat forests should be part of a successful carbon storage strategy (Seidl et al., 2014). However, including the initial and subsequent impact of windthrow damage in the model is not simple, and stand volume cannot be reduced by windthrow risk alone. Subsequent windthrow damage increases as stand edges are reshaped and the internal structure of the stand changes, both as a result of natural disturbances and management actions, such as thinning and clearfelling of adjacent stands (Montoro Girona et al., 2019). Even though the current (i.e., at model start year) stand stocking, and indirectly stand volume, in Coillte's Woodstock model is reduced based on windthrow recorded during forest inventories, and these data are continuously updated, the potential impacts of future windthrow damage is not included in their model. The windthrow risk model, used in this study, only estimated the probability that at least 3% of the stems in a stand have been damaged by windthrow—it made no assumptions on the actual proportion of windblown trees or how a stand with high windthrow risk would be affected during subsequent years.

Monte Carlo simulation is often used in forest modelling to evaluate the potential impact of natural disturbances (Davis and Keller, 1997). A Canadian study that modelled the average annual forest area affected by wildfire found that Monte Carlo simulation resulted in highly imprecise annual estimates, even though long time series were available (Armstrong, 1999), and this might also be true for windthrow damage. However, Monte Carlo simulation can only be utilised in Woodstock models that use simulation, and not those that use linear programming (Walters, 1993). To properly include the impact of windthrow, it might be better to adjust the yield tables or include a mandatory windthrow action, where in a certain percentage of the stands the stocking is lowered. However, this method would need to utilise a generalised damage level, instead of the irregular nature of catastrophic windthrow events and the individualised windthrow damage at a stand level (Scott and Mitchell, 2005). On the other hand, spatial specificity to reflect increased windthrow damage in stands adjacent to clearcuts or heavily wind damaged stands would likely increase the accuracy in modelling such damage at the landscape level (Seidl et al., 2009).

Biodiversity Impacts

Except for coarse deadwood volume, all biodiversity indicators increased in all modelled scenarios. The biodiversity indicators were not greatly impacted by the global scenarios since they were not directly influenced by the objective function. The fact that the biodiversity indicators were not greatly reduced in any of the global scenarios indicates that initial indicator values in the forest landscape were low to begin with, which is often the case in production oriented forest landscapes dominated by exotic tree species (Marto et al., 2018). The increases were largely due to additional broadleaf volumes resulting from the creation of buffer zones and more large diameter trees in older stands, either due to their protection status or as a result of the unprofitability of their clearfelling and future management. Unprofitable forests and protection status also caused the area of old forest to increase in all scenarios. Natural mortality volumes decreased in all scenarios, and almost all coarse deadwood in the landscape originated from coniferous trees. The yield tables used for broadleaves did not include natural mortality as they were based on intensively managed forests where trees were thinned out before natural mortality could take place. The yield tables used for conifers included more natural mortality associated with unthinned Sitka spruce stands (which most of the Sitka spruce stands in the CSA were), whereas lodgepole pine stands produced more harvest residue during clearfelling, for stands of the same age on the same site. Thus, most of the reduction in coarse deadwood volume was due to the replacement of Sitka spruce with lodgepole pine, since aboveground deadwood from harvest residues accounted for only around 10% of all aboveground deadwood. High levels of biodiversity ES have been found to contribute to improvements in the provision of many other ESs (Lefcheck et al., 2015), especially with regards to overall ecosystem multifunctionality rather than individual ESs (Hector and Bagchi, 2007; Gamfeldt et al., 2008). Although this blanket peat dominated study landscape is very limited in its ability to grow a wide range of tree species, studies have found that even small increases in tree diversity contribute to increased ecosystem multifunctionality (Van Der Plas et al., 2016). Further, Duncker et al. (2012) found that modified forest management can have positive effects on biodiversity at fairly low costs. Thus, sacrificing only a small amount of NPV by implementing relatively minor management changes can lead to increased biodiversity and multifunctionality of Ireland's western peatland forests.

Water Quality

Water quality was assessed based on N and P emissions. The N emissions were not changed by forest management actions, but the P emissions were assumed to increase for 4 years after clearfelling before returning to previous levels. Thus, water quality was indirectly negatively affected by higher timber assortment prices, as these led to an increase in the total clearfell area in the S1 and S3 scenarios. However, even in the absence of clearfelling, the forests and all other land-use parcels in the CSA emit a background amount of P. Whether the emitted P would actually significantly impact the ecological status of downstream rivers and lakes depends on water discharge rates, other diffuse and point sources of P in the landscape, which catchments were affected, the temporal distribution of P, as well as the ecological threshold and current status of the waterbody receiving the additional P (Cummins and Farrell, 2003; Mockler et al., 2017). Some of these factors could be included in a Woodstock landscape management model, but others are much more difficult to capture, especially since most P is emitted from forests during heavy rainfall events (Rodgers et al., 2012). The P emission values from the Source Load Apportionment Model framework were area averages and applied to all land parcels, regardless of slope and distance to watercourses. In reality, harvesting sites close to watercourses release more P into the watercourse, but these additional P emissions could be avoided by increasing the width of buffer zones, especially in areas receiving more overland water flow (Ó hUallacháin, 2014). However, buffer zones on blanket peat sites, which dominate in the CSA, are unlikely to sequester large amount of nutrients, especially P (Kelly-Quinn et al., 2016). Proper planning and implementation of forest operations in sensitive catchments, such as avoiding tracks near the watercourses, are paramount to limiting nutrient emission runoffs. The methodology presented here can easily be integrated into Coillte's Woodstock model to produce rough estimates of the long-term P emissions at a catchment and sub-catchment level, which are required for FSC certification (FSC, 2012). Furthermore, governmental authorities implementing the Water Framework Directive could utilise this method to assess total nutrient emissions from all land-uses in a catchment (forestry, agriculture, and other point and diffuse sources), not just the current level, but also future emissions based on rural development scenarios.

Cultural Services

Overall there was a small increase in RAFL-index values over the planning horizon in all scenarios, but there were no large differences between the global scenarios. The increase was mainly due to increased buffer zone areas that also increased the broadleaf volume, and an increased area of over-mature forest. The change from Sitka spruce to lodgepole pine caused no major change in either landscape aesthetics or Hemeroby-index, as both species are exotic conifers, but it did affect the stewardship score. The volume of harvest residue from clearfelled lodgepole pine is higher than the volume of harvest residue from Sitka spruce according to the yield tables, and this factor negatively affects the aesthetics of forests (Edwards et al., 2012). In contrast, unthinned Sitka spruce contained more natural mortality volume than unthinned lodgepole pine, and as natural mortality decreased in the landscape, the wilderness score decreased. Changes in the stewardship score were the main reason for the fluctuations in RAFL-index changes over the planning horizon and were due to differences in the size and temporal distribution of clearfell areas between the scenarios. Clearfelling followed by reforestation increased the number of trees per hectare, reduced the stand age and increased the volume of harvest residues—factors that all contributed to temporarily lowering the RAFL-index. It is important to note that the limits for the RAFL-index attributes were set subjectively and were based on achievable values within the CSA. For example, the maximum share of broadleaves was set to 5% as this is what would be biophysically possible to achieve in the CSA, since the blanket peats, wet mineral soils, mountainous areas and marginal agricultural land are not suitable for broadleaves. The CSA is representative for the western half of Ireland, where much public afforestation was done in the 20th century. For Ireland as a whole, the maximum share of broadleaves would more appropriately be set somewhere in the range of 55–67%, based on the soil types in the current forest estate, although only around 33% of the national estate would have commercial potential for broadleaves (Forest Service, 2018). Finally, the RAFL-index was based on a landscape average and ignored the likelihood that local areas might have high aesthetic values, where recreation activities could be concentrated.

Management Implications and the Improvement of ES Provision Levels

High levels of carbon, regulatory, biodiversity, and cultural ES indicators and low levels of P emissions were all achieved by not clearfelling any trees, allowing forests to mature, as in the BAU scenario. However, due to the windthrow instability of blanket peat forests and the fact that stands that have been opened up by initial windthrow are likely to experience more windthrow in subsequent years, many of these stands can be expected to have their standing volume reduced (Montoro Girona et al., 2019), which would reduce the provision levels of most ESs, and possibly shorten rotation periods due to salvage felling. Therefore, it is necessary, for a better utilisation of the land, for forest managers to look outside the box for new types of management intervention in these stands. Management actions such as planting low stocked forests, restoring bog habitat and promoting natural regeneration of native vegetation could be used to redesign many blanket peatland forests. Such actions could result in long-term increases in biodiversity, cultural services, and water quality from the forest landscape, compared to the results of this study. Additionally, this would reduce the overall windthrow risk by clearfelling more forest stands, which would avoid the negative impacts of having over-mature conifer trees falling into watercourses and impacting water ecology (Lynch et al., 1985), or unmanaged stands becoming a breeding ground for bark beetles in the future (Weslien and Schroeder, 1999). Therefore, it is advisable to decommission most Sitka spruce stands on blanket peat and harvest most standing Sitka spruce timber, recovering most of the extractable value (Lundholm et al., 2019). Sitka spruce is expected to suffer reduced growth due to climate change, and restrictive use of fertiliser in forestry makes it less likely as a reforestation option on peatlands in the future, further driving the argument to replace Sitka spruce with other species and, perhaps, move away from commercial forest management of many blanket peat forests. However, the profitability of peatland forests could improve if demand for biomass increases as part of climate change mitigation practices. In such a case, the best strategy could well be the continued management of forests on blanket peat sites with medium to high productivity. The future development of economically marginal peatland forests, their increasing windthrow risk, and how they should be managed are relevant issues to address for all Irish western peatland forest (Tiernan, 2008) and also for many forests along the Atlantic seaboard of western Europe.

Future Research

Some potential future research areas are: (1) inclusion of disturbance impacts; (2) investigation of the impact of the spatial resolution of climate change on the results; and (3) assessment of alternative forest management systems on peatlands. Not including the impact of disturbances risks skewing the results, so a better understanding of their long-term abiotic and biotic impacts on mortality and stand development is necessary to properly assess the future provision of ESs. Climate change impacts vary locally and regionally, meaning large-scale climate models often have too low a resolution to provide detailed enough information for proper decision making (Koca et al., 2006). The Climadapt climate change data, used in this study, is scaled down from low-resolution projections (Ray et al., 2009). Thus, the forecasting precision and accuracy of the climate change impacts on species suitability and productivity could be improved by using higher resolution climate data. This aspect refers not only to the CSA, but generally to the resolution of climate change data that should be used in forecasting studies in the whole of Ireland, in Europe, and globally. Alternative management of Ireland's peatlands has been proposed both in this study and by other authors (Tiernan, 2008; Renou-Wilson and Byrne, 2015). Before initiating the redesign of the forested landscape, the expected ES provision resulting from the use of alternative forest management systems should be carefully modelled. It is also be important to establish tests sites to increase our knowledge of suitable alternative management systems, especially regarding the natural development of clearfelled sites, the development of low-stocked stands, and the cost-effective potential to seed or plant areas with native broadleaf species for biodiversity.

CONCLUSION

The Remsoft Woodstock based ALTERFOR FMDSS was used to model climate change and dynamic prices in Ireland by using modifiers on volume and price outputs, meaning that yield tables did not have to be changed, but the availability of reliable data is essential to get realistic results. Although the modelling framework presented here can be used to compare long-term ES provisions between regions and countries, the model results presented in this study are only applicable to Ireland's western peatland forest landscape. The model objective was to maximise NPV, and, as a result, this indicator was most affected by the global scenarios. The ES indicator values varied between the scenarios, mainly due to the level of clearfelling, which was affected by the global scenario impacts, especially the changes in assortment prices. The largest differences in ES indicator values between scenarios were observed in carbon storage and windthrow risk, with smaller differences for biodiversity, water quality and cultural services. The scenarios exhibited the same overall trends, due to the nature of the linear programming model and its objective function. Biophysical limitations, e.g., the poor soil conditions, and policy restrictions, e.g., the prohibition on aerial fertilisation, made lodgepole pine the only eligible reforestation species on blanket peat soils, which dominated the results for the scenarios. Recently introduced forest policy led to larger buffer zone areas and, consequently a smaller productive forest area, but impacted positively on several ES indicators. Single objective optimisation is not the best method to analyse the complex interactions between the ES indicators. However, the aims of this study were to analyse forest management impacts on ESs indicators under global scenarios and not to find the best possible combination of ES provision levels. Therefore, linear programming was an appropriate tool to use in this study, as well for the subsequent analysis of the impact of alternative management actions on ESs.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

AUTHOR CONTRIBUTIONS

MN: conceptualization and funding acquisition. AL, KB, EC, and MN: methodology. AL, KB, and EC: software. AL: formal analysis, data curation, writing–original draft preparation, and visualization. AL and EC: investigation. AL, KB, EC, and MN: writing–review and editing. All authors: contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00200/full#supplementary-material

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Quantifying Long-Term Bird Population Responses to Simulated Harvest Plans and Cumulative Effects of Disturbance

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There is interest in linking outputs from land use simulators to bird species distribution models to project how boreal birds will respond to cumulative effects of caribou (*Rangifer tarandus*) conservation, harvest, fire, and energy-sector development in Alberta. Our hypotheses were: (1) species associated with older mixed-wood stands would decline more if harvest was shifted away from areas used by caribou to areas with more mixed-wood; and (2) species associated with older forests would be more negatively affected by the combined effects of harvest, fire, and non-forestry footprint than by harvest alone. We used vegetation data from two harvest scenarios produced in Patchworks as inputs for density models of 20 boreal forest songbird and woodpecker species in Alberta. We projected abundance of these species over 50 years under: 1) two scenarios created in Patchworks, without fire but with and without deferral of timber harvest within a caribou conservation zone on lands tenured to Alberta-Pacific Forest Industries Inc.; (2) a scenario with fire but no human footprint; and (3) five scenarios in ALCES Online, in which habitat was affected by Patchworks harvest locations, fire (1–2 × current rate), and energy sector development (present or absent; with or without seismic line reclamation to improve caribou habitat). In the Patchworks scenarios, we found similar projected numbers of each bird species over time, whether harvest deferral occurred or not. Both harvest plans increased habitat and numbers for most species associated with older forests over 50 years, while most species associated with younger forests declined in both harvest plans, because average projected forest age increased over 50 years. Fire and other footprint generally reduced relative amount of habitat for species associated with older forests, which still increased over time, while other species responded positively or less negatively to fire. Seismic restoration created habitat for three-quarters of species that responded negatively to energy sector development over

50 years. As projections depended on whether just harvest, fire or all footprints were analyzed, multiple human impacts over time beyond harvest should be considered in conservation and land use planning based on long-term predictions about wildlife in anthropogenic landscapes.

Keywords: cumulative effects, harvest, species distribution model, boreal birds, caribou, simulators, Patchworks, ALCES Online

INTRODUCTION

Canada's boreal forest is continually being altered by human activities like forestry, energy sector development, agriculture, and climate change (Carlson and Stelfox, 2014; Gauthier et al., 2015). The cumulative effects of these activities are affecting the amount and suitability of habitat for wildlife (Schneider, 2019). Forestry operations are a dominant source of land-use change in Canada's boreal forest and generally shift the age-distribution of forests toward younger successional states (Kuuluvainen and Gauthier, 2018; Lavoie et al., 2019). Fragmentation by roads and other linear features (e.g., pipelines, seismic lines, power transmission lines) are also a concern if these features reduce forest patch size or increase edge effects (DeLong and Tanner, 1996; Dyer et al., 2001, 2002; Schneider, 2019). To reduce such effects on wildlife, many forestry companies have begun adjusting the spatial pattern, size distribution, and timing of harvests to better approximate natural disturbances like forest fire (Hobson and Schieck, 1999; Huggard et al., 2014). The goal of approximating natural disturbance is that it provides a coarse-filter approach that should be better at maintaining habitat for more wildlife species than traditional harvesting (DeLong and Tanner, 1996; Dzus et al., 2009; Kuuluvainen and Grenfell, 2012). However, such strategies come with economic costs, so it is important to assess the environmental benefits of different harvesting strategies. Future simulation tools that project outcomes for forestry yields, harvesting costs, and habitat quantity or quality for different species (e.g., caribou, boreal birds) are a crucial component of such evaluations (Sturtevant et al., 2007; Carlson et al., 2014, 2019).

Coarse-filter habitat management by forestry companies can be complicated by the needs of declining species. In western Canada, woodland caribou (*Rangifer tarandus*) have declined in many areas, leading to calls to defer logging in caribou zones (Dyer et al., 2001, 2002; Wittmer et al., 2007). In the boreal plains ecoregion, harvesting of caribou habitat (black spruce dominated bogs and fens) is very uncommon as the trees are too small to be commercially valuable. However, within caribou zones, there are patches of upland, mesic, deciduous or white spruce stands, which are of low value to caribou *per se*, but are valuable commercial timber. Deferring or shifting logging away from upland patches adjacent to or within caribou zones has been proposed as a tool to minimize the risk that wolves (*Canis lupus*) and their primary prey (e.g., white-tailed deer [*Odocoileus virginianus*], moose [*Alces alces*]) are attracted to the early seral habitats created by forestry companies while also minimizing fragmentation caused by road construction (Latham et al., 2011). However, whether this fine-filter habitat management approach creates a conflict with other species at risk is not particularly clear (Villard et al., 1999; Drapeau et al., 2000; Imbeau et al., 2001).

While many qualitative assessments of caribou management on other species have been done, relatively few studies have used quantitative models to test the value of caribou as an umbrella species (however see Bichet et al., 2016; Drever et al., 2019). Previous studies on the value of caribou as an indicator species focus on the co-occurrence of other species with caribou using relatively coarse maps of species distribution, rather than projecting abundance of species based on detailed abundance - habitat relationships. Similarly, past work has tended to rely on relatively simple simulated landscapes or conservation networks rather than harvesting plans that will actually occur on the landscape. Declines in boreal birds may be exacerbated by a caribou-centric harvest strategy if forest harvest is concentrated in more contiguous older mesic upland forests, rather than in the small patches of upland interspersed in the lowland complexes preferred by caribou. To understand how long-term changes in land use to benefit one species affect other species, we can use spatial simulation modeling to create future landscapes. By linking spatial simulation models to species distribution models (SDMs) of abundance, it is possible to make predictions about how the size of bird populations may change under different harvest plans that vary in their objectives.

Quantitative predictions about bird response to forest harvest are only as realistic as the assumptions that go into each scenario. For example, in ecosystem-based management where harvests are designed to emulate natural disturbances, fire is usually assumed to be the most important disturbance influencing forest age and boreal forests can be stratified into areas naturally subject to and manageable with different fire or harvest frequencies ("ASIO model" *in* Angelstam, 1998; Kuuluvainen and Grenfell, 2012). Depending on the forest region, other disturbances or sources of tree mortality such as drought, wind storms or insect outbreaks may be more important disturbances in other regions (Seidl et al., 2017; Navarro et al., 2018). Forest harvest planning is often also based on the assumption that forest harvest is the sole disturbance setting forest age. Forestry companies design harvest strategies with the goal of approximating the distribution of forest fires, but an assumption underpinning these strategies is that fire control reduces the area burned sufficiently to allow for harvest to occur. It is becoming increasingly evident in western Canada that harvest and forest fires jointly affect forest age and the habitat available to different birds, despite best efforts at suppressing fire (Arienti et al., 2006). Furthermore, there is good evidence that bird abundance often differs between recently burned and recently harvested forests (Hobson and Schieck, 1999; Schieck and Song, 2006; Robertson and Hutto, 2007), particularly in the first 10–20 years post-disturbance (Schieck and Song, 2006; Huggard et al., 2014). Fires leave snags and patches of unburned vegetation and create temporary habitats for some species like woodpeckers and flycatchers (Schieck and Song, 2006) and some of these habitat attributes may be absent from some types of harvest blocks (Huggard et al., 2014). Whether or not there are significantly large differences in responses by species to fire and harvest in meaningful space and time remains a key question (Andison, 2003; Messier et al., 2003). SDMs that account for difference in bird response to harvest versus fire provide a much better way to assess whether forestry plans are maintaining birds within the natural range of variation (NRV) that would be expected when uncontrolled fire is the dominant disturbance agent. Simulating landscapes based on NRV in forest age and structure provides a way of estimating species abundance in the absence of human footprint, although the effects of a lack of harvest are confounded with the effects of increased fire due to a lack of fire suppression by humans.

While forest management plans often treat forestry as the only anthropogenic disturbance, there are an increasing number of other land-users in many areas of the western boreal forest. Assessing the impact of different sectors becomes a key priority in assessing overall risk to species and what the most effective management actions to conserve species might be. In western Canada's sedimentary basin, oil and gas development cumulatively deforest and/or alter vegetation structure of large areas each year (Brownsey and Rainer, 2009; Carlson and Stelfox, 2014; Pickell et al., 2015). Climate change is also increasingly influential, with recent studies suggesting that boreal forests are seeing and will be subject to even higher rate of burning (Stralberg et al., 2015, 2018), drought, wind storms, and insect outbreaks (Seidl et al., 2017; Navarro et al., 2018). Given that landscapes are being transformed by multiple agents of change, wildlife management decisions that focus solely on timber harvest may be ill-equipped to actually achieve management objectives if other disturbances are not accounted for. While integrated landscape management is recommended as a best practice, in reality it is rare in most jurisdictions (Kennett, 2006) as data from planned development by all relevant industries is usually unavailable. Decision support tools that simulate and incorporate multiple land uses (e.g., energy, forestry, agriculture, settlements, transportation, mining) and natural disturbances are needed (Carlson et al., 2014). By linking SDMs to simulation tools, the consequences of management strategies in the presence of the full suite of drivers can be assessed (Carlson et al., 2014, 2019).

We linked detailed bird SDMs with several landscape simulation models in order to: (1) compare how populations of 20 boreal bird species of interest respond to forestry over the next 50 years with and without deferrals of harvest in caribou habitat; (2) predict the NRV in those species' populations in the absence of human footprint but with historical fire rates; and (3) predict cumulative effects to these species from forestry, other land uses (bitumen development, settlements), and fire (present burning rate and a doubled burning rate). We focused on species of conservation interest to Canada or Alberta or of management interest to foresters in Alberta. Thirteen of these species use older coniferous, mixed-wood, or deciduous forests as habitat. We predicted that species associated with older mixed-wood, or deciduous forests would decrease with deferral of harvest in caribou habitat, while species associated with older coniferous forests would increase with harvest deferral. We also expected bird species associated with older forests to respond negatively to forest disturbance by fire and non-forestry land use, and positively to restoration of land use footprint. Seven of our 20 species use younger or open habitats, and we predicted these species would respond positively to harvest, fire, and other land use.

MATERIALS AND METHODS

Study Area

The study area was the Alberta-Pacific Forest Industries Inc. (Al-Pac) Forest Management Area (FMA) (∼6,300,000 ha) in northeastern Alberta, extending north from the towns of Athabasca and Lac La Biche to the Birch Mountains (∼340 km) and west from the Alberta/Saskatchewan border to Lesser Slave Lake. The predominant ecosystem is boreal forest, dominated by black spruce (*Picea mariana*) and tamarack (*Larix laricina*) in lowlands and by trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), and white spruce (*Picea glauca*) in mesic uplands. Another climax species, balsam fir (*Abies balsamea*), is uncommon due to the frequency of forest fires. Drier uplands are dominated by jack pine (*Pinus banksiana*). The merchantable land base comprises 31% of the FMA (Alberta-Pacific Forest Industries Inc, 2015). The FMA is divided into 12 Forest Management Units (FMUs) varying in size and the amount of forest stands that are suitable for harvest. A Forest Management Plan is produced every 10 years for the entire FMA but there are separate management targets for each FMU (Alberta-Pacific Forest Industries Inc, 2015, **Figure 1**).

Bird Species Distribution Models

The SDMs that we used for boreal birds were produced by the Boreal Avian Modelling Project (BAM), Alberta Biodiversity Monitoring Institute (ABMI), and Environment and Climate Change Canada (ECCC). The modeling process has been described in detail elsewhere and has been applied in other simulation and modeling studies (Ball et al., 2016; Sólymos et al., 2020b). Briefly, point count data were collated and standardized (n = 141,557 survey visits from 33,002 unique stations) from multiple boreal bird studies in Alberta's boreal forests (1993–2017). Boreal birds select habitat at multiple spatial scales (Mahon et al., 2016); thus, predictor variables in the SDMs were assessed at two spatial scales for each survey station. Local-scale variables were assessed in a 150-m radius of each station. Stand-scale variables were assessed in a 564-m radius (1 km^2) of each survey station. This stand scale was chosen for pragmatic reasons to match the mapping unit in our predictions and because it roughly corresponds to the scale deemed most appropriate for landscape variables based on smoothing kernel estimates for landscape variables (Chandler and Hepinstall-Cymerman, 2016). At the local scale, land cover was assessed for each survey station using provincial land cover

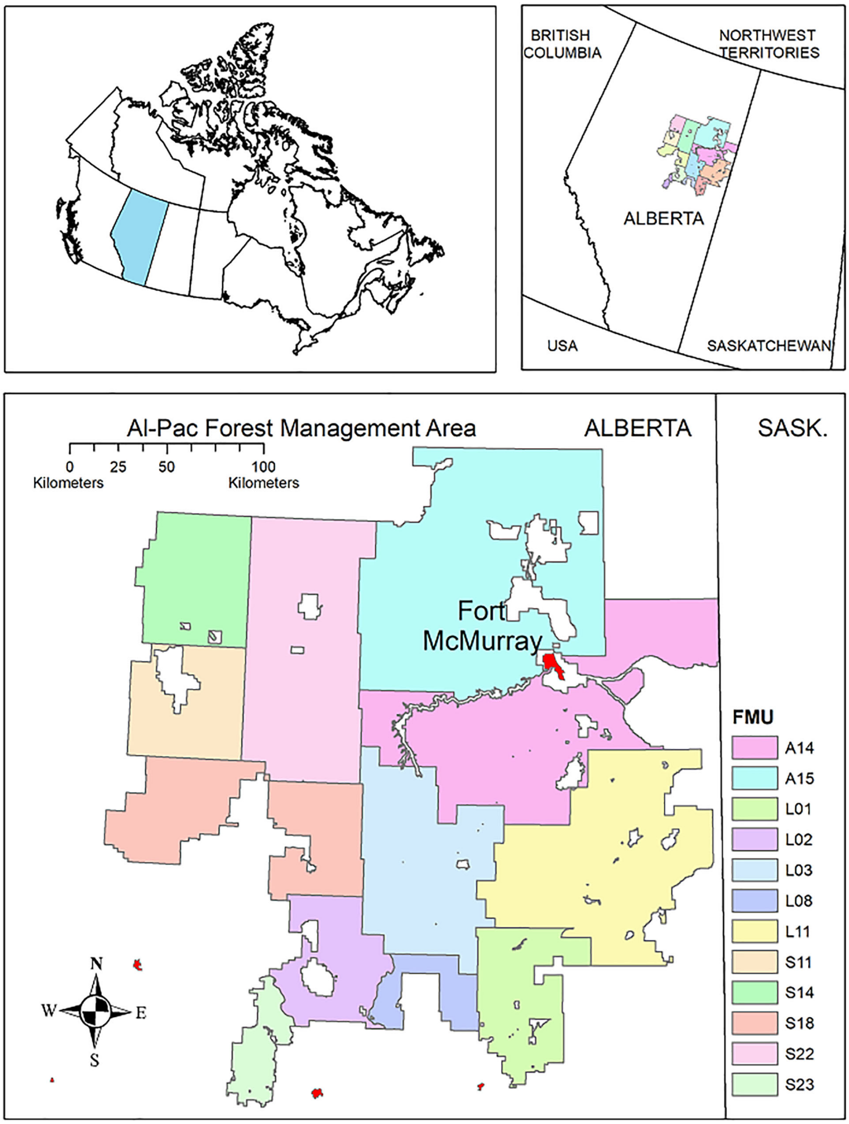

FIGURE 1 | Study area, in the Al-Pac Forest Management Area (FMA) area in northeastern Alberta. There is one Forest Management Plan for the FMA, but the FMA is divided into 12 Forest Management Units (FMUs). Separate harvest targets are set for individual FMUs within the plan, and FMUs vary in size and the amount of habitat for individual bird species.

information (Alberta Biodiversity Monitoring Institute, 2017, 2018; Allen et al., 2019). Vegetation type included deciduous, mixed-wood, white spruce, pine, black spruce, tamarack fen, shrub, grass/herb, graminoid fen, marsh, and swamp cover types. Human footprint was assessed at each survey point based on the year of sampling. Footprint type included cultivation, forestry, urban-industrial (mines, well sites, urban areas, industrial, rural residential), hard linear (road and rails), and vegetated soft linear (seismic lines, pipelines, power lines, road verges) features. Proportional area of the land cover types was calculated at the local scale, and the dominant vegetation type was assigned to each survey station based on a simple majority rule. Various data sources (Alberta Biodiversity Monitoring Institute, 2017) were used to estimate the years since last disturbance (i.e., forest age) relative to year of sampling for birds. Age was calculated as the area-weighted average of the forested polygons within 150 m of survey stations. When the dominant land cover was a harvest block, the pre-disturbance vegetation type but not age was assumed based on available forest inventory data in the local 150-m buffer. Doing so treated harvested areas as young forest rather than a separate land cover type. We also created a contrast variable that ranged between 1 (harvest) and 0 (converged to natural stands) to describe the convergence trajectory of forestry cut blocks. We assumed that convergence is complete at 60 years after harvest. This allowed us to differentiate young forests of natural (i.e., fire) versus anthropogenic (i.e., timber harvest) origin. Stand-scale variables included: the amount of open water in a 1-km^2 buffer around each survey location; the proportions of total human footprint, vegetated footprint types, non-vegetated footprint types, linear footprint, non-linear footprint, cultivation, and non-cultivation footprint types; and the proportion of suitable habitat for each species (**Table 1**). The suitable land cover classes were determined based on the binary classification of land cover types into suitable and unsuitable classes by maximizing the Youden index (Youden, 1950).

Geographic variation was captured by including latitude, longitude, and climate (mean annual precipitation, mean annual temperature, potential evapotranspiration, annual heat moisture index, frost-free period, mean warmest and coldest month temperature at 0.5° resolution; Wang et al., 2012) (**Table 1**).

The final SDMs were Poisson generalized linear models with a log link function. The response variable was the number of male birds of a species counted per survey. The QPAD approach was used to account for differences in sampling protocol and nuisance parameters affecting detectability (time of day, time of year, tree cover, habitat composition; Sólymos et al., 2013). This approach converts sampling distances and durations to a common standard through statistical offsets and adjusts for differences in detection error and sampling area related to broad vegetation types and timing of surveys. As a result, the results allow us to estimate density of birds (individuals per hectare), in a spatially explicit manner, allowing us to use forest stand type, fire or harvest origin, stand age, and human impact coefficients in scenario modeling.

Bird densities for the various scenarios were estimated based on the local stand, its spatial location, and the characteristics of the surrounding polygons. We modeled the effect of forest age on bird density by using weighted age and a quadratic or square root transformed terms as covariates to fit non-linear responses to age. We incorporated interactions between forest type and age, climate variables, latitude, and longitude (**Table 1**). The stand level effects of suitable habitats and human footprint allowed us to differentiate between locally suitable habitats that are surrounded by suitable vs. unsuitable land cover types. The stand-scale predictors effectively measure patch size in a species-specific manner, i.e., suitable habitat was assessed for each species individually, to best describe their optimal habitat characteristics.

We extracted habitat variables, and depending on the scenario, human footprint and climate variables, which served as inputs to the SDMs for predicting abundance of bird species at specific locations. For the Patchworks harvest scenarios and NRV scenario, these locations were individual quarter-sections throughout the Al-Pac FMA and we extracted proportions of different forest-origin type-age-classes per quarter-section. The quarter-section IDs were linked to latitude and longitude locations stored with climate variables and interaction terms in the cure4insect R package (R Core Team, 2020; Sólymos et al., 2020a). For the ALCES Online cumulative effects scenarios, we extracted variables from 200-m square raster cells including the proportion of each cell occupied by a specific vegetation-origin type or human footprint, the proportion of land within 1 km^2 of each cell in different vegetation-origin types or human footprints, the weighted-average forest age in that cell, latitude, longitude, climate variables, and any interaction terms among these variables. Instead of importing these variables as inputs to SDMs within the cure4insect package, we constructed individual species indicators and ran each species indicator through the cumulative effects scenarios in ALCES Online (**Table 1**) using a set of parameter estimates from models that included the 1 km^2 scale predictor variables as described in Ball et al. (2016). Model coefficients and indicator formulae for species are stored online at https://github.com/borealbirds/ABMI-bird-models-ALCES-Online.

We focused on 20 bird species in three key groups: (1) federally threatened species in Canada[1]; (2) provincially threatened in Alberta (Alberta Environment and Sustainable Resource Development, 2014), or (3) have specific habitat requirements that make them useful indicator species for forest managers in Alberta. Most of these species are associated with mature or older deciduous or mixedwood forests (Black-throated Green Warbler *Setophaga virens*, Brown Creeper *Certhia americana*, Canada Warbler *Cardellina canadensis*, Ovenbird *Seiurus aurocapillus*, Pileated Woodpecker *Dryocopus pileatus*, Yellow-bellied Sapsucker *Sphyrapicus varius*) or coniferous forests (Bay-breasted Warbler *Setophaga castanea*, Blackpoll Warbler *Setophaga striata*, Boreal Chickadee *Poecile hudsonicus*, Cape May Warbler *Setophaga tigrina*, Evening Grosbeak *Coccothraustes vespertinus*, Western Tanager *Piranga ludoviciana*, White-winged Crossbill *Loxia leucoptera*). The remaining species are of conservation or management interest but use younger or open habitats (American Three-toed Woodpecker *Picoides dorsalis*, Black-backed Woodpecker *Picoides arcticus*, Northern Flicker *Colaptes auratus*, Olive-sided Flycatcher *Contopus cooperi*, Palm Warbler *Setophaga palmarum*, Rusty Blackbird *Euphagus carolinus*, Western Wood-pewee *Contopus sordidulus*).

Harvest Planning for Caribou Management

Many forest planners in Alberta create their operating harvesting plans using the harvest-scheduling simulator software Patchworks[2]. Patchworks is used because it optimizes economic and ecological tradeoffs when selecting which stands to harvest, in what areas, and when (Sturtevant et al., 2007). We used Patchworks to create two spatial harvest plans for the Alberta-Pacific FMA in northeastern Alberta that are being submitted as options for harvest to provincial regulators.

The first Patchworks scenario solves for different tradeoffs to maximize harvesting pulpwood and timber with relatively even harvest levels over time, while (1) minimizing costs of road construction and maintenance; (2) adjusting harvest area size, shape, and distribution to approximate the size, shape and distribution of natural forest disturbances like fires; and (3) applying other constraints (Hebert et al., 2003; Dzus et al., 2009). We describe this scenario as the Ecosystem-Based Management/Natural Disturbance Model ("EBM") scenario.

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[1] https://www.registrelep-sararegistry.gc.ca

[2] https://spatial.ca/patchworks/

TABLE 1 | Predictors used in the species distribution models to predict density and abundance of each analyzed bird species within individual Forest Management Units and over the Al-Pac Forest Management Area (FMA) over 50 years within the two Patchworks spatial harvest scenarios, the NRV scenario, and the ALCES Online cumulative effects scenarios described in this paper.

Term	Definition	Values or range	Model stage	Model description	Square-root term tested	Quadratic terms tested	Interactions
Intercept	**Y-intercept**	**Species-specific constant**	**0**	**Initial null model**			
HAB	Land cover type within 150 m of point count	13 classes	1	Local-scale habitat			
YSD	Year since disturbance	0–160 years	2	Habitat × Age	Yes	Yes	With HAB
isM	HAB = Mixedwood	0 or 1	2	Habitat × Age			With YSD
isP	HAB = Pine	0 or 1	2	Habitat × Age			With YSD
isW	HAB = White Spruce	0 or 1	2	Habitat × Age			With YSD
isC	HAB = Conifer (Pine, White Spruce, Black Spruce, Larch)	0 or 1	2	Habitat × Age			With YSD
isLC	HAB = Lowland Conifer (Black Spruce, Larch)	0 or 1	2	Habitat × Age			With YSD
FOR	Stand origin (natural disturbance or harvest)	0 or 1	3	Forest Origin			
ROAD	HAB = Roadside	0 or 1	4	Roadside or not			
SLIN	Vegetated linear features within 150 m		4	Roadside or not			
ARU	Point counts collected by ARU or human	3 classes	5	Survey method			
CTI	Compound topographic index	5.0–26.8	6	Wetness			With WET
LAT	Latitude	50.27–60.01 degrees	7	Space/climate		Yes	With LONG
LONG	Longitude	−120 to −110 degrees	7	Space/climate		Yes	With LAT
PET	Potential evapotranspiration	288–645	7	Space/climate			
MAT	Mean annual temperature	−4.6 to 3.6 degrees Celsius	7	Space/climate			
MAP	Mean annual precipitation	347–1902 mm	7	Space/climate			
FFP	Frost free period	46–122 days	7	Space/climate			
AHM	Annual heat-moisture index	4.4–34.7	7	Space/climate			
MWMT	Mean warmest month temperature	7.2–17.7 degrees Celsius	7	Space/climate			
MCMT	Mean coldest month temperature	−27.1 to −8.7 degrees Celsius	7	Space/climate			
SSH 1 KM2	Species-specific total preferred habitat at 1 km^2 scale	0–100%	8	Landscape-level habitat	Yes		
WET	Wet land cover within 1 km^2	0–100%	6	Wetness		Yes	With CTI
THF	Total human footprint at 1 km^2 scale	0–100%	9	Landscape-level footprint		Yes	
SUCC	Successional footprint (harvest, seismic) at 1 km^2 scale	0–100%	9	Landscape-level footprint		Yes	
ALIEN	Alienating footprint (cropland and other non-successional) at 1 km^2 scale	0–100%	9	Landscape-level footprint		Yes	
LIN	Linear features at 1 km^2 scale	0–100%	9	Landscape-level footprint		Yes	
NLIN	THF-LIN (non-linear) at 1 km^2 scale	0–100%	9	Landscape-level footprint		Yes	
YR	Year of survey	1997–2015	10	Survey year			

For the Patchworks harvest scenarios and NRV scenario, we extracted the proportions of different forest-origin type-age classes from each quarter-section in the Al-Pac FMA, since quarter-section IDs were linked to latitude and longitude locations stored with climate variables and interaction terms in the cure4insect package. For the ALCES Online cumulative effects scenarios, we extracted the proportion of each 200-m square cell occupied by a specific vegetation-origin type or human footprint, the proportion of land within 1 km of each cell in different vegetation-origin types or human footprints, the weighted-averaged forest age in that cell, latitude, longitude, climate variables, and any interaction terms among these variables. We constructed individual species indicators using the extracted data with model coefficients from SDMs to run indicator under different scenarios in ALCES Online.

The second scenario is known as the Preferred Forest Management ("PFM") scenario and corresponded to the spatial harvest strategy used by Al-Pac in their 2015 Forest Management Plan. The PFM scenario also solves for the tradeoffs described in the EBM scenario but it also defers large tracts of habitat within Woodland Caribou range (primarily black spruce/larch bogs and fens) from harvest for the first 20 years of the simulation. After the 20-year deferral model allocation within the Caribou Zone is permitted. Both scenarios were run separately on each of Al-Pac's 12 Forest Management Units (FMUs) as required by provincial planning standards (Government of Alberta, 2006).

From each of the two scenarios, we extracted year 0, year 10, year 20, and year 50 outputs as shapefiles for each of Al-Pac's 12 FMUs in each scenario, describing the polygons harvested, when they were harvested, age at harvest, cutblock size, type of cover class, and harvest volume (**Figure 2**). We spatially unioned these layers with an Alberta quarter-section shapefile layer clipped to each FMU's boundaries. This allowed us to calculate the cumulative area of each forest age-forest type per quarter-section. We classified forest age-classes based on the management age of each forest stand since its origin, based on the stand and age-class categories used in the bird SDMs. The abundance of each species per quarter-section based on predicted habitat conditions were computed from cure4insect for the 20 bird species for each time period and scenario.

The Al-Pac FMP model underlying the Patchworks scenarios in this paper assumes that the only action that can change the age of a forest stand is a harvest event. When a stand is harvested, stand age is reset to zero and the forest type remains the same (regenerating stands are the same as the original stand). Stand succession (the endemic process of senescence and renewal) is captured in the long-lived yield curves with the assumption that long-term standing volumes decline and stabilize at 50% of peak culmination.

Natural Range of Variation

Patchworks is an optimization tool for harvest scheduling, but does not explicitly allow for dynamic changes in fire or other human land-uses. Thus, we used a spatially explicit land use simulator called LANDMINE (Andison, 1996, 2005; Andison and Forest, 2000) to compare the effects of fire to the harvest results from Patchworks. Specifically, we compared the two harvest scenarios to a scenario devoid of human activities whereby forest age-structure was set back by fire instead of harvest. LANDMINE uses a dispersal algorithm to spread fires from one pixel to another probabilistically based on fuel-type and topography. Fire movements were calibrated to create different fire shapes and unburnt island remnants based on empirical data. Fire size was controlled by an equation representing the actual fire size distribution for each landscape. Ignition location probabilities were loosely based on historical lightning probabilities. Finally, the total amount of forest burnt in any single time step was based on historical areas burnt. A burn frequency of 63.5 years was used for the Al-Pac FMA. The "NRV" scenario was a Monte Carlo simulation that replaced human footprint with natural disturbance footprints (fire) through time, in which no logging nor any other human activity occurred. Once human footprint was removed, the NRV scenario was run for approximately 1000 simulated years (Andison and Forest, 2000). The NRV simulation of fire and the resulting forest-age structure was developed by DA at Bandaloop Landscape Ecosystem Services[3].

From the NRV simulation 100 snapshots – each separated by 10 years – of the Al-Pac FMA were extracted. Each snapshot consisted of a grid of 200-m square cells across the entirety of the Al-Pac FMA. Estimated forest age and dominant tree species or non-forest vegetation in each cell were calculated. The amount of each vegetation age-class varied by snapshot. We converted each snapshot to shapefiles and imported the shapefiles into cure4insect to calculate bird abundance in each cell (**Figure 3**). Once we had 100 abundance predictions of each species, we estimated the mean, standard deviation, and confidence interval estimates for those predictions.

Cumulative Effects

While Patchworks and LANDMINE are particularly good at spatially representing harvesting and fire strategies and optimizing solutions, they were not designed to track cumulative effects. To explore how boreal birds may respond to the cumulative effect of multiple land uses and fire, we created five scenarios using a spatially explicit land use cumulative effects simulator called ALCES Online[4]. To make these simulations as realistic as possible, we used the actual harvest plans from the PFM scenario in Patchworks (the most likely harvest plan) along with theoretical future trajectories for bitumen development and fire to determine how these drivers affect bird response over the next 50 years. The consequences of simulated anthropogenic and natural processes were assessed by tracking changes in landscape composition, forest age, and forest origin (i.e., burn or harvest). The simulator is cell based, with each cell's composition tracked as proportional coverage by various natural and anthropogenic cover types. ALCES was initialized by calculating the current proportional composition of each 200-m cell by forest types, other cover types, and footprints. Forest area, age, and origin was based on the Alberta Vegetation Inventory as in the Patchworks and LANDMINE tools. Coverage by different non-forest, terrestrial and aquatic vegetation types – which may also influence bird abundance - was calculated using the Earth Observation for Sustainable Development (EOSD) land cover and the AltaLIS hydrology datasets. Current location and extent of anthropogenic footprints other than harvest (roads, well sites, pipelines, seismic liens, mines, rural residences, settlements, transmission lines, industrial features) were obtained from the Alberta Biodiversity Monitoring Institute human footprint inventory as well as other sources such as Alberta Energy Regulator, CanVec, and OpenStreetMap. Proportional composition, age, and origin of each cell was then modified during simulations to track the effect of new developments, reclamation, and fire

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[3] https://friresearch.ca/partner/bandaloop-landscape-ecosystem-services

[4] https://www.online.alces.ca/

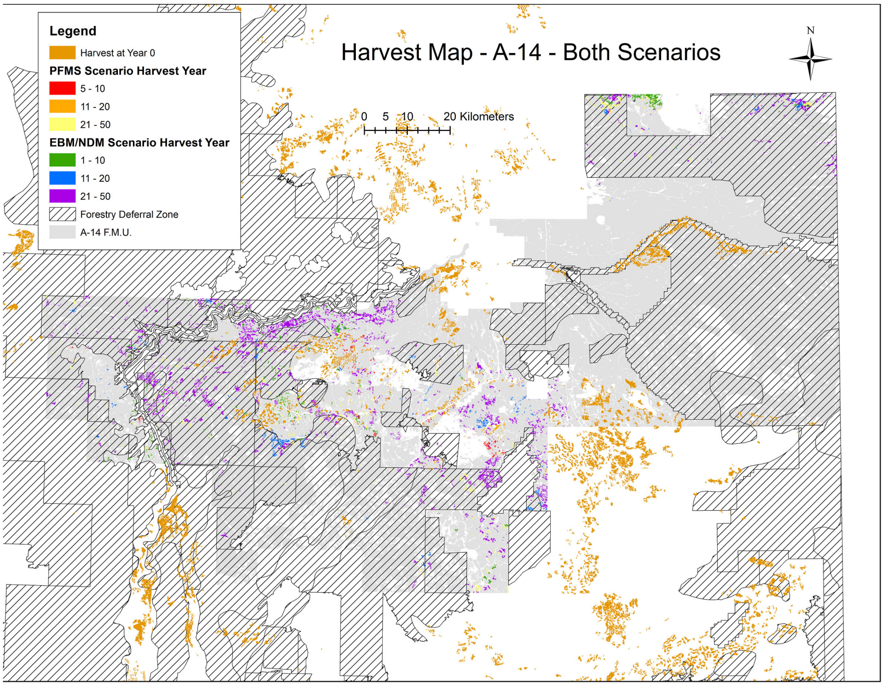

FIGURE 2 | Locations of existing harvested stands in Year 0 (start of simulation = 2016) and simulated harvested stands accumulated over 50 years under both the PFM and EBM scenarios in one of the Al-Pac forest management units (A-14), along with the locations of caribou conservation zones where harvest was deferred in the first 20 years of the PFM scenario. Existing harvest areas (brown) already present in A-14 at Year 0 could occur within the deferral zones as could harvests from the first 20 years of the EBM scenario (green, blue), but harvests from the first 20 years of the PFM scenario (red, orange) were excluded from the deferral zone. From Year 20 to Year 50, harvests under both scenarios could occur inside or outside the deferral zones and often the same harvest locations were selected under either scenario. Harvest over 50 years comprised a very small percentage of FMUs under either scenario, and overall forest age increased under both scenarios.

on landscape composition and age. A baseline "Al-Pac BAU" scenario incorporated forestry, bitumen, settlement, road, and gravel pit development as well as fire. The baseline scenario was modified to create the following additional scenarios: "Seismic Restoration," which restored seismic lines to improve woodland caribou habitat; "No Energy," which excluded the effect of future energy development; "No Fire," which excluded the effect of future fire; and "Increased Fire," which doubled the fire rate to incorporate the projected effect of climate change (Boulanger et al., 2014).

We used the following assumptions to simulate fire and non-forestry land use. Annual area burned (284.8 km2/year) and the fire size class distribution was based on fires occurring in the study area over the past 75 years (1940–2015) rather than on the NRV scenario. Fire location was influenced by forest type and age (Bernier et al., 2016). Simulation of *in situ* (i.e., well-based) and mineable bitumen development assumed production trajectories consistent with projections by the Alberta Energy Regulator (2016) and National Energy Board (2016) for the first 25 years, after which production plateaued based on the expectation that bitumen production will stabilize in the long-term (Millington and Murillo, 2015; Straatman and Layzell, 2015). The sequencing of mining projects during the simulation was based on anticipated project start-up dates. For the first 25 years of the simulation, *in situ* bitumen development occurred at operational, approved, and applied projects. Thereafter, location was influenced by bitumen pay thickness. The number of new production wells and mine area required through time to meet the production trajectory was based on productivity assumptions from previous studies (Wilson et al., 2008; Alberta Energy Regulator, 2015). Production wells and exploration footprint (exploration wells, seismic lines) were aggregated around central industrial plants, and pipelines linked the projects to the existing pipeline network. Energy sector footprints remained for the duration of the 50-year simulation because reclamation trajectories for footprints such as seismic lines (Lee and Boutin, 2006) and mines (Rooney et al., 2012) are slow and uncertain. The exception was the "Seismic Restoration" scenario for which seismic lines were reclaimed to natural land cover after 20 years. Rural residential and urban settlements were simulated to expand as per the Government of Alberta's population growth rate for the region. New rural residences (i.e., acreages) occurred within 1 km of existing rural settlement footprint, and urban expansion occurred at the periphery of Fort McMurray, the largest city in the study area. Simulated roads connected new well sites, acreages and timber harvest areas to the nearest existing road. New gravel pits were simulated based on the current ratio of road to gravel pit area; gravel pits were located within gravel deposits in proximity to new roads.

Rather than compute bird abundance by predicting total abundance using the various shapefiles created by Patchworks

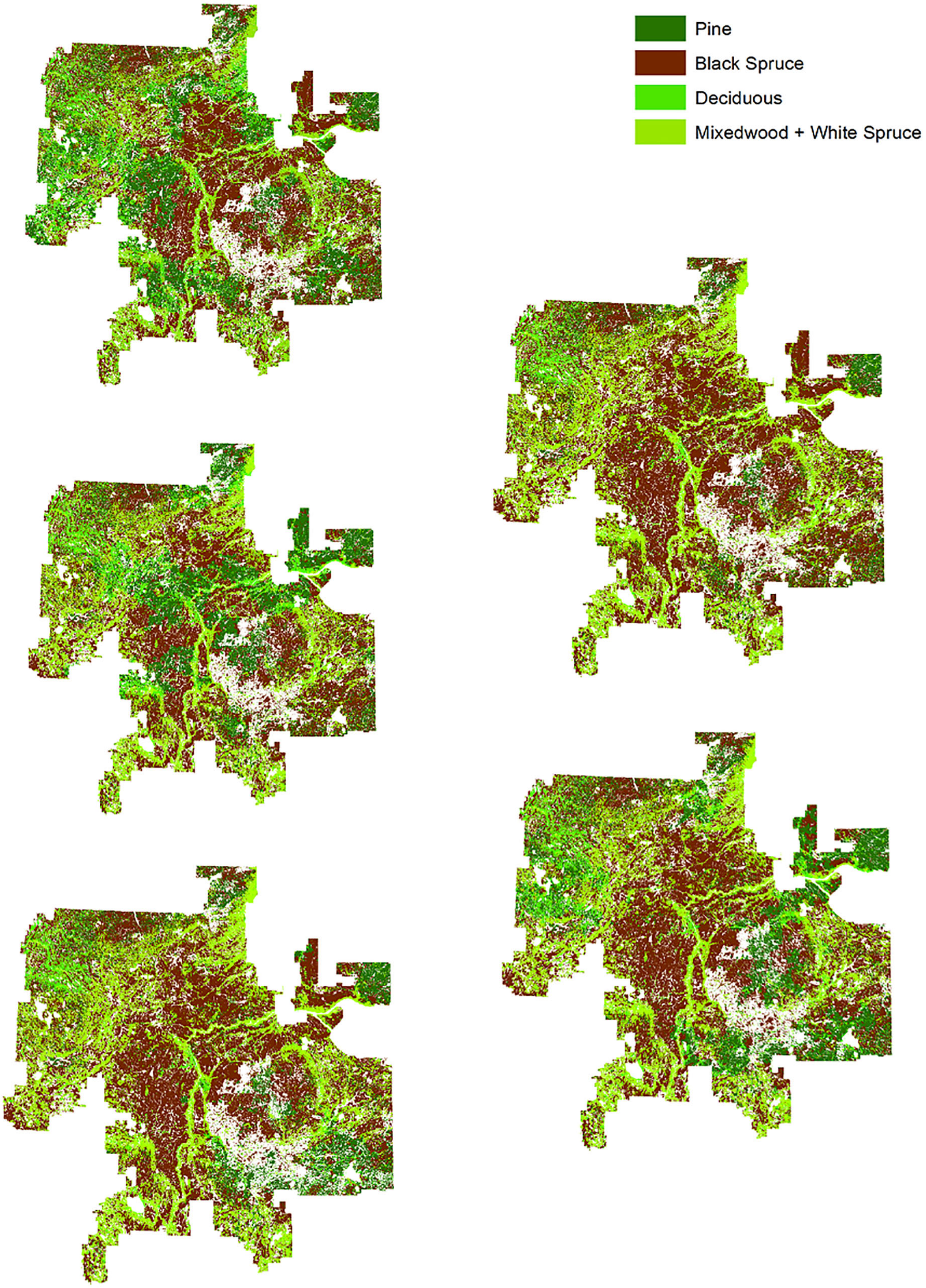

FIGURE 3 | Examples of “snapshots” of forest age-structure the Al-Pac FMA from simulations of natural disturbance (a 63.5-year fire cycle) in the total absence of human footprint (NRV scenario). In this program, younger forest stands resulted from fires which were also used to replace human footprint over 1000 years of simulated time. We ran this simulation for 1000 years, then used 100 “snapshots” from the simulation to estimate natural range of variation (NRV) of different forest stands and ages. Pure stands of white spruce were not included in the simulation due to their rarity in the Al-Pac FMA. In contrast to the NRV scenario, harvest was the only source of disturbance setting back forest stand age to 0 in the Patchworks scenario and given the small amount of each forest management unit harvested over 50 years in the Patchworks scenarios, forest age on average increased within individual FMUs over 50 years.

and LANDMINE as inputs in cure4insect, we took the underlying model coefficients from the SDMs in cure4insect to directly track birds as indicators in the Alces Online tool with reporting of mean density and population size at each 10-year mark in a 50-year simulation.

RESULTS

Harvest Planning for Caribou Management

Most bird species associated with mature and old deciduous and mixed-wood forests were predicted to increase over 50 years (**Figure 4**, **Table 2**, and **Appendix I**). Bird species associated with mature and old deciduous and mixed-wood forests tended to exhibit a larger population increase in the presence of caribou habitat deferral (PFM scenario) than without (EBM scenario). This included Black-throated Green Warbler (9% under PFM vs. 7% under EBM: 4701 more birds after 50 years), Brown Creeper (58% vs. 56%: 20849 more birds), Canada Warbler (36% vs. 30%: 18736 more birds), and Pileated Woodpecker (15.4% vs. 14.7%: 415 more birds). An exception was Ovenbirds, with 24375 fewer birds under the PFM scenario (−1.0% under PFMS vs. −0.6% under EBM), although the differences were small relative to the initial population of this species (5283326 Ovenbirds in Year 0). The density of species associated with older mixed-wood and deciduous forests tended to be lower in FMU A-14, which experienced a large forest fire in 2016 at the start of the simulation (**Figures 4–6** and **Appendix I**).

Bird species associated with older coniferous forests tended to respond more positively to the PFM scenario than the EBM scenario, although the difference was relatively minor. This included Bay-breasted Warbler (−6% under PFM vs. −7% under EBM: 38525 more birds under PFM after 50 years), Boreal Chickadee (13.7% under PFM vs. 13.5% under EBM: 7209 more birds under PFM), Cape May Warbler (19.8% under PFM vs. 19.7% under EBM: 3621 more birds), Western Tanager (13% under PFM vs. 12% under EBM: 7604 more birds), and White-winged Crossbill (2.1% under PFM vs. 1.8% under EBM: 1870 more birds). Two exceptions to these pattern were that harvest deferral was predicted to result in 6422 fewer Blackpoll Warblers (−46% under PFM vs. −44% under EBM) and 718 fewer Evening Grosbeak (20% under PFM vs. 21% under EBM). Species associated with older coniferous forests increased over 50 years except for Bay-breasted Warbler and Blackpoll Warbler (**Figure 4**, **Table 2**, and **Appendix I**).

Except for American Three-toed Woodpecker, species associated with younger forest or open habitat exhibited lower abundance under the PFM scenario compared to the EBM scenario. This included the Black-backed Woodpecker (−46% under PFM vs. −47% under EBM: 2108 fewer birds under PFM after 50 years), Northern Flicker (7% vs. 9%: 5719 fewer birds under PFM), Olive-sided Flycatcher (8.6% under PFM vs. 9.1% under EBM: 678 fewer birds under PFM), Palm Warbler (−20.3% under PFM vs. −19.9% under EBM: 7604 fewer birds under PFM), Rusty Blackbird (−7% under PFM vs. −3% under EBM: 4420 fewer birds under PFM), and Western Wood-pewee (0.7% under PFM vs. 1.5% under EBM: 3756 more birds under EBM). Black-backed Woodpecker, Palm Warbler, and Rusty Blackbird declined over 50 years under both harvest scenarios while other species increased (**Figure 4**, **Table 2**, and **Appendix I**).

When we compared forest age-class amounts in Year 50 from both harvest scenarios, we did not find large percent differences in the amount of each forest age-class. Four percent of the forest-age classes were ≥50% more abundant by Year 50 under the PFM scenario, particularly black spruce < 20 years old, but also some mixed-wood and white spruce 20–60 years old. Just over one percent of the forest-age classes were >50% less abundant under the PFM scenario than the EBM scenario, primarily pine <20 years old originating from harvest. Nearly 95% of forest age-classes across all forest management units showed smaller relative differences among the harvest scenarios (**Appendix II**).

Average forest age increased over time in both harvest scenarios. On average in Year 0, most quarter-sections in the FMA were dominated by deciduous and mixed-wood forests <60 years old and coniferous forests <80 years old. By Year 50 in both harvest scenarios, much of the FMA had become dominated by older forests (**Figure 7**), with relatively large gains in the percent cover of black spruce and pine >80 years old in each quarter-section. Mixed-wood and white spruce occupied small proportions of the FMA across the whole period and large tracts of older deciduous forest were strongly reduced in both scenarios over 50 years (**Figure 8**). However, by Year 50, declines in deciduous and mixed-wood forests >60 years old and white spruce >80 years old were offset by new older stands that developed from harvested areas existing prior to Year 0 of the harvest scenarios (**Appendices I, II**).

Natural Range of Variation

Most species associated with older coniferous, mixed-wood, or deciduous forests were projected to be more abundant under the harvest scenarios than in the NRV scenario (**Figures 4–6** and **Table 1**), or after 50 years were at the higher end of the number predicted in the NRV scenario. These increases are presumably due to greater amounts of older deciduous and coniferous (**Figure 8**) rather than mixed-wood forests after 50 years in both harvest scenarios, since older mixed-wood forests were still uncommon after 50 years in both harvest scenarios. We generally projected more deciduous and fewer young mixed-wood stands under the two harvest scenarios than in the NRV scenario (**Figure 9** and **Appendix II**). The amounts of deciduous and mixed-wood age-classes in the harvest scenarios were based on the initial amounts in the Alberta Vegetation Inventory, in which many natural mixed-wood stands had already been harvested and converted to either pure coniferous or deciduous stands during replanting (Hobson and Bayne, 2000). Blackpoll Warbler was less abundant under the harvest scenarios than the NRV scenario, possibly because fires in the NRV scenario created enough alternative habitat that this species could use.

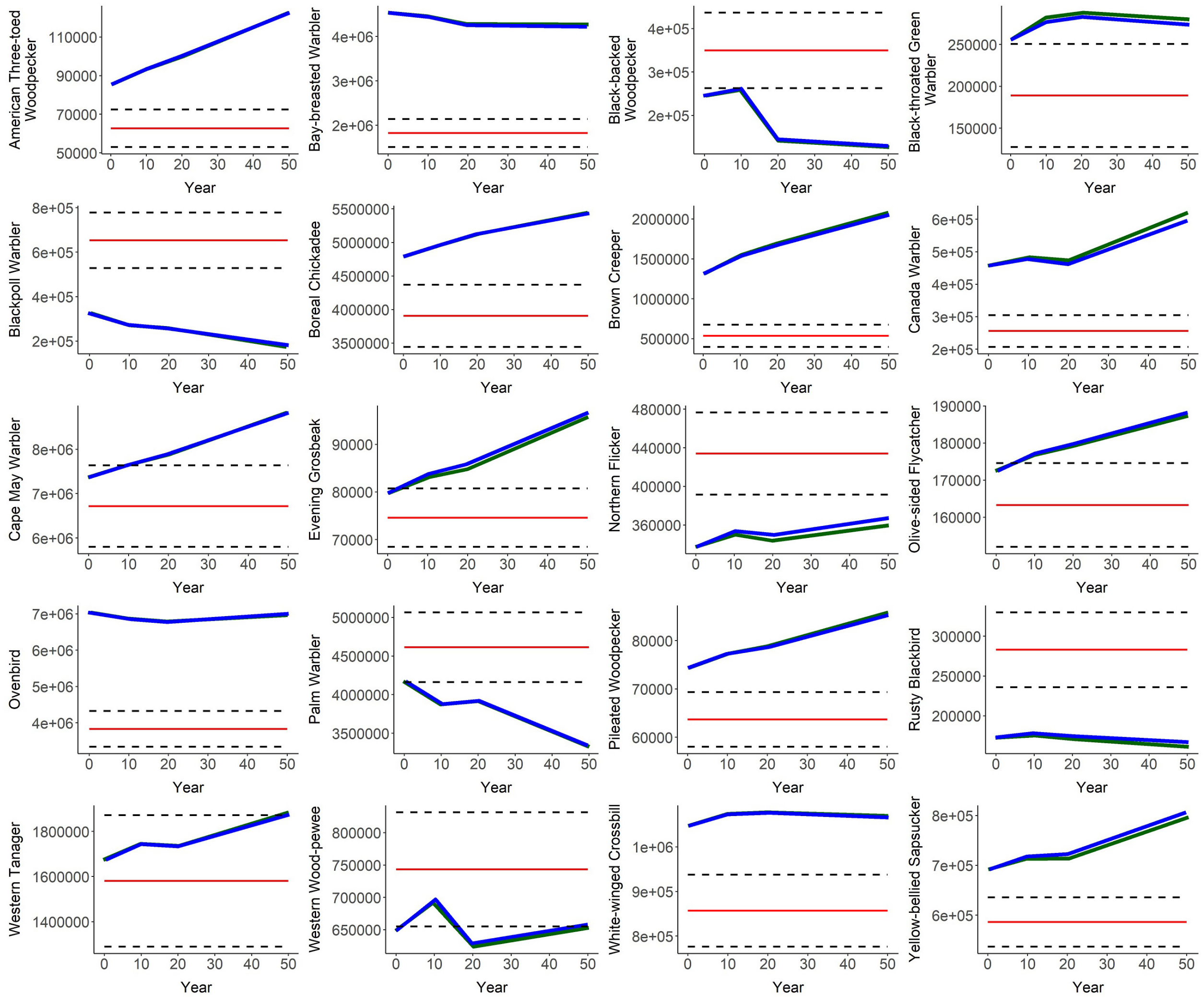

FIGURE 4 | Predicted abundance of 20 boreal bird over time (year 0–50, where year 0 = 2016) in the Al-Pac Forest Management Area (FMA), under two scenarios: (1) the Preferred Forest Management Scenario (PFM) that included harvest deferral within caribou habitats (green line); and (2) the Ecosystem-Based Management/Natural Disturbance Model Scenario (EBM) without harvest deferral (blue), relative to the predicted Natural Range of Variation (NRV) in abundance of each species in the absence of human footprint. Red line = mean predicted abundance in the FMA in the NRV Scenario. Black dashed lines = 95% confidence interval estimates in the NRV Scenario.

Most of the analyzed species that were associated with younger or open habitats in boreal forests were more abundant under the NRV scenario than either harvest scenario (**Figure 4** and **Table 1**). We reasoned that as the overall forest age structure became older, forests became less suitable for most of these species. Young pine and black spruce stands may have been less abundant while older pine and black spruce were more abundant under the harvest scenarios due to fire suppression: under the NRV scenario, fires were more likely to burn older pine and black spruce, converting burned stands to young stands (**Figure 9**). In contrast, American Three-toed Woodpecker and Olive-sided Flycatcher, which are associated with burns within boreal forests, were more abundant under the harvest scenarios than the NRV scenario, despite the fact that there would be fewer forests or open areas after 50 years in the harvest scenarios. Since these two are tree-nesters that forage on or from trees (in contrast to the other species that nest in trees or shrubs but forage in clearings), fire rates associated with the NRV scenario over 1000 simulation-years may be reducing some important habitat features for these species, even if fire is associated with habitat for these species.

While we focused on analyses of 20 bird species for this paper, we have included scripts for running the same Patchworks and NRV analyses on other species at https://github.com/borealbirds/Patchworks-NRV-cure4insect.

Cumulative Effects

When we considered cumulative effects of harvest, fire, and habitat conversion by non-forestry footprint, 13 of 20 species increased under current rates of fire, harvest, and energy sector

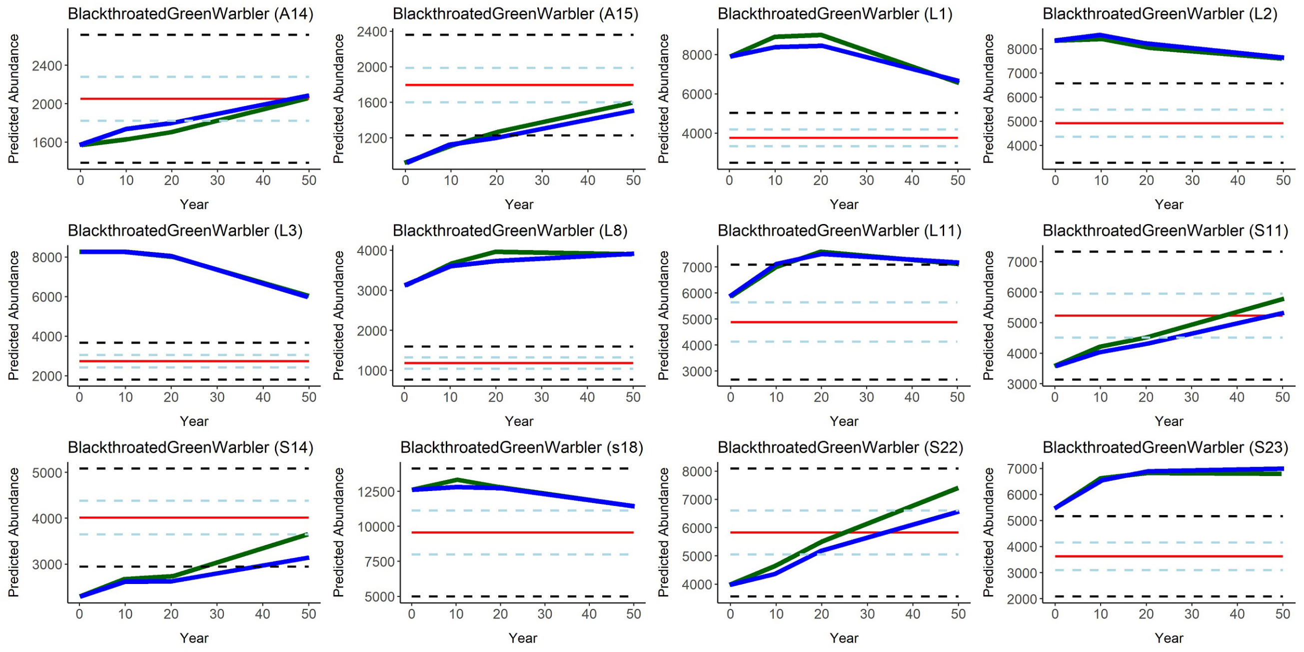

FIGURE 5 | Predicted Black-throated Green Warbler abundance over time (year 0-50, where year 0 = 2016) in all 12 Forest Management Units in the Al-Pac Forest Management Area, under two scenarios: (1) the Preferred Forest Management Scenario (PFM) that included harvest deferral within caribou habitats (green line); and (2) the Ecosystem-Based Management/Natural Disturbance Model Scenario (EBM) without harvest deferral (blue), relative to the predicted Natural Range of Variation (NRV) in Black-throated Green Warbler abundance in the absence of human footprint. Red line = mean predicted Black-throated Green Warbler abundance per Forest Management Unit in the NRV Scenario. Light blue dashed lines = 50% confidence intervals for mean predicted Black-throated Green Warbler abundance in the NRV Scenario. Black dashed lines = 95% confidence interval estimates in the NRV Scenario. SDMs predicted that Black-throated Green Warbler densities were highest in very old deciduous and mixed-wood stands (>80 years old) and average deciduous and mixed-wood forest age increased in most FMUs over 50 years in the Patchworks simulations, while average deciduous and mixed-wood forest age was reduced by simulated fires in the NRV scenario.

development ("Al-Pac BAU Scenario"), with the largest increases being observed for American Three-toed Woodpecker (126%) and Black-throated Green Warbler (120%). The declining species were Bay-breasted Warbler, Blackpoll Warbler, Ovenbird, Palm Warbler, and Rusty Blackbird (as in the harvest scenarios), and Boreal Chickadee and White-winged Crossbill (unlike in the harvest scenarios). The largest decrease was observed for Rusty Blackbird (42%) (**Figure 10** and **Table 3**).

In general, species that were more abundant under the harvest scenarios than the NRV scenario were relatively less abundant under a higher burn rate. This negative response was measured as a larger decrease or smaller increase in the "Increased Fire" scenario relative to the "Al-Pac BAU" scenario and/or as a larger decrease or smaller increase in the "Al-Pac BAU" scenario relative to the "No Fire" scenario (**Figure 11**). Most species associated with older forests, along with American Three-toed Woodpecker and Olive-sided Flycatcher, were more abundant in the harvest scenarios than the NRV scenario and also responded negatively to fire in the cumulative effects scenarios. The negative effect of fire on Olive-sided Flycatcher was small: Olive-sided Flycatcher increased in all scenarios but increased less over 50 years in the "Increased Fire" scenario (5%) than the "Al-Pac BAU" scenario (6%) and "No Fire" scenario (9%). The largest negative responses (≥25% difference between "Al-Pac BAU" and "No Fire" population projections at year 50) were for American Three-toed Woodpecker, Black-throated Green Warbler, Brown Creeper, Canada Warbler, and Cape May Warbler. An exception to the pattern was Ovenbird, which responded positively to fire in the cumulative effects scenarios. It is worth noting, however, that Ovenbird densities were initially reduced by a higher fire rate until near the end of 50 years in the cumulative effects scenarios (**Figure 10**). Other species that responded positively to a higher fire rate (Blackpoll Warbler, Black-backed Woodpecker, Northern Flicker, Palm Warbler, and Rusty Blackbird) were more abundant in the NRV scenario than the harvest scenarios (**Figure 10** and **Table 3**).

Most (16 of 20) species responded negatively to energy sector development in the cumulative effects scenarios. This negative response was measured as a larger increase or smaller decrease in the "No Energy" scenario relative to the "Al-Pac BAU" scenario and/or as a larger decrease or smaller increase in the "Al-Pac BAU" scenario relative to the "No Energy" scenario. The largest negative responses (≥25% difference between "Al-Pac BAU" and "No Energy" population projections at year 50) were observed for Black-throated Green Warbler, Canada Warbler, and Western Tanager. Species responding positively to energy sector development were limited to Blackpoll Warbler, Black-backed Woodpecker, Rusty Blackbird, and White-winged Crossbill (**Figure 10** and **Table 3**).

Twelve of sixteen species that responded negatively to simulated levels of energy sector development responded positively to restoration of seismic lines. The largest positive responses to seismic line reclamation ($\geq$5% difference between "Al-Pac BAU" and "Seismic Restoration" population projections at year 50) were observed for Black-throated Green Warbler, Brown Creeper, Canada Warbler, and Western Tanager (**Figure 10** and **Table 3**).

DISCUSSION

Harvest Planning for Caribou Management

In our study, outputs from Patchworks were used to predict bird species abundance under an ecosystem-based management versus caribou-conservation strategy. Differences in population projections for most birds were small with an absolute difference in percent population change between harvest scenarios < 6% on average for all species). While harvest locations differ considerably between the PFM and EBM scenarios in the first 20 years of the simulation, most forest stands over the entire FMA remained unharvested over 50 years in both scenarios as they have not yet become old enough to be harvested. We expected that the caribou-conservation strategy would have negative effects on birds that rely on large patches of older deciduous and mixed-wood forests. The SDMs on which bird population projections are based on emphasize habitat amount rather than habitat configuration *per se*. Our stand-level modifier that adjusts local bird density based on the amount of suitable habitat surrounding the survey location does indirectly account for patch configuration, because many metrics landscape fragmentation metrics are correlated with habitat amount (Wang et al., 2014). We also considered not only surrounding suitable habitat but amount of water and different types of human footprint at the landscape scale. We believe that a combination of these variables is predictive and interpretable, which were our main concerns from an application perspective. However, we also recognize that the concept of a patch for boreal birds is a fundamental challenge in these types of models as species with small territories may treat a clump of conifers in an otherwise deciduous-dominated forest as a patch, while a bird with a larger home range may view that same area as a mixed-wood. Taking a species-centric view of patch size is needed to address this issue in future simulations and will involve modeling local and landscape level stand characteristics by accounting for territory size differences among species (Westwood et al., 2019).

Importantly, total area harvested was similar in both the ecosystem-based management and caribou-deferral plans. After deferral ended in the PFM scenario, the same locations were eligible for harvest within both scenarios. Thus, even when large changes occurred in amounts of some forest age-classes underwent large changes, there ended up being similar amounts of most forest age-class types in both scenarios at the end of 50 years. As a result, habitat available for and predicted abundance of bird species in the FMA was similar in both scenarios after 50 years. Some studies suggest that habitat configuration and fragmentation effects are insignificant for boreal birds in landscapes where forest harvest is the primary agent of habitat conversion, except in extremely fragmented landscapes (Andren, 1994; Schmiegelow and Mönkkönen, 2002).

Our harvest scenarios explored the influence of harvest deferral on one major harvest strategy underlying EBM the location of harvest areas. Apart from varying size, shape, distribution and location, our harvest areas were all assumed to be clear-cuts based on the harvest practices modeled by our SDMs. Other EBM-based practices in Canada like partial cuts, shelterwood cuts, structural retention, and understory protection have been studied throughout Canada for their effects on tree mortality (Thorpe and Thomas, 2007), subsequent tree growth (Montoro Girona et al., 2017, 2018, 2019), understory protection (Burke et al., 2008), and biodiversity (Fenton et al., 2013; Huggard et al., 2014; Charchuk and Bayne, 2018). These harvest strategies may be more appropriate than traditional clear-cuts for emulating natural disturbance in regions where forest fires are less frequent than insect outbreaks and other disturbances. As regional SDMs are developed to account for the effects of these other harvest strategies on birds and other wildlife, it will become possible and desirable to project long-term bird abundance under these other strategies, using programs like Patchworks.

Since forest stand age was not set back by fire, other natural disturbances, or non-forestry human footprint in the Patchworks scenarios, increasing average forest age explains why we projected smaller numbers of bird species associated with younger forests in Patchworks relative to the absence of human footprint (including fire suppression) in the NRV scenario. Some bird species associated with younger forests, like Olive-sided Flycatcher, also use habitats that were not modeled in the harvest scenarios (e.g., larch fens, shrublands) (Robertson and Hutto, 2007). For this reason, simulators that also model non-forested vegetation, unlike Patchworks, may provide more realistic projections of habitat available for species such as these.

Previous studies (Bichet et al., 2016; Drever et al., 2019) have quantitatively assessed if conserving or managing habitat for woodland caribou also protects significant habitat for other species. While we did not explicitly test for the role of caribou as an umbrella species for boreal birds in our study, our harvest scenario results suggest that harvest deferral for 20 years within caribou conservation zones does not have large effects on the populations of bird species across the Al-Pac FMA over 50 years. Incidentally, deferral of harvest to benefit caribou in the Al-Pac FMA resulted in more available habitat created or remaining after 50 years for several species associated with older boreal forests. These species included the federally listed Canada Warbler[5] (see footnote 1) and some species of conservation interest in Alberta like Bay-breasted Warbler, Black-throated Green Warbler, and Cape May Warbler (Alberta Environment and Sustainable Resource Development, 2014). Harvest deferral was associated with reductions in two other federally listed species, Olive-sided Flycatcher (678 fewer under PFM after 50 years) and Rusty

TABLE 2 | Initial population size and projected percent change in population of 20 species in the Al-Pac FMA over 50 years, along with projected response of each species, under two scenarios: (1) the Preferred Forest Management Scenario (PFM) that included harvest deferral within caribou habitats; and (2) the Ecosystem-Based Management/Natural Disturbance Model Scenario (EBM) without harvest deferral, relative to the predicted Natural Range of Variation (NRV) in abundance of each species in the absence of human footprint.

		Habitat	Year 0	Percent change over 50 years under different scenarios		Response to	Abundance without	Response to
Group	**Species**	**Association**	**Population**	**With Harvest Deferral**	**Without Harvest Deferral**	**Harvest Deferral**	**Human Footprint**	**Fire in Absence of Harvest**
1	Black-throated Green Warbler	Older mixedwood	191831	9	7	More abundant	139460 (97040–181880)	Less abundant
1	Brown Creeper	Older mixedwood	987151	58	56	More abundant	323171 (236466–409876)	Less abundant
1	Canada Warbler	Older deciduous	343100	36	30	More abundant	162267 (130243–194291)	Less abundant
1	Ovenbird	Mature deciduous	5283326	−1	−1	Less abundant*	2545523 (2211689–2879357)	Less abundant
1	Pileated Woodpecker	Older mixedwood	55783	15	15	More abundant*	47764 (43519–52010)	Less abundant
1	Yellow-bellied Sapsucker	Older mixedwood	518940	15	17	Less abundant*	439581 (402442–476721)	Less abundant
2	Bay-breasted Warbler	Older coniferous	3402974	−6	−7	More abundant	743595 (616602–870588)	Less abundant
2	Blackpoll Warbler	Older coniferous	244752	−47	−44	Less abundant	490169 (396505–583833)	More abundant
2	Boreal Chickadee	Older coniferous	3593580	14	13	More abundant*	2928915 (2582035–3275794)	Less abundant
2	Cape May Warbler	Older coniferous	5526097	20	20	More abundant*	5037696 (4349961–5725431)	Neutral
2	Evening Grosbeak	Older coniferous	59820	20	21	Less abundant	55949 (51346–60552)	Neutral
2	Western Tanager	Older coniferous	1255702	13	12	More abundant*	1185285 (967163–1403406)	Neutral
2	White-winged Crossbill	Older coniferous	523613	2	2	More abundant*	428513 (388198–468828)	Less abundant
3	American Three-toed Woodpecker	Recently burned	64116	43	43	More abundant*	47036 (39765–54306)	Less abundant
3	Black-backed Woodpecker	Recently burned	184205	−48	−47	Less abundant	262288 (197045–327532)	More abundant
3	Northern Flicker	Open forest	253038	7	9	Less abundant	325561 (293678–357444)	More abundant
3	Olive-sided Flycatcher	Recently burned	129364	9	9	Less abundant	117624 (109682–125565)	Less abundant
3	Palm Warbler	Mature black spruce, Bog	3129020	−20	−20	Less abundant*	3461049 (3122518–3799580)	Neutral
3	Rusty Blackbird	Swamp	129599	−7	−3	Less abundant	212237 (176996–247479)	More abundant
3	Western Wood-pewee	Swamp	486388	1	1	Less abundant	557522 (491366–623677)	More abundant

"Increased" or "Decreased*" = less than a 1 per-cent difference in population after 50 years between scenarios with and without harvest deferral for caribou.*

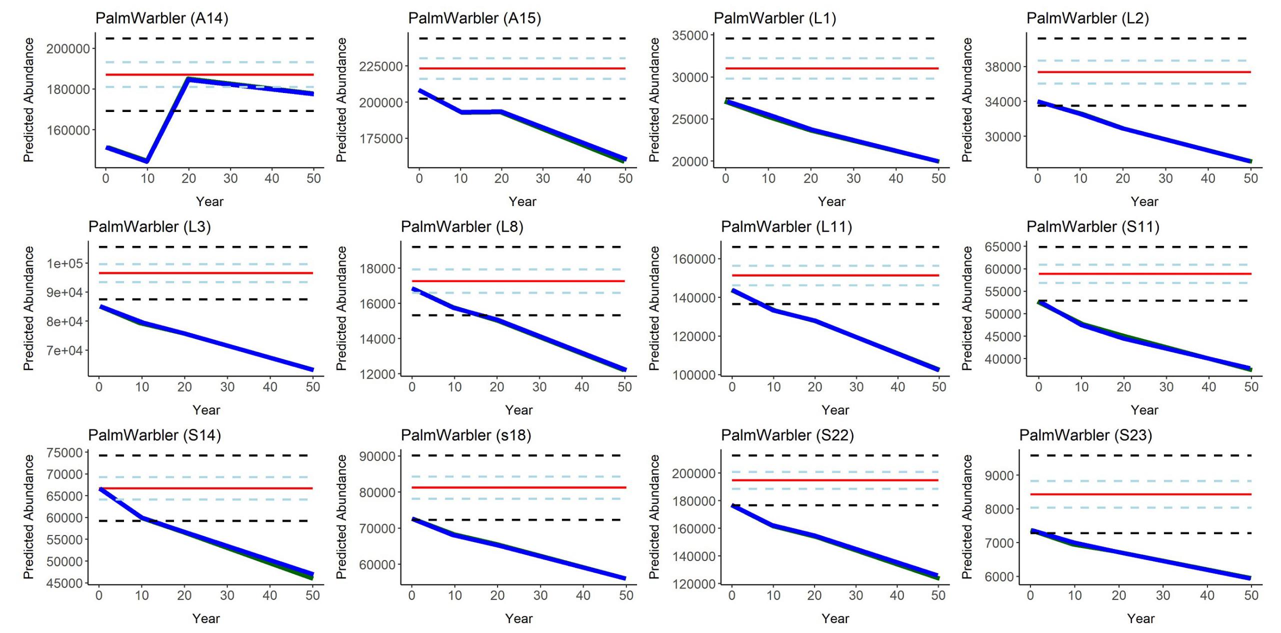

FIGURE 6 | Predicted Palm Warbler abundance over time (year 0-50, where year 0 = 2016) in all 12 Forest Management Units in the Al-Pac Forest Management Area, under two scenarios: (1) the Preferred Forest Management Scenario (PFM) that included harvest deferral within caribou habitats (green line); and (2) the Ecosystem-Based Management/Natural Disturbance Model Scenario (EBM) without harvest deferral (blue), relative to the predicted Natural Range of Variation (NRV) in Palm Warbler abundance in the absence of human footprint. Red line = mean predicted Palm Warbler abundance per Forest Management Unit in the NRV Scenario. Light blue dashed lines = 50% confidence intervals for mean predicted Palm Warbler abundance in the NRV Scenario. Black dashed lines = 95% confidence interval estimates in the NRV Scenario. SDMs predicted that Palm Warbler densities were in black spruce stands 40–80 years old, which are preferred as habitat by woodland caribou but are not harvested by Al-Pac; therefore habitat availability for and projected numbers of Palm Warblers were virtually the same under both Patchworks scenarios. Average black-spruce forest age increased in most FMUs over 50 years in the Patchworks simulations, reducing habitat for Palm Warblers, while simulated fires reduced forest age and increased habitat for these species in the NRV scenario.

Blackbird (4420 fewer under PFM after 50 years), but the percent population change over 50 years was small for both species (<5%). Based on the species we examined, shifting harvest pressure away from landscapes containing preferred caribou habitat does not appear to have large negative consequences for other species at risk and may incidentally benefit some declining birds as well. Additional management actions for those species at risk that do decline under the harvest deferral scenario could be considered within individual F.M.U.s where there is less harvest deferral occurring.

Natural Range of Variation

It may be intuitively surprising to expect average forest age and available habitat for birds associated with older forests to increase under harvest scenarios relative to the absence of human footprint. In addition to harvest, human footprint includes active suppression of fires. Recent fires like the Horse River Fire created many newly initiated forest stands in the Al-Pac FMA in the years just prior to this study. In fact, some of these fires may have been more severe in areas with a long history of fire suppression, due to accumulation of flammable material (Arienti et al., 2006). As a result, the average forest age in the Al-Pac FMA was low relative to other boreal forest regions in Alberta, in Year 0 of the Patchworks and ALCES Online scenarios. Since harvest resets forest age for only a small proportion of the total available forest, forest age will on average increase in the absence of other forest disturbances.

An assumption underlying some harvest scenario results (the projected increases bird species associated with older forests) is that fire suppression by humans is completely successful. If that assumption is unmet (Arienti et al., 2006), then projected increases of many bird species with increasing forest age will be smaller or even turn to decreases. It should also be noted that the NRV scenario was based on current burn rates but burn rates in boreal forests are predicted to increase with climate change in Canada (Bhatti et al., 2003; Krawchuk et al., 2009). Finally, it should be noted that the NRV scenario modeled only one natural disturbance, fire, but other disturbances like droughts, wind-throw, beavers, and insect outbreaks could also affect tree mortality and hence forest age structure and habitat availability for birds (Seidl et al., 2017; Navarro et al., 2018; Cadieux et al., 2020). These disturbances could further reduce habitat for species associated with older forests while creating habitat for other species. Furthermore, these disturbances are also expected to increase with climate change (Seidl et al., 2017; Navarro et al., 2018; Cadieux et al., 2020).

Cumulative Effects

Bird species associated with older forests (Black-throated Green Warbler, Brown Creeper, Canada Warbler, Cape May

TABLE 3 | Initial population size and projected percent change in population of 20 species in the Al-Pac FMA over 50 years under 5 land use scenarios, along with projected response of each species to simulated current fire rates, doubled fire rates, energy sector development without seismic line restoration, and energy sector development with seismic line restoration.

		Habitat	**Year 0**	**Percent change over 50 years under different scenarios**					**General response to**			
Group	**Species**	**Association**	**Population**	**BAU**	**BAU + Seismic Line Restoration**	**No Fire**	**Increased Fire**	**No Energy**	**Current Fire**	**Doubling of Fire**	**Energy Sector Footprint**	**Seismic Line Restoration**
1	Black-throated Green Warbler	Older mixedwood	255002	120	126	166	35	153	Decreased	Decreased	Decreased	Increased
1	Brown Creeper	Older mixedwood	1626827	9	14	35	−10	18	Decreased	Decreased	Decreased	Increased
1	Canada Warbler	Older deciduous	10830	42	50	103	14	77	Decreased	Decreased	Decreased	Increased
1	Ovenbird	Mature deciduous	2662259	−18	−19	−25	−14	−18	Increased	Increased	Decreased*	Decreased
1	Pileated Woodpecker	Older mixedwood	64325	11	13	27	3	13	Decreased	Decreased	Decreased	Increased
1	Yellow-bellied Sapsucker	Older mixedwood	212010	5	7	19	1	12	Decreased	Decreased	Decreased	Increased
2	Bay-breasted Warbler	Older coniferous	13432889	−13	−12	1	−26	−7	Decreased	Decreased	Decreased	Increased*
2	Blackpoll Warbler	Older coniferous	4450882	−10	−9	−53	23	−16	Increased	Increased	Increased	Increased*
2	Boreal Chickadee	Older coniferous	470621	−10	−10	−6	−14	−5	Decreased	Decreased	Decreased	Increased
2	Cape May Warbler	Older coniferous	1434837	68	68	95	44	79	Decreased	Decreased	Decreased	Increased*
2	Evening Grosbeak	Older coniferous	20348	3	6	16	−3	13	Decreased	Decreased	Decreased	Increased
2	Western Tanager	Older coniferous	338690	20	26	39	−6	76	Decreased	Decreased	Decreased	Increased
2	White-winged Crossbill	Older coniferous	416798	−5	−5	0	−12	−16	Decreased	Decreased	Increased	Decreased*
3	American Three-toed Woodpecker	Recently burned	70889	126	125	169	94	131	Decreased	Decreased	Decreased	Decreased*
3	Black-backed Woodpecker	Recently burned	149654	42	38	30	64	4	Increased	Increased	Increased	Decreased
3	Northern Flicker	Open forest	105020	19	18	17	22	22	Increased	Increased	Decreased	Decreased
3	Olive-sided Flycatcher	Recently burned	53166	6	7	9	5	13	Decreased	Decreased	Decreased	Increased*
3	Palm Warbler	Mature black spruce, Bog	1008685	−19	−19	−38	−5	−19	Increased	Increased	Decreased*	Increased*
3	Rusty Blackbird	Swamp	7877	−42	−42	−65	−8	−33	Increased	Increased	Increased	No change
3	Western Wood-pewee	Swamp	73514	5	5	5	0	10	No Change	Decreased	Decreased	No change

"Increased" or "Decreased*" = less than a 1 per-cent difference in population after 50 years between scenarios with and without a particular disturbance. All scenarios share the same amount and locations of harvest disturbances. "Al-Pac BAU" assumes that some forest habitat is either set back by fire or converted to other land uses by energy sector development but also by agriculture and urbanization. "Seismic restoration" assumes the same amount and location of fire, harvest, and non-forestry footprint as "Al-Pac BAU," but also assumes that seismic lines are successfully reclaimed and start regenerating to forests. "No Fire" assumes that no future forests are burned by fire, but levels of conversion to non-forest habitats are the same as in "Al-Pac BAU". "No Energy" assumes that no new energy sector development occurs, but levels of fire and conversion to other non-forest habitats are the same as in "Al-Pac BAU." "Increased Fire" assumes that the same amount of forest habitat is converted to other land uses like energy sector development, agriculture, and urbanization as "Al-Pac BAU," but twice the amount of forest is burned each decade, reducing older forests relative to "Al-Pac BAU."*

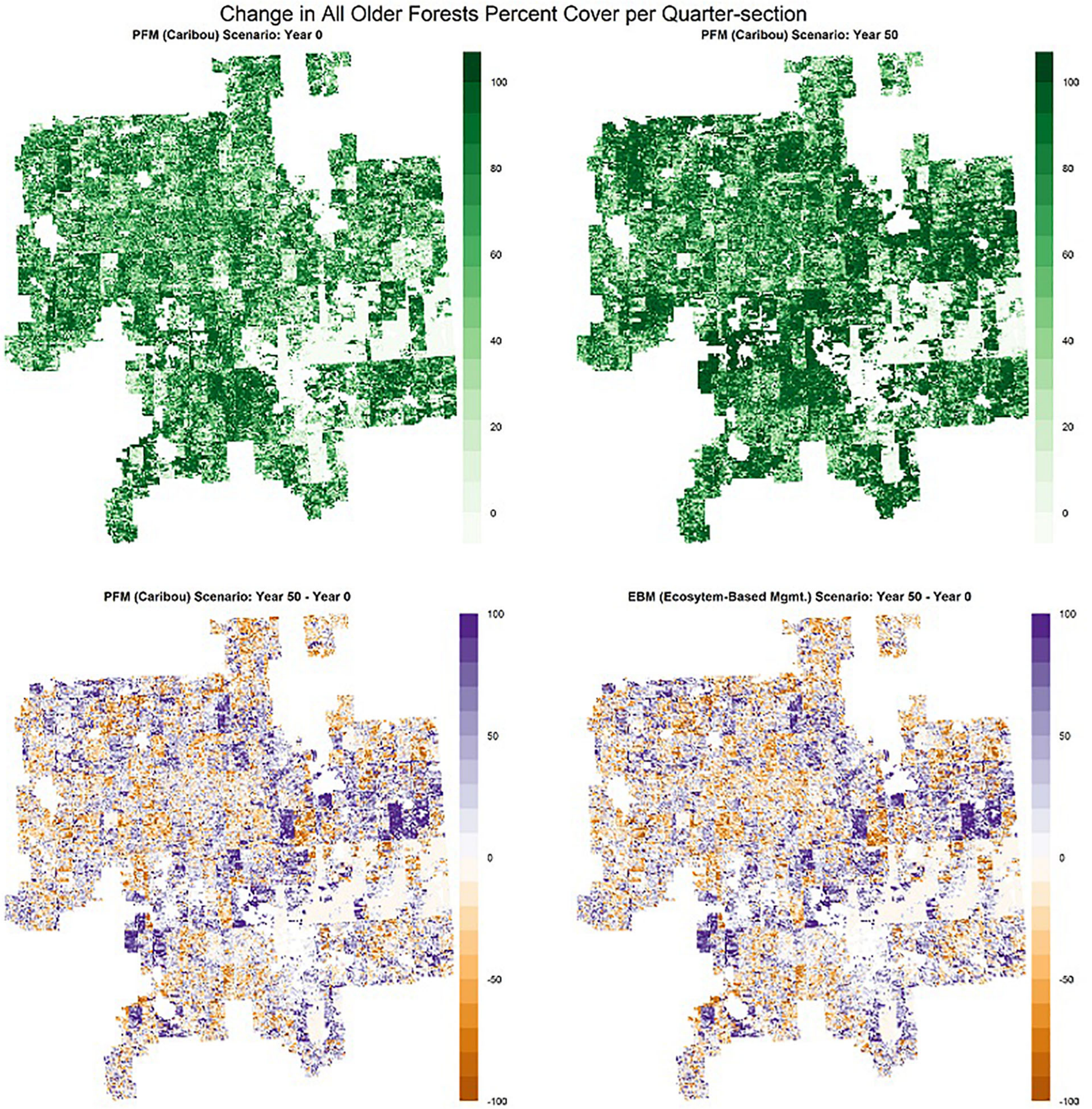

FIGURE 7 | Distribution of all older forests (deciduous and mixed-wood forest stands > 60 years old and black spruce, pine, and white-spruce stands > 80 years old, regardless of origin from fires or harvest) in the Al-Pac Forest Management Area (FMA): (1) mean percent cover per quarter-section by all older forests in Year 0 of the Preferred Forest Management (PFM) scenario that included harvest deferral within caribou habitats **(top left)**; (2) mean percent cover per quarter-section by all older forests in Year 50 of the PFM scenario **(top right)**; (3) change in mean percent cover per quarter-section by all older forests over 50 years under the PFM scenario **(bottom left)**; (4) change in mean percent cover per quarter-section by all older forests over 50 years under the Ecosystem-Based Management/Natural Disturbance Model (EBM) scenario without harvest deferral **(bottom right)**. The increase in percent cover of older forests over time was dominated by increases in older black spruce and pine.

Warbler) generally increased over 50 years in both the Patchworks and ALCES Online scenarios emphasizing that the forest age still increased over time throughout the Al-Pac FMA in the cumulative effect scenarios. However, fire and energy sector development generally reduced habitat for these species, resulting in smaller projected increases relative to the "No Fire" and "No Energy" scenarios. Forest disturbance by energy sector development in northeastern Alberta is substantial: in years prior to the global economic downturn of 2008 it was even comparable to the amount of harvest by the forestry sector (Schneider and Dyer, 2006; Brownsey and Rainer, 2009).

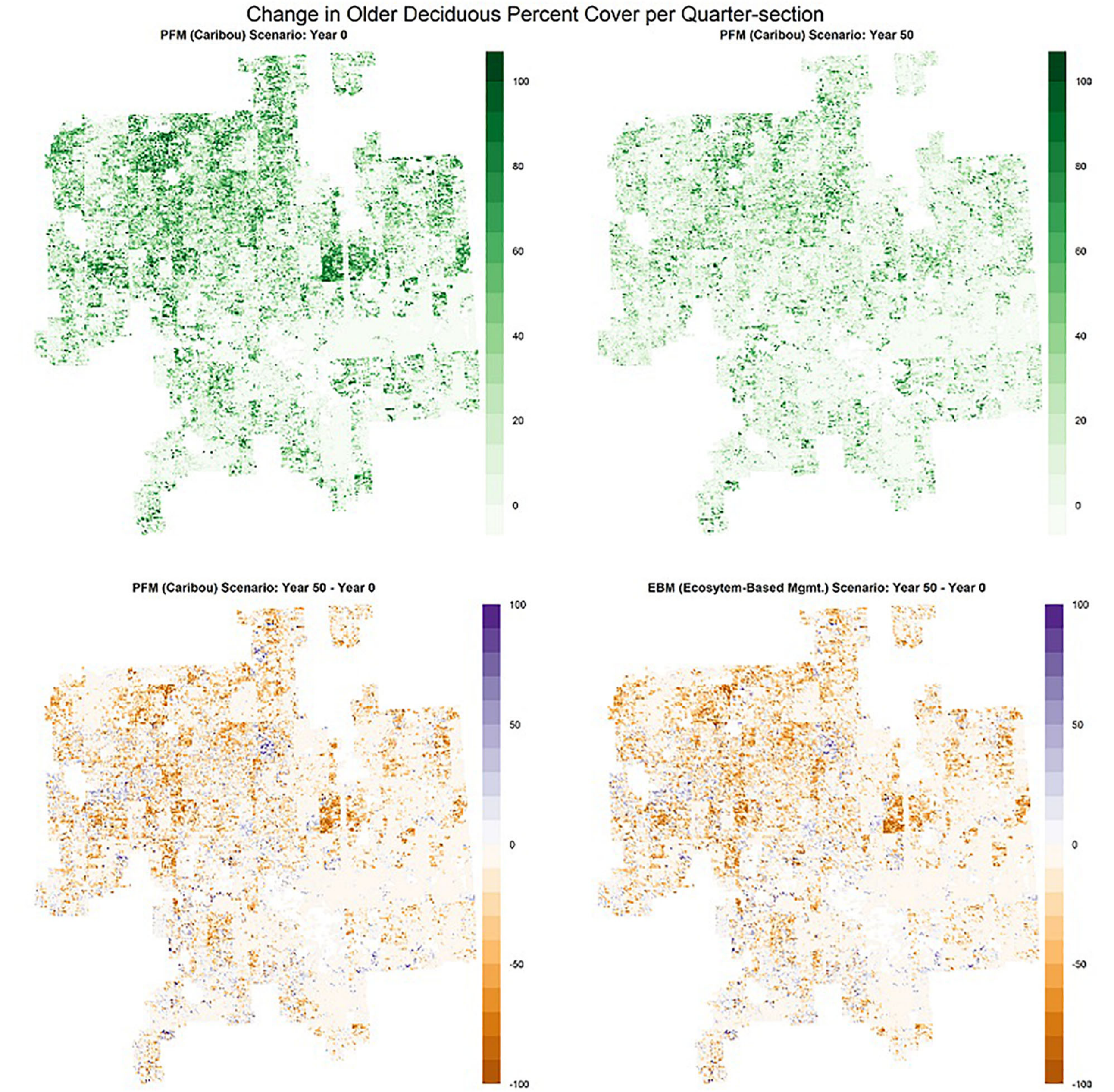

FIGURE 8 | Distribution of all deciduous forest stands > 60 years old, regardless of origin from fires or harvest, in the Al-Pac Forest Management Area (FMA): (1) mean percent cover per quarter-section by older deciduous forests in Year 0 of the Preferred Forest Management (PFM) scenario that included harvest deferral within caribou habitats **(top left)**; (2) mean percent cover per quarter-section by older deciduous forests in Year 50 of the PFM scenario **(top right)**; (3) change in mean percent cover per quarter-section by older deciduous forests over 50 years under the PFM scenario **(bottom left)**; (4) change in mean percent cover per quarter-section by older deciduous forests over 50 years under the Ecosystem-Based Management/Natural Disturbance Model (EBM) scenario without harvest deferral **(bottom right)**. The amount of older deciduous forests in some areas with larger concentrations was strongly reduced over 50 years in both scenarios, but new forests > 60 years old developed from cutblocks harvested prior to Year 0.

Surprisingly, fire and energy sector development also reduced habitat for Olive-sided Flycatchers in the NRV and ALCES Online scenarios, despite the species' preference for younger forest stands, burns, shrublands, and open lands as habitat (Robertson and Hutto, 2007). However, the negative response of Olive-sided Flycatchers to fire was small relative to species associated with older forests. Doubling the burn rate reduced the population growth rate of this species relative to the "Al-Pac BAU scenario) from 6% to 5% while a scenario lacking fire had 9% population growth. Since this species nests in coniferous trees, which had a higher burn probability in the scenarios, the simulated fires might have reduced some nesting habitat for

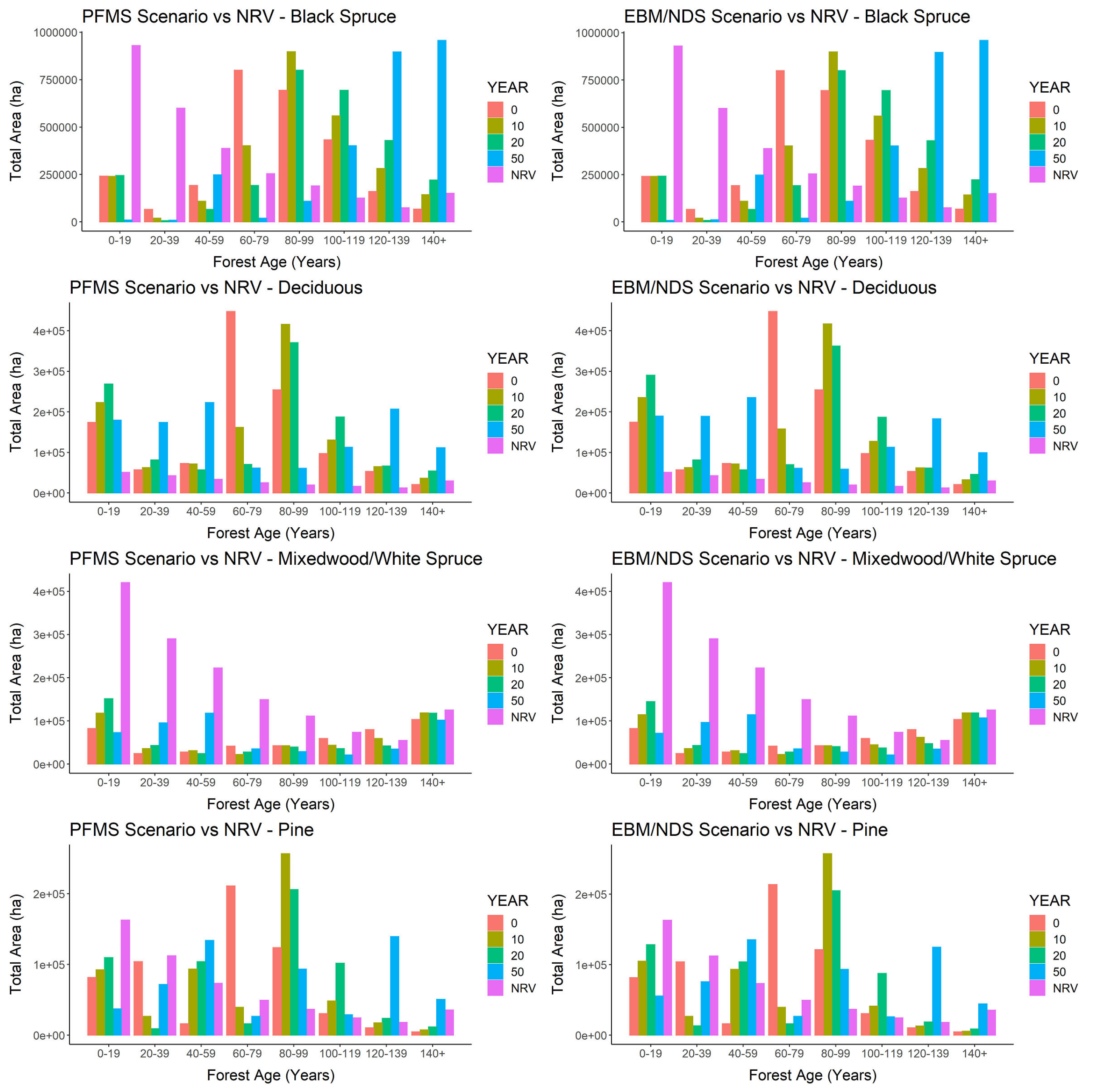

FIGURE 9 | Predicted amounts of different forest age-classes over time (year 0–50, where year 0 = 2016) totaled for the Al-Pac Forest Management Area, under two scenarios: (1) the Preferred Forest Management (PFM) scenario that included harvest deferral within caribou habitats (green line); and (2) the Ecosystem-Based Management/Natural Disturbance Model (EBM) scenario without harvest deferral (blue), relative to the median amount of those forest age-classes predicted from the Natural Range of Variation (NRV) Scenario in the absence of human footprint. (1) Forest types 0–9 and 10–19 years old were treated separately when predicting bird abundance but were combined to simplify display in these plots; (2) Mixed-wood and white spruce were treated separately when predicting bird abundance in the Patchworks scenarios but were combined in these plots for comparison against the NRV Scenario. The reason for doing so is that so little pure white spruce occurred in simulations of the NRV Scenario that white spruce was treated as older mixed-wood forests when predicting bird density.

this species even while theoretically creating more open habitat for this species.

Another surprising result was that Ovenbird responded positively to a higher fire rate, which was contrary to the species' lower abundance in the NRV scenario which also incorporated fire. Ovenbirds are associated with mature rather than old deciduous and mixed-wood forests and it is possible that simulated rates of fire in the ALCES Online scenarios created enough new suitable habitat over 50 years for Ovenbirds to exhibit a positive fire response. In contrast, the NRV scenario simulated rates of fire over 1000 years, which may have been long enough for fires to reduce the amount of suitable habitat

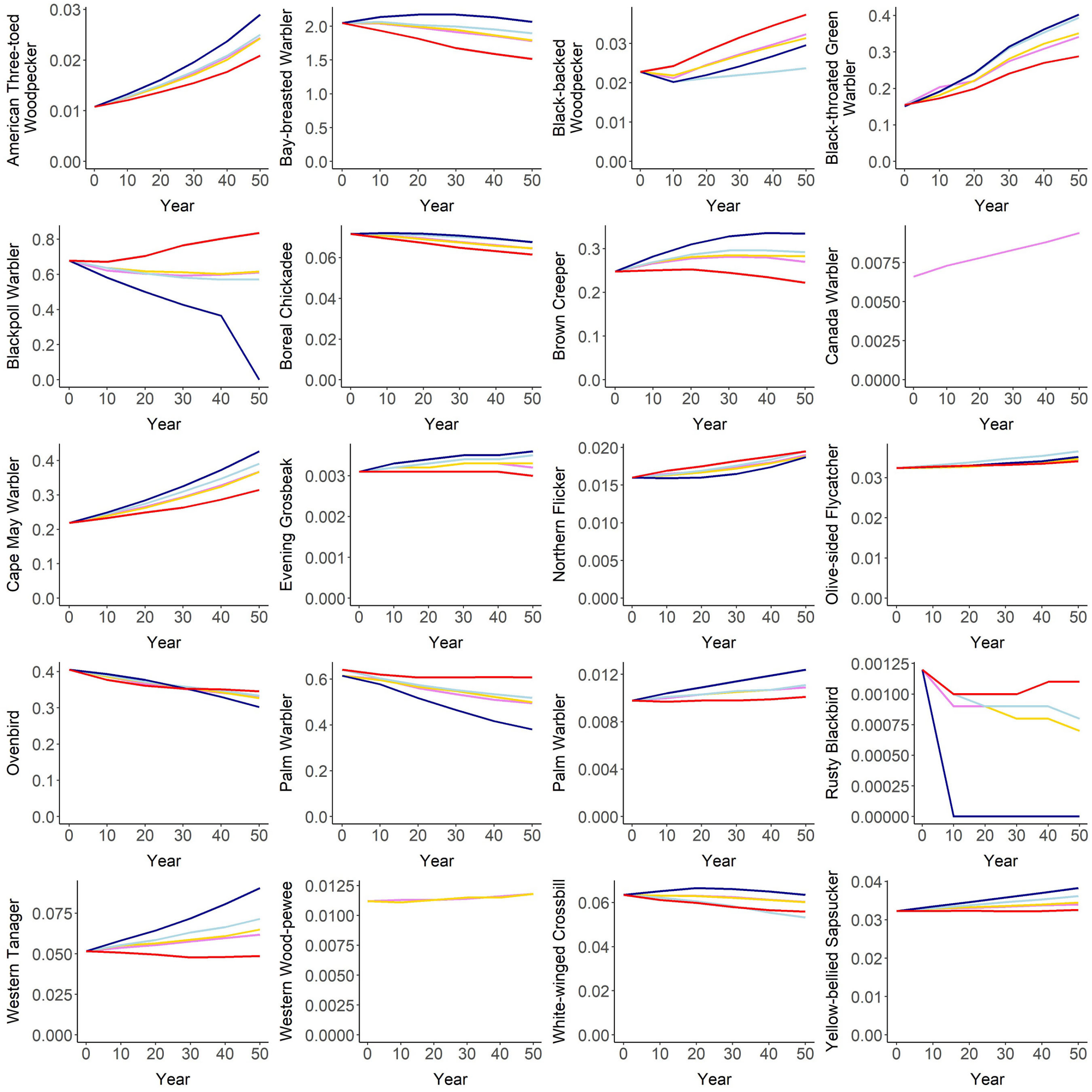

FIGURE 10 | Projected mean density (# males/ha) of 20 species in the Al-Pac Forest Management Area (FMA) over 50 years under 5 land use scenarios. Projected population size can be calculated by multiplying mean density by the number of hectares in the Al-Pac FMA (6,563,755). All scenarios share the same amount and locations of harvest disturbances. “Al-Pac BAU” (violet line) assumes that some forest habitat is either set back by fire or converted to other land uses by energy sector development but also by agriculture and urbanization. “Seismic Restoration” (gold line) assumes the same amount and location of fire, harvest, and non-forestry footprint as “Al-Pac BAU,” but also assumes that seismic lines are successfully reclaimed and start regenerating to forests. “No Fire” (dark blue line) assumes that no future forests are burned by fire, but levels of conversion to non-forest habitats are the same as in “Al-Pac BAU”. “No Energy” (light blue line) assumes that no new energy sector development occurs, but levels of fire and conversion to other non-forest habitats are the same as in “Al-Pac BAU.” “Increased Fire” (red line) assumes that the same amount of forest habitat is converted to other land uses like energy sector development, agriculture, and urbanization as “Al-Pac BAU,” but twice the amount of forest is burned each decade, reducing older forests relative to “Al-Pac BAU”. Generally as the amount of simulated disturbance increases from least (“No Energy,” “No Fire”) to most (“Increased Fire), species associated with older forests are more likely to decline or less likely to increase, while species associated with younger or mature forests are more likely to increase or less likely to decrease.

available on average to Ovenbirds. This incidental result suggests the importance of considering temporal scale when simulating cumulative effects on boreal birds.

When projecting future populations of species, the assumptions underlying forest disturbance, regrowth, and age matter greatly. Due to the assumptions underlying the

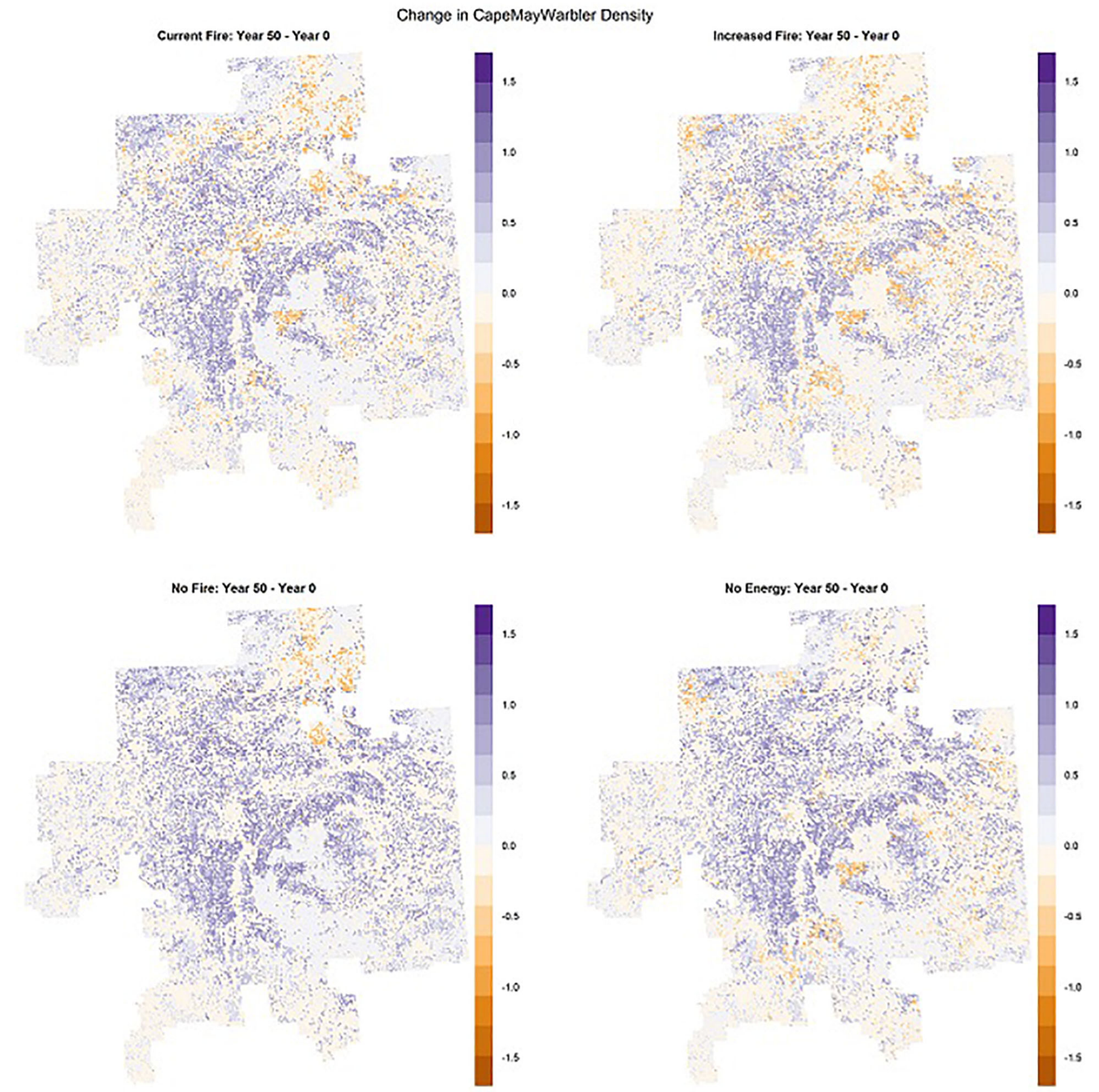

FIGURE 11 | Mean density (#birds/ha) and distribution of Cape May Warbler – a songbird that responded negatively to fire and energy sector development - in the Al-Pac Forest Management Area (FMA) under four cumulative effects scenarios in ALCES Online: (1) harvest from the Preferred Forest Management (PFM) scenario + current burn rate + moderate energy sector development over 50 years ("Al-Pac BAU" scenario) **(top left)**; (2) harvest from the PFM scenario + 2*current burn rate + moderate energy sector development over 50 years ("Increased Fire" scenario) **(top right)**; (3) harvest from the PFM scenario + no fire + moderate energy sector development over 50 years ("No Fire" scenario) **(bottom left)**; (4) harvest from the PFM scenario + current burn rate + no energy sector development over 50 years ("No Energy" scenario) **(bottom right)**.

harvest and cumulative effects scenarios, forests aged over time in the simulations and so habitat increased for bird species of older forests in our harvest scenarios. Although most species increased during the 50-year simulation period, the negative effect of a higher fire rate suggests that population declines could occur if anthropogenic climate change in Alberta's boreal forests results in more area burned than what we simulated (Bhatti et al., 2003; Krawchuk et al., 2009). Given that forest fire suppression is imperfect (Arienti et al., 2006), forest fires are likely to increase in the future in Alberta. Further, tree species successfully regenerate at different rates after fires (Lieffers et al., 2003; Johnstone et al., 2010) and different kinds of harvest

(Montoro Girona et al., 2017, 2018, 2019), so future simulation modeling efforts will need to account for differing levels and additional impacts of forest fires and other climate factors (e.g., increased drought) on stand replacement and habitat available to boreal birds (Cadieux et al., 2020). Exception for the higher fire rate scenario, we did not explicitly model climate change in our ALCES Online scenarios, which occurred over a shorter time frame than in Cadieux et al. (2020). The negative effect of doubling the amount of fire on the species we analyzed was consistent with negative population projections of boreal songbird species in other studies (Mahon et al., 2014; Stralberg et al., 2015; Cadieux et al., 2020).

Increases in non-forestry footprint, due mainly to the energy sector, were associated with larger reductions of bird species associated with older boreal forests, consistent with a previous study (Bayne et al., 2016). Some energy sector footprints like seismic lines are intended to be temporary and left to regenerate to forest, although regeneration has been variable along seismic lines in boreal forests (Lee and Boutin, 2006). The "Seismic Restoration" scenario created habitat for some federally or provincially listed species (66294 Bay-breasted Warblers, 16245 more Black-throated Green Warblers, 81555 more Brown Creepers, 820 more Canada Warblers, and 328 more Olive-sided Flycatchers) in the Al-Pac FMA over 50 years. Seismic restoration is one strategy being explored for improving woodland caribou habitat (Bentham and Coupal, 2015; Kansas et al., 2015). Our results suggest that just as deferral of harvest to benefit caribou did not have strong negative effects on boreal birds, restoring habitat for woodland caribou incidentally may have positive effects for some declining boreal bird species as well.

In theory, we could have tried to use one simulator to model all disturbances. ALCES Online can already do this for harvest, fire, non-forestry footprint. Another program, LANDIS-II, has been used to simulate multiple forest disturbance types like harvest, fire, windthrow, and insect outbreaks in many wildlife studies (e.g., Cadieux et al., 2020). However, these simulators do not yet account for many of the factors (e.g., socioeconomic) that must be considered in harvest plans, whereas Patchworks does. Similarly, Patchworks can now account for other disturbance types besides harvest, but these other disturbance types are not usually of interest to forestry companies, and simulators like ALCES Online are more versatile in modeling multiple disturbance types. ALCES Online can be used to remove human footprint from landscapes to simulate a lack of human footprint as in the NRV scenario; however, the NRV scenario simulator that we ran based on LANDMINE gave us estimates of uncertainty in habitat amounts, which allowed us to estimate uncertainty in bird abundance in the absence of human footprint.

CONCLUSION

This study is one of the first attempts to predict abundance of bird species under two harvest plans in response to habitat management for another species, and to compare those predictions with the likely NRV in those species' numbers in the absence of harvest, as well as with the presence of other human footprint in a northeastern Alberta landscape. By regulation, forestry companies develop forestry harvest plans in the absence of input and knowledge of activities from other industrial sectors in Alberta, because government oversight of industries is sector by sector and integrated land management is still uncommon (Kennett, 2006). In the case of forestry, forest management plans are updated every 10 years, thus allowing for the accounting of needs for both the forestry sector and wildlife such as caribou and boreal birds. Harvest scheduling software like Patchworks, when linked with wildlife SDMs, can be used to project the impact of strategic harvest plans on wildlife. In our study, we found that deferring harvest for 20 years in merchantable forest stands embedded within preferred caribou harvest was unlikely to adversely affect overall populations of boreal bird species associated with those stand types. These projections can make sense in the short-term because the location and extent of other industrial footprints are uncertain. However, given that substantial amounts of forest habitat can be removed by increases in fire (Bhatti et al., 2003; Krawchuk et al., 2009) and non-forestry sectors (Schneider and Dyer, 2006; Brownsey and Rainer, 2009), accounting for these additional non-forestry disturbances and sources of potential habitat loss is needed to evaluate fully how species could respond over the long term to "all" forms of disturbance. We found that inclusion of fire and energy sector development in addition to forestry led to lower habitat projections for most species that we analyzed, and that restoring energy sector footprint (seismic lines) to benefit caribou also benefited bird species. By projecting species abundance under a range of scenarios involving multiple industrial sectors and natural disturbance, cumulative effects simulators could facilitate future integrated landscape management for wildlife in Alberta.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation, to any qualified researcher.

AUTHOR CONTRIBUTIONS

LL developed the manuscript, figures, and appendix, created three ALCES Online scenarios modified from the baseline scenario created by MC, and generated predictions of bird species abundance for the Patchworks, NRV, and ALCES Online scenarios in this manuscript. EB and ED helped conceive the overall study design and edited the manuscript. PS developed the bird species distribution models used to make predictions in this manuscript, developed the cure4insect package in R for generating predictions from GIS outputs, and edited the manuscript. TM developed the Patchworks scenarios and simulations and edited this manuscript. DA developed the NRV scenario and simulation and edited this manuscript. DC edited this manuscript. MC developed the baseline ALCES Online scenario and Seismic Restoration scenario and simulations in this manuscript and edited this manuscript. All the authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00252/full#supplementary-material

APPENDIX I | Projected changes in 20 boreal bird species and multiple forest age classes over 50 years, based on the resulting forest age-structure over time from the Patchworks and NRV scenarios described in this paper. R project scripts are available online at https://github.com/borealbirds/Patchworks-NRV-cure4insect for readers to generate projections for other bird species from the raw data (habitat summaries per quarter-section for both the Patchworks and NRV scenarios), using model coefficients stored in the cure4insect package.

APPENDIX II | Projected changes in multiple forest age classes over 50 years, based on the resulting forest age-structure over time from the Patchworks and NRV scenarios described in this paper.

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Climate Change Is Likely to Alter Future Wolf – Moose – Forest Interactions at Isle Royale National Park, United States

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We evaluated how climate change and variable rates of moose browsing intensity, as they relate to wolf predation, might affect the forests of Isle Royale National Park, Michigan, United States by conducting a modeling experiment. The experiment consisted of contrasting three different scenarios of wolf management and with a static (current conditions) and changing climate (high emissions). Our results indicate that the interactive effects of wolf predation and climate change are likely to be temporally variable and dependent on biogeographic and forest successional processes. During the first 50 years of 120-year simulations, when the effects of climate change were less impactful, higher simulated rates of predation by wolves reduced moose population densities, resulting in greater forest biomass and higher carrying capacities for moose. However, over the longer term, early successional and highly palatable aspen and birch forests transitioned to late successional spruce and fir forests, regardless of climate or predation intensity. After 50 years, the effects of climate change and predation were driven by effects on balsam fir, a late successional conifer species that is fed on by moose. High-intensity predation of moose allowed balsam fir to persist over the long term but only under the static climate scenario. The climate change scenario caused a reduction in balsam fir and the other boreal species that moose currently feed on, and the few temperate species found on this isolated island were unable to compensate for such reductions, causing strong declines in total forest biomass. The direct effects of moose population management via reintroduction of wolves may become increasingly ineffective as the climate continues to warm because the productivity of boreal plant species may not be sufficient to support a moose population, and the isolation of the island from mainland temperate tree species may reduce the likelihood of compensatory species migrations.

Keywords: balsam fir, climate change, moose, trophic cascade, wolf

INTRODUCTION

Today's natural resource management agencies are tasked with anticipating how the effects of their decisions are likely to play out over the long term in the face of climate change. Near-term solutions to some environmental problems could range from counterproductive to ineffective to critically important as time passes and the climate warms. For example, most large mammalian herbivore populations (e.g., moose, elk, and deer) experience some form of population management given their iconic stature and/or importance for recreational and subsistence hunting (Danell et al., 2006). These animals can also alter the structure and function of ecosystems by preferentially foraging on some plant species and avoiding others (Hobbs, 1996; Pastor and Danell, 2003). Consequently, management agencies often use a variety of techniques to locally reduce herbivore populations (e.g., re-introducing predators or conducting controlled harvests) when their populations grow large enough to affect forest resources in ways that cause conflicts with other land management objectives (Demarais et al., 2012). While such actions can have important effects on the plant communities that these animal populations rely on (Terborgh et al., 1999; Ripple and Beschta, 2012), so too can climate change (Iverson et al., 2008). Will population management actions continue to be effective as the climate warms? Will population management actions become increasingly important? More generally, will the ecosystems that currently support large mammalian herbivore populations continue to do so in the future, with or without population management?

These are some of the questions facing the U.S. National Park Service (NPS) as they begin to manage the moose population of Isle Royale National Park via the reintroduction of wolves. Moose and wolves have co-existed at Isle Royale since at least the 1940s (Murie, 1934; Allen, 1993; Peterson and Page, 1988). For about the past 50 years, the moose population has generally fluctuated between 1 and 2 per square kilometers (km^2) (500–1200 individuals) while the wolf population has fluctuated between 25 and 50 per 1000 km^2 (15–30 individuals) (Peterson et al., 2014). However, inbreeding depression among wolves began to take its toll on the wolf population beginning in the early 2000s (Vucetich et al., 2012), reducing the population to just a lone pair by 2017. Following several years of increasing moose population density and a multi-year environmental impact assessment (National Park Service [NPS], 2017), the NPS began re-introducing wolves during the winter of 2018–2019. There are currently 17 wolves on the island and the goal of the project is to bring the population up to a total of 20–30 animals. The primary purpose of wolf re-introduction was to reduce the growing moose population and its effects to the forest ecosystem (National Park Service [NPS], 2017). Although the decision to re-introduce wolves to Isle Royale was made with some consideration of the effects of climate change (Fisichelli et al., 2013), there have been no systematic studies of the projected effects of climate change on the vegetation of Isle Royale, or how climate change might interact with moose browsing to alter forest dynamics. This is despite recognition that the island is already being exposed to significant climate changes (Monahan and Fisichelli, 2014). It is therefore unclear what the long-term effects of wolf re-introduction might be as the climate warms and the vegetation of Isle Royale responds to it.

Most of the forested area of Isle Royale is in boreal hardwood (∼35%) and boreal conifer (∼40%) cover (**Figure 1**; The Nature Conservancy [TNC], 1999). Moose browsing has been shown to accelerate forest succession from the shade intolerant and rapidly growing hardwood species such as paper birch (*Betula papyrifera*) and quaking aspen (*Populus tremuloides*) to the more shade tolerant and slower growing conifer species such as white and black spruce (*Picea glauca* and *P. mariana*) because moose preferentially feed on the former and avoid the latter (Snyder and Janke, 1976; McInnes et al., 1992). In most North American boreal forests, balsam fir (*Abies balsamea*) is also associated with later successional spruce-fir forests (Bergeron, 2000). But at Isle Royale, moose heavily feed on balsam fir during the winter, reducing its abundance in boreal conifer forests (Brandner et al., 1990). In areas that have received very high annual rates of moose browsing, moose-spruce-savannahs have emerged following the loss of nearly all woody plant species, except for unbrowsed spruce (Rotter and Rebertus, 2015). The remaining forest cover of Isle Royale is composed of species more frequently associated with temperate forests. Northern hardwood species such as sugar maple (*Acer saccharum*) and yellow birch (*B. alleghaniensis*) are locally abundant on the western end of Isle Royale but make up only 10% of the total forest area of the island, while northern conifer forests (northern white-cedar (*Thuja occidentalis*) make up the remaining 15% or so of total forest area (**Figure 1**; The Nature Conservancy [TNC], 1999). These communities are dominated by long-lived species, often typical of late-successional old-growth temperate forests, but moose feed on all of them. As a result, heavy browsing may slow the rate of forest succession to these communities depending on browsing intensity (Sell, 2007).

Isle Royale National Park is situated in the North American temperate – boreal forest transition zone (Goldblum and Rigg, 2010) and is therefore thought to be highly susceptible to effects of climate change (Fisichelli et al., 2013). Both the boreal and temperate tree communities found there are growing near their southern and northern range limits, respectively, and are therefore considered to be sensitive to changes in temperature and/or precipitation (Fritts, 1976; Reich and Oleksyn, 2008). The upper Midwest region has shown an upward trend in mean minimum, mean maximum, and mean temperature in all seasons from 1901–2011 (Handler et al., 2013. Future projections for the twenty-first century indicate upward trends in temperature for the Midwest between 2.8 and 4.9 degrees Celsius (°C) by the end of the century, depending on emissions scenario (Intergovernmental Panel on Climate Change [IPCC], 2007; Gonzalez et al., 2010; Kunkel et al., 2013). Further, a recent examination of temperature trends at Isle Royale National Park showed similar trends in both annual mean temperature and mean temperature during the warmest quarter (summer months) as found for mainland areas (Monahan and Fisichelli, 2014). While projected changes in precipitation are more variable, a general decrease in precipitation is projected for high emissions scenarios in the upper Midwestern U.S. summer months after 2050 (Stoner et al., 2012). Current measurements of greenhouse

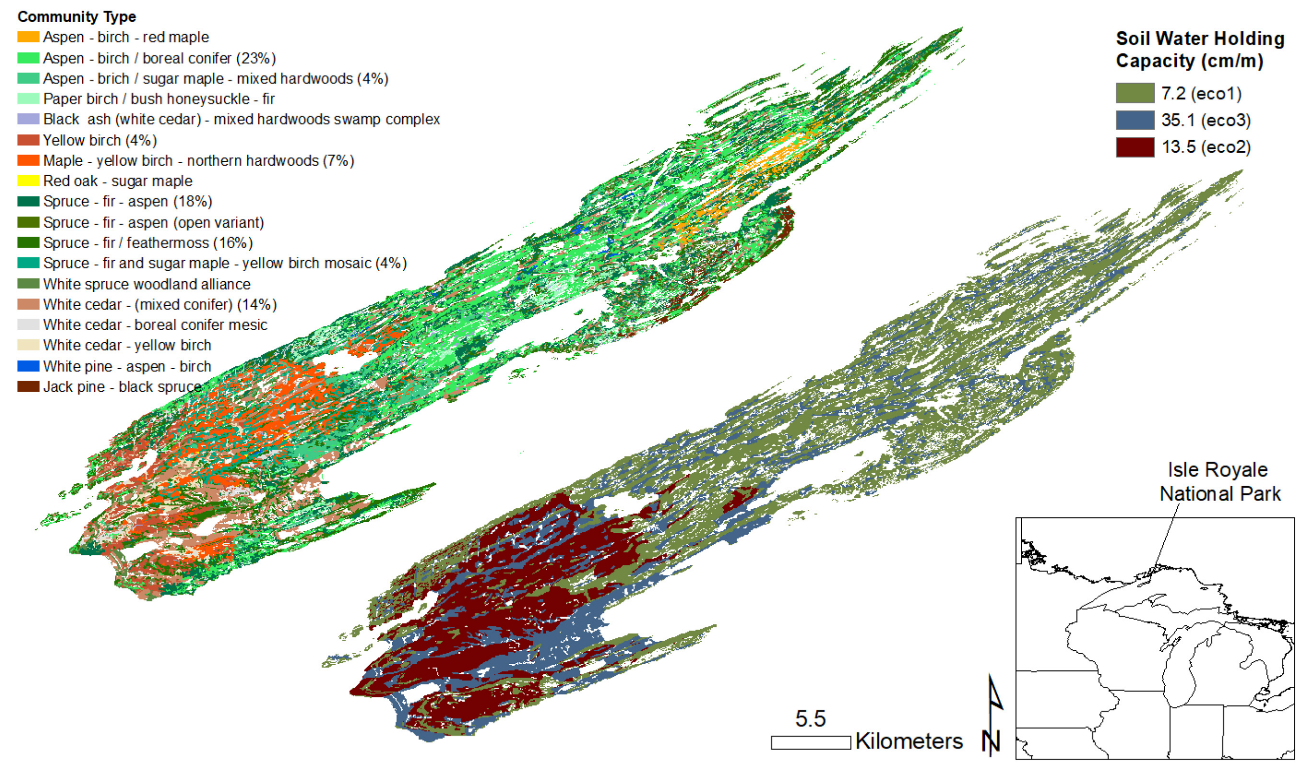

FIGURE 1 | Forest community types and soil water holding capacity representing initial conditions (c. 2006) at Isle Royale National Park. Percentage of total forest cover is provided for forest communities making up greater than 3% total forest cover. Forest plot data were imputed into the areas of similar forest community types to create the initial age and species distribution maps for modeling. Soil water holding capacity was used to delineate ecoregions, which influence rates of species establishment and growth.

gas emissions have been near the highest projected emissions scenario (A1FI) (Intergovernmental Panel on Climate Change [IPCC], 2007; Peters et al., 2012) and recent modeling studies indicate that the associated projected changes in temperature and precipitation for nearby northeastern Minnesota are sufficient to cause reductions in the establishment and growth rates of boreal tree species (e.g., spruce, fir, aspen, and birch), with less negative effects and some positive effects of climate change on a suite of temperate deciduous species [e.g., sugar maple, yellow birch, red maple (*Acer rubrum*), and red oak (*Quercus rubra*)] (Duveneck et al., 2014a). These results indicate that northern hardwood forests could begin to replace the boreal forests across Isle Royale. However, other studies also conducted in nearby northern Minnesota have shown that the negative effects of herbivory on the growth of temperate forest species could offset any positive effects of increasing temperatures, limiting the ability of temperate species to replace boreal species (Fisichelli et al., 2012). Furthermore, temperate species currently have a limited distribution at Isle Royale, and it is possible that the negative effects of climate change on boreal forests will outpace rates of dispersal by temperate species (Sanders and Grochowski, 2013). In either case, rather than simply experiencing a shift in the distribution of forest community types, Isle Royale could experience significant reductions in both forest productivity and biodiversity, and/or develop novel plant communities, with potentially significant implications for the ability of the landscape to support a moose population over the long term.

This study builds from earlier modeling studies to better understand and project the future forests of Isle Royale National Park under different scenarios of wolf management (De Jager et al., 2017b) and with projected effects of climate change on tree species establishment and growth rates (Duveneck et al., 2014a,b; Duveneck and Scheller, 2015a,b). While these previous modeling studies have examined effects of moose browsing and climate change independent of each other, the present study is the first to examine how they may interact with each other. Our objectives were to evaluate how climate change and variable rates of moose browsing intensity, as they relate to wolf predation, may affect the forests of Isle Royale National Park. We specifically addressed the following questions: (1) How does predation by wolves influence moose population dynamics and the effect of moose browsing on patterns of forest succession and productivity with and without climate change? (2) Are northern hardwood forests able to replace boreal forests as the climate warms and does this phenomenon depend on rates of wolf predation? (3) In general, can Isle Royale support both a healthy forest and a moose population over the long-term in the face of climate change, and how much does the answer depend on the rate of predation by wolves?

MATERIALS AND METHODS

Study Area

Isle Royale is an archipelago in the northwestern part of Lake Superior (**Figure 1**). The main island is ∼24 kilometers (km) from the shore of northeastern Minnesota, USA and southern Ontario, Canada, and is ∼534 km^2. The island has a distinct ridge and valley topography that reflects the angle of the most recent glacial stage [∼11,000 years before present (bp)]. De Jager et al. (2017a) recently characterized major differences in soils across the island, important for structuring vegetation communities. These differences were represented by calculating soil water holding capacity (SWHC) in units of centimeters per meter (cm/m) within 1 meter (m) of soil depth (Web Soil Survey, 2011). The data were then grouped into three zones of relatively homogeneous SWHC: thin soils over bedrock with low SWHC (mean of 7.2 cm/m), deeper soils (mean SWHC of 13.5 cm/m), and alluvial soils with high SWHC (mean of 35.1 cm/m). The climate of Isle Royale is similar to that of northeastern Minnesota, with mean daily high temperatures in summer (June, July, and August) of ∼20–21°C and mean daily high temperatures in winter (December, January, February) near -3°C. A recent assessment of climate change exposure for the U.S. National Parks found upward trends in mean annual temperature and mean temperature during summer for Isle Royale and other midwestern National Parks (Monahan and Fisichelli, 2014). Thus, Isle Royale, like the nearby mainland, is already experiencing significant climate change. Local observations indicate that there may be a gradient in temperature from the interior of the island to the shore of Lake Superior during summer. However, gridded climate data (PRISM, Daly and Gibson, 2002) described very little spatial variability in temperature or precipitation across the island. We therefore considered the entire island to be a single climate zone and developed an ecoregional geographic information system (GIS) coverage (50-m cell size) based on SWHC alone (**Figure 1**). This ecoregional coverage influences the potential establishment and growth rates of different tree species as described below (see "Landscape Simulation Modeling").

The vegetation of Isle Royale is characteristic of the temperate-boreal forest transition zone (Goldblum and Rigg, 2010; Sanders and Grochowski, 2013). For this study, we used a map of the vegetation communities developed in the late 1990s (The Nature Conservancy [TNC], 1999), which included 18 different plant community assemblages (**Figure 1**). The most abundant communities across the main island were Aspen-birch/boreal conifer forests (21%), spruce-fir-aspen forest (16%), spruce-fir/feathermoss forest 15%, white cedar- (mixed conifer)/alder swamp (13%), maple – yellow birch -northern hardwoods forest (7%). Although some communities were relatively rare (e.g., red oak – sugar maple forest, < 1%) we included them given their potential to expand under climate change. The species composition of forest inventory plots was then used to match each mapped forest community type with multiple forest inventory plots collected for the U.S. Forest Service Forest Inventory and Analysis (FIA) (Woudenberg et al., 2010) and the inventory plots were randomly imputed within each matched forest community type to develop a GIS coverage (50-m cell size) as described in previous modeling studies (e.g., De Jager et al., 2017a). Ages of each tree in the inventory dataset were then estimated using site index curves following the methods outlined in De Jager et al. (2017a,b). Finally, each tree was grouped into cohorts at 25-year age intervals, with all seedlings and any age 10 or younger tree assigned an age of 5 years. Although the current study used a similar methodology to develop this initial plant community dataset as that described in De Jager et al. (2017a,b), the present study included several additional rare temperate species and community types. Thus, results of this study may not be directly comparable to the previously published studies.

Landscape Simulation Modeling

We used the LANDIS-II forest simulation modeling platform (Scheller et al., 2007). LANDIS-II simulates successional processes, disturbances, seed dispersal, growth and mortality across a series of grid cells (i.e., the landscape). Such processes are represented with different extensions that allow users to determine the degree of complexity needed to represent different systems. We used the Biomass Succession Extension (version 3.2; Scheller and Mladenoff, 2004) to simulate establishment, growth, and competition across the landscape as these properties affect and are affected by the biomass of species-age-cohorts. Biomass Succession requires input parameters for potential species establishment probabilities (P_{est}), which represent the likelihood of establishment of a new cohort given a seed source and adequate light, and maximum growth rate ($\mathrm{ANPP}_{\mathrm{max}}$) and maximum aboveground biomass ($\mathrm{AGB}_{\mathrm{max}}$), which determine the potential aboveground growth of a cohort. These parameters can vary spatially and temporally as they relate to annual temperature and precipitation patterns and the underlying soil characteristics. We used previously published establishment and growth parameters for the species listed in **Table 1** developed by Duveneck et al. (2014a) in northeastern Minnesota for ecoregions of similar climate and soil conditions as that found at Isle Royale, and for two climate scenarios (current climate and high emissions, see below). Thus, the effect of climate change in this study was represented as a temporal change in the potential establishment and growth rates of the species growing on different soils at Isle Royale and in response to variable temperature and precipitation patterns. Duveneck et al. (2014a) used the PnET-II ecophysiology model (Xu et al., 2009) to estimate P_{est}, $\mathrm{ANPP}_{\mathrm{max}}$, and $\mathrm{AGB}_{\mathrm{max}}$ using input climate data for current climate conditions and that of the high emissions scenario (A1FI) for northeastern Minnesota and based on several species-specific physiological characteristics. These input parameters are provided in **Figure A1**, and provide some insights into potential species-specific effects of climate change. However, within the Biomass Succession extension, the actual growth of a cohort incorporates a species-specific growth parameter to determine how fast the actual growth rate (ANPP) reaches $\mathrm{ANPP}_{\mathrm{max}}$. Further, growth is also modified by competition and age. Competition is represented by the available growing space, and age-related mortality is represented by an increasing decline in growth as cohorts near longevity. Finally, actual species establishment rates are strongly affected by seed supply and

TABLE 1 | Tree species life history parameters used in forest simulation modeling for the species modeled at Isle Royale National Park.

Species	Longevity (year)	Maturity (year)	Tolerance		Seed Dispersal (m)		Vegetative reproduction (Prob)	Sprout age		Postfire regeneration
			Shade	Fire	Effective	Maximum		Minimum	Maximum	
A. balsamea	205	20	50	1	30	160	0	0	0	None
A. rubrum	150	10	4	1	100	200	0.1	0	60	Resprout
A. saccharum	300	40	5	1	100	200	0.1	0	60	None
B. alleghaniensis	300	40	4	2	100	400	0.1	0	180	None
B. papyrifera	165	25	2	2	200	5000	0.5	0	70	Resprout
F. nigra	150	35	2	1	100	200	0.1	0	75	Resprout
P. banksiana	205	17	1	4	20	275	0	0	0	None
P. glauca	225	40	3	2	30	200	0	0	0	None
P. mariana	200	22	3	3	80	200	0.1	0	100	Resprout
P. strobus	450	15	3	3	60	210	0.5	25	300	None
P. tremuloides	140	25	1	1	1000	5000	0.9	0	100	Resprout
Q. rubra	250	25	2	4	30	3000	0.5	25	180	Resprtout
Shrub	100	25	3	1	45	60	0.5	0	60	Resprout
T. occidentalis	300	35	5	1	45	60	0.5	50	300	None

light conditions. Thus, model outcomes depend on both the potential establishment and growth rates (**Figure A1**) and how local and landscape scale factors modify them over the course of model simulations.

We simulated the effects of predation on moose population density and dynamics and resulting feedbacks with browsing patterns and forest succession using the Dynamic Ungulate Browse Extension (Version 0.8). Readers are directed to De Jager et al. (2017a,b) for complete details of the browse extension as it is only briefly and generally discussed here. The browse extension simulates reciprocal interactions, at an annual time step, between an ungulate population and forest succession through annual estimates of available forage biomass. Available forage biomass is a fraction of the total species-cohort biomass considered to be available to a foraging ungulate across an entire year. These calculations take into account how long tree species remain within the height reach of a foraging animal and the fraction of total aboveground biomass in edible leaves (summer) and twigs (winter). In previous applications of the browse extension, total annual available forage biomass was generally near 0.1–0.2% of total forest biomass (De Jager et al., 2017b). The ungulate population is temporally dynamic and governed by a discrete-time quadratic model, with a carrying capacity term that is derived at each time step (year) based on how many animals could be supported by the total available forage biomass for all species-cohorts across the landscape. Thus, the carrying capacity of the landscape is an emergent property, rather than a pre-defined parameter estimate. This means that the animal populations density is also an emergent property, rather than being predefined. Other factors that can influence the annual moose population density include: (1) the intrinsic population growth rate, which was randomly selected each annual time step between 0.15 and 0.25, (2) random population mortality rate (0 to 0.1), (3) animal harvest rate (0), and (4) predation rate (see scenarios below). These parameter settings reflect empirical estimates derived from a long-term moose-wolf study conducted at Isle Royale National Park (Peterson et al., 2014 and references within). The initial population density was set to 1 moose per km^2, reflecting the long-term mean population density.

Within each year, the local ungulate population density (and hence how much forage biomass is removed from a site) is determined by downscaling and distributing the total population to each grid cell. This process is done using moving window calculations of site preference (forage quality and quantity) at each time step. Thus, the ungulate population can fluctuate from year to year and place to place based on how any factor influences the availability and quality of forage biomass over time and space, including the ungulate population itself. We derived estimates of forge preference (quality) based on previously published studies conducted at Isle Royle (**Table 2**). For estimates of annual forage preference, we relied heavily on Hodgson (2010) because that study utilized data collected annually (summer and winter foraging preferences). These parameter estimates represent the fraction of available forage biomass that the ungulate population would be expected to remove from each species present at a site, based on the literature identified in **Table 2**.

At each time step, the total available forage biomass removed from each grid cell (a site) is the amount needed to satisfy the requirements of the local ungulate population. How much biomass is removed from each species at a site depends on the preference of the population for each species (given in **Table 2**) at each site. Effects of removed biomass on the growth and survival of tree cohorts were simulated using threshold equations, whereby a user-specified proportion of biomass lost due to browsing triggers a negative growth response in the next time step, up to user-defined maximum negative effect at 100% removal of available forage biomass. We used the same parameter estimates for species preferences and effects of moose browsing on growth and survival as published in De Jager et al. (2017b) (see **Table 2**).

TABLE 2 | Species-specific model parameters for moose browsing preference and effects of browsing on growth and mortality.

Species	Preference	Growth reduction		Mortality	
		Threshold	Max	Threshold	Max
A. balsamea[1,2,4,6]	0.15	0.2	0.6	0.8	0.1
A. rubrum	0.30	0.2	0.6	0.8	0.1
A. saccharum[2,3,6]	0.15	0.2	0.6	0.8	0.1
B. alleghaniensis[2,3,6]	0.15	0.2	0.6	0.8	0.1
B. papyrifera[2,5,6]	0.25	0.5	0.4	0.9	0.1
F. nigra[1,2,6]	0	0	1	0.8	0.1
P. banksiana[1,2,6]	0	0	1	0.8	0.1
P. glauca[1,2,6]	0	0	1	0.8	0.1
P. mariana[1,2,6]	0	0	1	0.8	0.1
P. strobus	0.05	0.2	0.6	0.8	0.1
P. tremuloides[1,2,3,6]	0.30	0.5	0.4	0.9	0.1
Q. rubra	0.05	0.2	0.6	0.8	0.1
shrub[1,2,6]	0.25	0.5	0.4	0.9	0.1
T. occidentalis[1,2,6,7]	0.05	0.2	0.6	0.8	0.1

The threshold parameters represent the proportion of available forage biomass, that once removed trigger growth reduction or an increase in the probability of mortality. Growth reduction or mortality increase linearly to a maximum (Max) at 100% browse removal. [1]Hodgson (2010). [2]Risenhoover (1987). [3]Sell (2007). [4]De Jager et al. (2009). [5]De Jager and Pastor (2008). [6]Murie (1934). [7]Parikh (2015).

Climate and Predation Scenarios

We contrasted two climate scenarios: static or current climate, and a high emissions scenario as described in Duveneck et al. (2014a). Static climate was simulated by randomly selecting simulation years from 30 (1969–1999) past observed climate years (Daly and Gibson, 2002). We represented climate change using the A1FI high emissions scenario of the Intergovernmental Panel on Climate Change [IPCC] (2007) coupled to the Geophysical Fluid Dynamics Laboratory (GFDL) Global Circulation Model (GCM) given its sensitivity to emissions (Delworth et al., 2006). Our climate change scenario reflected an accurate representation of observed global emissions at the time it was developed (Raupach et al., 2007). Since then, additional climate change scenarios have been developed by the IPCC. Importantly, the high emissions scenario used here (A1FI) is similar to the more recent Coupled Model Intercomparison Projects (CMIP) scenarios CMIP5 (RCP8.5) and CMIP6 (SSP5-8.5), with similar end of century radiative forcing and global mean temperature projection (O'Neill et al., 2016). Briefly, the high emissions scenario indicates increased temperature in the Midwest in all seasons for the next 100 years with most of the increase in temperature after 2050. Likewise, the high emission scenario indicates variable but decreasing precipitation in summer months after 2050 (Stoner et al., 2012). We simulated climate (temperature and precipitation patterns) across the entire island using results from Duveneck et al. (2014a) for the coldest and northern-most climate region (climate region 1) in nearby NE Minnesota from 2006–2116. Thus, we compared a high emissions (climate change) scenario with a static (current climate) scenario. For a graphical representation of how projected temperature and precipitation patterns differ between our static and high emissions scenarios, see Duveneck et al. (2014a). It is important to note that within our modeling framework, climate change does not directly impact moose population density. Thus, impacts of climate change on carrying capacity or the moose population come about via indirect effects on plant growth.

We evaluated the effects of predation by varying the predation rates within the ungulate browsing extension. We contrasted a no predation scenario ($P = 0$) with a weak predation scenario ($P = 0.03$–0.10), reflecting long-term mean predation rates (Peterson et al., 2014), and finally a strong predation scenario ($P = 0.07$–0.15), reflecting above-mean long-term predation rates (Peterson et al., 2014). At each annual time step, a random predation rate between the above intervals was selected to represent stochastic variation in predation rates within a scenario replicate. Unlike the effects of climate change, simulated effects of predation directly reduce moose population density. Such effects can further feedback to alter plant growth and carrying capacity by reducing browsing effects. We simulated a total of 6 scenarios (3 predation X 2 climate scenarios) for 120 years (2006–2126, ∼100 years from today). For each scenario, we ran three replicates given the stochastic nature of the model.

Data Analysis

We evaluated moose population dynamics by estimating the island-wide population density, carrying capacity, and a habitat suitability index for each annual time-step. Population density and carrying capacity were calculated as the number of animals per island area (#/km^2). We calculated habitat suitability as the normalized sum of area-weighted total forage biomass (quantity) and site preference (quality) on a 0–100 scale. We evaluated forest successional patterns by calculating the total aboveground live biomass of different groups of indicator species. Black and white spruce were grouped into a single category (spruce); northern conifers included northern white cedar, white and jack pine; boreal hardwoods included aspen and paper birch; northern hardwoods included yellow birch, sugar maple, red maple, red oak, and black ash. For all outputs we calculated the mean and 2 standard deviations to evaluate statistical overlap among scenarios over time. These standard deviations were included in all figures, but in some cases were very small and not noticeable. For scenarios with standard deviations that appeared to be larger than others (e.g., strong predation under current climate), we ran additional replicate simulations to verify results were not driven by a single outlier replicate. We constructed maps for initial conditions (year 2006) and ending conditions (year 2126) for the scenarios that consisted of: (1) no climate change and no predation, (2) no climate change and strong predation, (3) climate change and no predation, and (4) climate change and strong predation. These maps can be found in **Figure A2**.

RESULTS

Moose Population Dynamics

Moose population densities were greatest at 3–4 moose per km^2 for the "no predation" scenarios. Indeed, moose population densities were largest for scenarios that did not include predation

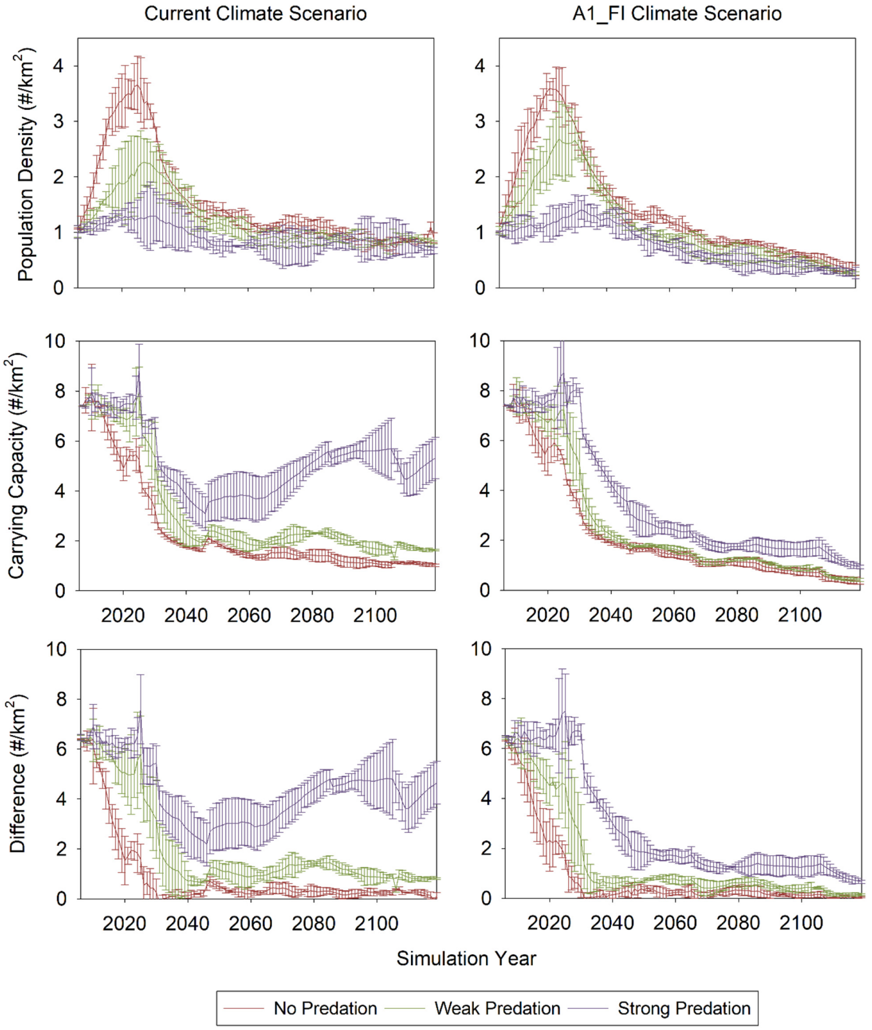

FIGURE 2 | Moose population density, carrying capacity, and the difference between the two for current climate **(left)** and high emissions scenarios **(right)** and three wolf predation scenarios. Data are area-weighted means ± 2 standard deviations from three replicate simulations within each scenario (climate × predation).

by wolves during the first 30 years of model simulations, regardless of the climate change scenario (**Figure 2**). Weak predation yielded peak moose population densities between 1.5 and 2.5 per km^2, while strong predation kept moose population densities below 2 per km^2 for the duration of model simulations.

In contrast to the near-term direct effects of predation on moose population density, climate change had almost no effect on population density in the near term, but had a minor effect on population density over the long term as it began to influence plant growth and establishment (forage production and carrying capacity) after 30 to 50 years. Late in the simulations (i.e., after 2060), moose population densities decreased for all three predation scenarios under the climate change scenario, in contrast to more stable moose population densities under the current climate scenario (**Figure 2**). These declines were due to reduced growth and establishment of boreal tree species in the diet of moose (**Figure A1**) and an apparent lack of compensatory growth by temperate species.

Differences in peak population density among scenarios had important consequences for longer-term estimates of carrying capacity, given the long-term effects of moose browsing on plant growth and available forage biomass. The lower peak population densities in the strong predation scenarios kept more forage biomass on the landscape and allowed for larger estimates of carrying capacity, especially under static climate conditions, but there were also more marginal effects under climate change (**Figure 2**). In these scenarios, predation continued to limit moose population density despite relatively higher carrying capacities, which in turn contributed to larger differences between carrying capacity and population density under both static and changing climate (**Figure 2**). The difference between carrying capacity and population density for the strong predation scenario was larger under current climate conditions than under the climate change scenario (**Figure 2**), reflecting a landscape much more suitable for moose (**Figure 3**). In contrast to the results for the strong predation scenarios, the higher initial peak population densities

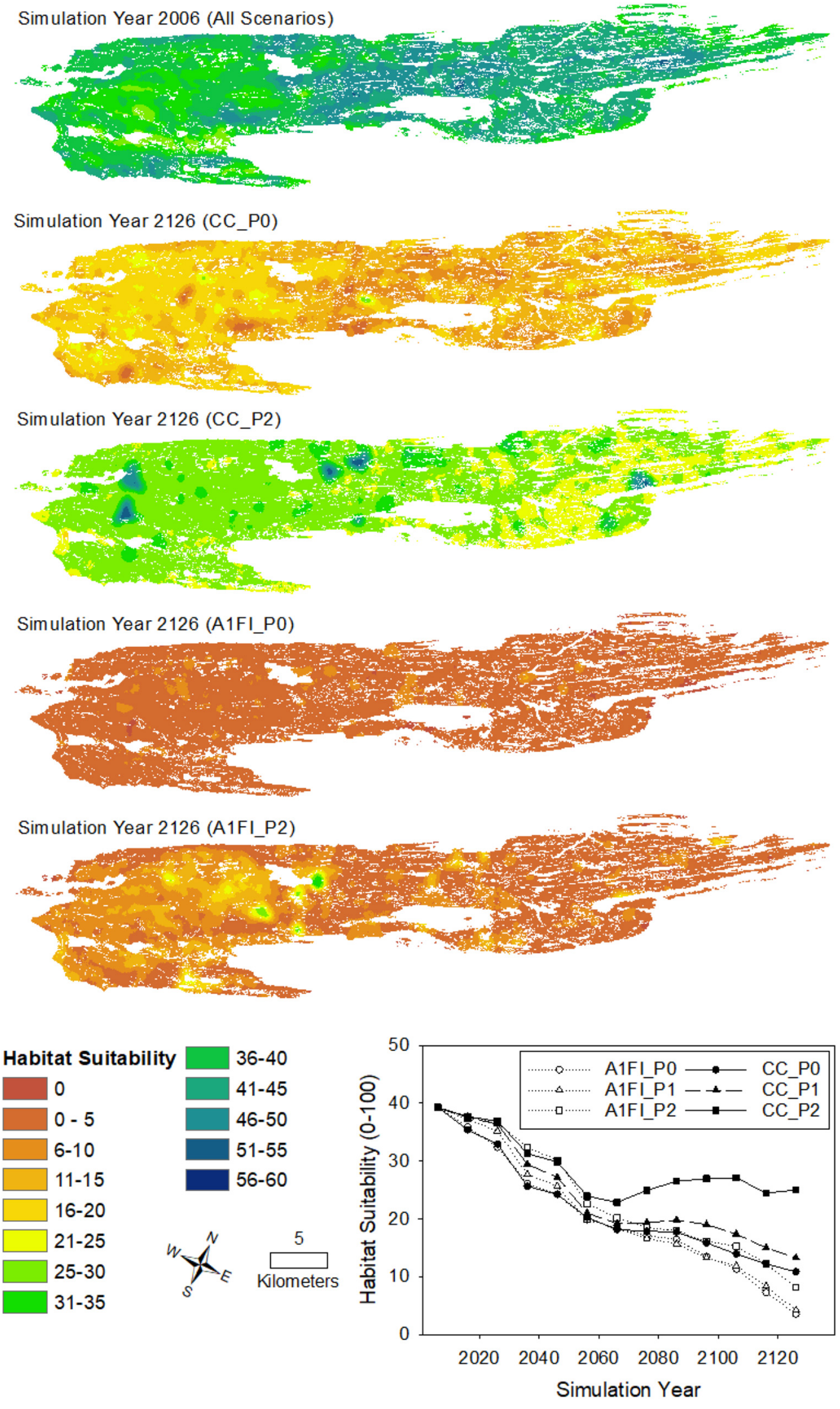

FIGURE 3 | Mapped distributions of habitat suitability for moose based on forage quantity and quality for initial model conditions (simulation year 2006) and after 120 years of current climate and no predation (CC_P0), current climate and strong predation (CC_P2), high emissions and no predation (A1FI_P0), and high emissions and strong predation (A1FI_P2). Inset graph shows the mean habitat suitability for each 10 years for all scenarios (CC_P1 is current climate with weak predation, A1FI_P1 is high emissions with weak predation).

in the weak and no predation scenarios contributed to lower long-term carrying capacities. This in turn limited long-term population density and kept the moose population much closer to the carrying capacity of the landscape. Thus, in the long-term, predation interacted with climate change to alter available forage biomass and the carrying capacity of the landscape. The largest estimates of carrying capacity and the largest difference between carrying capacity and population density was found for the strong predation scenario under current climate.

Interactive effects of simulated predation and climate also affected moose habitat suitability, which incorporated both the total available forage across the landscape and the quality of that forage (**Figure 3**). All three predation scenarios coupled to climate change resulted in lower habitat suitability than the current climate scenarios by simulation year 2126. The only scenario that produced significantly higher (non-overlapping CI's) and temporally stable estimates of habitat suitability was the strong predation scenario under current climate conditions. Thus, in our simulations, predation only contributed to a more suitable and sustainable landscape for moose under current climate conditions.

Finally, biomass removed from different species groups differed among predation scenarios early in simulations, during the period of time that predation was influencing population density (**Figure 4**). Later in simulations, when moose population density was similar across predation scenarios there were no differences in biomass removed among predation scenarios. However, late in the simulations (i.e., after year 2060) the amount of balsam fir removed from the landscape differed among climate change scenarios. Under current climate, the amount of balsam fir removed from the landscape tended to be greater than that removed in the climate change scenarios.

Forest Succession

The effects of climate change, predation, and forest successional processes also altered species biomass within different forest communities (**Figure 5**). Across the entire island, aspen and birch forests (boreal hardwoods) and spruce (white and black) forests had the highest initial mean estimates of forest biomass [∼4000 grams per square meter (g/m^2)] representing current conditions. Under all scenarios, these two species groups diverged immediately, with aspen and birch declining and spruce forests increasing in biomass. The simulated decline in more palatable aspen and birch biomass and increase in unpalatable spruce biomass contributed to the initial declines in both carrying capacity and habitat suitability that also occurred for all scenarios (**Figure 2**), indicating that forest successional changes had a large effect on moose population dynamics, regardless of the effects of climate change or predation. Though the decline in aspen and birch biomass occurred similarly for all scenarios, the increase in spruce biomass was only similar across scenarios until the year 2070, at which point it began to decrease in response to climate change. The change in spruce biomass drove overall declines in total forest biomass in response to climate change (**Figure 5**).

The other groups of species made up a much smaller proportion of total forest biomass, but tended to be much more sensitive to the interactive effects of predation and climate change and less dependent on forest successional processes. For example, strong predation aided the biomass of northern hardwood species under both climate scenarios, with the highest estimates of biomass found for current climate conditions, followed by the scenario that included strong predation and effects of climate change. For balsam fir, climate change caused a decline in aboveground biomass, regardless of predation. However, predation maintained a much higher above ground biomass of balsam fir under current climate conditions (**Figures 5**, **6**). The temporal trends in balsam fir biomass were similar to those observed for habitat suitability, indicating that the effects of climate change and predation on this species played a role in both forest succession and moose population dynamics. Yet, balsam fir and northern hardwood species made up just 5% or less of total forest biomass and thus these changes had no effect on this response variable.

DISCUSSION

Effects of Predation in a Warming Climate

Isle Royale National Park has long provided insights into the nature of predator-prey relationships in a forest ecosystem (Peterson et al., 2014). Past research has indicated that wolf predation can play a significant role in reducing and/or redistributing the intensity of moose browsing across the island (Vucetich et al., 2011; Peterson et al., 2014) and that reductions to moose browsing intensity would be expected to change rates of forest succession (Pastor and Naimen, 1992; Pastor et al., 1993; Pastor and Danell, 2003). However, in the absence of a coupled moose browsing-forest successional model, it is not possible to fully evaluate the potential long-term feedbacks between browsing and forest successional changes. In combination with previous modeling results (De Jager et al., 2017a,b), our simulations reveal the importance of the plant life history characteristics that influence rates and trajectories of forest succession, the foraging preferences of moose, and physiological responses to anticipated climate changes. In general, our results demonstrate that predation by wolves can alter how moose interact with forage resources and thereby alter rates and trajectories of forest succession. Such changes can have significant effects on the carrying capacity of the landscape for moose and thus on future moose population density in a dynamical system. However, our simulations also show that such interactions are likely to play out very differently as the forests of Isle Royale continue to shift toward late successional conifer species and especially as the climate continues to warm.

The primary effects of wolf predation were to lower peak moose population densities and maintain a higher abundance of high-quality forage. These effects were primarily found over the first 30–50 years of model simulations, before major changes in succession and before the effects of climate change had yet to significantly affect forest growth and development (see **Figure A1**). In these earlier simulation years, high rates of predation maintained a landscape with relatively high suitability for moose, even as forest successional changes were shifting

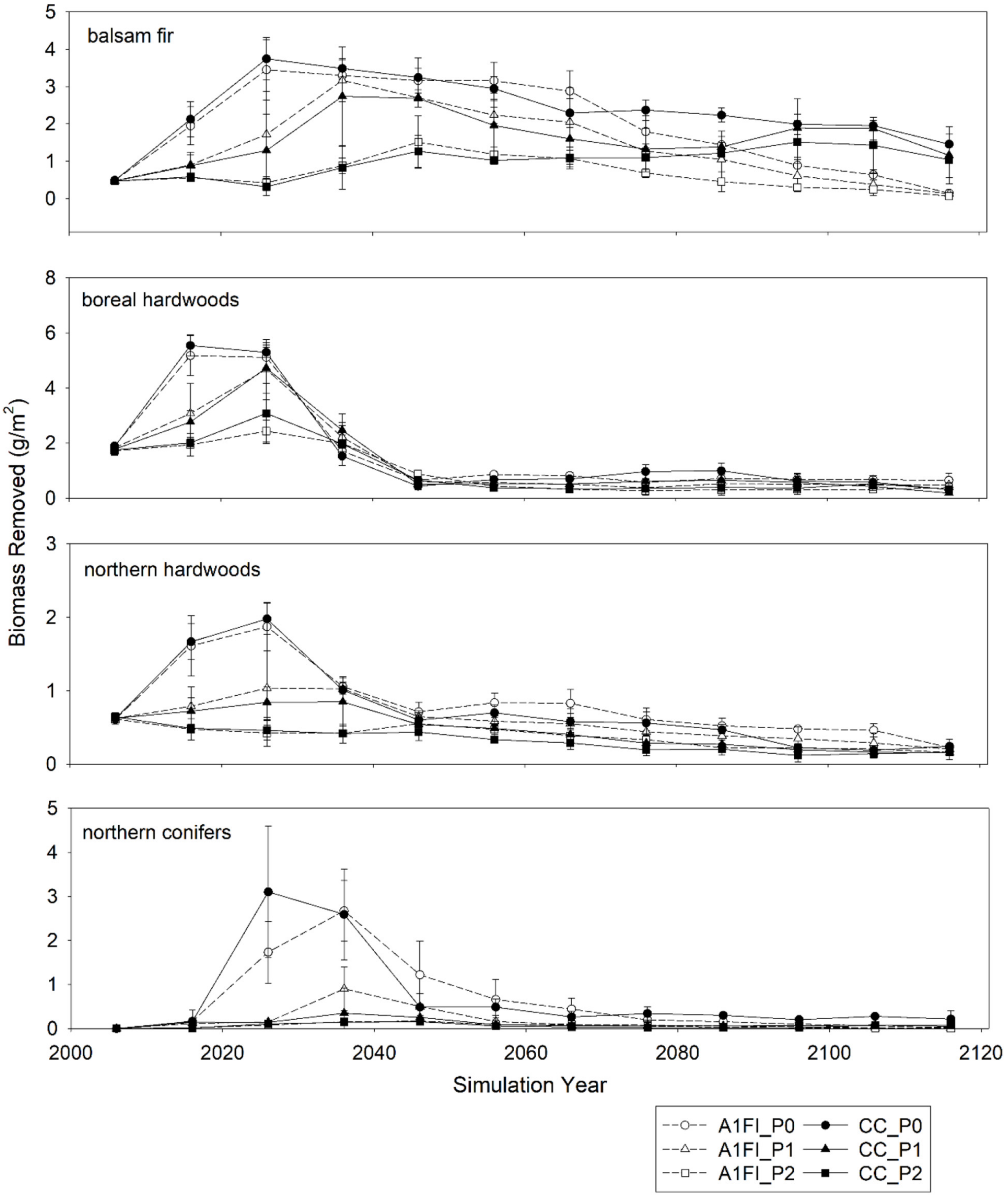

FIGURE 4 | Biomass removed due to browsing and browsing related cohort mortality for different predation and climate change scenarios. Data are area-weighted means ± 2 standard deviations for three replicate simulations for each scenario.

the landscape away from the shade intolerant and fast growing early successional species that moose highly prefer (e.g., aspen and birch) and toward the shade tolerant and slower growing species that they do not eat (spruce). These effects have also been shown in previous modeling studies (De Jager et al., 2017a,b) and exclosure studies (McInnes et al., 1992). However, our model draws attention to the only late successional conifer species that moose feed on, balsam fir. This species benefited most from wolf predation under current climate conditions and appeared to support the moose population over the long-term. Without predation, the successional changes and heavy browsing by moose decreased the carrying capacity of the landscape because browsing and successional changes negatively affected the growth of highly palatable early successional species (e.g., birch and aspen). Climate change further reduced the carrying capacity and suitability of the landscape for moose after 50 years by negatively influencing the growth of balsam fir. These effects were due to increased temperatures later in model simulations as shown in Duveneck et al. (2014a).

Effects of Climate Change and Herbivory in an Island Setting

Just as Isle Royale has served as a model predator-prey system, it also has characteristics (e.g., it is relatively small, isolated, and

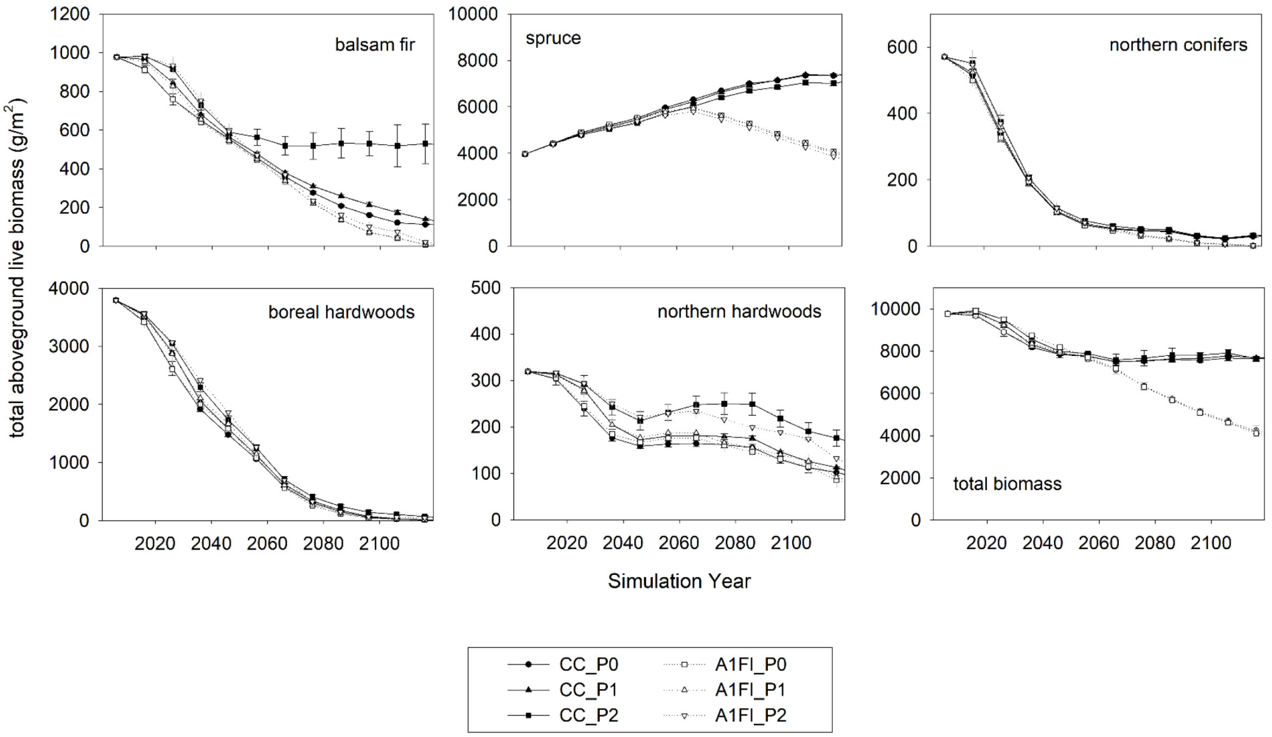

FIGURE 5 | Mean (± 2 standard deviations) total aboveground live biomass of three replicate simulations at 10-year intervals for 120 years of current climate and no predation (CC_P0), current climate and weak predation (CC_P1), high emissions and no predation (A1FI_P0), high emissions and weak predation (A1FI_P1) current climate and strong predation (CC_P2), and high emissions and strong predation (A1FI_P2). See methods for species included in each grouping. In some cases some scenarios overlap each other and are therefore not visible (e.g., total biomass outputs).

has a simplified flora) that can provide insights into the effects of island biogeographic processes on adaptations to climate change. Larger and more well-connected landscapes generally support higher levels of biodiversity, which would be expected to improve the odds of successful species migrations under changing environmental conditions (Cabral et al., 2014). Isle Royale is farther from the mainland than the estimated dispersal distances of several tree species that have been suggested to perform well in a warmer climate (Frelich and Reich, 2009; Sanders and Grochowski, 2013). Thus, without some form of assisted migration of additional temperate species or to expand the distribution of those already present, the vegetation of Isle Royale could begin to shift toward novel plant communities, with implications that extend to the moose population. In our simulations the biomass of temperate forest species, which may be favored with climate change, was not able to fully compensate for the declines in boreal communities as the climate warmed, and predation only marginally influenced this outcome. It is important to note that some of these species (e.g., yellow birch and sugar maple) are relatively shade tolerant and have long lifespans, increasing their importance as forage for moose in late successional forests. Previous studies have indicated that heavy moose browsing may reduce rates of expansion of such northern hardwood forests at Isle Royale National Park (Sell, 2007; De Jager et al., 2017b). Even when aided by potentially positive effects of climate change, browsing by white-tailed deer has been shown to limit the ability of temperate species to replace boreal species (Fisichelli et al., 2012). While our results support the idea that predation by wolves could reduce effects of moose browsing on northern hardwood forests, such effects were insufficient to allow for the expansion of these communities from their initial distributions in the high emissions scenario (**Figure A2**). Moose may also feed on some of the temperate conifer species that we simulated, such as white and jack pine. However, all temperate species currently have a very limited spatial distribution at Isle Royale, and the rate of climate change may have simply outpaced their ability to disperse as found in other systems (Vanderwel and Purves, 2013; Liang et al., 2017). Furthermore, the simulated effects of climate change on the potential establishment and growth rates of the two most abundant temperate species at Isle Royale (yellow birch and sugar maple) were not uniformly positive (**Figure A1**). Both species showed initial increases in potential establishment, followed by later declines, and either neutral or negative effects of climate change on potential growth rates. While these effects were less negative than found for boreal species, they did not allow them to compensate for the declines in the biomass of boreal species.

Management Implications

Our results are not meant to provide precise predictions of the future. Large inherent uncertainty encompasses the processes that we simulated. We cannot predict precise future

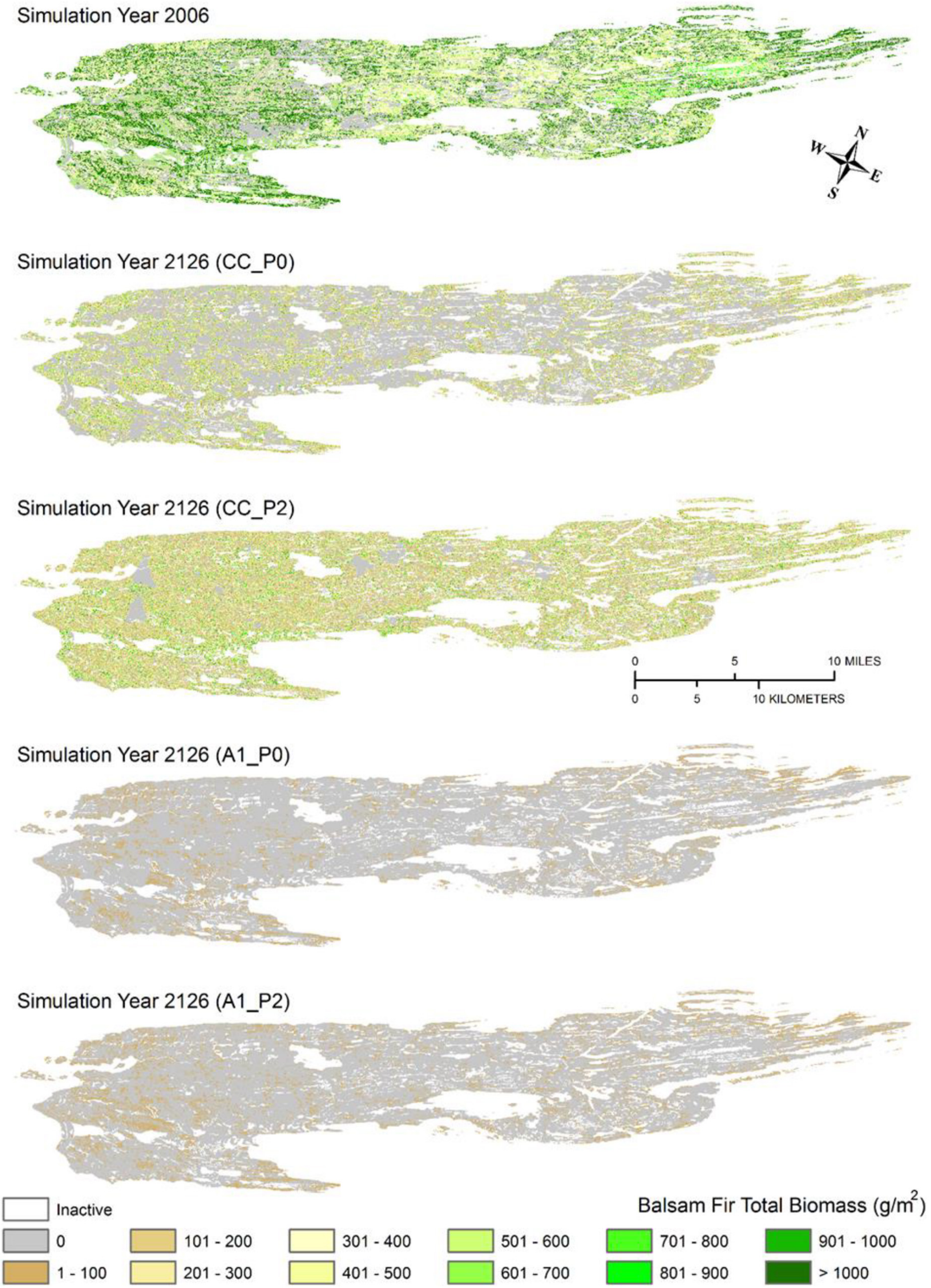

FIGURE 6 | Mapped distributions of balsam fir biomass for initial model conditions (simulation year 2006) and after 120 years of current climate and no predation (CC_P0), current climate and strong predation (CC_P2), high emissions and no predation (A1FI_P0), and high emissions and strong predation (A1FI_P2).

climate in general (Intergovernmental Panel on Climate Change [IPCC], 2013) or for Isle Royale National Park, and we cannot represent every individual species interaction. Additionally, our simulations are based on models and model parameterization that introduce additional uncertainty. In general, our predictions regarding near-term dynamics (< 50 years) are probably more robust than those for the longer term (after 100 years). Our near-term projections reflect an initial landscape with a mix of boreal conifer and hardwood species with a relatively high suitability for moose. Although our process for imputing forest plot data into cells across the landscape introduces some uncertainty, the degree of uncertainty is likely much less than for model projections of plant communities 100 years into the future. In addition, the uncertainty in the magnitude of climate changes and their effects on plant growth and establishment increase with time. Thus, our insights into the way management agencies might think about the roles of predation, ungulate population, and forest management in a changing climate could be interpreted considering the assumptions and uncertainty inherent to our methods.

Our primary finding is that the direct effects of moose population management via reintroduction of wolves is likely to be effective while wolf-moose interactions play out on the current mixed boreal forest landscape of Isle Royale and under a climate suitable for boreal plant species. However, in the longer term, and perhaps considered with a greater degree of uncertainty, the effects of predator reintroduction may become increasingly ineffective as the forest shifts toward late successional conifers and as the climate continues to warm because forest composition and productivity may not be sufficient to support a moose population at all. On the other hand, the marginal effects of predation under the climate change scenario could be viewed as essential to maintaining a small moose population and prevent that population from exhausting the few forage resources that remain. Even so, our projections imply that Isle Royale is likely to undergo changes in composition and productivity that make the island increasingly unsuitable for moose.

Our modeling efforts assume that the National Park Service will continue to allow the forests of Isle Royale to undergo forest successional changes in absence of major stand replacing disturbances such as fire or timber harvesting. This is a feature of Isle Royale that makes it different from most other boreal forests that support large moose populations (e.g., Alaska, Sweden). At the start of our model simulations, a mixed landscape of boreal hardwood and conifer forests supported a relatively large carrying capacity for moose and moose were removing biomass from the landscape in accordance with published foraging preferences (boreal hardwoods > balsam fir > northern hardwoods > northern conifers). But the boreal hardwood and conifer communities diverged within the first 30 to 50 years of our simulations, regardless of the effects of climate change or predation. As these successional changes occurred, the carrying capacity of the landscape for moose declined significantly and moose began to rely increasingly heavily on later successional balsam fir.

The abundance and initial age structure of the early successional aspen and birch forests may reflect a history of small-scale timber harvests and forest fires that were coincident with copper mining and tourism on the island during the early 1900s (Krefting, 1974). Then, in 1936 a large fire reset the forest successional sequence over a large central portion of the island and may have been responsible for sustaining the moose population (Scarpino, 2011), as there were reports that the population had exhausted its food supply (Krefting, 1974). Since that time period there have been no large-scale stand replacing disturbances on the island and the current aspen-birch forests are approaching their longevity. We did simulate smaller-scale wind patch disturbance events reflecting the low intensity and high frequency wind blowdown events on the island (Kirschbaum and Gafvert, 2012). These simulated wind events created local increases in forage availability of select species (**Figure A2**) but did not alter the landscape as dramatically as a much larger disturbance, such as the 1936 fire would, for example. The absence of larger scale forest disturbances or management actions to regenerate these early successional forests resulted in significant declines in both the quantity and quality of forage for moose across the island and changes in foraging behavior that do not correspond with published observations from earlier successional forests. Finally, it has been suggested that the frequency and/or intensity of large scale fires could increase at Isle Royale under a changing climate (Fisichelli et al., 2013). In the near-term, while climate change impacts on the establishment and growth of early successional boreal species such as aspen and birch are projected to be more minor, stand replacing fires would be expected to increase the suitability of Isle Royale for moose. However, it is less clear how such disturbances would impact the suitability of this landscape for moose late in time, when the effects of climate change on these species is stronger.

Finally, in this study, we focused our attention on the effects of climate change on plant growth and establishment rates, and how such effects may interact with variable rates of moose browsing to alter forest dynamics in space and time. However, it has been suggested that climate change may directly impact moose survival, especially in areas near their summer range limit (Thompson et al., 1998; Murray et al., 2006; Lenarz et al., 2010). Within our modeling framework, increased moose mortality due to the direct effects of heat stress would result in lower moose population densities and weaker effects on forest resources than we simulated in the strong predation/high emissions scenario. A recent global analysis by Timmermann and Rogers (2017) found that 10 of 15 moose populations near their summer range limit were stable or increasing, including the Isle Royale population, and indicated that climate change may pose no immediate threat to moose populations. However, the projected changes in climate that we simulated here are larger than what has been observed during the recent past and could become physiologically unsuitable for moose over the next 100 years. More generally, our approach to modeling moose population dynamics relies on estimates of carrying capacity, which are derived from annual estimates of the total available forage across the landscape and the estimated yearly forage requirements for an average moose. As a result, our estimates of carrying capacity are likely an over-estimation of the population density expected to be supported by forage resources. A more physiologically based approach would allow for an evaluation of the direct effects of climate change on the moose population or any other factor that may cause moose mortality long before the population reaches carrying capacity based on forage quantity alone.

DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. This data can be found here: https://www.nps.gov/im/vmi-isro.htm.

AUTHOR CONTRIBUTIONS

ND conceived the study, conducted the modeling, analyzed the results, and wrote the manuscript. JR prepared the input data files, conducted GIS analyses, and edited the manuscript. MD provided the input parameters derived from previous climate change modeling work and edited the manuscript. All authors contributed to the article and approved the submitted version.

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Forest Biodiversity, Carbon Sequestration, and Wood Production: Modeling Synergies and Trade-Offs for Ten Forest Landscapes Across Europe

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Europe’s forests provide vital habitat for biodiversity and essential ecosystem services whose provision must be sustained or enhanced over the coming century. However, the potential to secure or increase forest ecosystem services, while securing the habitat requirements of taxa remains unclear, especially within the context of uncertain climate and socio-economic developments. To tease out the associated trade-offs and synergies, we used 10 case study landscapes within nine countries throughout Europe. Starting with the current status of the forests in the case study landscapes, we simulated forest development 100 years into the future. Simulations were embedded in three combined climate and socio-economic frame scenarios based on global and European policies which varied in their climate change mitigation efficiency. Scenarios were translated into country specific projections of climate variables, and resultant demands for wood products. Forest management regimes were projected to vary in response to these scenarios at local scales. The specific combinations of alternative forest management practices were based on parallel research and input from local forest stakeholders. For each case study, a specific forest growth simulator was used. In general, the climate scenarios applied did not cause fundamentally different ecosystem service outputs at the case study level. Our results revealed almost no reduction in outcomes for biodiversity indicators with an increase in wood production, and in some cases synergistic results occurred when diversity was actively promoted as part of the management concept. Net carbon uptake was not strongly correlated with biodiversity, indicating that biodiversity-friendly forest management doesn't need to curtail carbon sequestration. Notably, we obtained heterogeneous results for the relation between sustainable wood production and net carbon uptake. Most scenarios resulted in a more or less reduced net carbon uptake over the long term, often due to stand age class distribution shifts. Levels of sustainable wood production varied widely during the simulation period, from significant increases (Sweden, Lithuania) to minor changes (Slovakia, Turkey) and slight decreases (Ireland, Netherlands). We place our results within the larger context of European forest policy and the challenges of simulating and contrasting forest biodiversity and the ecosystem services that societies depend on.

Keywords: ecosystem services, biodiversity, wood production, carbon sequestration, forest management, sustainability, simulation, Europe

INTRODUCTION

Forests provide vital habitat for biodiversity and essential ecosystem services (Brockerhoff et al., 2017). Forest biodiversity, and the associated goods and services provided, must be sustained or enhanced over the coming century to meet the resource requirements of the global human population, and to halt the biodiversity crisis (IPBES, 2019). However, the potential to secure or increase forest ecosystem services, while simultaneously securing the habitat requirements of taxa remains unclear, especially within the context of uncertain climate and socio-economic developments (Plas et al., 2016; Felton et al., 2020). Whereas, the *wake theory* (cf. Knoke et al., 2017) suggested that desirable forest ecosystem services would be delivered "in the wake" of sustainable wood production, empirical studies have repeatedly challenged this assumption. Habitat loss and the depleted delivery of at least some ecosystem services is frequently associated with forests managed primarily for wood provision (Paillet et al., 2010; Gamfeldt et al., 2013; Felton et al., 2016b).

A recurring theme in assessing forest ecosystem services provision is the relation between a landscape's biodiversity and wood biomass production (Jucker et al., 2014; Bugalho et al., 2016; Felton et al., 2020). Possible conflicts, but also synergies have been discussed in relation to forest (Maes et al., 2012; Biber et al., 2015; Borges et al., 2017; Dieler et al., 2017) and agricultural natural resource management (Tscharntke et al., 2005; Whittingham, 2011; Harrison et al., 2014). Of growing and related importance is determining how best to optimize the carbon sequestration capacity of forest lands; in specific terms whether the intensive harvest or setting aside of forest land is best suited to mitigating climate change (Winjum et al., 1993; Leighty et al., 2006; Profft et al., 2009; Daigneault et al., 2010). Addressing these issues also requires deciphering to what extent forest biodiversity and forest carbon sequestration influence each other, and how forest management can be altered to achieve both biodiversity conservation and climate change mitigation goals (Boscolo and Vincent, 2003; Caparrós and Jacquemont, 2003; Bekessy and Wintle, 2008; Díaz et al., 2009; Felton et al., 2016a).

Few empirical or modeling studies address the trade-offs and synergies that can occur among forest biodiversity, biomass production, and carbon sequestration, at landscape scales. A key obstacle to such assessments is the need to contrast less readily quantifiable aspects like biodiversity, across a wide variety of forest types and biogeographical and socio-economic conditions. Although the tools used to do so are still in their infancy, in recent years promising new approaches have been developed for evaluating forest biodiversity despite such varying conditions, including those by Blattert et al. (2017, 2018) and Biber et al. (2020, submitted: "A Fuzzy-Logic Based Approach for Evaluating Ecosystem Service Provision Applied to a Case Study in Southern Germany"). The assessment of carbon sequestration likewise requires careful attention and unambiguous categorization if large scale or cross-national comparisons are to be made. This is because outcomes strongly depend on how the boundaries of the analysis are drawn and which aspects are incorporated, i.e., developments solely within the forest ecosystem itself, or inclusive of wood products and emission substitution effects (Peckham et al., 2012; Pukkala, 2014). In contrast, the quantification of wood production can seem relatively simple, largely because forest science has provided clear definitions of key variables since its earliest days. However, even wood production has traditionally been evaluated using a range of different variables, including periodic annual increment, mean annual increment, standing volume, and total volume production.

Under some circumstances, for example those in which evidence-based guidance for forest stakeholders is sought, clearer insights can be achieved by condensing the inevitably multidimensional outcomes for biodiversity, and selected ecosystem services, into a single robust indicator for each ecosystem service and overall biodiversity. With this in mind, here we use recently developed approaches to contrast and evaluate the outcomes of forest management decisions and developmental trajectories for carbon sequestration, wood production, and forest habitat availability for biodiversity. To do so, we assess—based on the methodological considerations made above-—10 case study landscapes across Europe, where future forest development scenarios have been simulated for 100 years. These scenarios are defined by detailed silvicultural measures which in turn are embedded in combined socio-economic and climate frame scenarios. We explore expected trade-offs and synergies between biodiversity, carbon sequestration and wood production and place our results within the context of forest management and policy formulation in Europe.

MATERIALS AND METHODS

Case Study Landscapes

Our research was based on case study areas (CSAs) in nine European countries (from North to South: Sweden, Lithuania, Ireland, Netherlands, Germany, Slovakia, Italy, Portugal, and Turkey). Except Germany, which hosted two CSAs, there was one CSA per country, resulting in a total of 10 CSAs (**Figure 1**, **Table 1**, **Supplementary Table 1**). CSAs were forest landscapes covering areas between several thousands and several hundred thousands of hectares (**Table 1**). They were selected to capture the most important issues relating to sustaining habitat for biodiversity, and the goods and services forests provide, operating at the interface of forest management and forest policy. Usually, the case studies' significance is not solely restricted to the country within which it is located, but extends to comparable biogeographic circumstances in their respective climate zone (cf. **Supplementary Table 1**). For example, the results of the Irish case study can be used to represent the vast peatland areas throughout Northern Europe. For all CSAs, state-of-the art simulation models and decision support systems (DSSs) were available (see **Table 1**). These had the advantage of being adapted to the circumstances within which they were applied. The drawback, however, is that the output variables were not *a priori* comparable across CSAs, due to e.g., different definitions and input variables. This has been a major obstacle for previous European-wide studies (Biber et al., 2015; Orazio et al., 2017). For this reason, a pre-condition for inclusion in this study was that all CSAs need to apply a common standard for output information that was defined and established across all simulation models and DSSs (Nordström et al., 2019).

Frame Scenarios

Three nation-level frame scenarios provided by the International Institute for Applied Systems Analysis (IIASA) provided the foundation for silviculturally detailed forest development scenarios for application within the CSAs. These scenarios represent different levels of climate change mitigation effort, and related wood demand for material and bioenergy purposes, which can directly impact on wood production, biodiversity and carbon sequestration in the forest landscape. The three scenarios combined the RCP (Representative Concentration Pathways)-SSP (Shared Socioeconomic Pathway) scenarios developed for the International Panel for Climate Change (IPCC) (Fricko et al., 2017) with policy targets for the European Union (Forsell et al., 2016), and are defined as follows (see Forsell and Korosuo, 2016 for details):

- The *Reference scenario* projects future development pathways based on historical development trajectories. This scenario takes into account EU policies and targets until 2020 in current legislation, and thereafter continues with development toward climate outcomes that follow pathways experienced in the past. In addition, the global economic growth and population development are assumed to be consistent with pathways experienced in the past. Climate change is somewhat mitigated via additional policies on greenhouse gas emission mitigation and through the development of carbon capture technologies. Global temperatures will significantly increase, and reach 3.7°C above the pre-industrial level by 2,100.
- The *EU Bioenergy scenario* projects rapid development of the EU bioenergy sector. This scenario takes into account EU policies aiming at an 80% reduction in carbon emissions by 2050, with some global climate policies also in place. In this scenario, the emission reduction targets in the EU for 2030 and 2050 are assumed to be fulfilled. The biomass demand for energy is assumed to remain stable thereafter in the EU. However, the importance of woody biomass as feedstock for building materials is projected to increase. Outside of the EU, it is assumed that additional climate change mitigation policies are in effect, so that global temperatures at 2,100 will increase by 2.5°C above the pre-industrial level.
- The *Global Bioenergy scenario* projects global development toward climate targets. It is assumed that climate policies are enacted globally, with both stringent EU policies and strong global climate mitigation. In the EU, the same targets until 2050 are in place as in the previous scenario (EU Bioenergy). Additionally, strong global mitigation actions are expected to be taken in all sectors and the bioenergy demand is expected to increase due to the investments in renewable heat and power. This leads to a temperature increase of 1.5–2.0°C by 2,100, compared to pre-industrial level.

Forest Management Scenarios

Forest management scenarios were developed for each CSA, for which detailed silvicultural actions were applied to the forest as guided by surveys of important stakeholders in each CSA (Marques et al., 2020; Trinh et al., 2020). As can be taken from **Table 1**, these stakeholders cover a wide range of interests, from commercial private forest owners to environmental NGOs. The management alternatives implemented in the different scenarios considered the interests and opinions of the stakeholders in the CSA. The heterogeneity of stakeholder constellations led to different solutions among the case studies. For example, in Portugal and Turkey, one forest management scenario was applied under all frame scenarios. Some case studies decided to define different forest management scenarios that were directly linked to the frame scenarios (Sweden, Netherlands), whereas others applied different management scenarios inside each frame scenario (Italy, Slovakia, Germany, Ireland, Lithuania). Note that if a forest management scenario was applied to more than one frame scenario, it had to be adapted in order to take account of the different market and climate developments associated with the frame scenarios. For example, increased bioenergy demand in the EU Bioenergy or Global Bioenergy frame scenario might

FIGURE 1 | Locations of the case study landscapes.

require more harvesting compared to Reference conditions, even within the same forest management scenario. This occurred in Sweden, Ireland, the Netherlands, Slovakia, Italy and the German case study AWF (cf. **Supplementary Table 3**). While these forest management scenarios were designed to achieve goals at the landscape level, this often was achieved using a variety of silvicultural treatments at the level of individual stands.

Despite heterogeneity in forest management scenarios (**Table 2**), they can be usefully categorized into four different types. Often, a CSA covers more than one of these scenario types. There are scenarios striving to maximize the economic profit (type 1, found for Sweden, Lithuania, Netherlands, Germany, Slovakia). Related scenarios also involved a focus on production and profit, however with the addition of environmental restrictions, or efforts to mitigate production risk by e.g., increasing the share of deciduous species (type 2, found for Ireland, Lithuania, Netherlands, Slovakia, Sweden). Other scenarios did not prioritize wood production above other ecosystem services, and strived to achieve a variety of goals at the same time (type 3, found for Portugal, Turkey, Germany, Italy, Slovakia, Netherlands). The fourth category of scenarios prioritized ecosystem services other than wood production, including nature protection and recreation (found for Germany, Italy).

Simulation Tools

The simulation tools used for this study (**Table 1**, **Supplementary Table 2**) are among the leading instruments available in the field of management-oriented forest modeling. Their construction, validation, and utilization has been documented in a large body of publications, the most recent of which are listed at the bottom of **Table 1**. All of the models were adapted to the information supply and demand of the specific case studies they were applied to.

TABLE 1 | Case study landscapes used in this study [taken from Biber et al. (2019), modified].

(Country code) Name(s)	Area, 1000 ha (% forest)	Forest ownership (%)	Main stakeholders	Main ecosystem services	Available simulation models or DSS
(SWE) Kronoberg county	847 (77)	83 Private 17 Public	Forest owners' association, environmental organizations, forest industry, Swedish Forest Agency, public	Timber, biodiversity, water, recreation, carbon sequestration	Heureka[a]
(LTU) Telšiai	254 (34)	63 Private 37 Public	State forest managers, private forest owners, environmental organizations, regional park	Timber, biodiversity, water, recreation, carbon sequestration	Kupolis[b]
(SVK) Podpolanie	34 (57)	7 Private 93 Public	State forest managers, private forest owners, environmental organizations, general public	Timber, biodiversity, water, recreation, carbon sequestration	Sibyla[c]
(IRL) Barony of Moycullen	81 (16)	22 Private 78 Public	Forest service, advisory services, private forest owners, environmental organizations, industries, public, fisheries, investment bodies	Timber, biodiversity, water, recreation, carbon sequestration	Growfor[d] Remsoft[e]
(ITA) Veneto	76 (100)	74 Private 26 Public	Forest owners' association, logging enterprises, municipalities, regional forest administration, environmental organizations	Timber, biodiversity, water, erosion control, carbon sequestration	InVEST[f] VALE
(PRT) Sousa Valley	15 (10)	90 Private 10 Public	Forest owners' association, forest owner federation, forest industry, forest service, local municipality, other non-governmental organizations	Timber, regulatory services (related to wildfire risk), soil erosion, recreation, carbon sequestration	StandSim[g] SADfLOR[h]
(GER) Augsburg Western Forests (AWF)	150 (33)	50 Private 50 Public	Private forest owners, environmental organizations, forest service, forest industry, general public (stable ownership structure for decades)	Timber, biodiversity, recreation, water, soil protection, carbon sequestration	SILVA[i]
(GER) Lieberose –Schlaubetal, Neuzelle (LSN)	90 (37)	44 Private 56 Public	Private forest owners (their share steadily increasing), forest service, environmental organizations, forest industry, general public	Timber, biodiversity, recreation, soil protection, carbon sequestration	SILVA[i]
(NLD) Netherlands	3,734 (11)	52 Private 48 Public	Government: National, Regional and Owners: Owner association, State forestry, National Trust, private non industrial forest owners, general public	Timber, recreation, biodiversity, carbon sequestration	EFISCEN-space[j]
(TUR) Gölcük	81 (49)	9 Private 91 Public	Gölcük state forest enterprise, timber processing companies, nature protection agency, forest cooperatives and contractors, forest villagers	Timber, biodiversity, soil conservation, recreation, water, carbon sequestration,	ETFOP[k]

[a] Wikström et al. (2011).
[b] Petrauskas and Kuliešis (2004).
[c] Fabrika (2005) and Fabrika and Durský (2006).
[d] Purser and Lynch (2012).
[e] Walters (1993).
[f] Kareiva et al. (2011).
[g] Barreiro et al. (2016).
[h] Marto et al. (2019).
[i] Pretzsch (2009, p. 515 ff.) and Pretzsch et al. (2002).
[j] Schelhaas M. et al. (2018) and Schelhaas M.-J. et al. (2018).
[k] Kadıoğulları et al. (2018).

However, the simulation tools used by CSAs differed extensively from each other due to differences in the available input data (e.g., remote sensing data sources vs. terrestrial grid inventories), their fields of application (e.g., commercial forestry vs. multifunctional management, which implies a different focus in the set of output variables), model conception (e.g., empirical vs. theory-based), and DSS capabilities (e.g. automatic optimization procedures available or not). See **Supplementary Table 2** and Nordström et al. (2019) for more details; see **Table 1** for model names and key references. To overcome some methodological differences, all models had to adequately take into account the climate and wood demand developments predicted in the global frame scenarios (Nordström et al., 2019), with outputs provided as a standard set of variables. Due to the structure of their DSS, the Italian case study could not provide the full set of standard variables.

Evaluation Methods

We assess the value of the simulated development of forests for biodiversity, sustainable wood production and carbon sequestration. As stated above, each of these categories is considered to be a complex and multi-dimensional construct

TABLE 2 | Overview of the forest management scenarios used in this study [after Biber et al. (2019), modified].

Country	Forest management scenario name	Concept	Used with global frame scenarios
Sweden	High wood production	Better regeneration and more pre-commercial thinnings, shorter rotations, more Scots pine, hybrid larch, fertilization in pine forests, Norway spruce clones	Global Bioenergy
	More diverse forest management (EU version)	More diverse forest management. More Scots pine, more oak for wood production, include border zones without management, spruce-birch admixtures, continuous cover forestry	EU Bioenergy
	More diverse forest management (Reference version)	More diverse forest management. More Scots pine, more oak for wood production (compared to EU Bioenergy), more spruce-birch admixtures (compared to EU Bioenergy), include border zones without management, Douglas fir, continuous cover forestry	Reference
Lithuania	Adaptive rotation ages	Maximize forest rent/present net value, applying rotation ages depending on soil types	All
	Care for deciduous	Adjust silvicultural priorities toward deciduous species, while conifers still remain important	All
Ireland	Environmentally constrained profit maximization	Increase profit of blanket peat forests while having low environmental impact. Low stocked planting of lodgepole pine, create good conditions for native broadleaf species, Sitka spruce under birch nurse, include zones for bog restoration	All
Netherlands	Reference gfdl	Slightly adapted management based on current developments (gfdl 8.5 climate)	Reference
	Reference hadgem	Slightly adapted management based on current developments (hadgem 8.5 climate)	Reference
	Wood	Focus on timber production (hadgem 4.5 climate)	EU Bioenergy
	Bioenergy gfdl	Focus on local sustainability and bioenergy (gfdl 2.6 climate)	Global Bioenergy
	Bioenergy hadgem	Focus on local sustainability and bioenergy (hadgem 2.6 climate)	Global Bioenergy
Germany (both case studies)	Multifunctional	Establish and maintain (uneven-aged) mixed stands in order to provide a broad range of ESs	All
	Production	Maximize wood production with monospecific even-aged conifer forests, reduce share of other forest types	All
	Setaside	Landscape is treated as a strictly protected area; no active silviculture	All
Slovakia	Conservative	Management goals determined by natural conditions and species composition	All
	Liberalized	Management goals determined by the forest owner	All
Italy	Recreation and habitat selectivity	Close to nature, improve recreational and cultural forest functions, maintain biodiversity	All
	Uniform shelterwood and coppice	Uniform shelterwood in oak-hornbeam forests, transform coastal forests into holm oak coppice with standards	All
Portugal	Combination of eucalypt, pine, broadleaf, cork oak and riparian forest management	Address challenges related to the management of eucalypt plantations, risk of fire, fragmented land ownership, lack of management and abandonment; develop a landscape mosaic that provides the full range of ecosystem services (e.g., wood and non-wood products, resistance to wildfire, biodiversity, carbon, soil erosion protection, and cultural values)	Reference[a], EU Bioenergy[a]
Turkey	Continuous Cover Forestry	Provide a multitude of ESs by creating and maintaining uneven aged mixed stands	All

Supplementary Table 3 *provides complementary information about the mean annual harvest amounts and areas modeled for the scenarios.*

[a] *These are local scenarios provided by the Clipick tool (Palma, 2017)—Global Bioenergy is not considered due to lack of precipitation data.*

that cannot be measured directly and/or objectively. Based on earlier work, we constructed indicators for each of these services that integrate along these different dimensions. For biodiversity and sustainable wood production we used a fuzzy logic approach (Biber et al., submitted) to qualitatively indicate the interaction effect between the dimensions, whereas for carbon sequestration we assumed its different dimensions were quantitatively additive (Biber et al., 2018). The methods we used to evaluate biodiversity, sustainable wood production, and carbon sequestration at forest landscape levels were possible due to the standardization of CSA model outputs outlined above. Standardization allowed us to collate comparable estimates for outcome variables from all CSAs.

Biodiversity

Our primary aim was to provide a means of contrasting important forest features for biodiversity across biogeographical regions in a way that was readily interpretable, and considered fair, by all those involved. Thus, for assessing forest biodiversity, we used a rule-based approach modified from Biber et al. (submitted). This method estimates a forest landscape's biodiversity based on a range of forest compositional and structural variables of demonstrated importance to forest biodiversity (Felton et al., 2016b). These variables, calculated as area-weighted mean stand values at the landscape scale were (i) the amount of coarse deadwood, (ii) tree species diversity, and (iii) the abundance of big trees. Coarse deadwood was measured in m^3/ha, and the abundance of big trees was expressed as the volume (m^3/ha) of trees with a diameter at breast height of 60 cm or more. The importance of deadwood (Müller and Bütler, 2010; Ranius et al., 2018) tree species diversity (Gamfeldt et al., 2013; Ampoorter et al., 2020) and large trees (Lindenmayer and Laurance, 2017) to the conservation of forest biodiversity is supported by reviews of the available empirical data.

Defining what constitutes a "big" tree is challenging because it is an ecosystem- and tree species-dependent concept, for which definitions vary even among researchers working within the same region, and depending on whether scientific or legal requirements are considered (Lindenmayer and Laurance, 2017). So for our purposes, we erred on the side of caution and consistency across CSAs, and chose a threshold size limit that was securely within a tree size range demonstrably beneficial for biodiversity regardless of which biogeographical region was under consideration (Lindenmayer et al., 2012; Felton et al., 2017). Concurrently, this threshold was below that commonly used in Europe for maximum target diameter cutting [i.e., 70–80 cm dbh (Vandekerkhove et al., 2018)], to allow for the potential presence of such trees even in commercially harvested forests. Whereas, some tree species may be sufficiently old to begin producing key features of importance to biodiversity (tree hollows, large crowns, large branches, deep bark fissures) at smaller diameters and within some regions, e.g., northern Europe (Felton et al., 2010), varying the size threshold by tree species and region to capture this lower limit was considered to potentially add bias and limit the comparative interpretation of outcomes.

In contrast to Biber et al. (submitted), we used the Shannon Evenness (Pretzsch, 2009, p. 280) to measure tree species diversity. We calculated it as

$$E = \begin{cases} \frac{-\sum_{i=1}^{s} p_i \cdot \ln(p_i)}{\ln(s_{\max})} & if\ s > 1 \\ 0 & if\ s = 1 \end{cases} \tag{1}$$

with s being the number of tree species and p_i the volume share of species i. The numerator of the equation for $s > 1$ is the usual unstandardized Shannon diversity index (Shannon, 1948; see also Pretzsch, 2009, p. 279). By dividing it by the natural logarithm of the number of species, which is the maximum Shannon index for the given number of species, we obtained the Evenness. The Evenness is standardized to the interval $[0, 1]$, whereby 1 indicates the maximum diversity that can be obtained from the tree species pool available. This was advantageous because it acknowledges that the potential maximum number of tree species differs considerably among the regions included in this study (e.g., a number of tree species considered "rich" in Northern European landscapes, could still be considered "poor" in some Southern European landscapes). We also took into consideration that different combinations of frame scenarios and forest management scenarios can result in different numbers of tree species within the same CSA. This means that for different scenarios in the same case study the maximum number of species obtained across all scenarios was used for standardization. Thus, to standardize the Shannon index to the Evenness in Equation (1), we used $\ln(s_{\max})$, with $s_{\max}$ as the maximum number of tree species occurring in any simulation run for a given CSA.

Using the species' volume shares p_i, instead of tree number shares, added another advantage: if in a scenario e.g., old monospecific conifer stands are transformed into multispecies forests, the tree number shares of the new species will increase very quickly due to the high number of small trees per unit area. However, as the volume of these small trees is negligible compared to the older trees, tree number shares can overemphasize the actual presence of the newly introduced tree species.

To translate the three input variables into a single biodiversity assessment, we applied the fuzzy logic rule system developed by Biber et al. (submitted). The full rule system is graphically shown in **Table 3**. To illustrate, one rule from **Table 3** reads as follows: "*IF the coarse deadwood amount is low AND the volume of big trees is low AND the Evenness is high, THEN the biodiversity is medium.*"

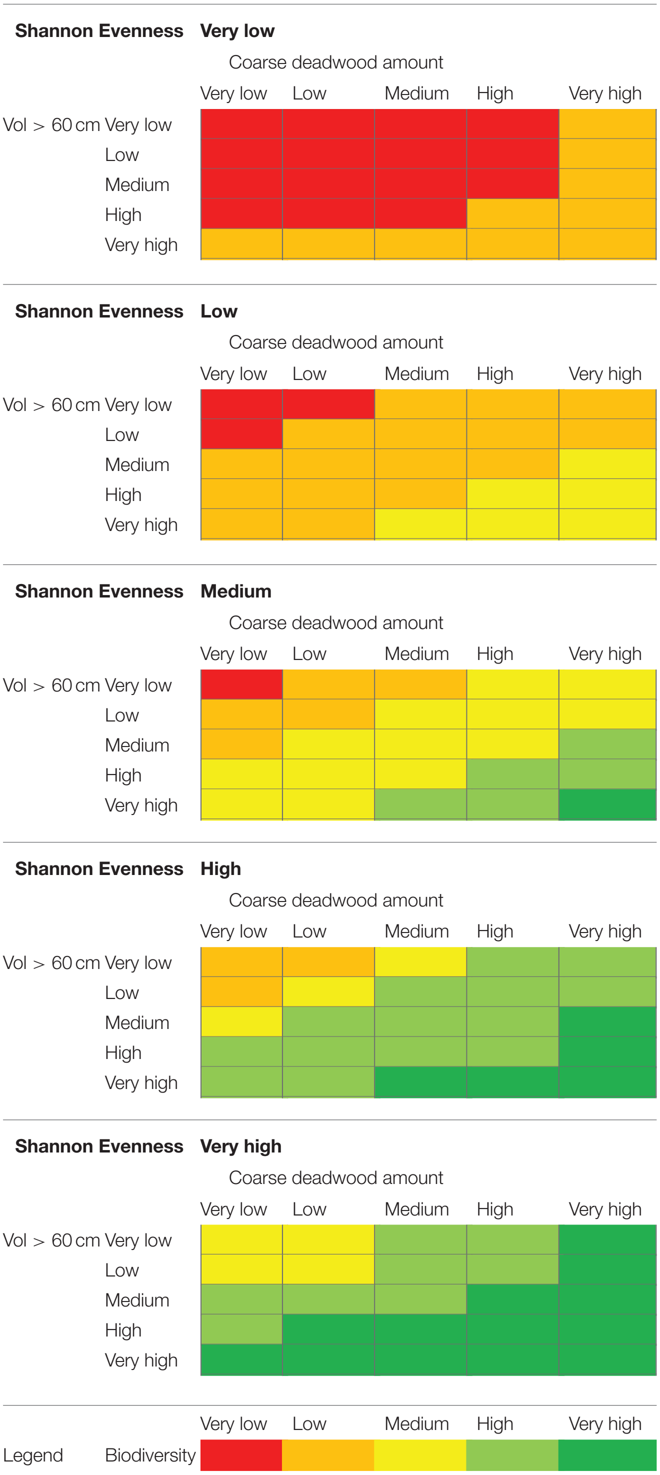
All input variables are mapped to the categories *very low*, *low*, *medium*, *high*, and *very high* by way of equally spaced overlapping triangular fuzzy sets, and the output—the assessed biodiversity–is mapped to the range $[0, 1]$, with 0 being *very low* and 1 representing *very high* [see Biber et al. (submitted) for details]. For coarse deadwood, the typical values for very low and very high were 0 and 50 m^3/ha, respectively [taking into account evidence based recommendations for Europe by Müller and Bütler (2010)]; the same range for the volume of big trees was 0 and 50 m^3/ha (adjusting downwards the levels assumed by Biber et al. (submitted), which were made specifically for highly productive forest sites), and for the Evenness these extremes were given by their natural range [0, 1].

While the use of fuzzy logic for assessing the provision of ecosystem services is discussed in detail by Biber et al. (submitted), we should mention here that fuzzy logic has already demonstrated its usefulness in numerous fields where human evaluation and assessment processes are to be mimicked (Reynolds et al., 2014; Marto et al., 2018). As such, it is highly useful in situations where expert knowledge is used for assessment purposes. The rule system laid down in **Table 3** is based on expert knowledge provided by contributing authors who are forest biodiversity specialists.

Sustainable Wood Production

To assess sustainable wood production, another fuzzy logic evaluation system developed by Biber et al. (submitted) was

TABLE 3 | Fuzzy rule set for biodiversity assessment (modified after Biber et al., submitted).



Shannon Evenness Very low

	Coarse deadwood amount				
	Very low	Low	Medium	High	Very high
Vol > 60 cm Very low	🟥	🟥	🟥	🟥	🟧
Low	🟥	🟥	🟥	🟥	🟧
Medium	🟥	🟥	🟥	🟥	🟧
High	🟥	🟥	🟥	🟧	🟧
Very high	🟧	🟧	🟧	🟧	🟧

Shannon Evenness Low

	Coarse deadwood amount				
	Very low	Low	Medium	High	Very high
Vol > 60 cm Very low	🟥	🟥	🟧	🟧	🟧
Low	🟥	🟧	🟧	🟧	🟧
Medium	🟧	🟧	🟧	🟧	🟨
High	🟧	🟧	🟧	🟨	🟨
Very high	🟧	🟧	🟨	🟨	🟨

Shannon Evenness Medium

	Coarse deadwood amount				
	Very low	Low	Medium	High	Very high
Vol > 60 cm Very low	🟥	🟧	🟧	🟨	🟨
Low	🟧	🟧	🟨	🟨	🟨
Medium	🟧	🟨	🟨	🟨	🟩
High	🟨	🟨	🟨	🟩	🟩
Very high	🟨	🟨	🟩	🟩	🟢

Shannon Evenness High

	Coarse deadwood amount				
	Very low	Low	Medium	High	Very high
Vol > 60 cm Very low	🟧	🟧	🟨	🟩	🟩
Low	🟧	🟨	🟩	🟩	🟩
Medium	🟨	🟩	🟩	🟩	🟢
High	🟩	🟩	🟩	🟩	🟢
Very high	🟩	🟩	🟢	🟢	🟢

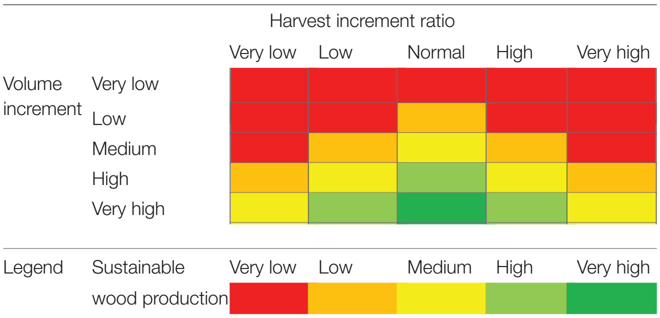
Shannon Evenness Very high

	Coarse deadwood amount				
	Very low	Low	Medium	High	Very high
Vol > 60 cm Very low	🟨	🟨	🟩	🟩	🟢
Low	🟨	🟨	🟩	🟩	🟢
Medium	🟩	🟩	🟩	🟢	🟢
High	🟩	🟢	🟢	🟢	🟢
Very high	🟢	🟢	🟢	🟢	🟢

		Very low	Low	Medium	High	Very high
Legend	Biodiversity	🟥	🟧	🟨	🟩	🟢

The rule set consists of five matrices, each one for a fuzzy value of the Shannon Evenness (very low, low, medium, high, very high). Each matrix combines the volume of trees with dbh > 60 cm with the coarse deadwood amount (using the AND operator). The color codes "red", "orange", "yellow", "green", "dark green" represent the biodiversity assessments "very low", "low", "medium", "high", and "very high", respectively". More explanations in the text.

TABLE 4 | Fuzzy rule set for the assessment of sustainable wood production (according to Biber et al., submitted).



		Harvest increment ratio				
		Very low	Low	Normal	High	Very high
Volume increment	Very low	🟥	🟥	🟥	🟥	🟥
	Low	🟥	🟥	🟧	🟥	🟥
	Medium	🟥	🟧	🟨	🟧	🟥
	High	🟧	🟨	🟩	🟨	🟧
	Very high	🟨	🟩	🟢	🟩	🟨

		Very low	Low	Medium	High	Very high
Legend	Sustainable wood production	🟥	🟧	🟨	🟩	🟢

The rule set consists of a matrix which combines the annual wood volume increment per unit area with the ratio of harvest and increment. In this rule system, all combinations use the AND operator. The color codes "red", "orange", "yellow", "green", "dark green" represent the sustainable wood production assessments "very low", "low", "medium", "high", and "very high", respectively".

applied. Here the periodic annual volume increment (of each 10 year simulation period) at landscape level was used to determine the amount of wood currently produced in the forest landscape, whereas the harvest increment ratio (i.e., the ratio of wood harvested and the volume increment from the same period) indicated the sustainability of wood production. The more this ratio deviates from 1, the less sustainable the situation is, either due to over- or underharvesting. While the non-sustainable aspect of overharvesting is self-evident, underharvesting also must be considered unsustainable, as it does not utilize the forest landscape's potential and leads to overly dense, instable, calamity-prone stands, which limits the choice of future silvicultural options for decades [see the extensive review provided by Cameron (2002)]. The concept of the evaluation is that the absolute increment defines the potential level of sustainable production, while an unsustainable harvest-increment ratio moves the forest landscape away from that level. The corresponding fuzzy rule system is shown in **Table 4**. Whereas, this follows the same approach as the biodiversity assessment (e.g. *IF volume increment is high AND harvest increment ratio is normal, THEN sustainable wood production is high*), in this case it is much shorter as only two input variables are taken into account (volume increment and harvest increment ratio). Just as with biodiversity, both input variables are mapped to the categories *very low*, *low*, *medium/normal*, *high*, and *very high* (typical very low, low, medium, high, and very high volume increments: 0, 4, 8, 12, and 16 m^3/ha/a; typical very low, low, normal, high, and very high harvest increment ratios: 0, 0.5, 1, 1.5, 2) by equally spaced overlapping triangular fuzzy sets, and the resulting assessment of sustainable wood production is mapped to the range $[0, 1]$, with 0 being *very low* and 1 representing *very high* [see Biber et al. (submitted) for details].

Carbon Sequestration

We used a generic tool for calculating carbon sequestration and carbon balancing, that was developed by P. Biber and K. Black (Biber et al., 2018). Its application is described in detail in

Schwaiger et al. (2019). This software tool can be applied *post hoc* to the output data of forest simulation models. The most important information required includes, timelines of growing stock, species shares, annual increments, harvest amounts and how these are split into main assortments and the amount of wood remaining in the forest. Dead wood and product stocks are dynamically calculated based on typical, and adjustable, half-life times. This software traces the most important carbon stocks in the forest (including above and below ground living tree biomass and deadwood), wood usage and wood products as well as carbon emission savings due to the usage of wood instead of other materials. This enables an encompassing approach to carbon balancing, which includes carbon found in the forest itself, the related wood products, and emission savings, while ensuring the avoidance of double counting.

While the framework provided by this carbon balancing tool is generic, it allowed numerous parameters to be adjusted to the requirements of a CSA. Most importantly (but not exclusively) such adjustments related to the shares of different harvested wood assortments being attributed to different kinds of use (energetic, pulp, wood-based-products, sawn wood), half-life times of wood products, and shares of harvest residuals that remain in the forest (see Schwaiger et al., 2019 for more details). For this study, we used the mean annual total carbon balances for each 10 year simulation period. "Total" meant that the balance included the whole system forest-wood products-emission savings. These annual balances were expressed in tC per ha forest area, which also included the wood product stocks related to that area. Positive values indicated a net carbon uptake, while negative values indicated net carbon release.

Compared to the carbon stocks mentioned above, the soil-bound carbon stocks and their balances are of less importance to modeling outcomes, especially in relation to the extensive effort required for their inclusion. However, soil-bound carbon could not be neglected for the Irish and the Lithuanian case study where the mineral soil is mostly covered by a thick organic layer. In the Irish case we subtracted 0.91 t/ha/a from all the annual balances obtained with our model, in order to represent the C emissions from organic soils. This value was derived from the UNFCCC greenhouse gas inventory (Duffy et al., 2020). For the Lithuanian case study we applied the IPCC guidelines' default soil carbon emission rate for this region of 0.68 t/ha/a for organic soils in cold wet temperate conditions, plus 0.31 t/ha/a for C runoff; amounting to soil carbon losses of 0.99 t/ha/a (Intergovernmental Panel on Climate Change (IPCC), 2006).

RESULTS

Here we present the results for the three target variables of this study, sustainable wood production, biodiversity, and carbon balance. Additional information beyond that presentable in this publication, including the simulated development of all input variables for each CSA, is freely available online (Biber et al., 2019).

Country Specific Results

We display the CSA results (roughly clockwise by cardinal direction, starting in the North) with a standard set of three "trade-off" diagrams. We explain this setup using the results from Sweden as an example (**Figure 2**). In order to visualize the four-dimensional relationship of biodiversity, sustainable wood production, carbon balance, and time in an interpretable way, we prepared three two-dimensional diagrams per CSA. Each diagram plots two of our three variables against each other, thus covering all possible combinations of two. Inside each diagram we plotted the time trajectory of the particular variable combination (a so-called "phase diagram"). We marked the starting point (initial time) with a • symbol and the endpoint (final time) with a ▲. This allowed the development of all variables to be followed in relation to each other over time, and possible trade-offs and synergies to become visible, even if they are only temporary. In these diagrams the variables "biodiversity" and "sustainable wood production" obtained from the fuzzy logic assessments were scaled over the range [0, 1], with the extremes "very low" at 0, "very high" at 1, and "medium" in the middle. In contrast, we scaled the carbon balance from −3 to +3 tC/ha, which was slightly wider than the most extreme range we obtained from the analyses. As a result, values near the center of a diagram showed either medium values (for the fuzzy based variables) or a neutral total carbon balance. Values in the upper right quadrant indicated above average values of both displayed variables, with the opposite indicated by values in the bottom left quadrant. The upper left quadrant indicated good values for the y-axis variable and less desirable ones for the x-axis variable, with the bottom right quadrant showing the opposite.

Sweden

For Sweden, the simulations started with sub-optimum biodiversity, and middle to low sustainable wood production (**Figure 2**, left). Sweden applied a different forest management scenario with each global frame scenario (**Table 2**), with the reference and the EU bioenergy scenarios aimed for more diversified forest management, and the global bioenergy scenario mainly focused on wood production. This was reflected by the Reference pathway, which ended with quite high biodiversity and with small increases in sustainable wood production (**Figure 2**, left). The EU bioenergy trajectory followed almost the same path but ended slightly less advanced. The global bioenergy scenario substantially increased sustainable wood production, as well as biodiversity. However, biodiversity increased significantly less than in the other two scenarios. As **Figure 2** (middle) shows, this comparably small gain in biodiversity in the global bioenergy scenario came with the steepest drop in carbon sequestration from about 1.5 down to 0.5 tC/ha/a. The other two scenarios showed only a slight decline in the C-balance with increasing biodiversity; in the reference scenario it fully recovered to the highest biodiversity level of all scenarios. When sustainable wood production and the carbon balance were plotted against each other (**Figure 2**, right), the intuitively expected correlation between both did not occur. The moderate increase in sustainable wood production in the reference and the EU bioenergy scenarios was achieved with no or only a

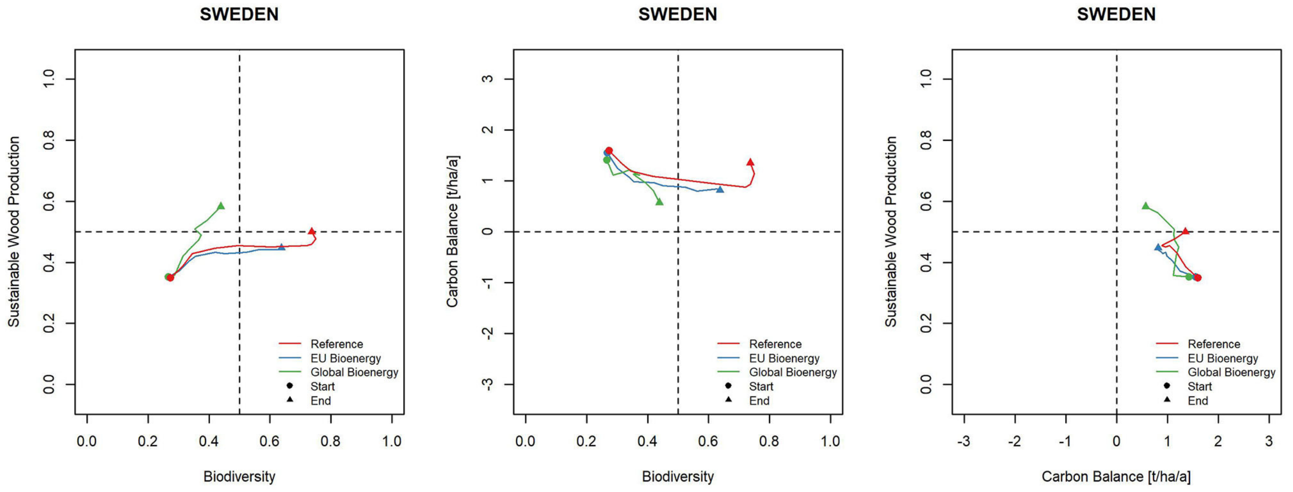


FIGURE 2 | Trade-off diagrams for Sweden.

slight loss in net carbon sequestration, while the carbon balance ended up lowest in combination with the highest sustainable wood production in the global bioenergy scenario. Increasing forest product stocks and C-emission avoidance effects could not compensate for lower C-stocks in the forest, due to lower average stand volumes.

Lithuania

For the Lithuanian case study two different silvicultural concepts were applied under all three global frame scenarios (**Table 2**). One strived to maximize financial benefits from the forest, while the other one moderately increased the share of deciduous species, while the conifers remained important. As all diagrams in **Figure 3** show, there was almost no difference among the scenarios (i.e. close overlap in the trajectories), as all managed to substantially increase sustainable wood production from low values to intermediate ones (**Figure 3**, left). The runs which introduced more deciduous species ended up with slightly higher biodiversity scores, but the difference was negligible. Comparing the carbon balance and biodiversity (**Figure 3**, middle), the carbon balance increased from about −1 tC/ha/a, up to only slightly negative and neutral values, without impairing biodiversity, which remains low. The C-balance and sustainable wood production (**Figure 3**, right) were related in such a way that, for all scenarios, the substantial increase in the carbon balance occurred quite early, prior to the substantial increase in wood production. The latter was accompanied by a slight reduction in the C-balance.

Ireland

In the Irish case study, one silvicultural scenario was applied to all three global frame scenarios (**Table 2**). The goal was profit maximization with the caveat of certain environmental constraints that included bog restoration and increased native broadleaf species. Biodiversity under these conditions remained low, at the long-term expense of sustainable wood production which, after an intermediate maximum, drops down to low values (**Figure 4**, left). Differentiation among the global frame scenarios was hardly visible. As **Figure 4** (middle) shows, the carbon balance dropped steeply down from about 2 tC/ha/a, before stabilizing around −0.5 tC/ha/a; whereas biodiversity again remained constant. With respect to the trajectory of sustainable wood production vs. carbon balance, a spiraling pattern with initially high amplitudes but distinct stabilization was observed (**Figure 4**, right). An early increase in wood production came with a strong decrease in C-sequestration, which continued even as wood production decreased again. In the later phases of the simulation, both values oscillated around small negative carbon balances and low sustainable wood production.

The Netherlands

For the Dutch case study, five silvicultural scenarios were calculated, one fitting to the EU bioenergy frame scenario, and two each for the reference and the global bioenergy scenarios (**Table 2**). The reference frame scenario was covered with two analogous silvicultural scenarios (slightly adapted current management), under the gfdl (Geophysical Fluid Dynamics Laboratory) and hadgem (Hadley Centre Global Environmental Model) 8.5 climate scenarios. Global bioenergy was covered in a similar way but with a silvicultural focus on local sustainability and bioenergy, as combined with gfdl and hadgem 2.6 climate scenarios. For the EU bioenergy frame scenario, only one run was simulated. It had a silvicultural focus on wood production that was combined with the hadgem 4.5 climate scenario.

In contrast to the case studies shown before, the Dutch case study started and remained at a high level of biodiversity (**Figure 5**, left and middle). As also seen in previous case studies, differentiation among the global frame scenarios in the Dutch case study is not pronounced. Virtually unconnected to the biodiversity response, sustainable wood production started at a low to moderate level, rose to moderate, before falling back to below the initial value (**Figure 5**, left). When looking at the

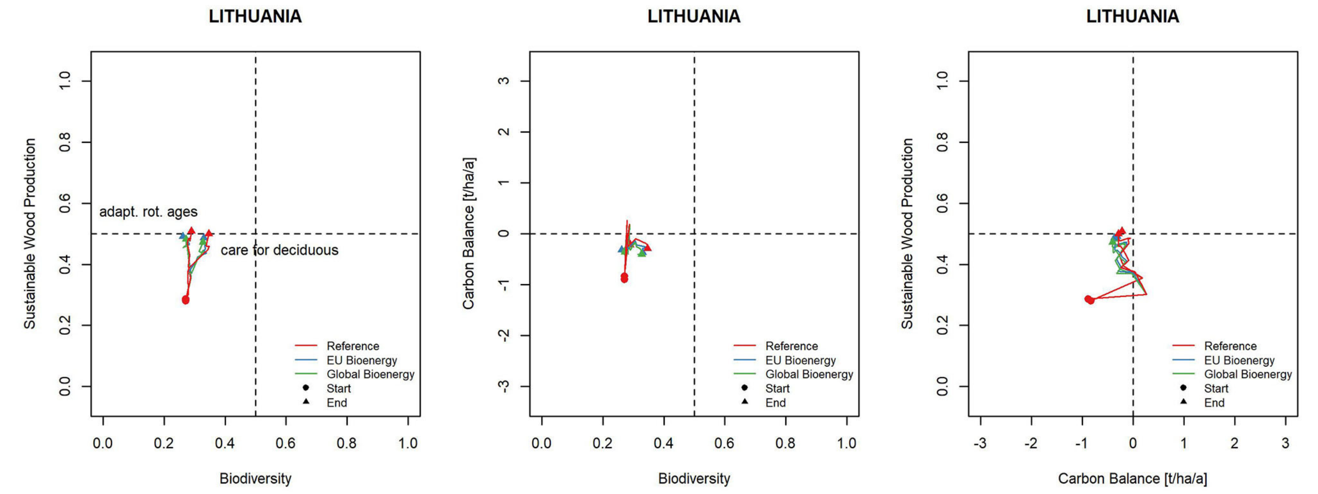


FIGURE 3 | Trade-off diagrams for Lithuania. The forest management scenarios “adaptive rotation ages” and “care for deciduous” are labeled in the left diagram.

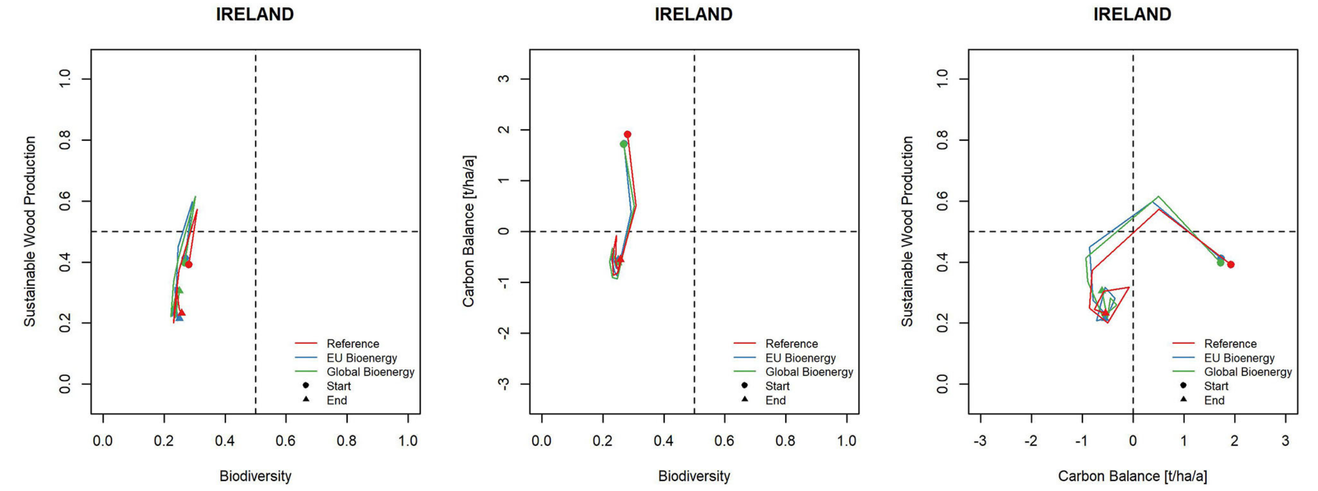


FIGURE 4 | Trade-off diagrams for Ireland.

carbon balance in relation to biodiversity (**Figure 5**, middle), all scenarios remained at high levels, even though there was a tendency to lower carbon balances at the end of the simulations. Relating the carbon balances to sustainable wood production (**Figure 5**, right), a positive correlation was visible, comprising the above-mentioned tendencies of both variables, with the global bioenergy related scenarios resulting in the smallest ranges.

Germany

In Germany, two case study areas were investigated, namely the north-eastern German case study “Lieberose-Schlaubetal, Neuzelle” (LSN), and the southern German region “Augsburg Western Forests” (AWF). The former was dominated by Scots pine (*Pinus sylvestris* L.) stands on low-growth sites, whereas the latter was dominated by Norway spruce (*Picea abies* (L.) H.KARST.) on productive sites. For the CSAs and global frame scenarios, three silvicultural scenarios were calculated, namely “Multifunctional”, “Production”, and “Set aside” (**Table 2**). Whereas, the “multifunctional” scenario involved establishing uneven-aged mixed stands, and the “production” scenario attempted to maximize wood production using conifer plantations, the “set aside” scenario simply maximized nature protection by stopping active forest management.

Considering the northeast case study (LSN) first (**Figure 6**, upper panel), differentiation among the frame scenarios was as low as for the previously shown case studies. In terms of the silvicultural scenarios, the set aside scenario stood out from the others. Considering biodiversity and sustainable wood production (**Figure 6**, upper panel, left), these started at very low and low values and remained as such for the whole simulation time span. The trajectories for the

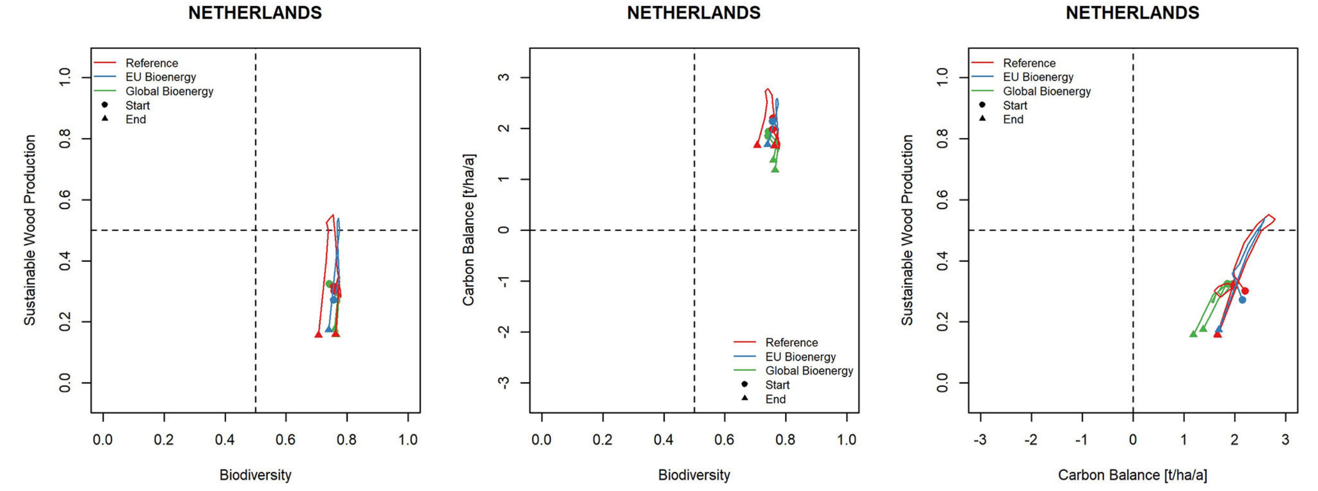


FIGURE 5 | Trade-off diagrams for the Netherlands.

multifunctional and the production-oriented scenarios were hard to tell apart. While almost no change in biodiversity occurred (remained at a low level), sustainable wood production fluctuated between low and medium, with the production scenario ending with higher production than the multifunctional forest scenario. Notably, the production forest scenario ended with very low biodiversity in the global bioenergy scenario. In all scenarios, carbon sequestration fell from values of >1 tC/ha/a, down to neutral or almost neutral values, while biodiversity remained virtually constant except for the global bioenergy effect mentioned above (**Figure 6**, upper panel, middle). When considering the carbon balance and sustainable wood production (**Figure 6**, upper panel, right), the set aside scenario resulted in very low sustainable wood production over the entire time span, while the carbon balance reduced with time. However, the net carbon uptake in the set aside scenarios remained higher over the long run than in all management scenarios. Despite no harvest taking place under the set aside conditions, sustainable wood production did not have a zero value. This reflected the fact that wood was produced within these "reserves," even though it was not harvested (categorized as not sustainable). While arriving and stabilizing at approximately neutral C-balances, the production forest scenarios managed to do so with an oscillating but on average increased sustainable wood production, while the wood production under multifunctional management remained at a relatively lower level.

The most pronounced differentiation among silvicultural scenarios inside any case study was evident for the southern German case study area "Augsburg Western Forests" (AWF, **Figure 6**, lower panel). Most noticeable were the strong oscillations of the production scenarios in all diagrams. These oscillations resulted from an uneven age-class distribution, which was not dampened by the silvicultural actions. Considering biodiversity and sustainable wood production (**Figure 6**, lower panel, left), the production scenario led—despite oscillations—to the lowest levels of biodiversity, especially in the global bioenergy scenario. Sustainable wood production was low to intermediate in phases of low harvest and high at times where high harvest volumes coincided with high volume increment. In the multifunctional forest, sustainable wood production remained stable at an intermediate to high level, with biodiversity consistently increasing from intermediate to high. The least movement was visible for the set aside scenarios where biodiversity remained at high levels, and sustainable wood production was low to intermediate. The latter resulted from high volume increments which were not harvested, and accumulated in the forest (categorized as a low degree of sustainability). Relating the carbon balance against biodiversity, similar patterns were obtained (**Figure 6**, lower panel, middle). At intermediate to low biomass levels, the carbon balance oscillated between almost −3 and 3 tC/ha/a. The most negative values occurred at times when a surplus of mature stands was harvested; the opposite was the case when high increment met low harvesting, leading to rapid C-accumulation in the forest. With increasing biodiversity, as mentioned before, the multifunctional scenarios showed a quick initial reduction in the C-balance, followed by a stabilization at about 1 tC/ha/a. Detailed analyses revealed that this was almost exclusively from substitution effects, due to the use of wood instead of other materials. A consistent decrease in the C-balance without any stabilization was evident for the set aside scenarios, accompanied by biodiversity remaining at a high level. Remarkably though, the multifunctional approach caught up with these biodiversity values in the long run. More than the other diagrams, **Figure 6** (lower panel, right) revealed a tendency toward higher sustainable wood production over the longer term in the production forest scenarios, while the C-balance oscillated without any clear tendency. The trajectories of the production scenarios formed a loop in the quadrant of high wood production and high carbon balances, which enclosed the entire trajectories obtained for multifunctional management. This indicated stability in multifunctional management at a high constant level. For the set aside scenario, wood

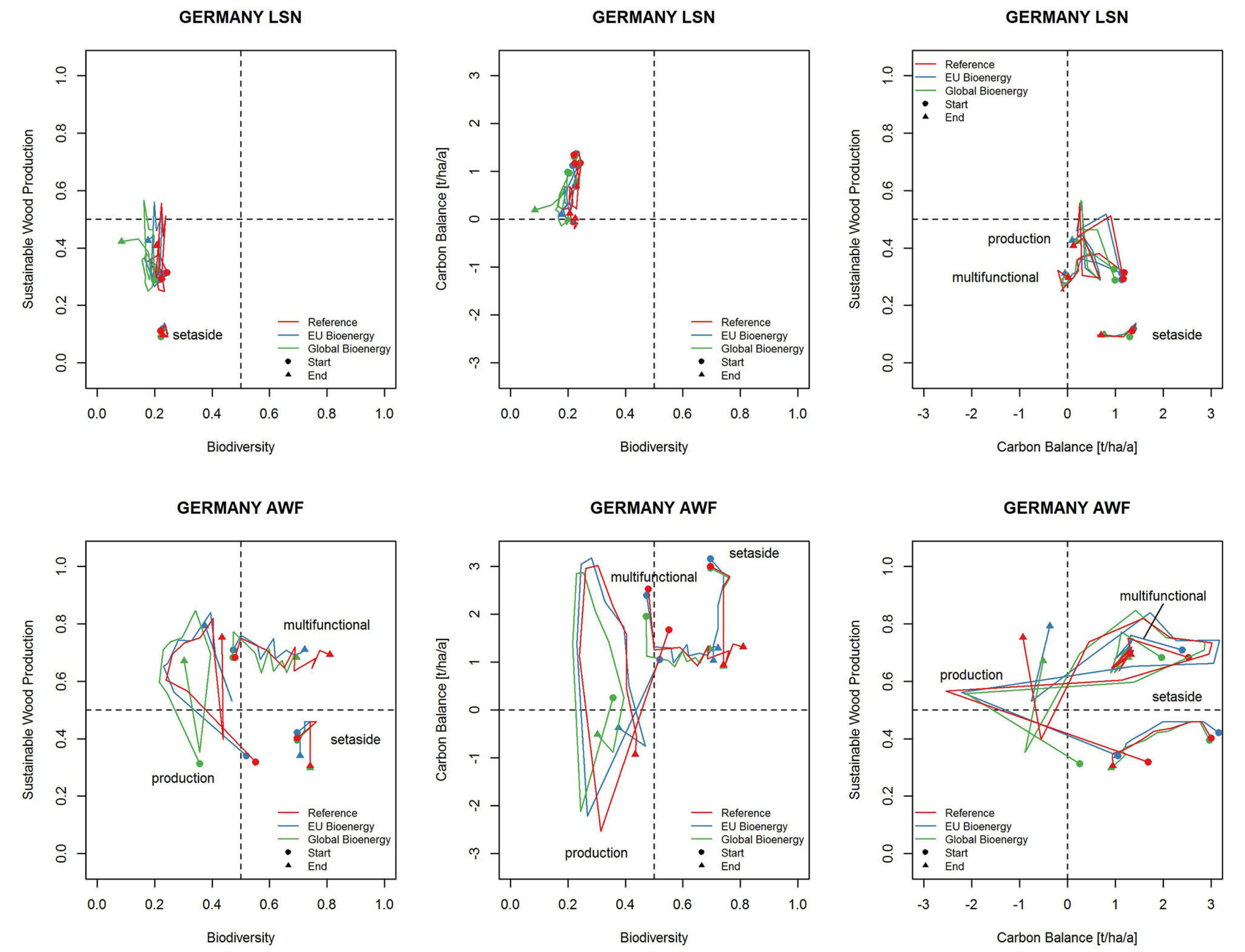


FIGURE 6 | Trade-off diagrams for the two German case studies. Upper panel: Northeast German case study “Lieberose-Schlaubetal, Neuzelle” (LSN). The trajectories of the “set aside” scenarios are labeled in the left and rightmost diagram. In the latter, also the multifunctional and production scenarios are marked. Lower panel: Southern German case study “Augsburg Western Forests” (AWF). The trajectories of all three silvicultural scenarios (multifunctional, production, and set aside) are labeled.

production fell down from medium to low levels along with a decreasing positive carbon balance. This indicated that high amounts of wood are produced “on reserve,” storing high amounts of C in the forest. This happened, however, with a decreasing trend, as the stands approached their maximum standing volume.

Slovakia

For Slovakia, two silvicultural scenarios were available inside each frame scenario. The first (“conservative”), was based on business as usual approaches whereby management objectives were mainly determined by site conditions and the species composition of the forest. The other one (“liberalized”), was based on liberalized planning approaches whereby the management objectives depended mainly on the decisions of forest owners. The liberalized management scenario represented a very innovative management option in a former socialist country. In spite of the large conceptual differences in the management scenarios compared, a very small differentiation among the silvicultural scenarios was registered from the landscape perspective of the study (**Figure 7**). In addition, **Figure 7** showed certain reactions of the goal variables to the frame scenarios, but no clear distinct effects (careful consideration of the graphs shows a somewhat smaller distance of the end-points among the silviculture scenarios than among the frame scenarios. This was mainly caused by the outlying reference scenario). The average biodiversity remained low and almost invariable, while sustainable wood production varied slightly in the low/intermediate zone with a decrease in the Reference scenario and an increase in the others (**Figure 7**, left). Very similarly, the total carbon balance was stable, oscillating slightly around 0.5 tC/ha/a without any visible correlation with biodiversity (**Figure 7**, middle). The same stability occurred when the carbon balance was compared with sustainable wood

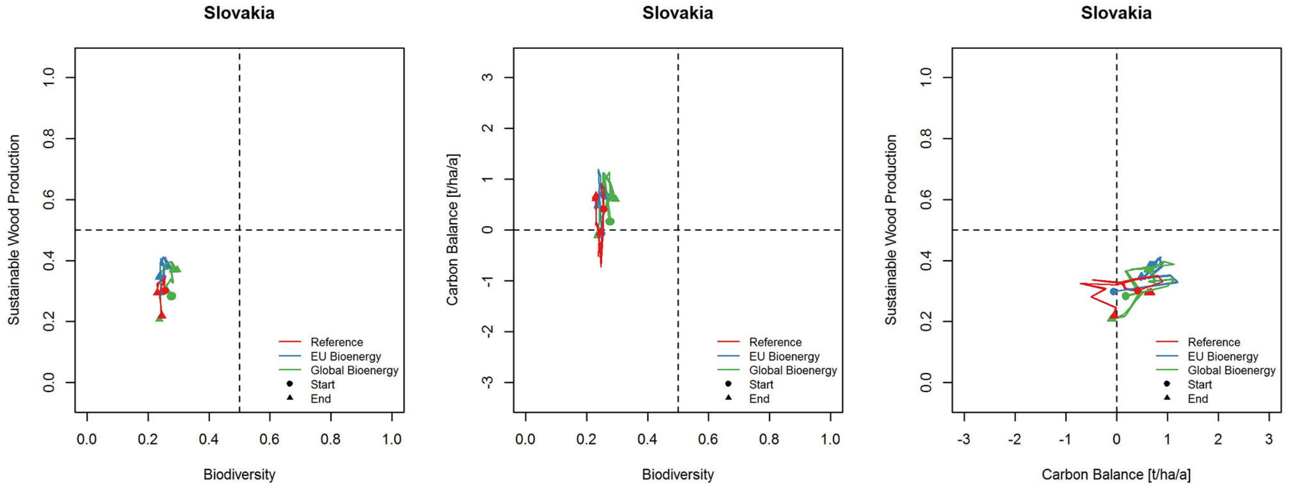


FIGURE 7 | Trade-off diagrams for Slovakia.

production (**Figure 7**, right). The amplitudes were so small that potential correlations would not play a decisive role.

Italy

As indicated in the methods section, the Italian case study was an exception insofar as no data were available that allowed us to evaluate biodiversity with the approach shown above. Therefore, only sustainable wood production and the carbon balance could be evaluated (**Figure 8**). There were two different silvicultural scenarios, each of which was applied in combination with all three frame scenarios (**Table 2**). The first silviculture scenario introduced close-to-nature forestry with the goal of maintaining biodiversity while improving recreational and cultural forest functions. The second scenario applied uniform shelterwood in important hardwood stand types, while transforming coastal forests into holm oak (*Quercus ilex* L.) coppice with standards. As **Figure 8** shows, the scenario differentiation was remarkably small. All trajectories moved around low to medium sustainable wood production with C-balances mostly between 0.5 and 1.0 tC/ha/a. The only exception was for the scenario with a constant high carbon balance and an increasing trend in wood production. This was the uniform shelterwood scenario in the Global Bioenergy frame scenario. The high wood demand in this frame scenario seemed to induce the strongest reaction from silviculture in terms of increased production.

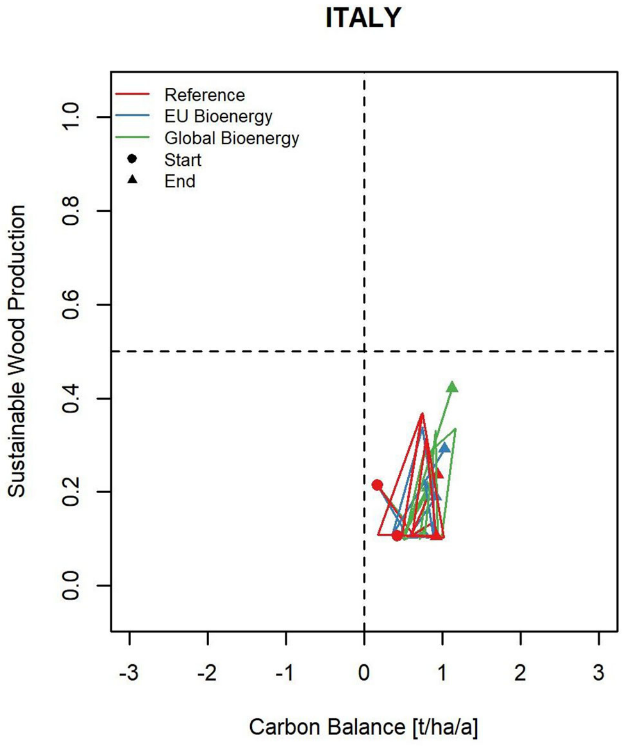


FIGURE 8 | Trade-off diagram for Italy. For the Italian case study, no data were available for the assessment of biodiversity based on this study's approach. Thus, only the trajectories for sustainable wood production and the carbon balance can be shown.

Portugal

In the Portuguese case study, a multifunctional silvicultural concept was applied (**Table 2**), which attempted to provide regulatory (wildfire resistance), cultural services, biodiversity, erosion control and wood production, within a spatially optimized approach (cf. Marto et al., 2019). Due to a lack of appropriate climate data for the Portuguese DSS, only the Reference and the EU Bioenergy frame scenarios were covered (**Figure 9**). While the frame scenarios did not make a large difference to outcomes, the silvicultural treatment resulted in interesting patterns. While for all three variable combinations the start and the endpoints did not vary extensively, there were wide fluctuations and clear correlations along the intervening path. As **Figure 9** (left) showed, sustainable wood production and biodiversity both co-fluctuated between low and intermediate levels. This happened with a clear linear-like correlation;

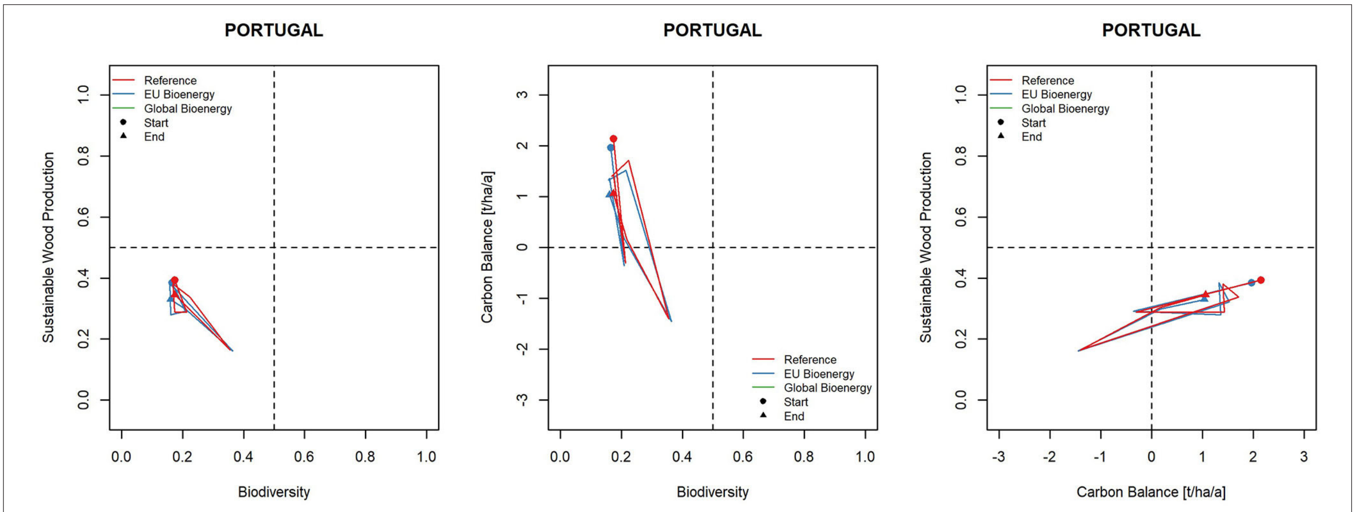


FIGURE 9 | Trade-off diagrams for Portugal.

intermediate biodiversity only occurred with low sustainable wood production and vice versa. The relatively low levels of assessed biodiversity resulted from the absence of large trees (>60 cm) as well as from the very small amounts of coarse dead wood, both resulting from silvicultural practices.

Stronger than that found in most other case studies, the total carbon balance correlated positively with sustainable wood production; the latter varying widely between −1 and +2 tC/ha/a, but mostly staying within the positive zone (**Figure 9**, right). Consequently, biodiversity correlated negatively with the total carbon balance (**Figure 9**, middle).

Turkey

In the Turkish case study, a multifunctional silviculture concept, which included continuous cover forestry as an alternative forest management scenario, was applied in all three global frame scenarios (**Table 2**). With no considerable frame scenario differentiation, we saw a slight increase in sustainable wood production (from very low to still low levels) along with a considerable increase in biodiversity (from low to intermediate, **Figure 10**, left). The main driving factor for the increased biodiversity in the Turkish case study was the increased abundance of big trees. This was due to an ongoing conversion from coppice to high forest while maintaining the existing set of production tree species.

This development, however, came with a decrease in the total C-balance, from about 1.5 down to 1.0 tC/ha/a, despite an increased sustainable wood production (**Figure 10**, middle). The decrease of the C-balance came in parallel with an age class shift toward younger stands at the end of the simulation period. Thus, whereas wood production and biodiversity were positively correlated, and the correlation between biodiversity and carbon sequestration was negative, a negative correlation between wood production and carbon sequestration was evident in **Figure 10** (right).

Synopsis

With **Table 5** we provided a synopsis of the results presented above, as visually interpreted correlations between our three target variables–sustainable wood production, biodiversity, and the carbon balance. In general, taking all case studies into consideration, correlations were not clear. Sustainable wood production did not show a clear correlation with biodiversity in either direction. In the case of Sweden and Turkey there seemed to be a positive relationship, while a negative correlation between both was evident in Portugal, as a consequence of the importance of eucalypt plantations to the sustainability of the overall timber supply. Additional correlations existed between sustainable wood production and the carbon balance. Positive correlations occurred in Ireland, the Netherlands, Portugal, Lithuania, where higher wood production meant more C-sequestration. However, there were also tendencies toward negative correlations in Sweden and Turkey. Correlations between carbon balance and biodiversity were also inconsistent. In six out of nine cases no correlation occurred, with the only identified correlations being negative (Portugal, Turkey, Sweden). Nevertheless, in the case of Portugal, this was explained by the importance of eucalypt plantations for both wood supply and C-sequestration, and its association with lower values of biodiversity.

DISCUSSION

Climate and Forest Management Sensitivity

Across all of the case studies, there were no fundamental differences in the outcomes from the climate scenarios. One could argue that this was due to a lack of sensitivity in the simulation models applied, which is possible, despite the standards demanded (Nordström et al., 2019). However, we deem this explanation unlikely to be the only one, as the models covered a broad range of conceptual types (from statistic

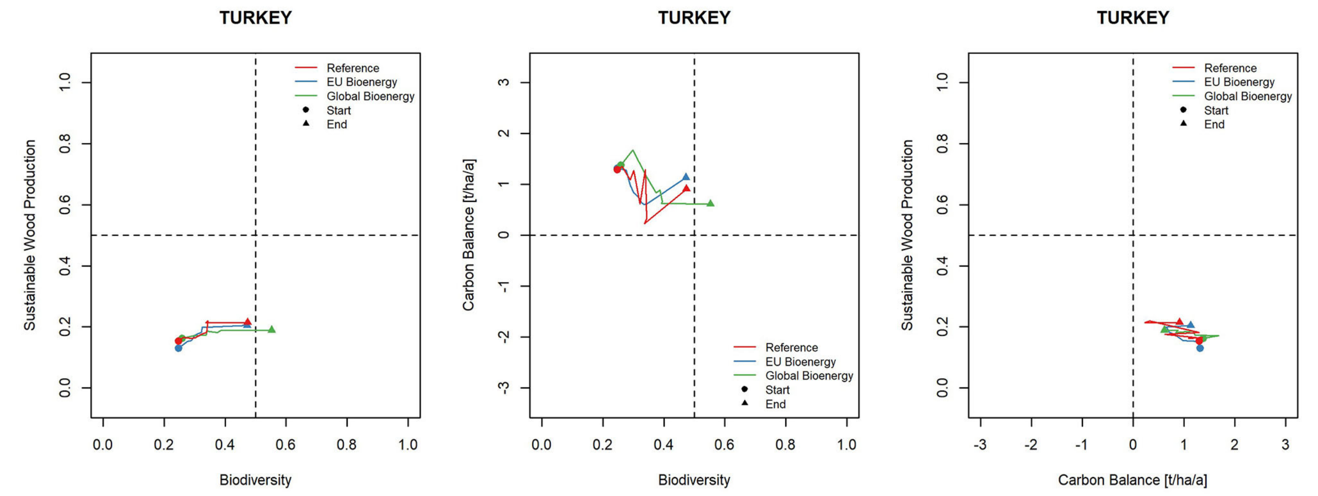


FIGURE 10 | Trade-off diagrams for Turkey.

TABLE 5 | Country-wise correlations between the goal variables of this study, by visual interpretation of the trade-off diagrams (**Figures 2–10**).

Country	Wood vs. Biodiversity	Carbon balance vs. Biodiversity	Wood vs. Carbon balance
Sweden	+	–/0	–/0
Lithuania	0	0	0/+
Ireland	0	0	+
The Netherlands	0	0	+
Germany (LSN)	0	0	0
Germany (AWF)	0	0	0
Slovakia	0	0	0
Italy	n.a.	n.a.	0
Portugal	–	–	+
Turkey	+	–	–

The symbols "+", "–", "0" indicate correlations we interpret as considerably positive, negative, or not existing, respectively. Two symbols separated by a "/" means that both correlation types are observed in different scenarios of the related case study.

and hybrid, to mechanistic models, and from simulation to optimisation). Certainly, this result was also caused by the gradual nature of the temperature increase underlying the frame scenarios, and it can be contrasted with those provided by distinct forest management scenarios. In those case study areas for which several forest management scenarios were developed, the differences among these in biodiversity and ecosystem service outcomes were generally more pronounced than those driven by climate and market differences, as long as the management scenarios were sufficiently different (see below). An exception was Slovakia, where case study specific frame conditions prevented a significant differentiation of management outcomes. But even in the case of Portugal, which reported an optimized version of its generic management concept for both climate scenarios, the contrast between optimal and non-optimal solutions under each climate scenario was greater than the contrast between solutions, i.e., management scenarios across climate scenarios. There was, however, another significant caveat regarding this conclusion. While our models addressed the effects of mean annual climate on forest dynamics, they did not include any changes to the probability of extreme events and disturbances such as wildfires, storms and droughts (Lindner et al., 2010; Clark et al., 2016; Reyer et al., 2017). The combination of both facts in reality is the reason for the seemingly paradoxical situation that we observe accelerated forest growth in large parts of Europe, despite accumulating evidence for increased damage to these forests associated with climate change (Allen et al., 2010; Carnicer et al., 2011; Milad et al., 2011; Lindner et al., 2014; Seidl et al., 2014). The need to address disturbances and extreme events by forest simulation models and DSS is clearly an issue which requires attention in future studies (Reyer et al., 2017). For interested readers, we note that all of the scenarios presented in this study were also evaluated for the provision of regulatory services, i.e., resistance against typical disturbances. However, this information was not available at a generic enough level to be included in this study (see Biber et al., 2019 for these results).

In contrast to the generally small effects of climate, our results suggested, at least in principle, the considerable potential to alter biodiversity and ecosystem service outcomes by varying the silvicultural approach applied. However, this did require substantial differences in the silvicultural approaches used, such as those applied in the southern German case study AWF, to achieve large differences over relatively short time periods. This is due to the pronounced inertia of forest systems, even to altered management regimes; it is not, as could be conjectured, an inherent inertia of our evaluation methods. Notably, the application of the same silvicultural scenarios made much less of a difference when applied to the low-growth region LSN in northeast Germany. If the silvicultural scenarios were relatively similar, or if the area shares of different approaches did not change fundamentally, the inertia of forest landscapes appeared difficult to overcome over the time period considered. Examples of this were the case studies of Italy, Slovakia and Lithuania, for which even seemingly diverse forest management concepts did not substantially alter the provision of the ecosystem services evaluated.

Evaluating Ecosystem Service Provision

While our carbon balancing followed a strictly quantitative approach, the assessment of biodiversity and sustainable wood production was based on expert rules which introduced a subjective element to the evaluations. Whereas the authors tried to incorporate the best scientific knowledge and expert experience available [see also Biber et al. (submitted)], some level of conjecture was unavoidable. In such a context, the transparency of the rule system used is crucial, and this is certainly an advantage of a fuzzy logic approach due to the intuitive formulation of the rule systems (Reynolds et al., 2014).

In addition, due to the standardized requirements of the case studies, our evaluations were limited to a few cornerstone input variables that were only available as landscape level averages. While this provided the overview picture required for this study, it had the potential to obscure more fine-grained results that are of interest to decision makers at the case study and finer level. For example, detailed analyses of the Slovakian case study showed effects of biodiversity-friendly management practices which were not distinguished from the perspective of this study. Likewise, in the Portuguese case study, the inclusion of additional taxa in the biodiversity assessments, such as shrubs and herbaceous plants, was advocated by local experts as a means to improve result outcomes. The reader is encouraged to see the case study specific reports in Biber et al. (2019) for related information.

Another methodological issue were the estimates of tree species diversity, which were of direct relevance to biodiversity assessments. Our approach did not distinguish between the "ecological quality" of the tree species, i.e., species are weighted the same without distinguishing whether they are indigenous, exotic species or even cultured clones. This might bring about over-optimistic biodiversity assessments in silvicultural scenarios which rely on increasing production by introducing non-native and industrially bred species, as was the case in Sweden's global biodiversity scenario. Another point which is beyond our approach are climate-change related shifts in species distributions, and the potential losses to forest biodiversity in this century induced by more extreme greenhouse gas emission scenarios and associated disturbances (Felton et al., 2014; IPBES, 2019). Our study, in its simulation and evaluation methods, is limited to using variables that are available from forest inventories. Tackling this problem, in contrast, required (meta-) population modeling of key plant and animal species in a dynamically changing forest landscape (Wintle et al., 2005).

A Closer Look at the Outcomes

Our outcomes were constructed from two primary components: (i) the static component, i.e., the initial situation (in terms of our target variables) in each case study, including the existing trade-offs and synergies, and (ii) the dynamic component, i.e., the changes observed with simulated forest development. With regard to the static component, virtually all case study areas started at low to moderate biodiversity, combined with low to moderate sustainable wood production. In this regard, low to moderate biodiversity and wood production was associated with high levels of net carbon uptake. Regarding the dynamic component, our results suggested that in most case studies there was not a trade-off between biodiversity and sustainable wood production. This result is supported by recent studies Dieler et al. (2017) and Schulze (2018). We observed almost no reduction in biodiversity indicators associated with an increase in wood production, except in the Portuguese case study. The importance of the eucalypt pulpwood in the overall wood supply explained the trade-off observed in Portugal. Whilst the presence of eucalyptus may be instrumental to generating financial resources which can be used to support set-aside conservation areas, introduced eucalypt stands generally have low inherent biodiversity value (Deus et al., 2018).

In some cases (Sweden, Turkey) synergistic results occurred when diversity was actively promoted as part of the management concept [similar results were obtained by Biber et al. (2015)]. However, due to unbalanced forest age class distributions, we observed relatively large oscillations in ecosystem service provision in some case study areas (Ireland, Portugal, Germany AWF). In most cases, the net carbon uptake was not correlated with biodiversity, indicating that biodiversity-friendly forest management did not necessarily restrict carbon sequestration. However, conflict between biodiversity and carbon sequestration was projected in some case studies (Portugal, Turkey, partly Sweden). We feel these results are supported by a wide-scale review by Huston and Marland (2003), who argue that even win-win situations for C sequestration and biodiversity were possible given careful (spatial) planning.

Notably, we obtained heterogeneous results with respect to the relations between sustainable wood production and net carbon uptake. This was due to several issues: low-intensity forest management with low harvest volumes led to rapidly increasing forest-bound carbon stocks and thus resulted in a high net C-uptake. On the other hand, intensive management with high sustainable harvest levels could also increase carbon stocks in wood products and, even more important in the long run, maintained a high level of C-emission savings due to substitution effects. In addition, the effect of harvest volumes on the net carbon uptake of the whole system (forest, wood products, C-emission savings) depended to a large extent on what wood assortments (pulpwood, roundwood) were harvested, and how they were used (energy, pulp and paper, wood-based products, sawn wood), see Pingoud et al. (2010). Both harvested wood assortment shares and wood usage shares differed among the case study landscapes and management scenarios (Biber et al., 2019). If C-balancing is only considered in relation to the forest-bound C-stocks, a reduction in management intensity will always leads to an increase in the net uptake of C (assuming–forest carbon sinks are not yet saturated). However, we also took into account wood products and emission savings in our modeling. By so doing we see our work as helping to close a gap pointed out by Peckham et al. (2012), in the lack of whole forest system analyses with respect to C-balancing.

When we compared the outcomes for wood production to the wood demand described in the frame scenarios, we found that in almost all case studies production was considerably lower than the demand. Even though a statistical upscaling of the case studies to the EU level was not feasible, this could indicate that achieving the stringent renewable energy goals of the Global Bioenergy scenario is not realistic, or that the actual production potential was not fully utilized even in the production-focused silvicultural scenarios.

Implications

We believe that our study results are relevant to forest management and policy in Europe. Although our case studies were not selected for representativeness in a statistical sense, attention was payed to include circumstances with key properties of relevance at the European level. As the silvicultural scenarios were designed in consultation with the views of powerful stakeholders, they are not just utopian assumptions, but some aspects of them have a considerable chance of being implemented—as indeed, some already are. For practical forest management our results suggest that, at least with regard to wood production, biodiversity, and carbon sequestration, there are more degrees of freedom than may intuitively be assumed. This is certainly an advantage, because it indicates a considerable range of forest management options that do not automatically trade off one of the three ecosystem services against the others. On the other hand, this result highlights the necessity of forest management planning and assessment down to the regional and landscape scale in order to avoid improper generalizations with resulting suboptimal outcomes. Furthermore, this study shows that state-of-the-art optimisation and simulation models and DSSs are available throughout Europe which, however, require enhancement. As mentioned above, a necessary extension that these tools require in the future is to include the effects of extreme events like droughts or storms. Seen across all case studies, our results form a very heterogeneous picture, which indicates the diversity of forest management in Europe and the diversity of pathways along which it is expected to develop in the future. For European forest policy this suggests that strict top down regulations might not be the best approach to optimize ecosystem services provision. As far as forest management is concerned, a policy sometimes called “Europe of the Regions” (Luedtke, 2005) may be advisable.

CONCLUSIONS

We conclude that the potential exists to steer the provision of biodiversity, sustainable wood production, and carbon sequestration from European forests, but this should not be overestimated. If no fundamental changes in silviculture are applied, changes in the provision of these ecosystem services will mostly take decades. Specifically, our results are likely to be optimistic, with respect to climate change associated disturbances, such as storms and extended drought periods, which were not taken into account in our analyses. In relation to European forest policy development, we conclude that subsidiary approaches, that allow regionally tailored solutions, were the most appropriate to optimize ecosystem services provision throughout Europe.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors on reasonable request, without undue reservation.

AUTHOR CONTRIBUTIONS

PB and AF designed the study and wrote the paper. Together with MN and ML who also contributed to writing, they structured and coordinated the study. PB designed the basis version of the ecosystem service evaluation system. PB, AF, MN, and ML adjusted it for the study at hand. KB and PB designed the carbon evaluation tool. All authors provided indispensable simulation data and interpretation. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.547696/full#supplementary-material

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Application of the Conservation Planning Tool Zonation to Inform Retention Planning in the Boreal Forest of Western Canada

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Retention forestry is an approach in which live trees and other components of forest structure are retained within harvested areas. A primary objective of retention forestry is to maintain biodiversity and to hasten post-harvest recovery of forest structure and function. Retention is now a key element in sustainable forest management practices in many regions of the world. However, locating where retention should be placed to best achieve management objectives is a challenging problem, and evidence-based approaches to operational applications are rare. We suggest here that harvest planners could benefit from the use of systematic conservation planning principles and methods to inform retention design. Specifically, we used a conservation planning—or prioritization—tool, Zonation, to create spatially-explicit scenarios of retention harvesting in a boreal mixedwood forest in northwestern Alberta, Canada. Scenarios were informed by several environmental variables related to site productivity; in particular, we used a metric of wetness (depth-to-water from the Wet Areas Mapping algorithm) that is based on airborne lidar-derived terrain models previously shown to correlate with patterns in post-harvest forest regeneration and biodiversity. The nine retention scenarios examined here related to the placement of retention focused to drier, mesic, or wetter sites in combination with other prioritization constraints. Results were compared with an existing harvest plan to assess differences in the spatial pattern of retention (e.g., percent overlapping area, number of patches, size of the patches). We also tested for the homogeneity of forest attributes (e.g., tree species, deciduous density) between scenarios and the existing harvest plan using multivariate dispersion analysis. Our results showed limited commonalities among scenarios compared to the existing harvest plan; they were characterized as having limited spatial overlap, and more and smaller patches with the use of a timber-cost constraint further affecting retention patterns. While modeling results significantly differed from current retention practices, the approach presented here offers flexibility in testing different scenarios and assessing trade-offs between timber production and conservation goals using a standardized conservation planning toolkit.

Keywords: conservation planning, prioritization model, retention, forest management, biodiversity, sustainable forestry

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INTRODUCTION

Disturbances are major drivers of forest structure and composition. In forests of western Canada managed for the production of timber, pulp, and other forest products, harvesting is one of them. Intensive forest management, which strongly emphasizes fiber production over other values, can threaten biodiversity by simplifying forest structure and composition at multiple scales, thereby reducing habitat and species diversity (Puettmann et al., 2009; Gustafsson et al., 2012; Venier et al., 2014). Retention has become an important paradigm of forest management; its aim is to minimize the differences between natural and managed forests, thereby conserving biodiversity (Attiwill, 1994; Bergeron et al., 1999, 2001; Burton et al., 2006). It also involves maintaining forest complexity at the stand scale through retention of biological legacies. This translates into leaving unharvested individual trees or tree patches during harvest, a practice known as variable retention harvesting (Franklin et al., 1997) or retention forestry (hereafter RF) (Gustafsson et al., 2012). Retention of tree structural complexity within the harvested stand provides refugia for elements of biodiversity otherwise not found in harvested areas (e.g., large live trees, snags, coarse woody material, and understory plant communities) (Franklin et al., 1997), thereby "lifeboating" species and ecosystem processes over the regeneration phase (Macdonald and Fenniak, 2007; Fedrowitz et al., 2014).

An important challenge to implementation of retention relates to deciding on the location of patches of retained trees within a harvested block. Finding an acceptable balance between designation of areas for RF to meet biodiversity objectives while limiting losses of timber revenue requires the development of spatially explicit scenarios to guide forest harvest planning (Ezquerro et al., 2016). Attempts to integrate biodiversity conservation goals while preserving timber revenues are recent (Ezquerro et al., 2016), often applied over large tracts of land (Hauer et al., 2010), and do not always provide spatial results directly applicable to planning purposes (Ahmad et al., 2018). In parallel, the wide adoption of systematic conservation planning (SCP) principles has facilitated the development of spatial prioritization tools that can be applied at a range of scales and for a variety of ecological questions, including forestry issues (Margules and Pressey, 2000; Moilanen et al., 2005; Moilanen, 2008; Lehtomäki et al., 2009). SCP is essentially based on spatial multi-criteria analysis in which a number of environmental features (e.g., land cover, forest stand age, umbrella species occurrence) are used as biodiversity surrogates (i.e., indicators) and combined in such a way that the selection of landscape characteristics is prioritized toward the conservation of representative biodiversity areas helping the completion of quantitative conservation targets (Margules and Pressey, 2000; Lehtomäki and Moilanen, 2013). While often used for the design of reserves at large scales (i.e., sub-national to global), the core concepts of prioritization and cost-effectiveness on which systematic conservation planning is based (Moilanen, 2008) are compatible with forestry needs and applicable at smaller scales typical of harvested landscapes, where retention patches can be thought of as analogs of biodiversity reserves in large-scale planning exercises (Work et al., 2003; Mazziotta et al., 2017).

To apply SCP in a forestry context, input data need to be assembled to capture variation in key forest ecosystem attributes at the cutblock scale, including biodiversity and timber quantity. These data can be assembled by combining vegetation inventory, satellite imagery, and lidar-derived vegetation and soil metrics. Topographic wetness has been shown to be relevant for forest management actions, including the establishment of infrastructure footprint minimizing soil disturbance (Ågren et al., 2014), forest stand type and structure characterization (Murphy et al., 2008a; Nijland et al., 2015b), site productivity (Bjelanovic et al., 2018), biodiversity in unmanaged and post-harvest forests (Bartels et al., 2018b, 2019; Echiverri and Macdonald, 2019), and managing soil carbon (Sewell et al., 2020). Fine-scale data on topographic wetness has become available for Alberta's managed forests by applying models to spatially extensive airborne light detection and ranging (lidar) data (White et al., 2012). Lidar also provides fine-scale data on forest structural attributes, e.g., tree height, cover and vertical complexity (Lefsky et al., 2002; Wulder et al., 2008), while satellite data can provide information related to forest productivity (Cook et al., 1989; Coops, 2015). Together, these data provide the necessary input for adapting a SCP tool to a forestry context involving the search for a spatial pattern of retention that balances both biodiversity and timber production objectives. It is also often acknowledged that, within the mesic portions of the landscape managed for timber production (i.e., the active landbase), wetter sites display higher levels of productivity and biodiversity; indeed, relative site wetness has been demonstrated to be related to biotic and edaphic (i.e., soil) properties of mixedwood boreal forests (Nijland et al., 2015b; Bartels et al., 2018a; Echiverri and Macdonald, 2019; Sewell et al., 2020). If wetter sites have higher biodiversity and productivity, managers face a challenge in achieving goals for maintaining biodiversity while extracting the greatest quantity of timber. However, this relationship is not always true among the three main forest types of western boreal forests (i.e., conifer, deciduous, mixedwood); in some cases the evidence suggests that targeting drier forest sites for retention would be better for conservation and recovery of biodiversity or forest regeneration after harvesting (Nijland et al., 2015a,b; Bartels et al., 2018a, 2019; Echiverri and Macdonald, 2020).

In this study, our main objective is to test an existing SCP toolkit, Zonation (Moilanen, 2007), for retention planning. We sought to assess the degree to which RF pattern and stand attributes (e.g., tree height, species) vary among scenarios built using different constraints, including prioritization of when levels of a high-resolution topographic wetness gradient (Murphy et al., 2007, 2011). Further, we examined which scenario(s) might best meet one of three possible objectives: (i) lowest cost (lowest volume of merchantable timber left in retention); (ii) maintenance of habitat patches (largest retention patches); or (iii) biodiversity (retention patches distributed so as to be broadly representative of the range of wetness classes). To put the results of the various scenarios in context, we compare the outputs of Zonation with an existing forest harvest plan to assess (dis)similarities with current retention practices based on forest practitioners' empirical knowledge. We then discuss the potential benefits of combining an SCP approach with information on topographic wetness used for designing RF schemes. We believe that this innovative approach based on an operational demand from forest managers, provides a simple and valuable contribution toward the development of sustainable forestry practices.

MATERIALS AND METHODS

Study Area

The study area was located in northwestern Alberta, Canada, in the Boreal Plains ecozone (**Figure 1**). The Boreal Plains are characterized by a continental climate and boreal mixedwood forests.

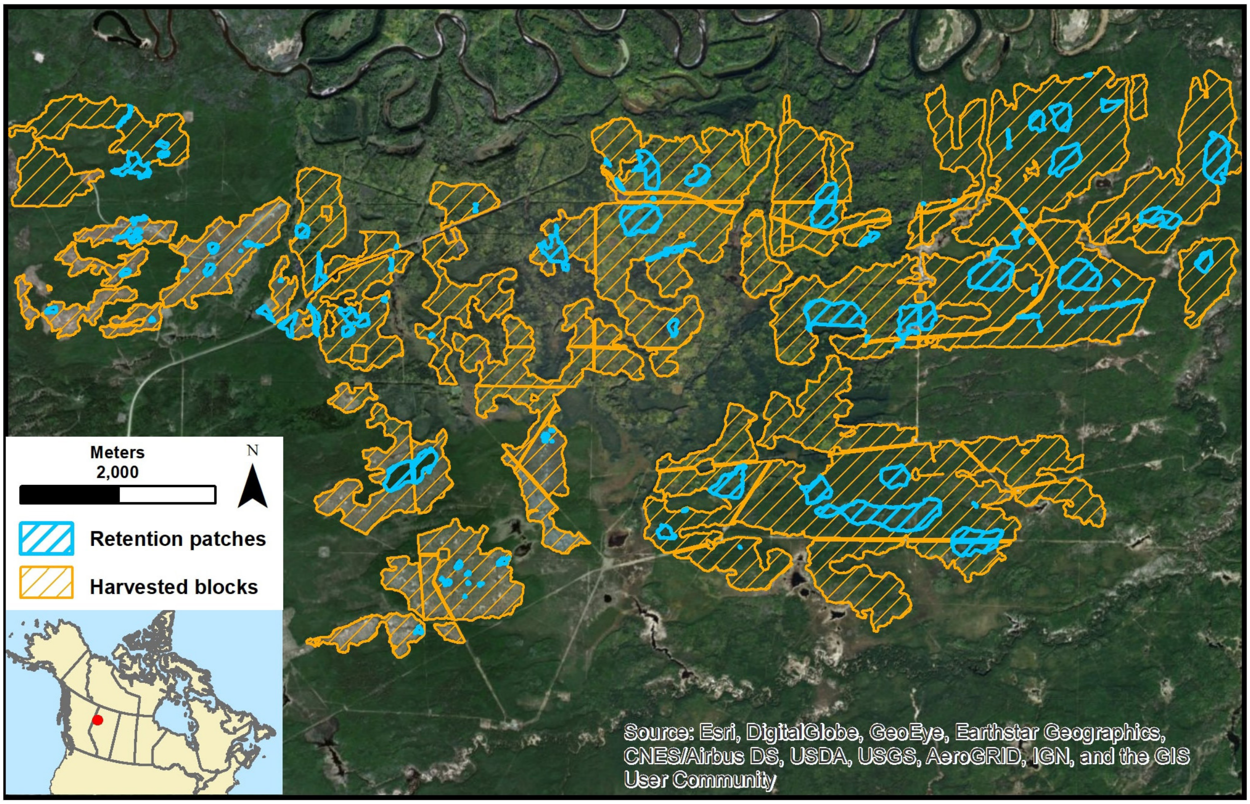
TABLE 1 | Details pertaining to the land cover in the area of interest, derived from the Alberta Vegetation Inventory (Alberta, 2017).

Land cover type	Area (km^2)	Proportion (%)
Trembling aspen	15.7	64.2
White spruce	1.2	5.0
Black spruce	0.3	1.2
Balsam poplar	0.1	0.5
Lodgepole pine	0.1	0.3
Grassland and Shrubland	6.9	28.3
Anthropogenic	0.1	0.6

Statistics only report the dominant land cover/species.

The harvested and retained perimeters on which our study focuses (**Figure 1**) covered a total of 24.4 km^2 and were dominated by trembling aspen (*Populus tremuloides*, **Table 1**). Retention patches, as planned by the forestry company responsible for managing the area, covered 1.95 km^2, or 8% of the total perimeter shown in **Figure 1**, and were dominated by trembling aspen ~72% cover), white spruce (*Picea glauca*,~10% cover) and black spruce (*Picea mariana*,~10% cover) (**Table 2**). Here, retention patches were defined as areas within harvested blocks, and this did not include other areas that were excluded from harvest blocks in connection with planning guidelines such as riparian buffers, inoperable areas, or areas set aside for other specific purposes (e.g., key wildlife habitat).

Alberta's forests fall primarily on public (Crown) lands, but most forest harvesting is carried out by private forestry companies who are granted tenure rights to timber resources by the provincial government. Companies submit forest management plans to the Province that describe the rate, pattern, and location of harvest. Alberta requires these plans to follow sustainable forest management principles by setting objectives for landscape and stand level biodiversity indicators (Alberta,



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

FIGURE 1 | Study area located in northwestern Alberta, Canada (118°15′ W, 56°52′ N). The map displays forested perimeters that were harvested or are planned to be harvested, as well as existing and planned retention perimeters. The modeling work and analysis presented in this study apply to these perimeters only.

TABLE 2 | Details pertaining to the land cover in the retention patches (as operationally implemented or planned); derived from the Alberta Vegetation Inventory (Alberta, 2017).

Land cover type	Area (km^2)	Proportion (%)
Trembling aspen	1.4	71.8
White spruce	0.2	10.3
Black spruce	0.2	10.3
Balsam poplar	0.04	2.0
Lodgepole pine	0.03	1.5
Grassland and Shrubland	0.03	1.5
Anthropogenic	0.05	2.6

Statistics only report the dominant land cover/species.

2006a). This includes the requirement to commit to a minimum percentage of within-harvest area retention. Riparian areas receive protection through requirements to leave unharvested buffers along watercourses (Alberta, 2006b), and these buffer strips contribute to the maintenance of structural diversity in harvested areas. Forest management plans in Alberta include a Structure Retention Strategy that describes the process the company will be using to identify, lay out, and monitor retention patches during harvesting operations.

Data

Base data showing harvested blocks and existing or planned retention patches were provided by Mercer International – Peace River Pulp [formerly Daishowa-Marubeni International Ltd., (DMI)] in vector format (**Figure 1**).

Topographic wetness was represented by the depth-to-water (DTW) metric; a product of the Wet Areas Mapping (WAM)[1] project supported by the Government of Alberta (White et al., 2012) and freely available to the public. DTW values were derived from one-meter spatial resolution bare-Earth digital elevation models (DEMs), which were interpolated from airborne lidar ground returns. This spatial processing equates to the modeling of soil wetness based on both the vertical and horizontal relationship of a given pixel to adjacent predicted steam lines, which were in turn also derived from the DEM. Higher DTW values represent lower relative site moisture (Murphy et al., 2008b, 2009; Oltean et al., 2016). Comparisons with existing wet area inventories in previous studies yielded a good correspondence and WAM has been extensively ground-truthed and validated in our study area (Murphy et al., 2007, 2009).

We used data on forest density and height, stand age, dominant tree species, and timber stocking derived from vegetation inventory, Sentinel-2 satellite imagery, and lidar-derived vegetation metrics. Detailed stand-level information on overstory and sub-canopy tree species composition and age was obtained from the Alberta Vegetation Inventory (Alberta, 2017). The normalized difference vegetation index (NDVI; Tucker, 1979) derived from the European Union Copernicus program's Sentinel-2 satellite data (Drusch et al., 2012) provided a proxy of site productivity, a measure that is complementary to DTW information (Nijland et al., 2015b), and provided information on post-disturbance recovery potential. Tree height data, as a proxy for forest structure and productivity, was represented by the 95th percentile of airborne lidar first returns, a metric that has previously contributed to the characterization of stand successional stage (Kane et al., 2010) and the creation of a lidar-based habitat index (Coops et al., 2016). We also used lidar-derived deciduous and conifer merchantable stem density per hectare, and gross merchantable volume (GMV) per hectare as a measure of standing-tree volume potentially available for harvest.

Input raster data were at a 10-meter spatial resolution and projected in NAD1983 UTM Zone 11 North. This required resampling the DTW data from one to 10 m and timber volume and density data from 20 to 10 m using bilinear resampling. All data processing was done in ArcGIS Desktop 10.5 (Environmental Systems Research Institute, 2017).

METHODS

Zonation and Systematic Conservation Planning

Zonation is a software described both as a conservation planning method based on the Zonation meta-algorithm and its implementation in the Zonation landscape prioritization software (Moilanen et al., 2005). Simply put, the Zonation meta-algorithm prioritizes the areas of a landscape deemed the most suitable for biodiversity conservation, either because of higher biodiversity levels (overlap in species habitats) or because of higher habitat quality, by iteratively removing areas of lesser values. Zonation ranks areas based on their ecological suitability with higher ranks—and so higher values—corresponding to areas of higher suitability. Although a number of studies demonstrated the capacity of Zonation to deal with large forested landscapes, particularly in the boreal environment (Lehtomäki et al., 2009), we are not aware of previous examples of its application to the challenge of selecting areas to be retained in an operational forestry context.

Selection of areas for conservation is often biased toward sites that are isolated and of low economic interest, thereby limiting the achievement of core conservation objectives such as representativeness (e.g., species, habitat) and long-term survival of the species and other elements of biodiversity they harbor (Margules and Pressey, 2000). Similarly, in early efforts to implement RF, economic considerations strongly influenced selection of retained areas in sites of low productivity (Mitchell and Beese, 2002). To mitigate the conflict between multiple objectives, SCP aims at constructing a well-informed, objective, and structured set of biodiversity indicators and protection targets, whose ecological and socio-economic relevance can be tested across land-management scenarios of varied complexity and scales resulting in an adequate conservation solution (i.e., the best trade-off between biodiversity and cost considering a set of management objectives) (Margules and Pressey, 2000; Lehtomäki and Moilanen, 2013). Conservation efforts based on SCP principles often start with the creation of spatially-explicit area prioritization schemes, which was the very point of building alternative RF scenarios in this study.

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[1] https://www.alberta.ca/hydrological-data.aspx

Systematic Retention Scenarios

Systematic conservation planning is based on the selection and use of biodiversity features, ideally species distribution data, which can be used as indicators of overall biodiversity for a given area of interest (e.g., total species richness), however, the availability and/or reliability of species distribution data is often limited over large territories, and the use of biodiversity coarse-filter surrogates, such as topographic wetness and forest structure, is a credible alternative. According to a number of recent studies in the western boreal forest of Canada (White et al., 2012; Nijland et al., 2015b; Bartels et al., 2018a, 2019; Echiverri and Macdonald, 2019, 2020), DTW is an effective surrogate for many conservation values, and different parts of the wetness spectrum can be prioritized for leaving retention, depending on the biodiversity targets to be reached by forest operators (**Table 3**).

Our study was based on the comparison of actual retention identified within an existing harvest plan to multiple hypothetical RF designs generated by Zonation. The former, referred to as the *reference* below, represented business-as-usual practice, whereas the latter represented a set of modeling scenarios in which RF within the planned harvest blocks was constrained by different sets of parameters, i.e., pixel aggregation rules; prioritization of wet, dry, or mesic site wetness; and pixel removal cost (**Table 4** and **Supplementary Material 1**). The process is summarized in **Figure 2**; in total, nine scenarios were modeled and their outputs were compared to the *reference.*

According to best practices listed by Moilanen et al. (2014), we first created a baseline scenario (EqualWeightDef) in which all biodiversity features had an equal weight and pixel aggregation rules that control output patchiness were relaxed. We also used an additive benefit function (ABF) since we were using surrogates instead of species-specific information with trade-offs between conservation values allowed and conservation investments maximized (i.e., greater conservation to investment ratio, Moilanen et al., 2014). ABF would therefore prioritize areas of the landscape (i.e., pixels) whose sum of surrogate values were higher than those of the surrounding areas.

TABLE 3 | Associations between soil wetness, biodiversity and ecosystem function (soil carbon and nitrogen) for three stand types in boreal mixedwood forest.

For conserving	**DDOM**	**MIX**	**CDOM**
Forest regeneration[1]	Drier	Drier	Drier
Bryophytes[2]			
Cover		Wetter	Wetter
Richness/Diversity	Drier	Wetter	Wetter
Composition	Dry (and wet)[6]	Wet (and dry)[6]	Wet (and dry)[6]
Specialist species	Drier	Wetter	Wetter
Vascular plants[3]			
Cover	Drier	Drier	Wetter
Richness/Diversity	Wetter	Wetter	Wetter
Composition	Dry (and wet)[6]	Wet (and dry)[6]	Wet (and dry)[6]
Carabid beetles[4]			
Richness/Diversity	Wetter	Wetter	Drier
Specialist species	Wetter	Wetter	Wetter
Soil[5]			
Carbon and nitrogen	Wetter		Wetter

Soil wetness is represented by Depth-to-Water (DTW). Blank means no clear trend. DDOM stands for Deciduous-dominated, MIX stands for Mixedwood, and CDOM stands for Conifer-dominated boreal mixedwood forest. [1] *Nijland et al., 2015a;* [2] *Bartels et al., 2018a, 2019;* [3] *Echiverri and Macdonald, 2019, 2020;* [4] *Ronzani et al. unpublished;* [5] *Sewell et al., 2020;* [6] *Indicates variation in composition along the DTW gradient with brackets indicating the part of the moisture gradient that was more resilient to harvesting.*

TABLE 4 | Details pertaining to the scenarios modeled using Zonation.

Scenario	**Description**
Reference	Existing harvest design
EqualWeightDef	Baseline Zonation run with equal weight given to all variables and a weak pixel aggregation constraint (default parameter)
EqualWeightAgg	Zonation run with equal weight given to all variables and a strong pixel aggregation constraint
EqualWeightCost	Zonation run with equal weight given to all variables, a strong pixel aggregation constraint, and a cost constraint (Gross merchantable volume, GMV)
DryWeightAgg	Zonation run with weight given to dry sites (> 2 m DTW) and a strong pixel aggregation constraint
DryWeightCost	Zonation run with weight given to dry sites (> 2 m DTW) and a strong pixel aggregation constraint, and a cost constraint (GMV)
MesWeightAgg	Zonation run with weight given to mesic sites (0.5–2 m DTW) and a strong pixel aggregation constraint
MesWeightCost	Zonation run with weight given to mesic sites (0.5–2 m DTW), a strong pixel aggregation constraint, and a cost constraint (GMV)
WetWeightAgg	Zonation run with weight given to wet sites (<0.5 m DTW) and a strong pixel aggregation constraint
WetWeightCost	Zonation run with weight given to wet sites (<0.5 m DTW), a strong pixel aggregation constraint, and a cost constraint (GMV)

We then built on this baseline scenario to create eight additional scenarios (**Table 4**) in which we controlled for spatial aggregation by using a Boundary Length Penalty (BLP) rule of 0.001; a higher penalty would produce larger, more compact patches of lower boundary length while decreasing their overall conservation quality, whereas lower penalty would create more patches of higher conservation quality. Although a lower penalty would lead to a more fragmented result, it would also provide more flexible solutions in terms of RF design options, hence making trade-offs between conservation and timber production easier to reach. BLP is a generalist rule fitted for general biodiversity management purposes (Moilanen et al., 2014), as imposed in forestry regulations.

Out of these eight scenarios, six were further constrained by prioritizing different levels of site wetness, i.e., dry, wet, and mesic according to DTW values (**Table 4**). Drier sites had DTW values greater than 2 m. Wetter sites had DTW < 0.5 m and depicted the "traditional" RF practice of retaining the wettest parts of the landscape. Mesic sites had DTW between 0.5 and 2 m and represented an intermediate situation in which a larger range of moisture conditions, and thus ecological conditions, was preferable. We reclassified DTW values in ArcGIS10.5 (Environmental Systems Research Institute, 2017) to emphasize

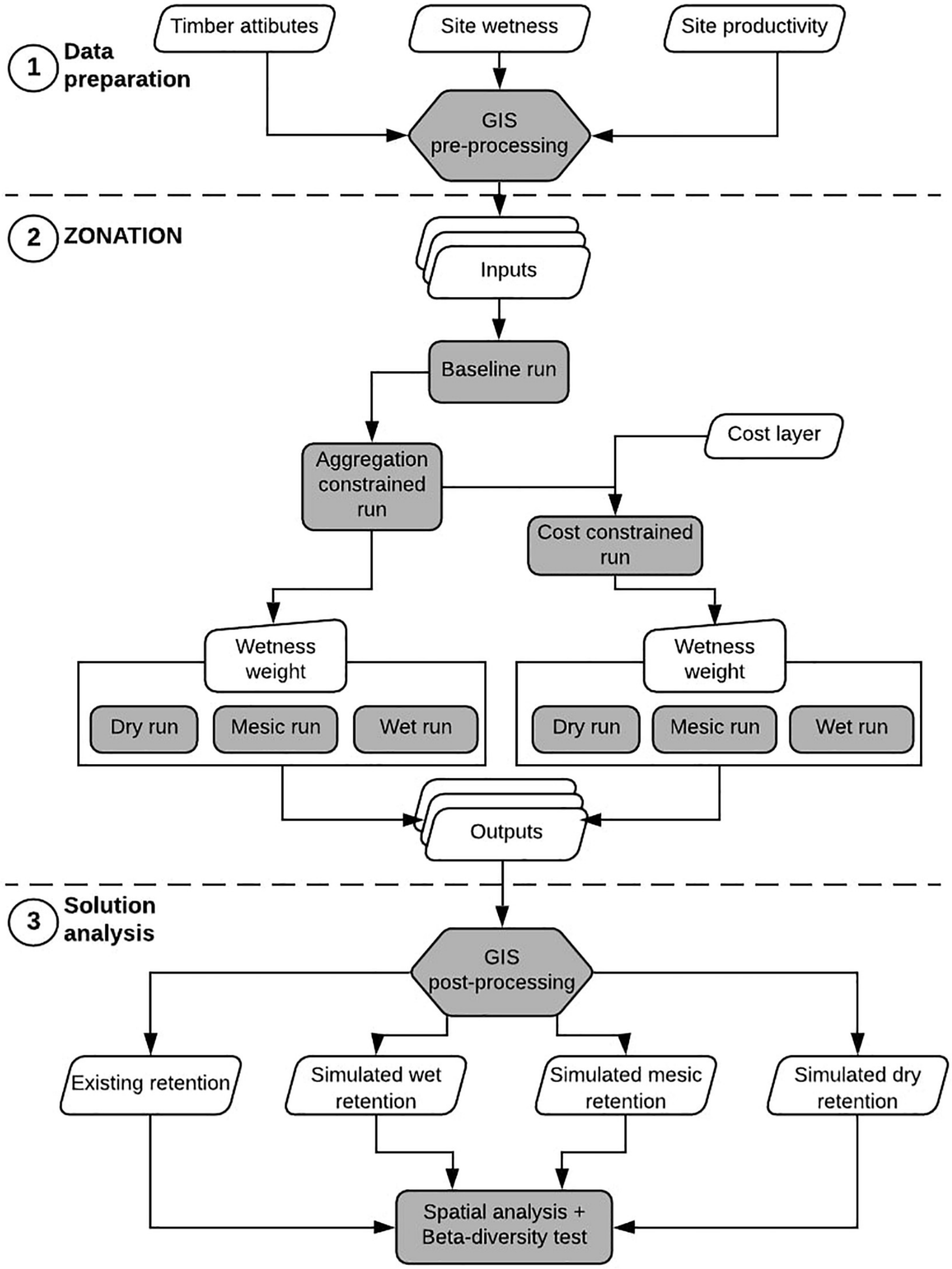

FIGURE 2 | Systematic retention p lanning flowchart representing the method used in this study. Step 1 was conducted in ArcGIS10.5 and step 3 was conducted in both ArcGIS10.5 and R3.6.3.

these different wetness levels: original DTW values were kept as-is so higher values correspond to the drier end of the spectrum; an inverse linear function was used to switch the range of DTW values, so higher values correspond to the wetter end of the spectrum; for mesic sites, we used a Gaussian function with a 1.25 m depth as the "midpoint" and a spread parameter of 0.75 m. For each of these wetness scenarios, the wetness layer was given a weight 10-times greater than the other layers to prioritize it.

Finally, out of these six scenarios, three were further constrained by the addition of a cost layer that prioritized the conservation of low-cost pixels (**Table 4**) to produce a RF design that would be less expensive to implement. By using gross merchantable timber values, we limited the selection of the most valuable timberland. This meant that areas displaying greater merchantable volumes would not be protected at the expense of timber revenues; therefore, Zonation would trade areas of high ecological value with areas that might be less important from an ecological standpoint but also more important from an economic standpoint. The same constraint was also applied to the baseline scenario ("EqualWeightCost," **Table 4**).

Analysis

We compared RF patches in the *reference* (i.e., as operationally planned) and RF patches modeled by Zonation in terms of their spatial pattern and forest attributes (e.g., tree species, mean tree height). Patches in the *reference* covered 8% of the area; therefore, we kept the top 8% of each Zonation output so only those pixels with the best conservation values per scenario were used for comparison. In other words, we only kept those 8% of pixels that the model classified as being the best from a conservation standpoint.

For each scenario, we first summarized the number of patches, the mean patch size, and the percent spatial overlap with the *reference* in an attempt to present differences in a synthetic manner. We also created a heatmap displaying the frequency at which each pixel was selected throughout the scenarios and the *reference*. It provided a simple visual to identify clusters of pixels that were selected in most of the scenarios, or on the other hand, those that were rarely selected. Complementary to the heatmap, for each scenario we computed average stand age, mean DTW, the average deciduous and conifer density, the average NDVI, the average of the 95th percentile of tree height, and the total GMV. We also collected information regarding forest composition. This information was necessary to assess (dis)similarities in the structural composition of RF patches between the *reference* and the scenarios.

Subsequently, we made overall comparisons of the *reference* and scenarios using all forest attributes by means of multivariate dispersion analysis, which was deemed a robust method to measure abundance-based beta diversity among multiple areas (Anderson et al., 2006). For a set of environmental variables or species distributed across multiple groups, the test uses a distance matrix to analyze the variance (i.e., ANOVA) of sample distance around a calculated multivariate median (i.e., the dispersion). Dispersion within groups is then compared among groups by permuting ANOVA residuals under the null hypothesis of homogeneity among groups (Anderson, 2006). In our study, groups were represented by RF scenarios, environmental variables were derived from forest attributes within retention patches, and samples were the retention patches (**Supplementary Material 2**). To compare each forest attribute independently, continuous attributes of the *reference* (i.e., year of origin, tree height) were reclassified into four classes using a four-quantile scheme whose class bounds were applied to the other scenarios. The year of origin attribute was reduced from 11 to five classes of 30 years each. Tree height was reclassified using a four-class equal interval classification. Then for each retention patch, the number of pixels of each class was extracted before running the dispersion analysis and the permutational test (4999 permutations, **Supplementary Material 3**). This analysis was done using the vegan v2.5-6 package for R3.6.3 (RStudio Team, 2015; Oksanen et al., 2019; R Core Team, 2019; **Supplementary Material 3**).

To examine how the different scenarios compared – to one another and to the reference – in terms of the three objectives we summarized information on the best-performing scenarios as follows: (1) For the "cost" objective – those scenarios resulting in the lowest gross merchantable volume left in retention patches; (2) For the "habitat patch" objective – those scenarios resulting in the largest mean patch size; and (3) For the "biodiversity" objective – the scenarios that resulted in a distribution of retention that was broadly representative of the range of DTW values; this is based on the evidence that both wetter and drier sites could be important, depending on the biotic group and the forest type (**Table 3**).

RESULTS

The *reference* (representing retention patches as operationally planned) had fewer, and thus larger, patches than most of the scenarios (**Table 5**). The number of patches in the *reference* was 103, compared to an average of 393 patches across the nine scenarios, with the baseline scenario (EqualWeightDef) resulting in the most patches (874). The addition of the aggregation constraint resulted in somewhat fewer and larger patches than the baseline scenario (726, 0.3 ha vs. 874, 0.2 ha). The addition of a cost constraint resulted in fewer and larger patches than the comparable scenario without a cost constraint, and thus the cost constraint scenarios were more similar to the *reference* (**Table 5**). In the scenarios with a cost layer there were no substantive differences among the wetness scenarios; in these three scenarios the number and size of patches were quite similar to those in the *reference* (an average of 98.7 patches, 1.96 hectare in size compared to 103 patches, 1.9 hectare in size in the *reference*). In contrast, scenarios based on the wetness level only showed consistently higher number and smaller size of patches, with an average of 0.42 hectare across the three wetness scenarios. Of the three wetness scenarios without a cost layer, the one prioritizing dry sites resulted in the fewest and largest patches, and was thus most similar to the *reference*; the mesic scenario had the most and smallest patches, and was quite similar to the scenario with only an aggregation constraint (**Table 5**).

The level of spatial overlap between retention patches in the *reference* and in the scenarios ranged from 1.67 to 20.42%, with an average of 10%. Cost-constrained scenarios showed a higher degree of overlap, being 19.1% on average. In contrast, scenarios based only on the wetness level showed much lower overlap with the *reference*, (2.7% on average).

The heatmap (**Figure 3**) reveals variable spatial commonalities among scenarios, including with the *reference*. Over 38% of the pixels were selected only one time (i.e., cold-spots), almost 93% of pixels were selected less than five times, and less than 1% were selected eight times (i.e., hotspots). A closer look at the spatial distribution of pixels indicates that those selected the least often correspond to the large patches existing in the *reference*

TABLE 5 | Basic landscape-ecology metrics for retention patches under the various scenarios (see **Table 4**).

Scenario	Number of patches	Mean patch size[1] (SD)	% overlap[2]
Reference	103	1.9 (3.5)	–
EqualWeightDef	874	0.2 (0.8)	2.87
EqualWeightAgg	726	0.3 (1.0)	2.83
EqualWeightCost	240	0.8 (3.0)	16.23
DryWeightAgg	238	0.8 (2.0)	1.67
DryWeightCost	104	1.9 (12)	20.08
MesWeightAgg	753	0.3 (0.8)	2.84
MesWeightCost	97	2.0 (13.8)	19.68
WetWeightAgg	411	0.5 (1.2)	3.45
WetWeightCost	96	2.0 (14)	20.42

[1] In hectares. [2] Percent area in retention patches in the reference that overlapped with those in the scenario.

RF design (see **Figure 1**), as well as isolated pixels coming from the scenarios. Pixels that were selected four to five times often match patterns seen in the outputs of the models that used a cost layer; in the south-eastern portion of the study area, these also line up with the RF pattern in the *reference*. Pixel hotspots were generally in areas of intermediate to lower relative wetness (i.e., mesic to drier sites).

A comparison of forest attributes shows no substantive difference in average stand origin (i.e., age) between the *reference* and any of the scenarios (**Table 6**). In the *reference,* and in all scenarios, most of the forest contained in retention patches originated in 1880–1909 or 1910–1939; the scenarios prioritizing mesic or wet sites had proportionally greater area in the older of these two age classes (**Figure 4**). Adding a cost constraint slightly increased the proportional area in the 1940–1970 age class. Mean DTW showed important differences, with an average DTW of 1.5 m from all scenarios being drier than the 0.4 m DTW in the *reference* (**Table 6**). Even the two "wet" scenarios (WetWeightAgg and WetWeightCost) had lower proportional area of wet sites than the *reference*, and these did not differ much from the comparable mesic scenarios (**Figure 4**). The baseline scenario and the one with only an aggregation constraint resulted in retention patches that were overall drier (higher DTW), as did the dry scenario with no cost constraint. The addition of a cost layer resulted in the selection of wetter sites (lower average DTW). Deciduous density in the wetness scenarios with no cost constraint was similar to the *reference,* whereas with the addition of a cost constraint it dropped, from 610 in the *reference* to an average of 450 stems/hectare. For conifer density, the results show an opposite pattern, with cost-constrained scenarios showing values closer to the *reference* (overall average of 246 versus 191 in the *reference*). Mean NDVI values and tree heights were quite similar in the *reference* and all scenarios. Most scenarios had higher gross merchantable volume values than the *reference.* The addition of a cost constraint slightly increased the area in low volume (**Figure 4**), resulting in these scenarios having somewhat lower GMV and thus being more similar to the *reference.* The wet scenario without a cost constraint had the highest GMV value of 478 cubic meters per hectare.

An examination of the forest composition shows that all scenarios had proportionally more area in grassland/shrubs than did the *reference*, although even the latter included some such area (**Figure 4**). Adding a cost constraint resulted in slightly less area in grassland/shrubs and more area dominated by black spruce stands at the expense of trembling aspen; this made the cost-constrained scenarios more similar to the *reference.*

Results from the multivariate dispersion analysis (**Supplementary Material 3**) indicate that all scenarios and

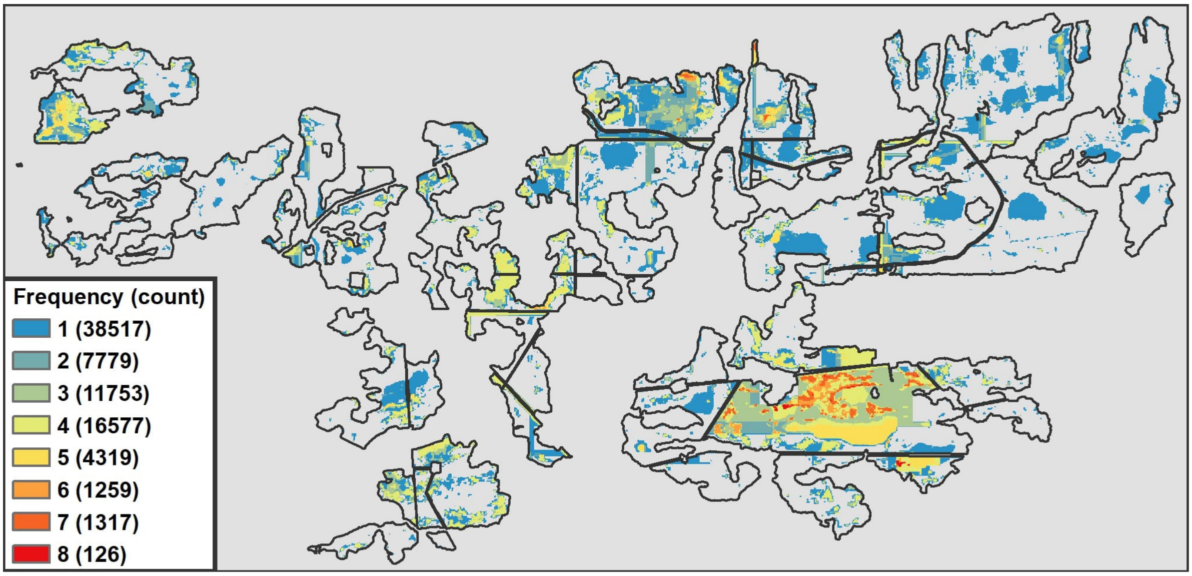

FIGURE 3 | Heatmap showing the frequency of pixel selection across scenarios, including the reference, i.e., pixels coded as "1" were selected in one scenario only, whereas pixels coded as 9 were selected in 9 out of 10 scenarios.

the *reference* were significantly different from one another based on the overall analysis including all forest attributes (p-value < 0.0002), however, pairwise comparisons suggested that cost-constrained scenarios tended to display forest attributes closer to the *reference*, statistically speaking.

In terms of the "cost" objective the EqualWeightCost was best, resulting in substantially lower gross merchantable volume left in retention patches than did the reference (**Tables 6**, **7**). For the "habitat patch" objective, the MesicWeightCost and WetWeightCost scenarios performed equally, but resulted in only a slightly larger mean patch size than the DryWeightCost or reference (**Tables 5**, **7**). In terms of the "biodiversity" objective, the DryWeightCost scenario resulted in the most even representation of all three wetness (DTW) classes with MesicWeightCost being only slightly more unbalanced (**Figure 4** and **Table 7**). In terms of meeting all three objectives, the DryWeightCost scenario would be best; it had mean patch size only slightly lower than the maximum, the best representation of the wetness gradient, and the second lowest gross merchantable volume.

DISCUSSION

We demonstrated an approach to informing the design of tree retention using Zonation, a prioritization software commonly used in SCP. Prioritization scenarios included consideration of site topographic wetness across different site moisture profiles – dry, mesic, and wet — thus emphasizing different gradients associated with biodiversity observable in the western boreal forest of Canada. Operationally planned RF patches were compared to those of nine scenarios in terms of spatial patterns and their (dis)similarities in forest composition. Our results show that use of such an approach is likely to result in a substantially different end result in terms of size, structure, and spatial location of retention patches than those selected by a planning forester in a business-as-usual approach. Notably, incorporating wetness levels into prioritization for retention patches yielded very different results. The addition of a cost-constraint to scenarios resulted in outputs closer to the *reference*; for some forest structure variables the addition of a cost constraint resulted in the wetness level being almost completely overridden. The scenarios performed differently in the context of different objectives for RF; thus, we cannot say there is one single optimal solution. However, our results suggest that this approach could be helpful in identifying approaches that could best achieve multiple, even sometimes competing, objectives. This study provides an example of how RF planning can be done in a systematic manner, thereby providing a range of results that can accommodate a variety of management priorities. Our approach should be complemented by the use of ecological and economic models using our results as inputs to explore the variable impacts of RF scenarios on, for instance, animal behavior and movement, and long-term timber yield.

Toward Systematic Retention Planning for Multiple Values

Although retention harvesting as an approach is practiced worldwide and argued to be an important tool in ensuring forestry is sustainable, challenges regarding its operational implementation remain (Bose et al., 2014; Stockdale et al., 2016). Planning retention necessarily involves consideration of a variety of objectives, which are often competing. Fortunately, forestry professionals now have available to them data that provides extensive coverage for a variety of important forest structure, productivity, and site variables linked to desired outcomes, such as biodiversity (this study; Van der Plas et al., 2018). The utilization of a systematic conservation planning approach, such as we demonstrate herein, holds much promise for facilitating utilization of such spatial data on ecosystem function in a planning framework designed to efficiently consider trade-offs.

Including biodiversity in forest planning is not new, but is not often attempted at this scale (i.e., operational), and not with this type of software that emphasizes prioritization based on potential benefits for biodiversity. Further, there is no comparable work using relative site/soil wetness as a biodiversity proxy to drive

TABLE 6 | Descriptive statistics pertaining to forest attributes per scenario.

Scenario	Mean stand origin[1]	Mean DTW[2] (SD)	Mean deciduous density[3] (SD)	Mean conifer density[3] (SD)	Mean NDVI[4] (SD)	Mean canopy height[5] (SD)	Total GMV[6] (SD)
Reference	1904	0.4 (0.5)	610 (307)	191 (252)	0.66 (0.05)	22.2 (5.8)	333 (138)
EqualWeightDef	1900	1.8 (1.1)	609 (209)	518 (228)	0.65 (0.08)	23.6 (2.4)	468 (81)
EqualWeightAgg	1900	1.8 (1.1)	609 (209)	519 (227)	0.65 (0.08)	23.6 (2.4)	468 (81)
EqualWeightCost	1906	1.2 (1.2)	477 (383)	150 (268)	0.65 (0.09)	21.5 (5.4)	218 (141)
DryWeightAgg	1910	2.7 (0.9)	712 (226)	270 (280)	0.64 (0.1)	23.7 (2.7)	388 (107)
DryWeightCost	1902	1.2 (1.3)	480 (303)	246 (247)	0.64 (0.09)	22.3 (5.5)	324 (195)
MesWeightAgg	1898	1.3 (0.2)	620 (219)	446 (238)	0.62 (0.1)	23.6 (2.4)	447 (81)
MesWeightCost	1899	0.9 (0.9)	420 (267)	295 (241)	0.62 (0.1)	22.0 (5.5)	332 (204)
WetWeightAgg	1898	1.35 (0.7)	591 (204)	550 (210)	0.65 (0.08)	23.6 (2.2)	478 (69)
WetWeightCost	1899	0.9 (1.0)	423 (271)	292 (242)	0.62 (0.09)	22.0 (5.5)	331 (204)

[1] Weighted mean based on pixel age classes; excludes grassland and shrubland, which had no age estimation. [2] Depth-to-water index in meters, lower numbers indicate wetter sites. [3] Number of merchantable stems per hectare. [4] Normalized Difference Vegetation Index, an index of site productivity derived from remotely-sensed images; [5] 95th percentile of tree height in meters; [6] Volume of merchantable stems per hectare, in cubic meters.

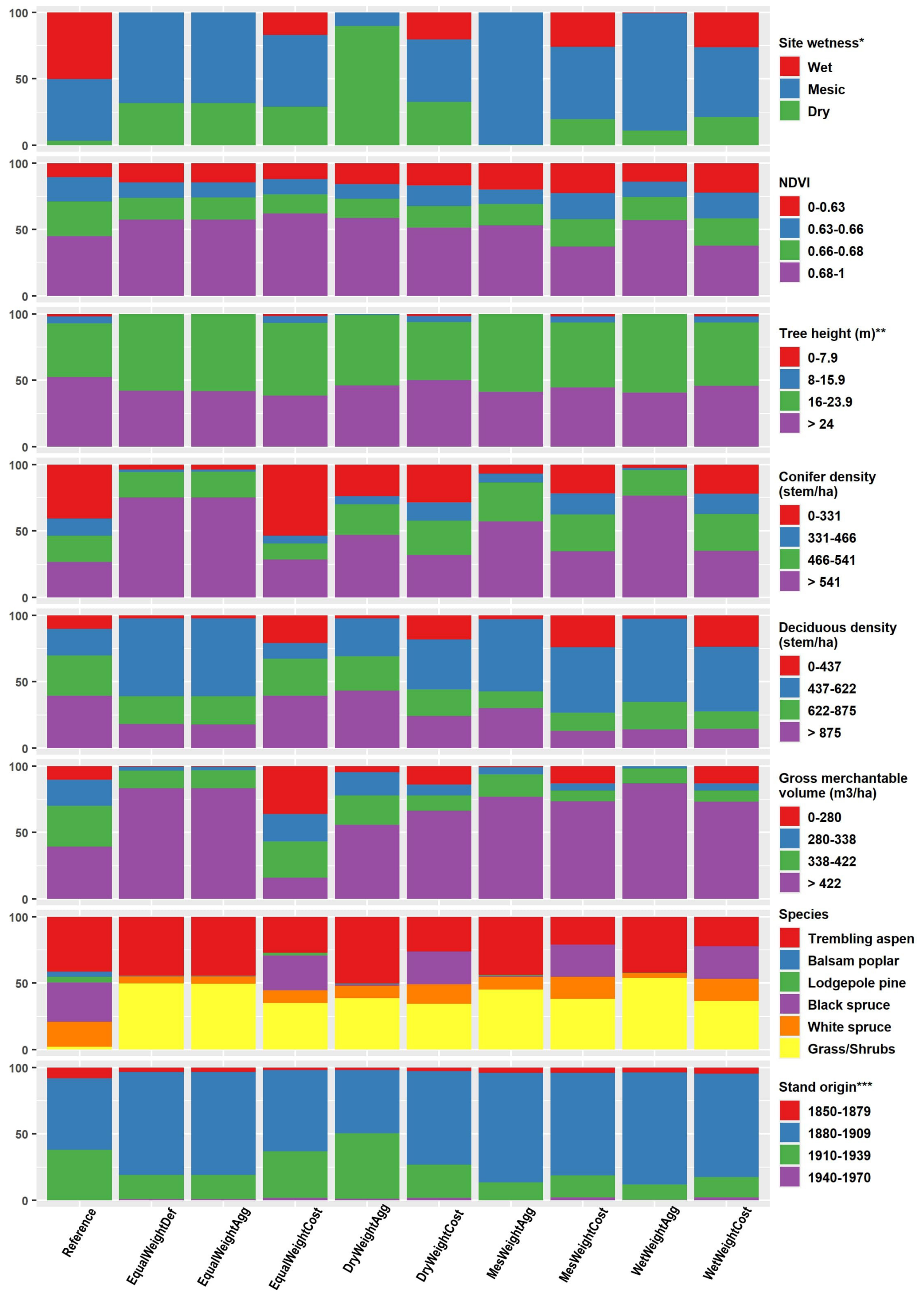

FIGURE 4 | Compositional plots comparing forest stand structure between the *reference* retention design and the scenarios resulting from Zonation. See **Table 4** for information on constraints included in the various scenarios. The *Y*-axis displays the percentage occupied by a class based on pixel counts within retention patches for a whole scenario. * Site wetness is classified by the Depth-to-Water Index as follows: Wet = 0–0.5 m; Mesic = 0.5–2 m; dry > 2 m. ** 95th percentile of LIDAR-derived tree heights. *** Year of origin of a given stand, used to calculate stand age; excludes grassland/shrubs patches which had no estimate of stand origin.

reserve design. According to Ezquerro et al. (2016, 2019), research to integrate biodiversity into operational planning (i.e., the scale of our study) remains limited. There is, therefore, room to further explore the possibilities offered by spatial tools coming from the field of conservation planning to provide insights to better guide modern sustainable forest management.

TABLE 7 | Assessment of the scenarios relative to three objectives: (i) lowest cost (lowest volume of merchantable timber left in retention); (ii) maintenance of habitat patches (largest retention patches); or iii) biodiversity (distribution of retention patches broadly representative of the range of wetness).

Scenario	**Total GMV (SD)**[1]
Objective: Cost (lowest GMV)	
Reference	333 (138)
EqualWeightCost	218 (141)
DryWeightCost	324 (195)
MesicWeightCost	332 (204)
Scenario	**Mean patch size (SD)** [2]
Objective: Habitat patches (largest)	
Reference	1.9 (3.5)
DryWeightCost	1.9 (12)
MesWeightCost	2.0 (13.8)
WetWeightCost	2.0 (14)
Scenario	**DTW class coverage**[3]
Objective: Biodiversity (representative wetness classes)	
Reference	Very low amount of "dry"
DryWeightCost	Most equal representation of the three wetness classes
MesWeightCost	Fairly equal representation of the three wetness classes

[1] *Mean volume of merchantable stems per hectare, in cubic meters, left in retention (standard deviation) (see* ***Table 6****).* [2] *Mean retention patch size in hectares (standard deviation) (see* ***Table 5****).* [3] *Site wetness was classified by the Depth-to-Water Index as follows: Wet = 0–0.5 m; Mesic = 0.5–2 m; Dry > 2 m (see* ***Figure 4****).*

Overall, the nine systematic retention planning scenarios resulted in quite different patterns and characteristics of retention patches than did the operational selection of retention, as represented in the *reference.* Operational planning of retention resulted in fewer and larger patches, which were located on wetter sites, with higher deciduous density, lower conifer density, similar stand age, and lower gross merchantable volume. The addition of a cost constraint resulted in patterns of retention that were generally more similar to the *reference* and that were very different than in the comparable scenario without a cost constraint: there were fewer and larger retention patches, and these retained areas were of comparable age, slightly shorter, less dense, had much lower GMV and NDVI, and showed a much higher degree of spatial overlap with the *reference* (**Figure 4**). The application of the aggregation or site wetness constraints had little effect on mean NDVI or canopy height. Differences among scenarios with the three site wetness levels were minimal when the cost constraint was in place; without it, a preference for drier sites resulted in higher deciduous density while a preference for wetter sites resulted in retention patches with higher conifer density and greater gross merchantable volume, with a larger proportion of older stands generally.

The comparison of the scenarios in the context of the three objectives demonstrated that they all performed as well or better than the reference. Further, those comparisons suggested that some scenarios could successfully achieve multiple objectives; for example, DryWeightCost.

An interesting outcome of the scenarios is that they included more areas identified as grassland/shrubland than did the *reference* (business-as-usual) approach. Although our study landbase was mesic upland boreal forest targeted for commercial forestry, it would naturally include some small patches with less dense, or lower height tree cover that would be identified as grassland or shrubland in the forest inventory. Our scenarios did not specifically prohibit the inclusion of such patches in retention. A planning forester would, however, be unlikely to map out such an area as a retention patch. It is worth considering the value of including such areas in an overall retention design, as they are an important part of finer-scale forest heterogeneity and there could be biodiversity benefits to leaving them undisturbed, particularly if they are contained within a larger forested retention patch.

The approach we demonstrate provides a variety of outputs that would be useful to a planning forester. In addition to metrics on size, number, and spatial distribution of retention patches under different constraints, the heatmap provides a simple tool for selecting areas for retention based on how often they were chosen under the varying scenarios. One benefit of Zonation comes from the ranked output. We limited our retention patches to the top 8% most valuable pixels in terms of biodiversity values to match the 8% of retention implemented by industry for ease of comparison in our example, but this threshold could be changed to match any retention objective. For example, in the Province of Alberta, retention objectives in forest management plans currently range from 3 to 15%. Another potential benefit of the approach we present here is the level of complexity that can be integrated. Considering the push toward the management of forests as complex networks fulfilling a range of functions and providing a range of ecosystem services (Messier et al., 2019), spatial conservation planning is promising as it can consider multiple values at once and allows for the creation of management scenarios that can then be fed into timber supply models to assess long-term yields. Plus, working on small landscapes, as shown here, can allow for the implementation of small-scale variable solutions, helping to fulfill different objectives across a larger landscape. This could include, for example, nesting finer-scale planning for retention within larger-scale residual planning, for example riparian buffers, in order to consider connectivity within the context of the "functional complex network" concept (Messier et al., 2019). Here, we focused on analyzing prioritization for retention within cutblock areas. A priority for future work with SCP tools would be to investigate, in a more integrated way, the joint influence of in-block retention and forest areas conserved in the course of planning prior to planning for retention (e.g., stream buffers etc.).

The use of tools such as Zonation could also help address more fundamental research problems related to emulation of natural disturbances, which is the inspiration for retention forestry in many parts of the world (Gustafsson et al., 2012). For example, in western Canada the practice of RF and the patterns created post-harvest (dispersed retention, patch retention) are inspired by forest fire residuals, or refugia. Previous empirical work provides a basis for understanding natural patterns resulting from wildfire in the boreal forest (Andison, 2012; Andison and McCleary, 2014), and other works suggest that landscape wetness could drive this pattern (Krawchuk et al., 2016; Rogeau et al., 2018; Whitman et al., 2018). In Alberta's managed forests, detailed spatial information on burned and unburned areas within most wildfires is now being delineated and may function as another point of comparison for outputs of prioritization from Zonation. In a time of fire regime change, this approach is valid for management and forest adaptation purposes.

Limitations

As RF becomes increasingly popular around the globe, there is an urgent need for the development of open-access tools and reproducible approaches, such as demonstrated herein, to plan retention in the face of competing objectives. Our goal was to contribute to this challenge by demonstrating the utility of a systematic conservation planning approach. Thus, we felt constrained to put it in the context of an existing retention plan for comparison purposes. Future work should consider application of various scenarios to more areas with a variety of operationally-planned retention.

Our paper focuses specifically on the placement of island retention patches within harvested areas and does not directly deal with larger landscape connectivity issues that are affected by cutblock placement and the unharvested areas between cutblocks. The latter is an important issue but is beyond the scope of this paper. Island retention does contribute to landscape connectivity values so future research could assess how island retention within cutblocks affects landscape connectivity but this kind of study would need to control for other landscape patterns that this study was not able to control for.

Our modeling work is a simplification of otherwise complex ecological processes controlling the occurrence of unburned patches (Stockdale et al., 2016), the inspiration for retention forestry (RF). However, simplicity is always advocated when starting conservation design, and this study did not try to reproduce the spatial pattern of what would naturally be occurring during a high-severity fire. That being said, our approach could gain from further testing and tuning of Zonation's parameters; in particular, there is a need to find the right set of parameters to create larger patches and to limit fragmentation. For instance, we used a low Boundary Length Penalty (BLP) value to give the model freedom to design small patches of high conservation value where needed; although such choice leads to a diversity of dispersed patch sizes that likely lines up with natural (and often random) fire refugia occurrence, it does not produce an economically viable solution for foresters. On the converse, too high a BLP value would lead to simpler patch shape and pattern, which would be easier to implement but would result in a strong decrease in conservation values. It is unknown at the moment if finding the "right" BLP value would suffice or if the best solution lies in the use of values within a "goldilocks" range.

Although we have incorporated multiple data streams into our analyses, future analyses may benefit from the inclusion of additional variables or by refining data inputs. First, in the absence of a comprehensive set of species distribution variables, using information on well-known umbrella species could help further refine the results (Meurant et al., 2018). Second, the cost layer could be refined in future work, as how "cost" is defined is a complex issue. For example, in this study, cost was defined simply as timber revenue loss, however, one can argue that there is also a cost of losing rare or endangered species' habitat or areas providing important, maybe irreplaceable, ecosystem services. From a forest management perspective, timber revenue loss could also be offset by reduction of other costs. For example, as retention patches facilitate natural regeneration, planting costs may be reduced. We argue that more work should be done developing a cost layer that mixes competing interests.

DATA AVAILABILITY STATEMENT

The data analyzed in this study is subject to the following licenses/restrictions: A part of the original datasets used in this study were provided by a private partner that does not allow public access to the information. Requests to access these datasets should be directed to Gordon Whitmore, gordon.whitmore@mercerint.com.

AUTHOR CONTRIBUTIONS

SN and SM developed the initial concept and obtained funding. F-NR and SN designed the study. JS, CB, CN, and SM provided updates on the study design. CB processed and provided the supplementary input data. F-NR prepared the inputs, performed modeling, and processed model outputs. F-NR, SN, CN, and SM analyzed the results. All co-authors helped with the writing of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.584291/full#supplementary-material

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Simulating Growth and Competition on Wet and Waterlogged Soils in a Forest Landscape Model

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Changes in CO_2 concentration and climate are likely to alter disturbance regimes and competitive outcomes among tree species, which ultimately can result in shifts of species and biome boundaries. Such changes are already evident in high latitude forests, where waterlogged soils produced by topography, surficial geology, and permafrost are an important driver of forest dynamics. Predicting such effects under the novel conditions of the future requires models with direct and mechanistic links of abiotic drivers to growth and competition. We enhanced such a forest landscape model (PnET-Succession in LANDIS-II) to allow simulation of waterlogged soils and their effects on tree growth and competition. We formally tested how these modifications alter water balance on wetland and permafrost sites, and their effect on tree growth and competition. We applied the model to evaluate its promise for mechanistically simulating species range expansion and contraction under climate change across a latitudinal gradient in Siberian Russia. We found that higher emissions scenarios permitted range expansions that were quicker and allowed a greater diversity of invading species, especially at the highest latitudes, and that disturbance hastened range shifts by overcoming the natural inertia of established ecological communities. The primary driver of range advances to the north was altered hydrology related to thawing permafrost, followed by temperature effects on growth. Range contractions from the south (extirpations) were slower and less tied to emissions or latitude, and were driven by inability to compete with invaders, or disturbance. An important non-intuitive result was that some extant species were killed off by extreme cold events projected under climate change as greater weather extremes occurred over the next 30 years, and this had important effects on subsequent successional trajectories. The mechanistic linkages between climate and soil water dynamics in this forest landscape model produced tight links between climate inputs, physiology of vegetation, and soils at a monthly time step. The updated modeling system can produce high quality projections of climate impacts on forest species range shifts by accounting for the interacting effects of CO_2 concentration, climate (including longer growing seasons), seed dispersal, disturbance, and soil hydrologic properties.

Keywords: forest landscape modeling, permafrost, forested wetlands, hydrology, LANDIS, Siberia

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INTRODUCTION

Changes in abiotic conditions (CO_2 concentration and climate) have the potential to greatly modify forest dynamics by altering disturbance regimes and changing competitive outcomes among tree species. These modified competitive and disturbance dynamics can, over time, result in range shifts within biomes, and shifts in biome boundaries themselves (Liang et al., 2018). Competitive outcomes are determined by a host of interacting factors, including the biotic factors of intrinsic growth rates, drought tolerance, shade tolerance, heat and cold tolerance, and the abiotic factors of CO_2 concentration, temperature, precipitation, soil texture, soil depth, and nutrients. Furthermore, many relationships and interactions are non-linear. Disturbances interact with competitive relationships when they remove dominant cohorts or completely reset the successional sequence (Coop et al., 2020). Range expansions (or contractions) involve displacement of existing species or life forms through both dispersal and competitive superiority, although displacement may lag considerably behind a change in abiotic conditions in the absence of removal of extant cohorts by senescence or disturbance (Liang et al., 2018). Because of these many complex interactions, it is extremely difficult to predict future forest composition and individual tree species range shifts under the novel conditions expected in the future.

Waterlogged soils are common in many forested ecosystems, and can be produced either by topography, surficial geology, or permafrost at high latitudes. In glaciated landscapes without permafrost, the topography of glacial till and near-surface bedrock produces depressions that are perennially wet, and such conditions can occupy large portions of some landscapes. At high latitudes and elevations, permafrost can be the dominant driver of soil hydrology, limiting soil drainage to increase the occurrence of waterlogged conditions. A warming climate has the potential to alter permafrost hydrology such that the vegetation will change. Successional trajectories may move toward either a wetter or drier ecosystem in the near term (depending on specific conditions), but will ultimately become drier if the permafrost thaws completely where soils have good drainage (Jin et al., 2020). Predicting such successional trajectories is critical for forecasting shifts of species and biome boundaries and understanding impacts on carbon budgets.

Predicting the effects of global changes on forests requires models that formalize empirical knowledge acquired from field and laboratory experiments in terms of first principles to predict behavior under the novel conditions of the future (Gustafson, 2013). Assessments of the effects of global change on the dynamics of temperate and boreal forests have been conducted primarily using either eco-physiology models that simulate growth and materials fluxes within a forest plot or stand (e.g., Forest-GCB, Running and Gower, 1991; PnET-CN, Aber et al., 1997) or Dynamic Global Vegetation Models (DGVM, e.g., LPJ-DGVM, Quegan et al., 2011; CLM-FATES, Lawrence et al., 2018) that simulate competition among plant functional types (PFTs) at regional to global scales (Medlyn et al., 2011). Both of these classes of models tend to simulate the mechanisms of photosynthesis and competition for light and water, and are therefore relatively robust for making predictions for novel climatic conditions that are outside the conditions under which forests have been studied in the past (Gustafson, 2013).

Dynamic Global Vegetation Models play a key role for integrating climate-vegetation feedbacks within Global Circulation Models by projecting the spatial distribution of PFTs across the globe. However, it has been demonstrated that spatial processes not modeled by DGVMs (disturbances, seed dispersal and establishment, and the consequent sub-cell heterogeneity that results from those processes) degrade their ability to accurately scale up ecosystem processes to regional and global scales (Fisher et al., 2010), particularly in high-latitude biomes (Wullschleger et al., 2014), where disturbances (particularly fire) greatly alter living and dead carbon pools (Dolman et al., 2012). Also, because DGVMs model PFTs rather than individual species, the re-assortment of species into novel assemblages (and habitats) as climate and disturbance regimes change is poorly simulated. Alternatively, stand biophysical models (e.g., PnET, Aber et al., 1995; LINKAGES, Post and Pastor, 1996) also tend to have mechanistic formulations based on first principles, and can robustly account for competitive interactions, but they rarely include spatial interactions among stands, such as seed dispersal, contagious disturbances, and hydrologic links to the broader landscape. Such models are useful to predict stand-level responses to climate change and management interventions, but they omit many of the factors that operate at broader spatial scales and determine forest dynamics at landscape and regional scales.

Forest Landscape Models (FLMs) have proved useful for projecting future forest dynamics because they explicitly account for most of the factors that structure forested ecosystems at landscape spatial and temporal scales (He, 2008), and simulate seed dispersal and disturbances such that their interactions play out as an emergent property of the climate inputs, abiotic environment and vegetation state. Unlike DGVMs, FLMs are spatially explicit at a relatively fine resolution (10–500 m cells) and most simulate competition and succession at the species level. Unlike stand models, FLMs include spatial interactions among stands. However, FLMs tend to have weak or indirect links between climate and growth, often using slowly changing climate averages that fail to account for the importance of extreme events in structuring forests (Gustafson, 2013). Virtually all FLMs are unable to dynamically link climate to changes in hydrology, especially in hydrologic systems where soil waterlogging is possible, although a couple examples of loosely coupling a hydrology model with an FLM have recently been described (De Jager et al., 2019; Speich et al., 2019).

The LANDIS-II FLM (Scheller et al., 2007) simulates growth, death and succession of tree species cohorts (rather than individuals, PFTs or forest types) on grid cells (10–500 m) that interact spatially through seed dispersal and contagious disturbances. LANDIS-II requires one of several available succession extensions to simulate growth processes, and has many optional extensions to simulate disturbances relevant to the system under study. A relatively mechanistic succession extension was developed for LANDIS-II that relies on first principles related to growth via photosynthesis

(De Bruijn et al., 2014). This extension (PnET-Succession) incorporates algorithms from the PnET-II eco-physiology model (Aber et al., 1995), and it represents a major advance in forest landscape modeling because it mechanistically simulates photosynthesis as in DGVMs and biophysical models, while LANDIS-II includes the spatial processes (e.g., seed dispersal and contagious disturbances) that are inadequately simulated in those models. This new modeling approach provides some key advances over other FLMs that operate at this intermediate scale. (1) Growth is tightly linked to climate and responds to climate dynamically at a monthly time step (vs. annual or decadal), better reflecting the major effect of weather extremes in structuring forests through growth and mortality. (2) Succession is an emergent property of species-level growth and competition under dynamic climate conditions rather than transition probabilities among forest types or assemblages (e.g., ALFRESCO, Rupp et al., 2000). (3) Mortality is mechanistic rather than probabilistic, occurring when carbon reserves drop below critical levels when photosynthetic output is insufficient to cover respiration costs. (4) Species cohorts compete for soil water, simulated using a relatively simple hydrologic bucket model. PnET-Succession also includes species-specific water stress parameters for both low (dry) and excessively high (waterlogged) water potentials. (5) The mechanistic approach integrates CO_2 effects on growth, conductance and water use efficiency; temperature effects on photosynthesis, respiration and evapotranspiration (including length of growing season); precipitation and consumption effects on water availability; incoming radiation and canopy layering effects on light extinction; and inter-cohort competition for light and water, all of which interact to determine species-cohort productivity and competitiveness under a given climate and hydrologic regime. It is virtually impossible to robustly simulate such interactions under novel climatic conditions using a phenomenological approach that uses the past to predict the future.

Despite the significant advantages of PnET-Succession for simulating the impacts of global abiotic change on future forest dynamics, its soil hydrology calculations assume that the water table is below the rooting zone and the simulation of hydrology has few links relevant to changes in climate other than precipitation inputs. Furthermore, the model assumes that water can drain through the soil profile into the water table sink, but it does not perform well when the water table normally fluctuates within the rooting zone (e.g., forested wetlands, flood plains) or when the size of the hydrologic "bucket" varies seasonally (e.g., permafrost). Therefore, to reliably simulate climate change effects on such forests, modifications are needed to more directly link PnET-Succession hydrology parameters to the monthly climate inputs of the model. Given that a large proportion of the world's forests are located on wet or frozen soils (Brown et al., 1997; Lehner and Döll, 2004) where waterlogging is an important factor driving competitive outcomes, this limitation is not trivial.

Our primary objective was to strengthen links in PnET-Succession between climate and hydrology to specifically allow simulation of (1) fluctuating saturation of lowland soils in swamps and bogs, and (2) permafrost dynamics and their effect on soil water. We modified the model and tested its ability to project changes in competitive outcomes among species occurring on soils subject to waterlogging under changing climate using hypothetical ecosystem and climate scenarios. A secondary objective was to evaluate the feasibility of simulating range expansion and contraction induced by climate change at high latitudes by conducting simple experiments on a hypothetical landscape grid.

MATERIALS AND METHODS

A major strength of PnET-Succession is its basis in well-established principles of tree physiology, so our first inclination was to take a first principles, mechanistic approach to improve the hydrologic component of the model. However, we quickly realized that doing so would add a prohibitive computation and parameterization burden to the model that would make it intractable at landscape scales. Mechanistically simulating water table dynamics is extremely complex and requires 3D terrain and soil data to compute vertical flow of water within the soil and bedrock profile as well as surface and subsurface horizontal flow of water between grid cells. Additionally, it is important to account for catchment-scale features such as natural and man-made impoundments, aquifer recharge and discharge areas, and broad-scale impervious soil layers (Carter, 1996). We therefore chose to implement relatively simple, intuitively understood hydrologic parameters that are linked to climate inputs to alter the hydrological behavior of individual cells in response to temperature and precipitation inputs at a monthly time scale. Our goal was to produce a generally realistic hydrologic response to climate that accounts for the soil type in each "ecoregion" in a map that represents the abiotic landscape within LANDIS-II. Ecoregions (i.e., biophysical land units) can be defined by a variety of characteristics, including soil characteristics, elevation, and disturbance regimes. In this paper, we use the ecoregion construct to define soil water saturation regimes reflective of lowland (i.e., saturated, excess water, etc.) versus upland (i.e., sufficient drainage to avoid saturation) biophysical land units. These capabilities are therefore necessarily phenomenological and somewhat simplistic, but they add a critical link to climate that is appropriately precise for the broad spatial and temporal scales at which landscape models operate.

Description of PnET-Succession

In PnET-Succession (De Bruijn et al., 2014), species-cohort (not individual tree) growth rates are calculated as a function of photosynthesis, which is fundamentally limited by water and light. Soil water availability is determined by precipitation inputs, loss to evaporation and runoff, leakage through the soil and consumption by species cohorts. Cohorts compete for water and light in each grid cell, and cohort biomass determines the priority of access to light, but not water. Growth is modeled as a competition of tree species cohorts at a monthly time step, and cohorts die when their respiration requirements chronically exceed their productivity (as determined by access to light and water). Maximum net photosynthetic capacity (*Amax*) is fundamentally determined by foliar nitrogen (FolN), and actual photosynthesis in a given month depends on the limiting (reduction) factors accounting for light, water, temperature, CO_2 concentration, age and optionally, ozone concentration. Each reduction factor is a multiplier (0.0–1.0) applied to species Amax to determine net photosynthesis (*A*) in each time step, such that a reduction factor of 1.0 is not limiting, and a value of 0.0 is limiting enough to completely shut off photosynthesis. Light availability varies vertically through the canopy, with canopy layering in the model represented by major canopy layers and subcanopy layers within each major canopy layer (Gustafson et al., 2020a). The light available in a given subcanopy layer is dependent on radiation at the top of the canopy, leaf area and extinction coefficients of cohorts in higher canopy layers. Temperature limits growth as it departs from the species-specific optimal temperature and as respiration costs increase with elevated temperatures. Length of growing season is annually dynamic and species-specific, beginning and ending when mean monthly daytime temperature is above user-defined thresholds. Mortality by extreme cold is simulated whenever minimum temperature drops below a species' cold tolerance. We use the methods of Court (1951) to estimate minimum daily temperature in winter months from the standard deviation (WinterSTD) of empirical hourly temperatures, with WinterSTD being an ecoregion parameter. The coldest temperature extreme in a month is estimated as Tave-(3*WinterSTD), where Tave is the average of the monthly minimum and maximum temperature inputs for the month. Elevated CO_2 increases photosynthetic capacity (with acclimation) by increasing CO_2 concentrations within the leaf and increasing water use efficiency (Franks et al., 2013) as described in Gustafson et al. (2018). The age reduction factor gradually decreases photosynthesis as age approaches longevity to reflect senescence, ultimately causing respiration to exceed productivity. The age reduction factor interacts with the other reduction factors such that older cohorts are more likely to die when stressed.

Soil water can limit photosynthesis by either excess or scarcity, modeled as a reduction factor that reduces the maximum possible photosynthesis rate of the cohort in proportion to water stress. Soil water is tracked at the grid-cell level using a bulk-hydrology ("bucket") model based on precipitation, loss to foliage interception, evaporation, runoff and percolation out of the rooting zone, and consumption by vegetation. A maximum rooting zone depth parameter (RootingDepth) defines the depth of the "bucket" and soil texture determines the maximum available water capacity of the "bucket," calculated as the difference between field capacity and wilting point (Saxton and Rawls, 2004). Soil water potential is a function of soil texture, and the volumetric water content resulting from inputs and outputs (**Supplementary Figure S1**). The water stress reduction factor (fWater) is a multiplier that is calculated for each sub-layer within the canopy in each month as a function of the soil water potential of the grid cell after sub-layers having higher priority access to light have transpired the water required to support simulated photosynthesis. The order in which cohorts are processed for access to light and water is randomized within each layer, with the incoming monthly precipitation and/or snowmelt partitioned into a discrete number of precipitation events (defined by an ecoregion parameter) to increase chances for cohorts to get access to water. There are four species-specific soil water potential threshold parameters (H1–H4, Feddes et al., 1978) that determine water stress (fWater) at each month. H1 and H2 control species response to waterlogging and H3 and H4 control response to dry soil (drought tolerance). H1 specifies the water potential at which waterlogging completely shuts down photosynthesis (fWater = 0.0), and can be given a negative value to allow some photosynthesis on completely saturated soils (**Figure 1**). H2 specifies the water potential above which reductions in photosynthesis caused by waterlogging begin to occur. H3 specifies the soil water potential below which reductions in photosynthesis caused by dryness begin to occur and H4 specifies the potential at which photosynthesis completely shuts down. fWater is 1.0 (no reduction) at water potentials between H2 and H3. PnET-Succession uses water potential units of the absolute value of pressure head (m).

In PnET-Succession, each grid cell has a hydrological budget that is independent of other cells of the landscape (i.e., there are no horizontal flows). The single water input is monthly precipitation in the form of rain or snow melt, with incoming water (but not snowmelt) reduced by foliage interception in proportion to the cohort foliage (PrecIntConst). Fixed fractional losses of this input are controlled by three user-specified parameters: loss to surface runoff due to slope or impermeability (PrecLossFrac), sublimation of snow (SnowSublimFrac) and percolation out of the rooting zone (LeakageFrac). Dynamic losses vary according to conditions on the site, and include evaporation (a function of vegetation on the site and temperature), runoff (inputs in excess of water holding capacity), and consumption by vegetation (transpiration). Water is unable to enter the soil when frozen, so any input that occurs with a frozen soil surface (including snow melt) is lost as runoff.

Simulation of Forested Lowland Dynamics

In PnET-Succession, soil texture and rooting depth parameters define the water capacity of the soil "bucket" on each cell (**Figure 1**), and the leakage parameter determines the ability of the soil to drain to field capacity. Water inputs that exceed saturation are assumed to run off and are not tracked. Depth to water table is also not tracked, but it is assumed to be below the rooting depth and to function as an infinite sink for water draining through the soil. In the real world, water table height is a function of topography, presence or absence of an impermeable subsurface layer, evaporation, interception, transpiration demand, and precipitation inputs (Richardson and Ritchie, 1973). Forested lowlands (also known as forested wetlands) have a water table near the surface primarily because they are surrounded by higher ground that greatly impedes runoff, and because their topographically low position produces soils that are high in silt, clay and organics (Falkner and Richardson, 1989), which can impede drainage (leakage). In a lowland forest system, water is lost by normal rates of evaporation, interception and transpiration, but with relatively low rates of runoff and/or leakage (Carter, 1996). Waterlogging

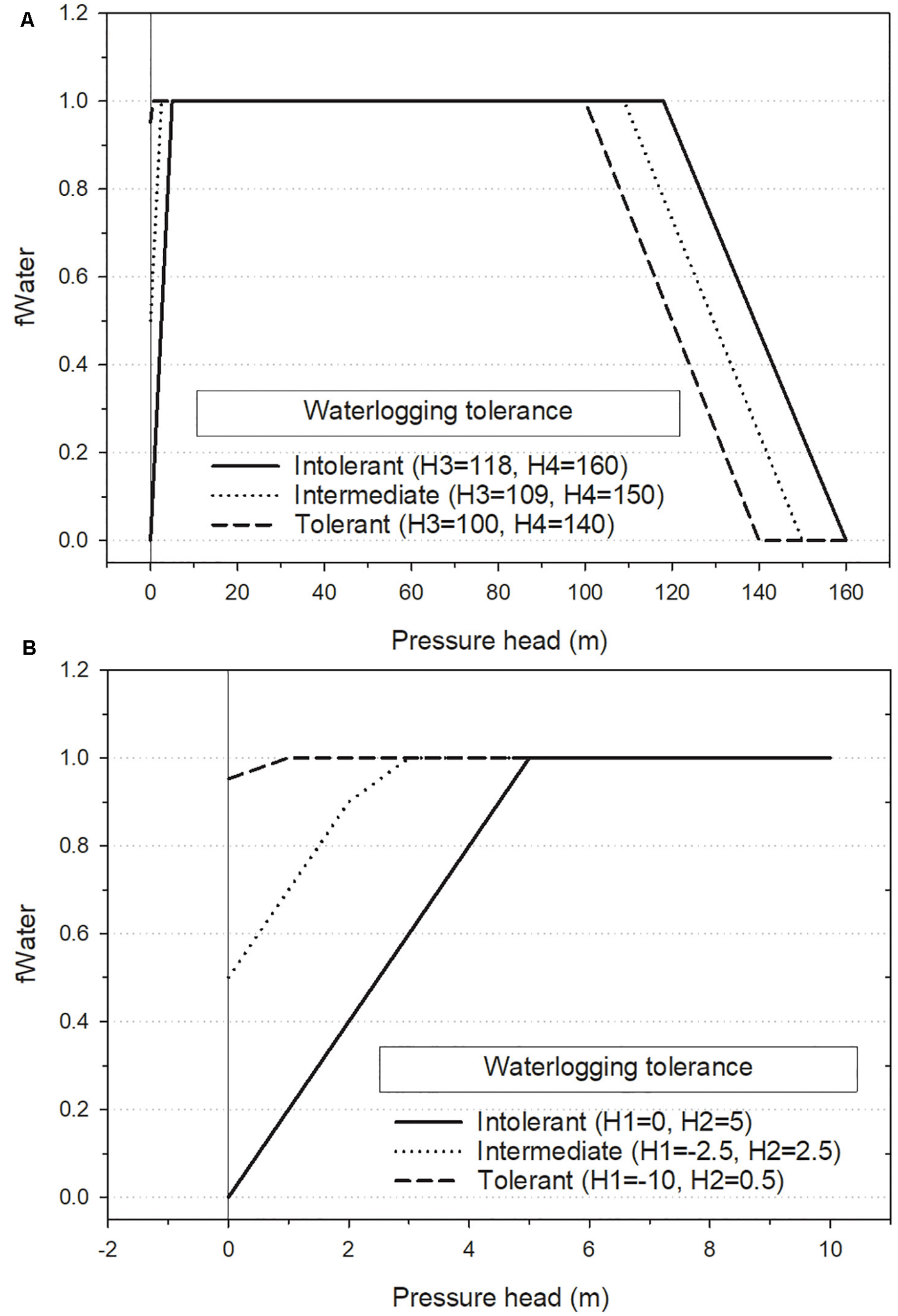

FIGURE 1 | Effect of soil water potential threshold parameters (H1–H4) on water stress (fWater) for the hypothetical species used in the single-cell lowland and permafrost experiments. fWater is calculated by linear interpolation between parameters H1–H4, with values of 1.0 resulting in no water stress. **(A)** Shows H1–H4 parameters and **(B)** shows the detail around H1 and H2. Note that pressure head (Ψ) can never fall below zero (vertical reference line), so negative values of H1 are used to determine fWater when Ψ = 0.

effects vary with the height of the water table, such that the soil is saturated (water potential = 0) when the water table is at or above the surface, drains normally when the water table is below the rooting zone, and has mixed drainage properties when the top of the water table is within the rooting zone (Ernst, 1990).

In this context, we modified PnET-Succession to improve its ability to simulate growth and competition in response to dynamic lowland hydrologic conditions. First, we added an ecoregion-specific parameter [RunoffCapture-the maximum height above ground level that excess water (runoff) can accumulate] that can be used to reduce some or all of the runoff within lowland ecoregions so that soil water can remain above field capacity and reach (or exceed) saturation, and this excess water is retained as surface water that contributes to the soil "water bucket." Thus, the soil remains excessively wet until runoff (beyond that allowed by RunoffCapture), evaporation, interception, transpiration and leakage (if any) collectively exceed cumulative precipitation inputs and any surface water (i.e., have consumed all excess water). In practice, the boundaries of the lowland ecoregions defined in model inputs would be derived from a DEM or by the location of existing lowland vegetation, and RunoffCapture would represent the average maximum depth of standing water, or could be calibrated to match the distribution of empirical water potentials given climate inputs or potentials consistent with the vegetation currently found in the ecoregion. For upland ecoregions (non-lowlands where runoff is generally unimpeded), RunoffCapture would typically be set to 0 (mm), and PnET-Succession would behave as in prior versions.

Second, the existing PnET-Succession ecoregion parameter LeakageFrac can be used to prevent some or all of the water from draining out of the rooting zone, to reflect the permeability of a non-porous layer and the basin configuration [i.e., ability of water to exit the lowland basin(s)]. This parameter could be estimated to reflect known sub-rooting-zone soil permeability, or to match empirically observed rates that water potential drops during drought and returns to a saturated condition after a drought is broken. These two simple modifications allow maximum flexibility for parameterization and calibration of lowland water dynamics with the addition of just one new parameter. The RunoffCapture parameter is conceptually linked to the mechanism of topographic position that impedes runoff, and the LeakageFrac parameter is linked to the mechanism of soil permeability at or near the bottom of the rooting zone.

With these modifications, water stress in lowland ecoregions can respond dynamically to monthly climate inputs and vegetation without the computational burden of mechanistically simulating hydrology across the entire landscape. Waterlogging stress can result whenever cumulative precipitation inputs chronically exceed the cumulative removal of water by runoff, evaporation, leakage and transpiration, and the growth of species with higher waterlogging tolerance would be favored. Lower water potentials can develop when vegetation growth increases transpiration rates sufficiently, or if precipitation declines for an extended period (e.g., drought, climate change). Climate change can also remove more water by increasing evaporation under higher temperatures. Most importantly, waterlogging stress responds dynamically at a monthly time step to variation in cumulative precipitation inputs and vegetation characteristics. Competitive interactions among species respond directly to available soil water through their drought and waterlogging tolerance parameters (H1–H4) and indirectly because establishment probability in PnET-Succession is dynamically proportional to the suitability of the light and water environment on each cell for growth of each species.

Cell-Scale Lowland Forest Experiment

We tested the effects of these new capabilities for modeling forested wetland dynamics using a single-cell factorial experiment with two treatment factors: biophysical unit [encapsulating soil water loss (RunoffCapture/Leakage)] and precipitation (each with 3 levels). A hypothetical baseline climate mimicking monthly temperature and precipitation typical of high latitude forests was used, and the high and low precipitation levels were generated by adding or subtracting 50% from baseline precipitation. The RunoffCapture (mm) and Leakage (fraction) levels were concurrently set to represent upland (unimpeded runoff and drainage), intermediate and very wet biophysical units (ecoregions) (**Table 1**). Temperature and precipitation levels were held constant across years within each level, and all other abiotic inputs were held constant across treatments, including CO_2 (400 ppm) and latitude. We initialized each cell with an assemblage of 3 hypothetical species (age = 20), each having a different waterlogging tolerance (**Supplementary Table S1**). We set species optimal temperature for photosynthesis equal to the mean growing season temperature of the baseline climate input. All other parameters were constant across all treatments, and establishment of new cohorts was prevented to avoid confounding competitive interactions among the three initial cohorts. All input files are given as **Supplementary Material**. Three replicates of 50 years simulations were generated. We quantified the effect of the treatments using GLIMMIX (SAS v9.4) to compute 95% confidence intervals and investigate interactions among the treatment factors on mean net photosynthesis and water stress (fWater) of each cohort across the growing season months of the last decade of the simulations. GLIMMIX estimates marginal means over a balanced population and confidence intervals are adjusted for the covariance parameters in the model.

Our expectation was that upland sites should have higher photosynthesis because of less waterlogging stress, and that increased precipitation should increase photosynthesis by reducing drought stress. Greater waterlogging tolerance should allow cohorts on Intermediate and Very wet sites to maintain photosynthesis by reducing waterlogging stress.

Simulation of Soil Ice Dynamics

To optionally simulate seasonal soil ice dynamics (specifically, over permafrost), we modified PnET-Succession to make active rooting depth and leakage fraction dynamic at a monthly time

TABLE 1 | Factor levels used in the lowland forest experiment.

	Level		
Factor	**Low**	**Intermediate**	**High**
Precipitation (% of baseline)	−50	+0	+50
RunoffCapture (mm)*	0	300	600
LeakageFrac (fraction)*	1.0	0.3	0.0

**Note that RunoffCapture and LeakageFrac were set concurrently to form a single treatment factor (soil water loss), resulting in a 2 × 3 factorial experiment (soil water loss and precipitation).*

step, driven by the temperature inputs to the model. Active rooting depth in this case is understood to represent the mean depth to the ice layer (0°C isotherm) in the month, although rooting depth is constrained in the model not to exceed the user-defined maximum depth that tree roots can typically extend (RootingDepth). When the ice layer retreats further below the rooting depth, we assume that the water column within the root zone is increasingly able to drain, and the effective leakage fraction is therefore increased linearly from 0.0 * LeakageFrac (when an ice layer is present within the rooting zone) to 1.0 * LeakageFrac when the ice layer is below the root zone by a user-specified depth (LeakageFrostDepth). Thus, the presence of an ice layer varies the available soil water within the rooting zone (active layer) according to temperature dynamics.

Soil temperature, T_{soil} at depth z (m) at month m is used to determine the depth to the ice layer as described for the LPJ DGVM in the appendix of Sitch et al. (2003):

$$\mathrm{T}_{\text{soil}}\,(z, m) = \; T_{\text{ave}} + A \times exp\left(\frac{-z}{d}\right) \times \sin\left(\Omega m - \frac{z}{d}\right) \tag{1}$$

where T_{ave} is average air temperature for month m, A is the amplitude of air temperature over the previous 12 months, d is the damping depth (m), and Ω the angular frequency of oscillation (radians/month). The damping depth, d, and angular frequency of oscillation (Ω) are calculated as:

$$d = \sqrt{\frac{2k}{\Omega}} \tag{2}$$

$$\Omega = \frac{2\pi}{12} \tag{3}$$

where k is the thermal diffusivity (mm^2 mo^{-1}) of the soil.

Thermal diffusivity (k) is estimated using the methods of Farouki (1986) and Jong van Lier and Durigon (2013), with inputs of total porosity (m^3/m^3), water content (m^3/m^3) and fraction clay (proportion), which make it dynamically dependent on the soil texture and its water content each month. These methods are generally consistent with those used in the LPJ DGVM (Beer et al., 2007), and produce dynamic soil temperature profiles (**Supplementary Figure S2**).

Equation [1] was additionally adapted to account for the insulating properties of snow and moss vegetation. As noted by Sitch et al. (2003), the $exp\left(\frac{-z}{d}\right)$ component of this equation effectively represents the reduction in temperature oscillation amplitude, which is due to the cumulative insulating properties of the soil at depth z. We used the same approach to apply snowpack and vegetation (i.e., moss, litter) impacts on the temperature oscillation by introducing two additional reduction factors.

$$\begin{aligned} T_{\text{soil}}\,(z, m) = \; & T_{\text{ave}} + A \times D_{\text{soil}} \times DR_{\text{snow}} \\ & \times DR_{\text{moss}} \times \sin\left(\Omega m - \frac{z}{d}\right) \end{aligned} \tag{4}$$

where D$_{\text{soil}}$ = $exp\left(\frac{-z}{d}\right)$ as above, and DR$_{\text{snow}}$ and DR$_{\text{moss}}$ follow the damping ratio formulation from Liang et al. (2014):

$$DR_{\mathrm{z}} = \; e^{-z\left(\frac{\Omega}{2k}\right)^{1/2}} \tag{5}$$

The calculations for snow include estimating thermal diffusivity (k$_{\text{snow}}$), thermal conductivity (λ_{snow}, W m-1 K-1 [Jordan, 1991]) and volumetric heat capacity (c_{snow}, kJ m^{-3} K^{-1}) based on the established heat capacity of snow (2090 J kg^{-1} K^{-1}):

$$DR_{\text{snow}} = e^{-snowdepth\left(\frac{\Omega}{2k\ \text{snow}}\right)^{1/2}} \tag{6}$$

$$k_{\text{snow}} = \frac{\lambda_{\text{snow}}}{c_{\text{snow}}} \tag{7}$$

$$\begin{aligned} \lambda_{\text{snow}} = {} & (\lambda_{\text{air}} + \left(\left(0.0000775 \times p_{\text{sno}}\right) + \left(0.000001105 \times p_{\text{sno}^2}\right)\right) \\ & \times (\lambda_{\text{ice}} - \lambda_{\text{air}})) \times 3.6 \times 24 \end{aligned} \tag{8}$$

$$c_{\text{snow}} = \frac{2090 \times p_{\text{sno}}}{1000} \tag{9}$$

The values for thermal conductivity of air (λ_{air}) and ice (λ_{ice}) are 0.023 and 2.29 W m^{-1} K^{-1}, respectively (Jordan, 1991). Snow density (p$_{\text{sno}}$, kg m^{-3}) is estimated using a relationship estimated from Figure 4a of Jonas et al. (2009), with density increasing over the length of winter:

$$p_{\text{sno}} = 165 + 1.3 \times WinterDays \tag{10}$$

The calculations for moss use the same general damping ratio formula, with estimates of moss heat capacity (c$_{\text{moss}}$ = 2500 kJ m^{-3} K^{-1}) and thermal conductivity (λ_{moss} = 432 kJ m^{-1} d^{-1} K^{-1}) from Sazonova and Romanovsky (2003):

$$DR_{\text{moss}} = e^{-mossdepth\left(\frac{\Omega}{2k_{\text{moss}}}\right)^{1/2}} \tag{11}$$

$$k_{\text{moss}} = \frac{\lambda_{\text{moss}}}{c_{\text{moss}}} \tag{12}$$

Soil warming in this model is not dependent on the albedo and radiation associated with site vegetation other than as they may affect air temperature in the climate inputs. Incoming precipitation and melting snow cannot enter the frozen portion of the soil, ensuring that the depth of an ice layer will dynamically determine how much snow melt can enter the soil "bucket." The water content of the soil when it thaws is the same as when it froze.

Cell-Scale Permafrost Experiment

We tested the effects of waterlogging induced by these permafrost dynamics using a simple single-cell factorial experiment with two factors: temperature and precipitation (3 levels each). The same baseline climate described above was used for the middle level of each factor, and the other factor levels were generated by adding or subtracting 3 degrees C from the baseline temperature and adding or subtracting 50% from baseline precipitation. Temperature and precipitation levels were held constant across years within each level, and all other abiotic inputs were held constant across all treatments, including CO$_2$ (400 ppm) and latitude. We used the same species parameters as for the forest lowlands test (**Supplementary Table S1**). All input files are given as **Supplementary Material**. To assess the consequences of omitting permafrost dynamics, we conducted the experiment with and without the simulation of soil freezing (ice), which served as a third experimental factor. We quantified the effect of the treatments using GLIMMIX (SAS v9.4) to compute 95% confidence intervals and investigate interactions among the treatment factors on mean net photosynthesis and water stress (fWater) of each cohort across the growing season months of the last decade of the simulations.

Our expectation was that increasing temperature in this high latitude experiment should increase photosynthesis by making more soil water available by increasing the depth of the active layer, that increased precipitation should increase photosynthesis by reducing water stress, and increased waterlogging tolerance should increase photosynthesis because permafrost reduces leakage and keeps soils wetter. We also expected an interaction between temperature and waterlogging tolerance, because increasing temperature should reduce soil wetness on permafrost sites.

Latitudinal Gradient Test Case

We then applied these new capabilities to a hypothetical "landscape" to evaluate the potential ability of PnET-Succession (v4.0) to model species colonization dynamics across a large latitudinal gradient in Siberian Russia in response to climate change. We constructed a simple 5 × 6 grid where each row represented a latitudinal zone located at approximately 100°E longitude, and each cell represented a typical forest stand. The grid is an artificial construct created to efficiently implement what is essentially a collection of single-cell experiments that also allow colonization to occur between adjacent cells. The upper row represented the tundra biome with a latitude of 74°N, initialized without woody vegetation. The second row was designated as latitude 70°N, initialized with a cold-tolerant shrub species (*Betula nana*) and Siberian larch. Subsequent rows represented latitudes 66°N (northern taiga), 62°N (middle taiga) and 58°N (southern taiga), initialized with Siberian species (**Table 2**) typically found at each latitude (**Supplementary Table S2**). The rows representing 66 and 58°N also had additional cells parameterized as forested wetlands and initialized with more waterlogging tolerant species, including a sphagnum (66N) and grass (58N) pseudo-species (not trees). We conducted a factorial experiment with two factors: future climate (RCP 2.6, 6.0, 8.5) for each latitude and biophysical unit (upland, lowland). Individual cells in each row were assigned a unique climate/biophysical unit (ecoregion), with climate projections through the year 2099 for each location generated by the Hadley GEM2-ES earth system model (Collins et al., 2011) (**Table 3**). The last 10 years of each climate projection was repeated for the final 100 years of each simulation. All sites were simulated using a loamy sand soil; upland sites had rooting depth = 0.9 m (1.0 at 58°N sites), LeakageFrac = 1.0 and RunoffCapture = 0 m, and lowland sites had a rooting depth = 0.7 m, LeakageFrac = 0.01 and RunoffCapture = 0.075 m. LeakageFracDepth was set at 3.0 m in all experiments. In this experiment, dispersal was simulated every 10 years, and was constrained to occur only between adjacent cells (including diagonal) to mimic colonization (range shifts) at ecotone boundaries, with establishment and growth being determined by the climate and extant competitors on each cell through time. Thus, the grid should not be interpreted as a spatially explicit landscape, but rather as a construct to conduct a highly controlled experiment, allowing colonization to occur between adjacent biomes. We evaluated simulations with and without a single stand-replacing disturbance (i.e., clear cut or wildfire, catalyzing species turnover) occurring independently on each cell at year 70. Four replicate simulations were run for 200 years to allow time for climate and disturbance effects to play out. All input files are given as **Supplementary Material**. For each treatment combination, we computed the change in species richness over 200 years, plotted the trajectory of biomass of each species on each cell, and quantified the number of invasions (species not initially present, but present after 200 years) and extirpations (initial species not present after 200 years) and maximum total biomass observed on each cell.

TABLE 2 | Siberian species used in the simulations.

Common name	Scientific name	Abbreviation
Siberian fir	*Abies sibirica*	abiesibi
Black alder	*Alnus glutinosa*	alnuglut
Dwarf birch	*Betula nana*	betunana
European white birch	*Betula pendula*	betupend
Siberian larch	*Larix sibirica*	larisibi
Siberian spruce	*Picea obovata*	piceobov
Siberian pine	*Pinus sibirica*	pinusibi
Scots pine	*Pinus sylvestris*	pinusylv
European aspen	*Populus tremula*	poputrem
Sphagnum	*Sphagnum* spp.	sphagnum
Generic steppe grass	N/A	genegrss

Our expectation was that biomass should (1) increase as emissions increase because of CO_2 fertilization and longer growing seasons, (2) decrease with increasing latitude because the growing season is shorter, and (3) decrease with disturbance because cohorts are younger. Richness should (1) be unchanged even as assemblages change in response to changing climate (i.e., the number of niches is not changed), and (2) increase with disturbance (intermediate disturbance hypothesis). Invasions and extirpations should (1) increase with disturbance because niches are opened, (2) increase with climate change because ranges shift, and (3) decrease at lower latitudes because change in climate is less.

RESULTS

Cell-Scale Lowland Forest Experiment

Model outputs confirmed that the model appropriately produces saturated or drained soils given the inputs for biophysical unit and precipitation, with corresponding water stress varying according to waterlogging tolerance (**Figure 2**). Surface flooding also responded appropriately to inputs (**Table 4**). Both biomass growth and water stress clearly responded to all three treatment

TABLE 3 | Projected change in temperature and annual precipitation by 2099 made by the Hadley GEM2-ES earth system model under each CO_2 emissions scenario for each latitude of the latitudinal gradient test case.

RCP emissions scenario	CO_2 in 2100 (ppm)	74 N (°C)/(mm)	70 N (°C)/(mm)	66N (°C)/(mm)	62N (°C)/(mm)	58N (°C)/(mm)
2.6	421	4.22/4.33	2.62/9.92	2.17/5.59	2.39/2.39	1.82/3.19
6.0	670	10.15/15.85	6.95/21.55	6.84/9.58	6.04/10.94	5.24/4.67
8.5	936	13.79/19.04	10.26/27.36	10.03/7.75	9.46/6.04	8.55/5.70

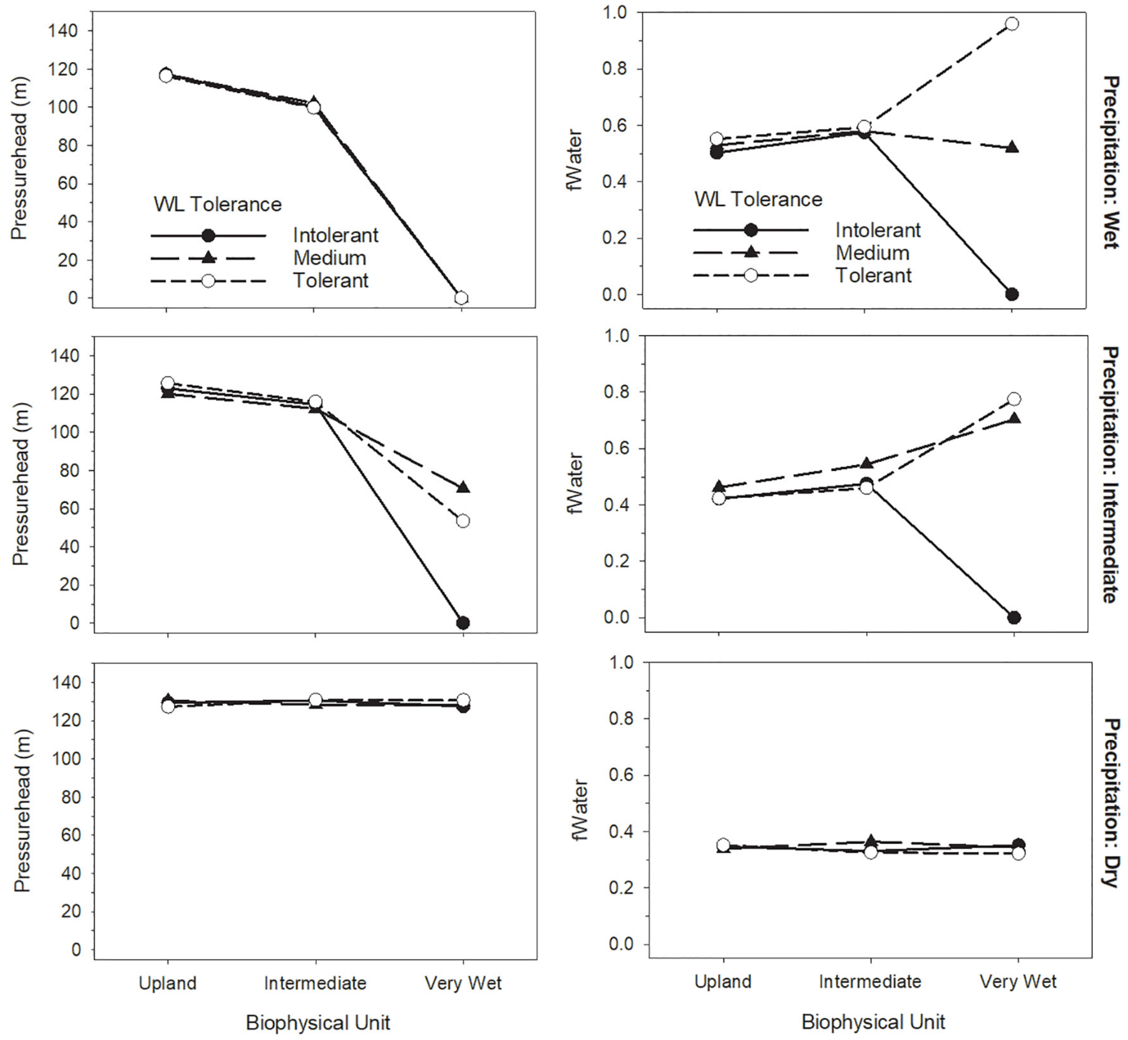

FIGURE 2 | Response of water stress (fWater) during the growing season months of the last decade of the simulations to soil water potential (pressure head) as a function of biophysical unit, precipitation and species waterlogging tolerance.

factors in the forested lowlands test case (**Figure 3**). Species waterlogging tolerance was the strongest determinant of net photosynthesis (**Figure 3A**), followed by precipitation, with biophysical unit also having an effect such that the treatments producing the wettest conditions were the most productive. This result, along with the pressure head showing consistently high values expect for the wettest biophysical unit (**Figure 2**) suggests that the arbitrary drought tolerance parameters and relatively dry climate were perhaps too limiting on upland biophysical units. All interactions among treatment factors were highly significant (not shown), and biophysical unit appeared to have its greatest influence as it interacted with waterlogging tolerance. Water stress differed primarily based on species waterlogging tolerance and precipitation inputs, with biophysical unit having a less clear effect (**Figure 3B**). There was a highly significant interaction between biophysical unit and waterlogging tolerance ($F = 32.45$, $p < 0.0001$), reflecting the fact that the waterlogging tolerance parameters used were able to maintain productivity in very wet biophysical units, often allowing waterlogging tolerant species to overtop the others. Water stress can result

TABLE 4 | Evaluation of surface flooding in response to treatments in the lowland forest experiment (on a SALO soil*).

Biophysical unit	Precipitation −50%	Precipitation + 0%	Precipitation + 50%
Upland	113.26 (55.14)	120.97 (34.25)	128.24 (35.05)
Intermediate	100.95 (26.68)	132.94 (41.68)	147.68 (44.57)
Very Wet	101.33 (26.96)	582.35 (274.45)	824.80 (171.22)

Values are mean (std dev) of available soil water (mm) across all growing season months of the 50-year simulation experiment. Values above soil porosity (451.8 mm) indicate an average soil water height that is above the ground surface.
**Field capacity = 184 mm; wilting point = 81 mm.*

from two factors: waterlogging and drought. Our treatments produced both conditions, varying by treatment combination. Waterlogging tolerant species were parameterized to also be drought intolerant. However, because the baseline climate was relatively dry, our arbitrary parameters caused species responses to be more sensitive to waterlogging than to drought.

Cell-Scale Permafrost Experiment

Mean growing season depth to ice varied between 0.8 and 1.4 m by growing season month across all treatments, and was linearly related to mean growing season temperature (R^2 = 0.96, not shown), with wetter soil tending to thaw somewhat deeper, as expected. Net photosynthesis and water stress clearly responded to all three treatment factors in the permafrost test case (**Figure 4**). When we omitted the simulation of soil ice, the effect of temperature and precipitation on the response variables was little changed from the permafrost scenario, but waterlogging tolerance had virtually no effect without soil ice to impede drainage.

Latitudinal Gradient Test Case

The growth (biomass) of individual species responded to both emissions scenario and latitude as a function of competition and establishment (**Figures 5**, **6**). Trend lines with large uncertainty represent stochasticity, primarily of establishment and to a lesser extent, competition. We found that total biomass (all cohorts of all species) increased dramatically with increasing emissions scenario (**Figure 7**). This effect was more pronounced at higher latitudes, suggesting that temperature is an important driver. However the magnitude of the biomass increase seen under RCP 8.5 is likely related to longer growing seasons and the CO_2 fertilization effect. Biomass was generally higher without disturbance (**Figures 5**, **7**), and disturbance often facilitated a change in species composition (**Figure 6**).

Invasions were highest at latitude 66N and higher (**Figure 7**), partly because there were fewer extant species in the northern sites. Invasions tended to be higher with elevated emissions, although this did not hold true at all latitudes. Extirpations increased at lower latitudes, partly because there were more species initially at lower latitude sites. Extirpations did not consistently respond to emissions scenario. Disturbance appeared to have little effect on the number of extirpations, while disturbance generally increased invasions, presumably by opening up colonization opportunities.

On wetland sites, there was also a consistent trend of increasing biomass as emissions increased (**Figure 8**), but there was no clear trend for invasions and extirpations (**Figure 7**). Extirpations were primarily of tree species that were unable to survive for 200 years and unable to regenerate because of excessive wetness. Invasions were primarily by species highly tolerant of waterlogging, and sites tended to become dominated by one or two waterlogging tolerant species, mainly sphagnum and dwarf birch in the north, and grass and alder in the south. However, in the absence of disturbance, Siberian pine (*P. sibiricus*) cohorts were able to grow sufficiently large to reduce waterlogging by transpiration such that they were sometimes able to attain fairly high biomass. It appeared that temperatures became too warm for most species to thrive in southern sites during the last century of the RCP 8.5 scenario.

On upland sites, species richness tended to increase at the higher latitudes and decrease at the lower latitudes, and was higher as emissions increased (**Figure 9**). Disturbance generally produced higher species richness, although perhaps not substantially so. On wetland sites, richness always declined because only the highly waterlogging tolerant species that were initialized were able to persist (**Figure 9**). Disturbance did not have a clear effect on species richness on wetland sites, likely because outcomes were determined primarily by waterlogging tolerance so that only quite tolerant species persisted.

DISCUSSION

Our primary objective was to strengthen links in PnET-Succession between climate and hydrology to explicitly simulate the effects of permafrost and lowlands on soil water potential and forest response to waterlogging. This was done with the addition of only two new input parameters (RunoffCapture, LeakageFrostDepth). Our tests of these capabilities demonstrated a strong relationship between climate inputs, hydrologic response, and competitive outcomes. This represents an important advance for projecting the consequences of landscape management and climate change on future compositional and pattern dynamics on forested landscapes that have a large forested lowland component, or where permafrost is currently found. FLMs (including LANDIS-II) have typically had to either ignore the effect of waterlogging on forest dynamics (e.g., Lucash et al., 2018), or make assumptions about when waterlogging has an effect, and what those effects might be. In another study, these new capabilities added to PnET-Succession produced more definitive results about the effectiveness of climate-adaptive silviculture in a sub-boreal ecosystem in northern Wisconsin (United States) because investigators were not forced to ignore the management of the abundant forested lowlands in the study area (Gustafson et al., 2020b).

Insights From Case Studies

For the lowland benchmark test, our expectation was that lowland sites should have lower photosynthesis because of waterlogging, and that greater waterlogging tolerance should allow cohorts on Intermediate and Very wet sites to maintain

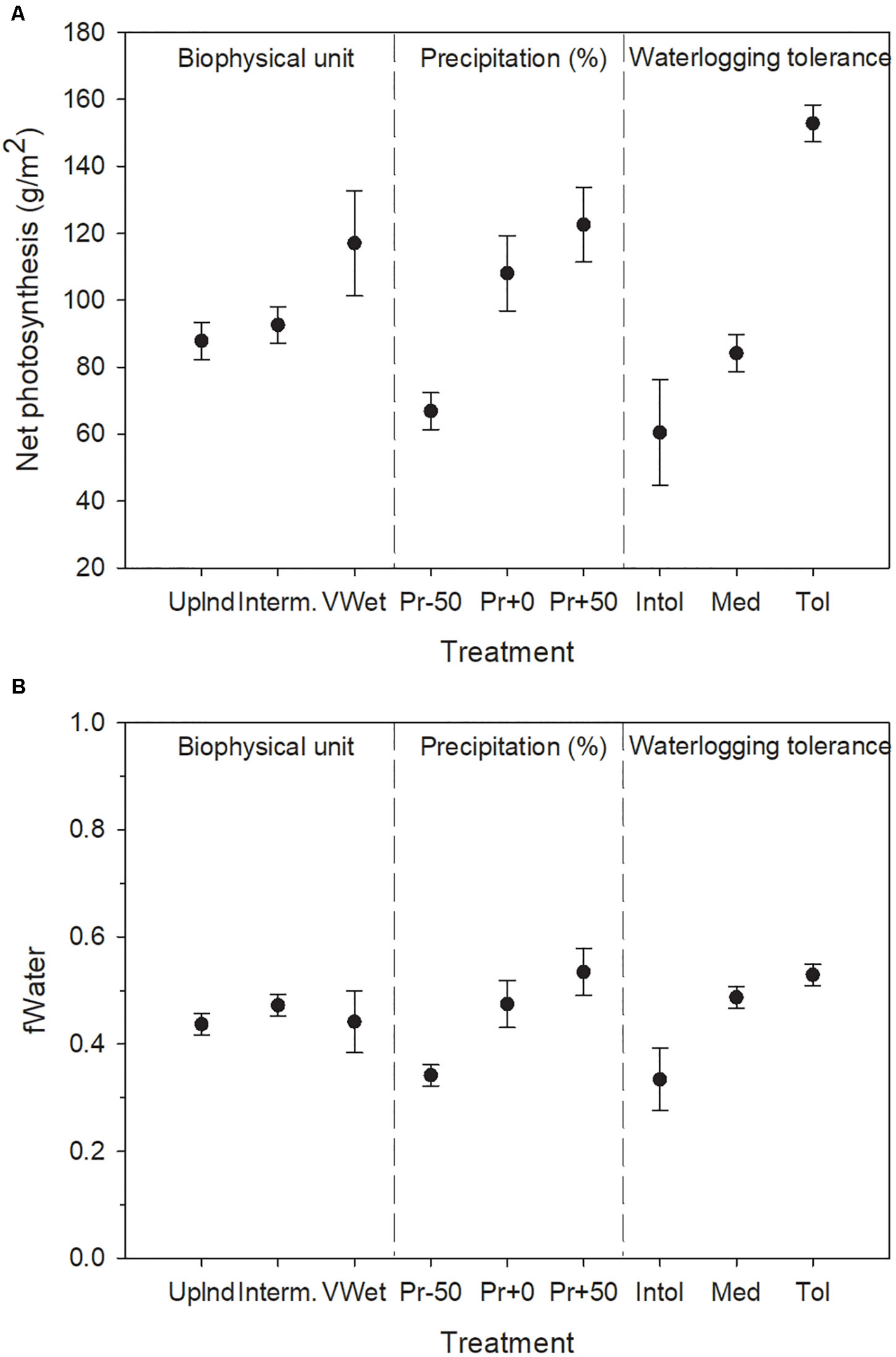

FIGURE 3 | Response of **(A)** net photosynthesis and **(B)** water stress to the treatment factors in the single-cell lowland forest experiment (soil ice not simulated). Water stress is inversely proportional to fWater. Error bars indicate 95% confidence intervals computed across the growing season months of the last decade of the simulations using least squares means of three replicates.

photosynthesis by reducing waterlogging. We found that in general, photosynthesis was greatest and water stress was least for scenarios with the most precipitation and for species with the greatest waterlogging tolerance (**Figure 3**). Upland sites had the lowest photosynthesis and the greatest water stress because our arbitrary water stress parameters produced more tolerance for wet soils than for dry soils and the climate produced relatively dry soils except when precipitation was high

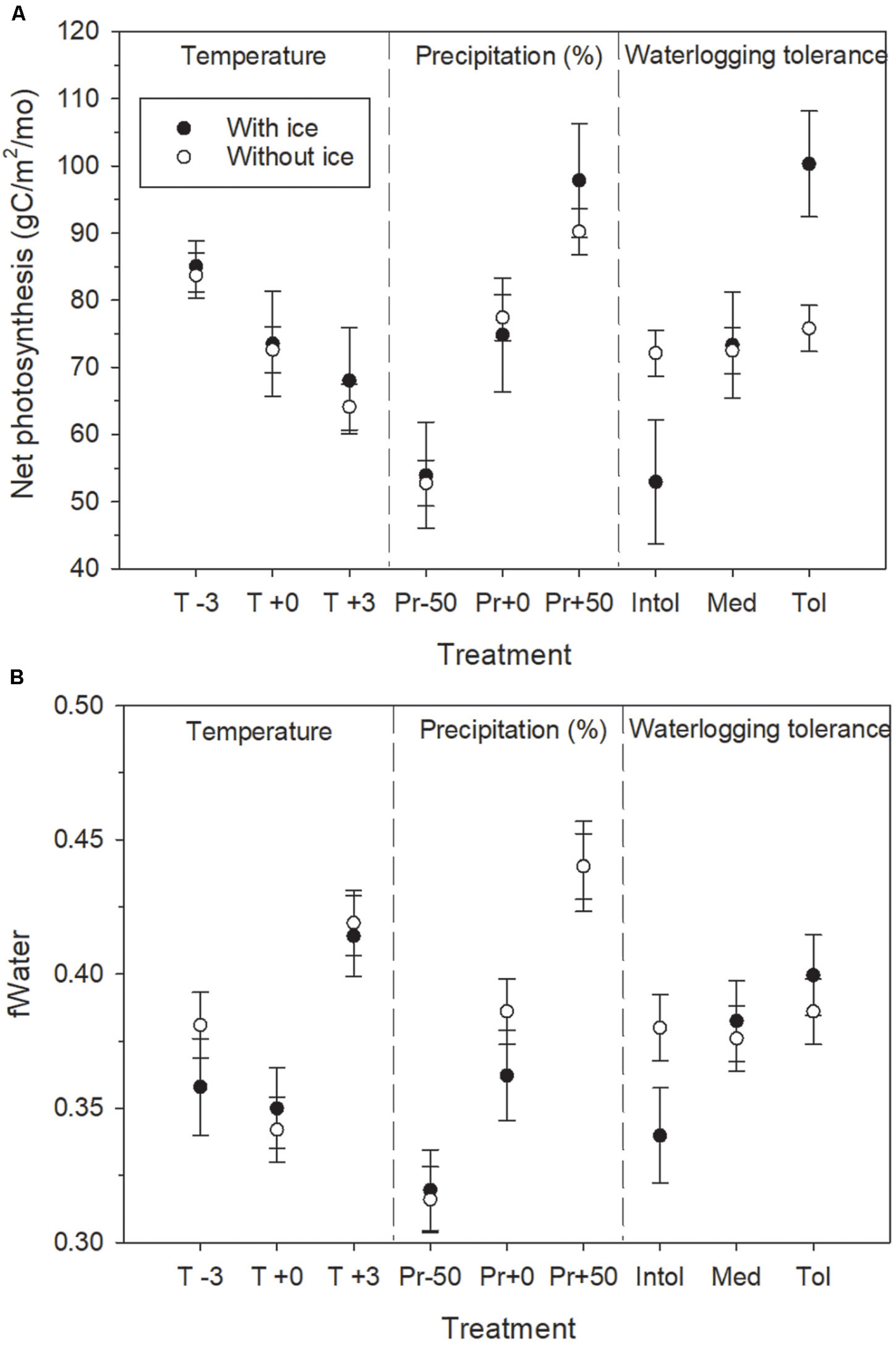

FIGURE 4 | Response of **(A)** net photosynthesis, and **(B)** water stress, to growing season water availability as a function of the treatment factors with and without permafrost simulated in the single-cell permafrost experiment. Water stress is inversely proportional to fWater. Error bars indicate 95% confidence intervals computed across the growing season months of the last decade of the simulations using least squares means of three replicates.

and/or leakage and runoff were constrained. It should be noted that dry conditions were possible on all biophysical units and precipitation treatments in some months in later years as cohorts grew large enough to become effective transpirers, perhaps explaining why fWater did not vary substantially by biophysical unit. **Figure 2** shows that the lack of overall change in fWater is because the effects on the different species canceled each other out to have little average effect, but a strong individual species effect. Overall, this test confirmed that the model appropriately produces surface flooding given the ecoregion and precipitation

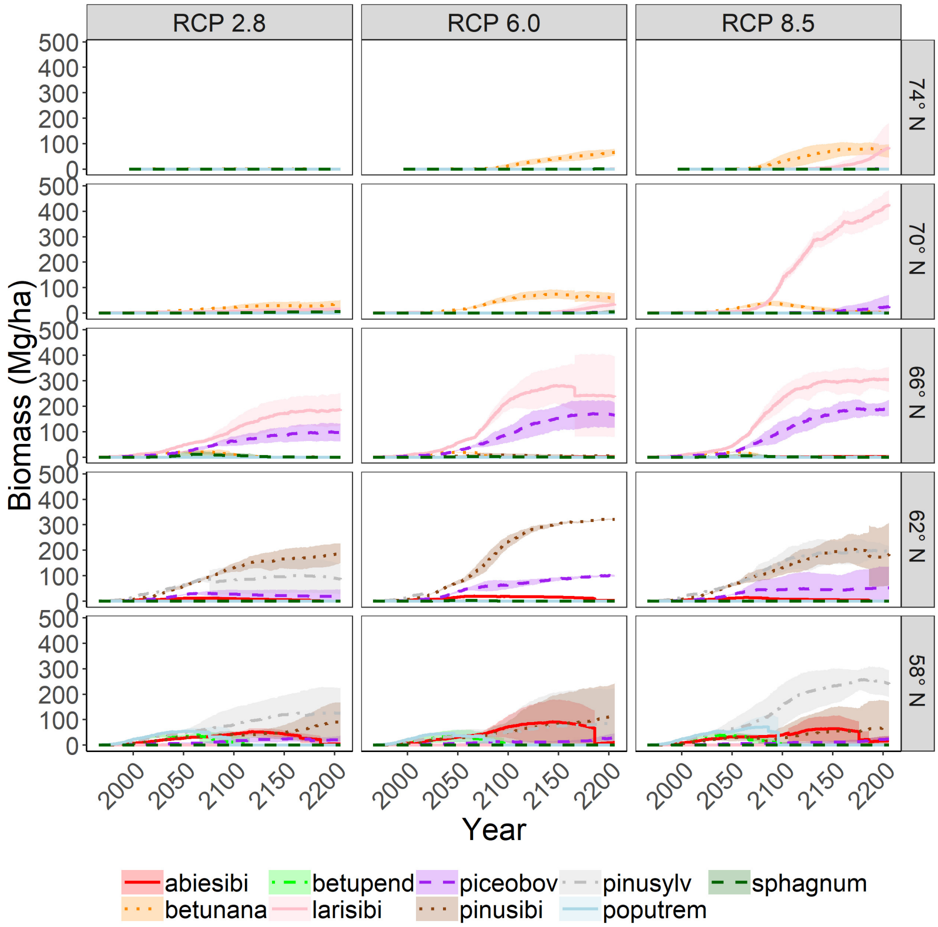

FIGURE 5 | Aboveground woody biomass of tree species through time in the absence of disturbance on upland sites. Shading represents one standard deviation of four replicates.

inputs, with equally appropriate species responses given their waterlogging tolerance.

Our expectations for the permafrost benchmark test were that increasing temperature should increase photosynthesis by making more soil water available (deeper active layer), that increased precipitation should increase photosynthesis by reducing water stress, and increased waterlogging tolerance should increase photosynthesis. We found that water stress (fWater) and photosynthesis were not tightly coupled in response to temperature (**Figure 4**), suggesting that other stressors (e.g., direct temperature effects on photosynthesis) had conflicting influence on the response. However, the two response variables responded similarly to precipitation and waterlogging tolerance. When we compared the outcome with and without soil ice simulated (**Figure 4**), we found that waterlogging tolerance only provided an advantage when ice was simulated, and that collectively, the species (covering the full range of waterlogging tolerances) were able to maintain as much biomass as they did when ice was not simulated. One consequence of this outcome is that the relative biomass of each species is affected by the presence or absence of ice (depending on waterlogging tolerance), and eventually composition may be altered as the prevalence of ice changes. We also expected an interaction between temperature and waterlogging tolerance, because increasing temperature should reduce soil wetness on permafrost sites, but this expectation was not supported ($F = 0.52$, $p < 0.0.7239$), likely related to our arbitrary waterlogging stress parameters.

The latitudinal gradient test demonstrated the interaction of the many factors that determine forest successional dynamics and species range shifts. The modeled factors include temperature effects (heat and cold stress, cold killing, growing season length), precipitation, CO_2 fertilization effects (enhancement of photosynthesis and water use efficiency), permafrost effects on hydrology, and light (latitude effects on day length, cloudiness). Our expectation for the latitudinal gradient test was that biomass should (1) increase as emissions increase because of CO_2 fertilization and longer growing seasons, (2) decrease with increasing latitude because the growing season is shorter, and (3) decrease with disturbance because cohorts are younger. These expectations were generally met. CO_2 fertilization effects were constant across latitudes, but temperature (including growing season length) and precipitation varied considerably by latitude

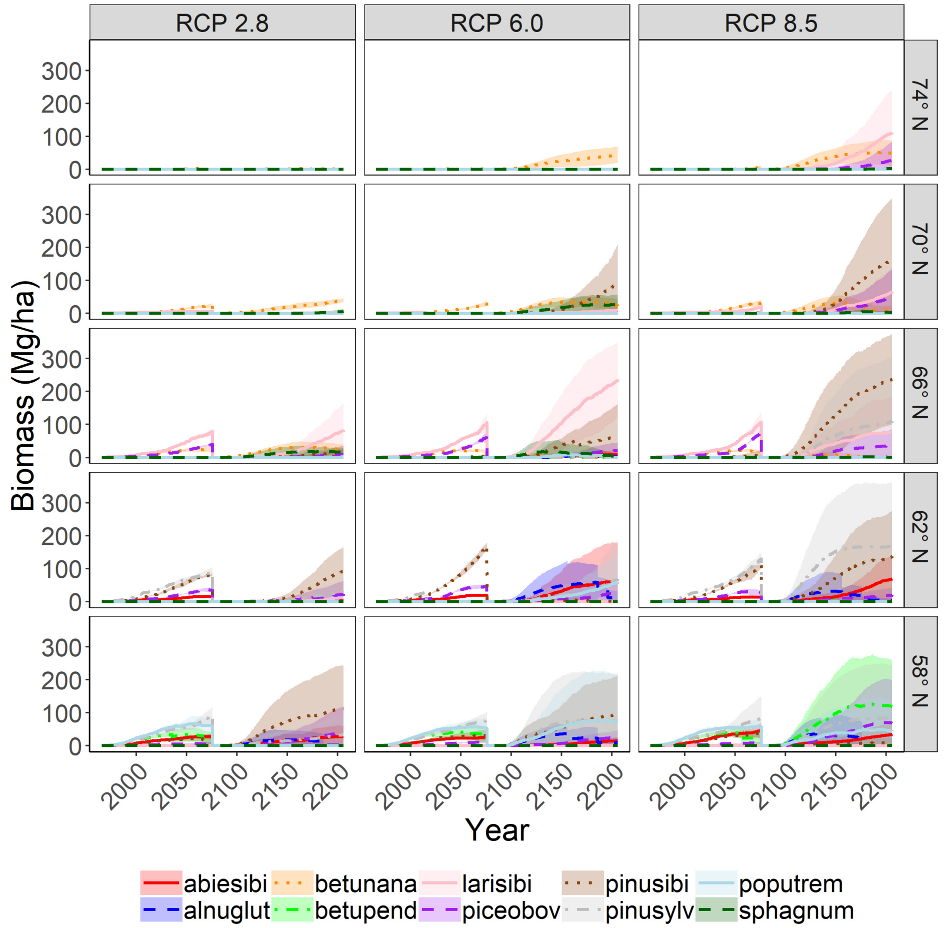

FIGURE 6 | Aboveground woody biomass of tree species through time with a single stand-replacing disturbance on upland sites. Shading represents one standard deviation of four replicates.

(**Table 3**). Thus, CO_2 fertilization effects can be seen across columns in the latitudinal gradient figures, and temperature and precipitation effects can be seen across rows. We note that scenarios with high CO_2 emissions greatly increased productivity at high latitudes, while productivity gains were limited at lower latitudes (similar to Shvidenko et al., 2008). We also expected that richness should (1) be unchanged, even as assemblages change (i.e., the number of niches is not changed), and (2) increase with disturbance (intermediate disturbance hypothesis). We found that on upland sites, richness was less changed in the absence of disturbance, and that richness tended to increase with disturbance, except at latitude 58N, where a large number of species were replaced with a small number of pioneers after disturbance. On wetland sites, richness always declined because only highly waterlogging tolerant species survived.

We expected that invasions and extirpations should (1) increase with disturbance because niches are opened, (2) increase with climate change because ranges shift, and (3) decrease at lower latitudes because change in climate is less. We found that disturbance sped up the process of climate-induced range shifts by reducing the dominance of established cohorts and giving pioneer species and new colonizers an opportunity to become a component of the new assemblage, consistent with Liang et al. (2018). Disturbance can also alter hydrology effects, primarily by reducing the transpiration rate on sites (increasing soil wetness), and also by potentially changing tree species composition to species with different drought and waterlogging tolerance. Disturbance (and warming climate) allowed larger-statured species to colonize and quickly become effective transpirers, altering hydrology and potentially displacing waterlogging-tolerant species, consistent with conclusions of Jin et al. (2020). In wetlands under climate change, disturbance was able to prevent development of effective transpirer cohorts (e.g., *P. sibirica*), maintaining the dominance of wetland species. Extirpations were higher and invasions were fewer on wetland sites compared to upland sites, reflecting the fact that most of the generalist tree species were not very competitive on saturated soil. However, wetland sites tended to have greater biomass than upland sites at the same latitude, presumably because large-statured species often became big enough to transpire the excess water, yet not be limited by low soil water availability.

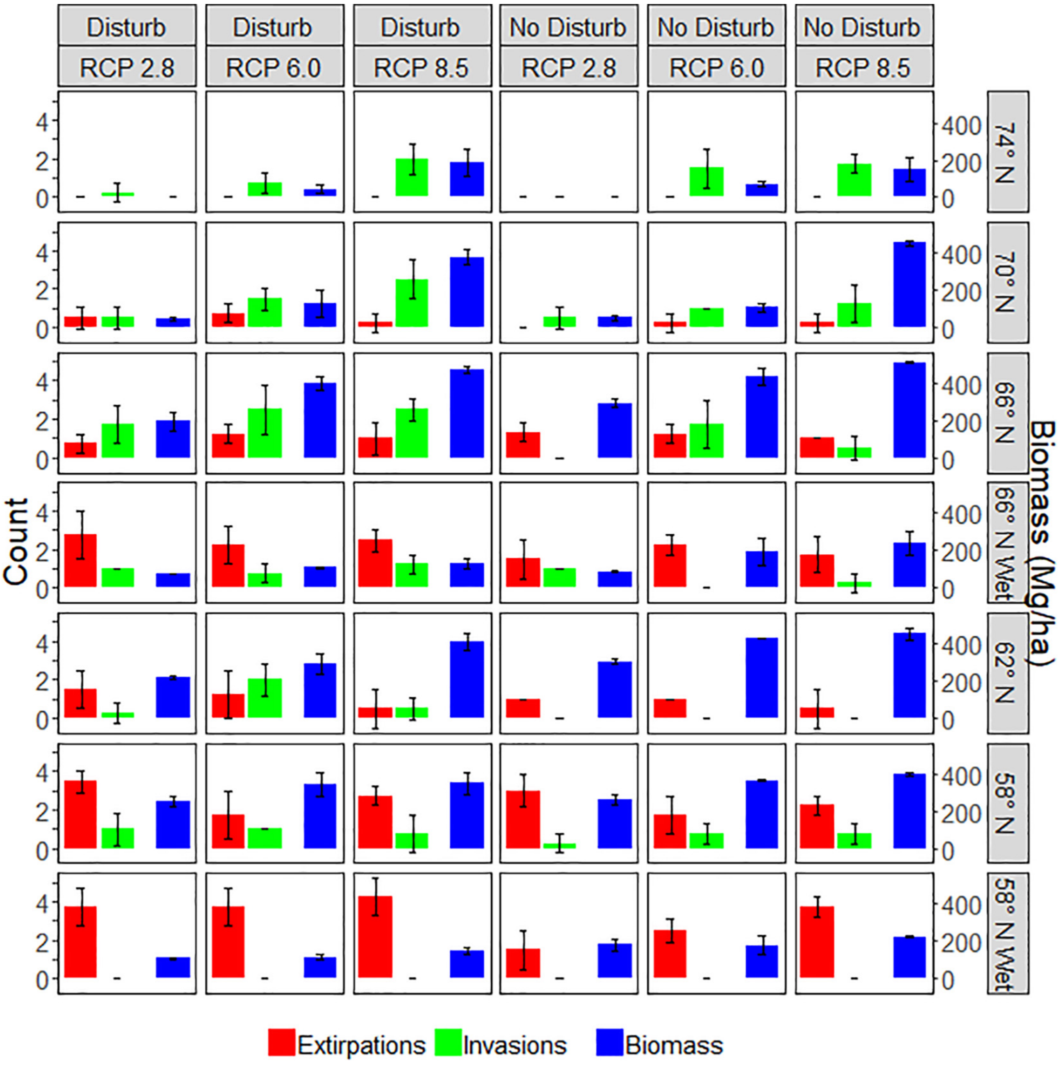

FIGURE 7 | Productivity and range shift responses to treatments on upland and wetland sites. Invasions are species present after 200 years that were not present at the start, while extirpations are species not present after 200 years that were present at the start. Biomass is the maximum aboveground woody biomass observed on the site over 200 years. Error bars represent one standard deviation of four replicates.

The design of the latitudinal gradient test did not allow us to quantify the effect of permafrost thawing relative to direct temperature effects on productivity and composition changes caused by altered hydrology. In the model, the air temperature photosynthesis reduction factor would be less altered by the climate scenarios used than the water stress reduction factor would be altered by the changes in hydrology induced by thawing of permafrost (increased depth of the active layer) observed in the simulations. We observed that active layer depths increased nearly three meters under the RCP 8.5 scenario compared to the RCP 2.6 scenario at high latitude sites. When the active layer is shallow, there is not much available water and it is unable to drain, so the soil tends to be saturated with just a small amount of liquid water. As permafrost thaws, the active layer deepens, resulting in more available water, although if the active layer is deeper than the rooting zone, it also begins to drain, which would reduce water. Species adapted to permafrost are able to tolerate both waterlogging and limited total water availability, so as climate warms, their competitive advantage may be lost, resulting in altered species composition.

One of our objectives was to evaluate the feasibility of using our modified model to simulate range expansion and contraction induced by climate change at high latitudes. We believe that our latitudinal gradient test demonstrated a general feasibility based on our considerable knowledge of Siberian forests. Further work is needed to implement the model on real high-latitude landscapes, including important specific disturbances, and calibrating and validating system behavior using empirical observations. Our experience in this study was that we were able to control most aspects of simulated species growth and competition on our hypothetical high-latitude landscapes using the parameters now available in the model.

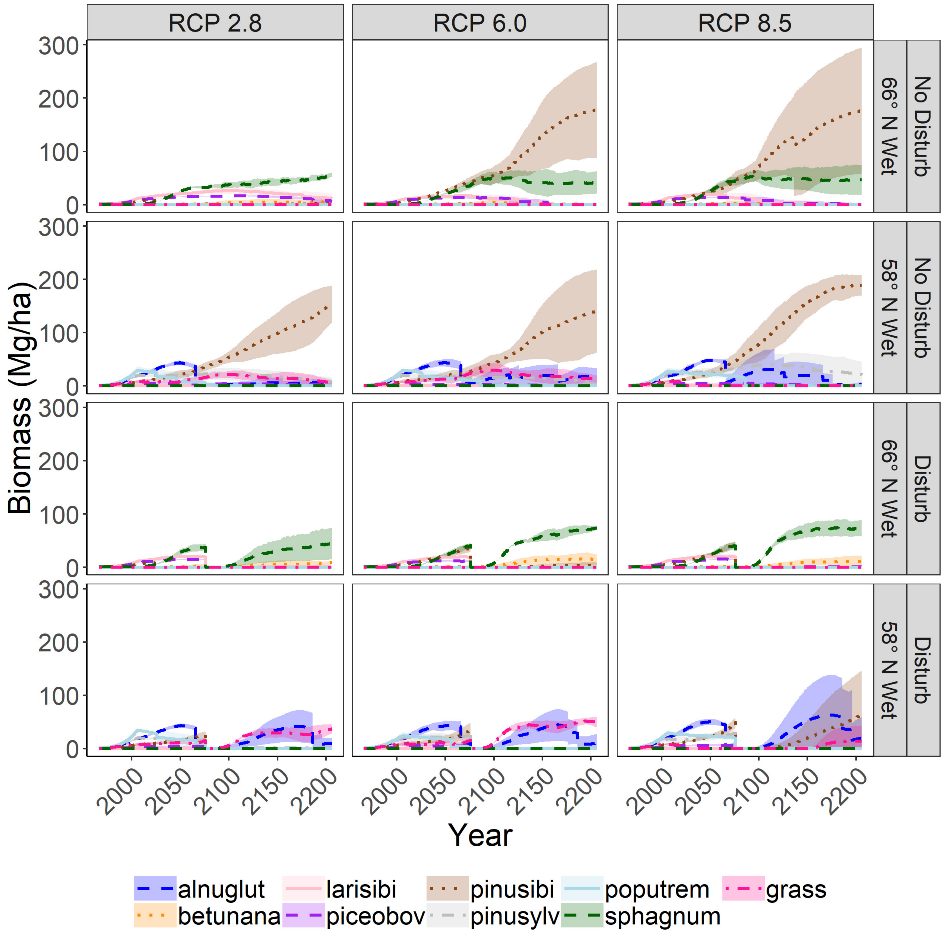

FIGURE 8 | Aboveground woody biomass of tree species through time on wetland sites. Shading represents one standard deviation of four replicates.

One consequence of climate change is greater temperature extremes, both hot and cold, and we observed that this can induce cold-killing of extant species, at least in the first 50 years. This result is perhaps not intuitively surprising, but it is a possible outcome of climate change that is not typically considered by forest managers and planners. If all cohorts of a species are catastrophically killed by a cold snap across entire landscapes, successional dynamics may not follow the path typically observed under past climate. This illumination of unexpected consequences of climate change illustrates another benefit of using a mechanistic FLM as part of any strategic forest management process that seeks to consider the effects of a changing climate.

In our attempts to find other landscape modeling results for comparison, we confirmed that there is indeed a need for these capabilities. We are aware of one other effort to simulate permafrost dynamics in a different LANDIS-II succession extension (DGS-Succession), but results have not yet been published (M. Lucash, personal communication). DGVMs use similar methods, having inspired our method, but their use of plant functional types instead of species cohorts makes direct comparison difficult. In a recent review of the impacts of climate-induced permafrost degradation on vegetation, Jin et al. (2020) call for improvement of process-based permafrost ecological models in order to predict and evaluate impacts of permafrost degradation on ecosystems and their adaptation.

Caveats

The interpretation of extirpations was confounded somewhat by the fact that many of the pioneer species at lower latitudes had relatively short longevity, meaning that some extirpations there were caused by senescence rather than competitive interactions. Similarly, invasions in the south may have been enhanced by a higher number of shade-intolerant pioneer species than found at more northerly latitudes. It should also be noted that there is a high degree of stochasticity associated with establishment, and therefore, invasion. For example, a species that establishes on a recently disturbed site decades before any other will likely dominate the site and exclude others more than in the case where several species establish simultaneously. The high variability seen in **Figure 7** mostly reflects this stochasticity.

Our results suggest that productivity is highest on the wettest biophysical positions (**Figure 3**), which is demonstrably

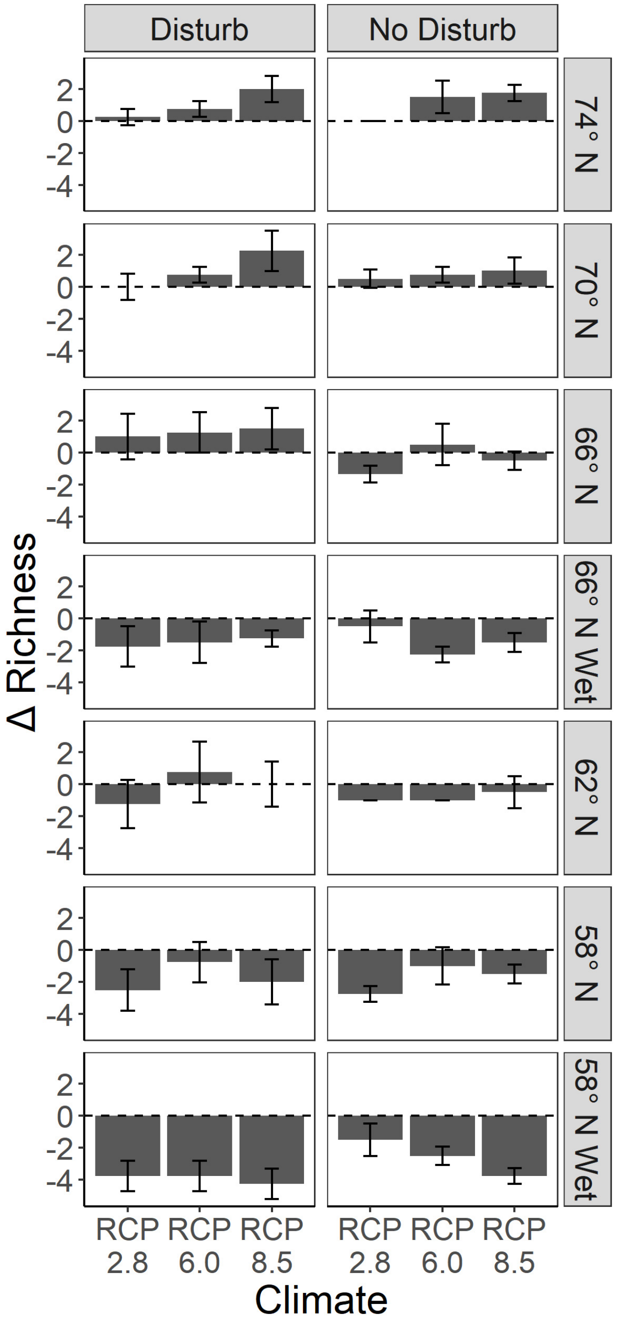

FIGURE 9 | Change in mean species richness (number of species) over 200 years on upland and wetland sites in response to the treatments. Error bars represent one standard deviation of four replicates.

false empirically (e.g., Iwasaki et al., 2009). This result is partly an artifact of the values we arbitrarily assigned to the waterlogging and drought tolerance parameters (H1–H4) when designing the lowland test prior to conducting test runs, although nutrient limitations also reduce productivity on many lowland sites, and nutrient limitations are not currently modeled in PnET-Succession. The baseline climate inputs also contributed to this result by generating mostly dry conditions that resulted in drought stress except under the wet combinations of factors, which is realistic for high-latitude landscapes. We could have modified the values of the waterlogging parameters *post hoc* to achieve more realistic results, but we believed that would reduce the legitimacy of the test. The model produces outputs that reflect the inputs, and this test clearly demonstrates that the model responds appropriately to the water tolerance parameters used given the water inputs and the site parameters that control hydrology.

There are no feedbacks in PnET-Succession between simulated vegetation and climate. The presence of live vegetation has no effect on ice depth other than its effect on soil water (which has high thermal diffusivity) through transpiration. LANDIS-II also does not simulate herbaceous vegetation that could modify establishment rates. PnET-Succession does not currently account for the effect of soil nutrients on growth. It is possible that some of the increase in productivity seen under the RCP 6.0 and 8.5 emissions scenarios may not be realized because of nutrient limitations. Adding soil nutrient and carbon dynamics into PnET-Succession is under discussion, but is not yet available.

We did not include the uncertainty in the climate projections used as inputs, nor the uncertainty associated with input parameters, to avoid confounding the signal from our experimental treatments. Thus, the uncertainty shown in our figures does not reflect the uncertainty that would be expected when using the model to make realistic projections of future forest dynamics under climate change. However, increasing the number of simulation replicates could be used to reduce such uncertainty to some extent.

Sphagnum is a bryophyte, lacking stomata (Silvola and Aaltonen, 1984). The photosynthesis algorithms in PnET-Succession are stomatally constrained (as in Biome-BGC, Bond-Lamberty et al., 2007), and therefore cannot mechanistically simulate sphagnum growth, forcing us to constrain growth using an unrelated parameter (FracActWd) to reduce foliage. Consequently, the projections of sphagnum biomass are highly uncertain, while the establishment of sphagnum is as reliable as the other species.

Future Work

Our study verified the ability of the new capabilities added to PnET-Succession to reasonably simulate the response of forests to hydrological dynamics induced by wet biophysical units and permafrost thawing. However, these capabilities should be more thoroughly tested against empirical data in a diversity of ecosystems before they are used to make definitive projections of forest response to waterlogged conditions. We have such work underway at four sites across a latitudinal gradient in Siberia, but other tests are needed. The model currently is not able to simulate periodic flooding of trees growing in riparian flood plains. However, we believe that such a capability may be feasible within the conceptual framework of the model (e.g., Bond-Lamberty et al., 2007), but considerable development and testing would be required.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

EG designed the study and led the model development, and wrote 95% of the manuscript. BM implemented the model design and contributed significantly to algorithm development. AS provided knowledge of Siberian forest ecology, and helped with model calibration and validation. BS contributed to analysis and interpretation. All the authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.598775/full#supplementary-material

Supplementary Figure 1 | Soil water potential (m pressure head) as a function of soil water content and soil texture. Curves end at the soil saturation point, and their shape as soil water potential values approach zero is relevant to waterlogging tolerance. Wilting point and field capacity in terms of pressure are defined as 153 and 3.4 m of pressure head, respectively. Soil acronyms follow FAO conventions. Data from Saxton and Rawls (2004).

Supplementary Figure 2 | An example of monthly soil temperature (T_{soil}) profiles on a sandy, saturated soil for a single year under a hypothetical high-latitude climate.

Supplementary Table 1 | Water stress parameters for the hypothetical species used in both the lowland forest and permafrost test experiments. Values given in units of m of pressure head.

Supplementary Table 2 | Selected PnET-Succession parameter values for Siberian tree species.

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Strengthening the Network of High Conservation Value Forests in Boreal Landscapes

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The natural and old-growth forests and their associated biodiversity continues to fade worldwide due to anthropogenic impact in various forms. The boreal forests in Fennoscandia have been subject to intensive clearfelling forestry since the middle of twentieth century. As a result, only a fraction of forests with long temporal continuity remains at the landscape level. In Sweden, some of these primary forests have been formally protected, whereas other forests with known high conservation values are not. Collectively, both protected and not protected known valuable primary forests are included in a nationally delineated network of high conservation value forests (HCVF). In addition to HCVF, older forests that have not been clearfelled since the mid-1900s, i.e., "proxy continuity forests," have recently been mapped across the entire boreal biome in Sweden. In this paper, we analyze how these proxy continuity forests may strengthen the HCVF network from a green infrastructure perspective. First, we evaluate the spatial overlap between proxy continuity forests and HCVF. Second, we perform a large-scale connectivity analysis, in which we show that adding proxy continuity forests located outside HCVF strongly increases the structural connectivity of the network of protected forests. Finally, by assessing habitat suitability for virtual species specialized in pine, spruce, and broadleaf forests, we find large regional differences in the ability to secure habitat and thereby functional green infrastructure by considering currently unprotected primary forest. We show that, by adding those forests to the network, the area of habitat for low-demanding species dependent on spruce or pine forests can be largely increased. For high-demanding species, additional habitat restoration in the landscape matrix is needed. By contrast, even counting all valuable broadleaf forests available is not enough to provide a suitable habitat for their associated species, which indicates a large need for landscape-scale habitat restoration initiatives, in particular, for broadleaf forests.

Keywords: continuity forests, primary forests, virtual species, Sweden, connectivity, green infrastructure, Scandinavian Mountains Green Belt

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INTRODUCTION

The loss of natural and old-growth forests and their associated biodiversity continues worldwide due to extensive anthropogenic impact (Ledig, 1992; Haddad et al., 2015; Kormos et al., 2017; Curtis et al., 2018). The area of "intact forest landscapes," defined as predominantly forested areas showing no or limited signs of human activity and large enough to maintain native biodiversity, is declining and thus their protection is a major conservation concern (Potapov et al., 2008, 2017; Watson et al., 2018; Svensson et al., 2020). In order to fulfill ecological, social, and economic roles of forests, the vital attributes of forest ecosystems must be maintained and, if necessary, restored (Christensen, 2014; Chazdon, 2017). Such attributes include biodiversity, key ecosystem processes, and resilience ensuring forests' capacity to recover from natural and anthropogenic disturbances, including impacts of climate change (e.g., Stanturf et al., 2014; Müller et al., 2019). In addition, to mitigate decades and centuries of degradation caused by intensive forest management, restoration of degraded forests and deforested areas are of great importance (Angelstam, 1998; Aerts and Honnay, 2011; Brancalion et al., 2018). For successful biodiversity conservation, sufficient functional conservation networks are pivotal (*sensu* Flather et al., 1997).

Among the different forest biomes of the world, boreal forest landscapes constitute important natural assets due to their size, ~30% of the global forest area (Brandt et al., 2013; Gauthier et al., 2015), circumpolar distribution, and a relatively high level of intactness (Potapov et al., 2008; Moen et al., 2014; Kuuluvainen, 2016). However, as demonstrated by Hansen et al. (2013) and, more recently, Curtis et al. (2018), ever-increasing anthropogenic pressure results in continuous and extensive loss of intact boreal forest landscapes with intensive forestry being the major driver of primary forest cover loss in Europe and, in particular, in Fennoscandia (Curtis et al., 2018; Ceccherini et al., 2020). The ecological consequences of this loss can presently not be fully assessed, in particular, in the context of the ongoing climate change (Gauthier et al., 2015).

In Europe, boreal forests cover large areas of the Fennoscandian shield, including Norway, Sweden, Finland, and Northwest Russia, where they have been intensively managed by systematic clearfelling since the middle of the twentieth century (Kuuluvainen, 2009). In Northwest Russia, the proportion of intact forests is still relatively high (Potapov et al., 2008). In Sweden, due to a long history and extensive impact of industrial forest management (Svensson et al., 2019), only a very small fraction of intact boreal landscapes still remain (Potapov et al., 2017; Svensson et al., 2020). Moreover, the main natural disturbance factor, wildfire, has been effectively suppressed in Sweden and other parts of western Fennoscandia since the middle of the nineteenth century (Rolstad et al., 2017) although there have been several incidents of larger wildfires during the most recent years (Gustafsson et al., 2019). As a result of intensive forestry and control of natural disturbances, many boreal species and several types of forest present in naturally dynamic boreal landscapes are threatened, and some successional phases (e.g., old-growth or aging broadleaf succession) are very rare (Berg et al., 1994; Esseen et al., 1997). In total, some 1400 species are included on the Swedish Red List as a direct and indirect consequence of forest harvesting (ArtDatabanken, 2020). These negative biodiversity and ecosystem function trends call for new initiatives that ensure a more favorable conservation status of boreal forests in Sweden and elsewhere in the boreal region in the future (e.g., Naumov et al., 2018; EEA, 2019; Jonsson et al., 2019).

Forestry in Sweden, as in other European countries, is maintained intense based on arguments that maximizing biomass production is justified in the transition toward a bio-economy (Börjesson et al., 2017; Lindahl et al., 2017; Jonsson et al., 2019; Verkerk et al., 2019). At the same time, the protection of natural values in Swedish boreal forests is highlighted in the Swedish forest legislation (Anon, 2018) and follows established international and national policies addressing sustainable use and conservation values. This includes formally protected areas, sites included in the European Union's Natura 2000 network, as well as areas voluntary set aside as a part of forest certification (Swedish Forest Agency, 2019). Similar to the situation in many countries, these conservation efforts collectively represent national implementation of the global Aichi Biodiversity goals (CBD, 2010), in particular, target #7 on sustainable management, biodiversity, and conservation; target #11 on protecting a minimum of 17% of terrestrial areas and ensuring their connectivity;, and target #15 on restoring degraded ecosystems.

At the European Union level, the concept of green infrastructure is being implemented or is in preparation for implementation in the member states (e.g., Slätmo et al., 2019; Chatzimentor et al., 2020). Green infrastructure aims to secure biodiversity, habitat resilience, and ecosystem services at multiple spatial scales (Liquete et al., 2015). One of the main objectives is to support protected areas through safeguarding connectivity of target habitats at multiple spatial scales (Hermoso et al., 2020). All these initiatives require the development of spatially explicit landscape plans concerning how much and where additional set-aside conservation and restoration areas are needed to conserve biodiversity and ecosystem services and to secure sustainable use of boreal landscapes (Snäll et al., 2016; Felton et al., 2017).

The increasing amount and accessibility of comprehensive remote sensing data on forests creates opportunities for more efficient and spatially explicit conservation planning at multiple scales (White et al., 2016; Torresan et al., 2017; Mikusiński et al., 2018). In Sweden, in addition to geographical data on formally protected forests, spatial data on known high conservation value forests (HCVF; Jennings et al., 2003; Anon, 2017) have been compiled. The HCVF-concept was primarily developed to systematically identify biodiversity and ecosystem services delivered by forest ecosystems to aid forest certification schemes (e.g., Senior et al., 2014), but it is also used in the broader sense for delineating forests important for biodiversity conservation. The major characteristics and values of HCVF are (1) diverse horizontal and vertical structure (e.g., mixed tree species composition, occurrence of old trees and large volumes of dead wood, diversified height of trees), (2) ecological functionality (e.g., erosion control, nutrient retention), (3) a long temporal continuity (not clearfelled), and (4) cultural ecosystem services and generically recreational with amenity values and cultural legacies (e.g., Patru-Stupariu et al., 2013; Boucher et al., 2016). In addition, a database delineating forests not clearfelled since the mid-1900s has been developed (proxy continuity forests—pCF) (Ahlcrona et al., 2017; Svensson et al., 2020). Both the HCVF and the pCF databases include forests that are not legally protected and thereby may be logged. Even if some pCF could have been subject to historical selective logging, one can assume that the two databases collectively encompass "primary forests" of boreal Sweden, i.e., naturally regenerated forests with native tree species in which there are no clearly visible signs of human interaction and in which the ecological processes are not significantly disturbed (FRA, 2020). Such forests are, in turn, a main component of "intact forest landscapes" defined above (Potapov et al., 2008).

Primary forests and intact forest landscapes are of profound importance for functional green infrastructures and, as such, essential in conservation planning. The functionality of green infrastructure, i.e., the ability to provide habitat for species and essential ecosystem services is, to a large extent, linked to the spatial configuration of its components (Andersson et al., 2013). For example, Svensson et al. (2020) have lately identified the Scandinavian Mountains Green Belt as a largely contiguous and structurally well-connected belt of intact forest landscapes formed by primary forests and surrounding near-natural forest areas. They concluded that the Scandinavian Mountains Green Belt is of utmost conservation importance on both the European and global scales.

Most recently, a new national-scale land-cover database has been published in Sweden (SEPA, 2019), which provides high spatial (10×10 m) and thematic resolution as well as high thematic accuracy. Together with the HCVF and pCF databases, this allows innovative approaches for analyzing the functionality of green infrastructure in providing suitable habitats for species with different habitat requirements and in mapping the premises for broad-scale ecological connectivity.

In this paper, we use these recently compiled spatial data sets describing primary forests with known and potentially high conservation value in an attempt to explore their abilities to support functional green infrastructure. More specifically, the aim of the study was to analyze and evaluate planning routes toward functional green infrastructure in boreal Sweden through analyses of spatial relationships between unprotected areas and the existing formally protected forests. The research objectives were (1) to estimate the spatial overlap of pCF and HCVF and explore how this overlap varies across the boreal region in Sweden; (2) to quantify the size, number, and distribution of the components of habitat networks for virtual species dependent on coniferous, i.e. spruce (*Picea abies*) or pine (*Pinus sylvestris*), or broadleaf forests based on formally protected forests; (3) to examine the potential increase of habitat area for virtual species when all identified primary forests are included and how this affects the functionality of green infrastructure; and (4) to assess how large-scale connectivity patterns varies among the protected primary forests, all primary forests, and all forestlands used as the baseline reference.

MATERIALS AND METHODS

Study Area

The study area covers northern Sweden, in total a 27.0 million ha terrestrial surface with a forest area equal to 18.9 million ha, corresponding to 67% of all forest land in Sweden (SLU, 2020) and to around 80% of the boreal forests. With the Scandinavian Mountains in the west, 18.4% (i.e., some five million ha) of the terrestrial surface is covered by non-forested alpine land. Flat terrain and sites with poor tree-growth conditions dominate over large areas and support open mires covering more than 4.4 million ha, i.e., 16.4% of the terrestrial surface (SLU, 2020). Of the total studied forest land, 80% is considered as productive (tree growth >1 m^3/ha/year on average per rotation cycle) with Scots pine dominating (44.0%) followed by Norway spruce covering 19.7% and mixed coniferous forests covering 12.6% (SLU, 2020). The study region includes all the subalpine mountain birch (*Betula pubescens* ssp. *czerepanovii*) forests in Sweden forming the alpine tree line in the western part of the study area and covering, in total, 1.1 million ha (Hedenås et al., 2016).

The history of forestry and other types of land use is extensive with more active forest harvesting since the 1600s and with the more intensive forest exploitation since the mid-1800s (Lundmark et al., 2013). Industrial rotation forest management with clearfelling, soil scarification, and replanting of monoculture genotypes dominates the last 60–70 years. From the middle of 1990s, the introduction of tree retention (i.e., retained solitary trees or trees in patches of about 0.01–0.5 ha on clearfelled areas or as buffer zones along streams, lakes, or mires) and a generally smaller size of single logged areas have, to some degree, ameliorated the environmental impact of forestry (Gustafsson and Perhans, 2010). However, the overall impact of forest management on the level of forest intactness has been massive with the majority of primary forests and intact forest landscapes transformed into intensively managed forests and landscapes (e.g., Jonsson et al., 2019; Svensson et al., 2019, 2020).

To reflect the biogeographical gradient and land use history, our analysis was done for eight subregions (**Figure 1**); four covering inland-to-mountain conditions (from south to north: Dalarna, Jämtland, Västerbotten west, and Norrbotten west) and four covering coast-to-inland conditions (from south to north: Gävleborg, Västernorrland, Västerbotten east, and Norrbotten east). Hence, we divided the two northernmost regions, Norrbotten and Västerbotten counties that stretch from the Scandinavian Mountains to the Bothnian Sea, into western and eastern parts.

Data

We used several different sources of spatial data on forests (details provided in the **Supplementary Material**). For data on HCVF, we used the national Swedish database provided by the Swedish County Administrations (Anon, 2017). The HCVF were delineated based on forest cover of the national topographic terrain (1:50,000) and road maps (1:100,000), and their high conservation values were validated via field surveys. This database provides the status up to 2016 and includes several

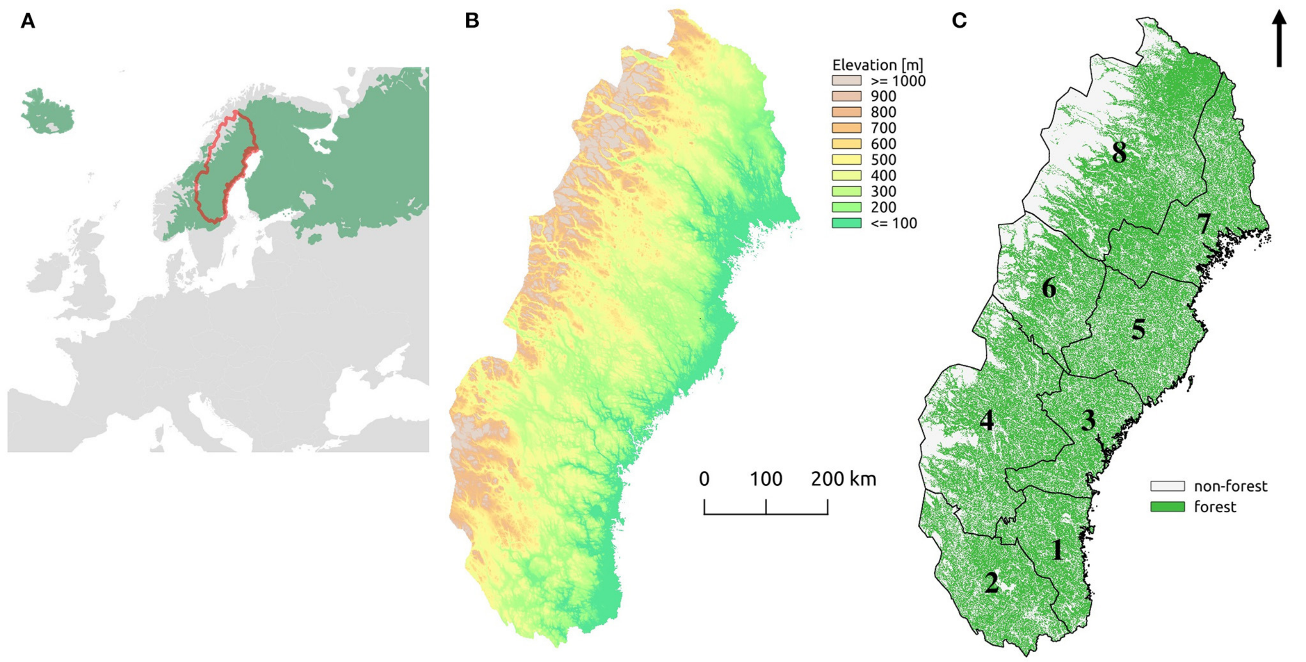

FIGURE 1 | (A) The location of the study region in Europe (red line) with the boreal biome highlighted in green. **(B)** The elevation (m) above sea level across the study region calculated from the elevation model. **(C)** Total forest land (green) with the eight subregions; (1) Gävleborg, (2) Dalarna, (3) Västernorrland, (4) Jämtland, (5) Västerbotten east, (6) Västerbotten west, (7) Norrbotten east, (8) Norrbotten west.

categories of long- and short-term formally protected, voluntarily set aside, and unprotected areas combined in two categories: protected and unprotected HCVF. The limitation of the HCVF dataset, or rather HCVF-dataset is that it includes only already known HCVF and, thus, excludes other forest areas not yet identified as valuable.

The pCF-dataset is a complete-coverage continuous raster layer mapped by retrospective analysis of remnant forest patches not being subject to clearfelling at least since the middle of the twentieth century. The pCF-mapping was performed as an automatic change-detection analysis of a time series of satellite images from 1973 to 2016, complemented with aerial photos from the 1950s and 1960s (Ahlcrona et al., 2017; Svensson et al., 2019, 2020). All forest patches 0.5 ha and larger and forest belts 20 m or wider were mapped across the entire boreal biome in Sweden. The inclusion of small patches in the database provides an opportunity to detect small-size, old-growth forest areas that function as stepping-stones linking larger forest patches, i.e., patches that are of interest in habitat distribution analyses. The limitation of the pCF-dataset is that it identifies only potentially valuable forests for conservation with no external validation of their ecological qualities.

Finally, we used the recently published high-resolution (10 m) national land cover database (SEPA, 2019). In this database the forest environments are classified into seven main forest types additionally divided into stands located on upland soils and on wet soils (14 classes in total).

Analyses

First, we combined different raster-based data sets (HCVF, pCF, land cover database) to quantitatively compare their spatial overlap. We used the original spatial resolution of 10×10 m of the pCF and national land cover databases and a rasterized HCVF vector layer at the same resolution. Next, we assessed large-scale structural connectivity (i.e., based on their spatial configuration and extent) between different primary forest categories relevant to conservation (HCVF protected, HCVF unprotected, and pCF) considering multiple scenarios. By expanding the area of primary forests from only including protected forest to including also unprotected HCVF and finally also to including pCF, we tested how their combined spatial configuration and extent can support the creation of a functional forest green infrastructure by maximizing the structural connectivity between the focal areas. Finally, we mapped habitats of virtual species (*sensu* Vos et al., 2001, Mikusiński and Edenius, 2006 and Angelstam et al., 2020; details provided in the **Supplementary Material**) that are dependent on pine, spruce, or broadleaf forest types with different spatial requirements in terms of the amount and distribution of the habitat available in the landscape perspective (low vs. high demanding). The virtual species approach group ecological profiles of organisms according to the characteristics that are important in their metapopulation response to the habitat amount and distribution in the landscapes. Thereby, in the meta-population context, individual area requirements are viewed as the dominant characteristic of species extinction risk in landscape patches and dispersal distance as the main determinant of the ability to colonize new patches (see also Vos et al., 2001).

To assess the large-scale structural connectivity of primary forests belonging to the two categories of HCVF (protected, unprotected) and pCF as well as composites of them, we used a connectivity model derived from circuit theory (McRae et al., 2008) and implemented in the Circuitscape software v5 (re)written in Julia programming language (http://www.circuitscape.org; Anantharaman et al., 2020). In this part of the study, we aimed at modeling the "global," i.e., for the whole study area, structural connectivity without focus on particular species or species group (thus, a "species-agnostic" model following Koen et al., 2014). We considered only two classes of land cover when designing the resistance surface used for the Circuitscape modeling: Class 1: clusters of primary forests (based on HCVF-protected, HCVF-unprotected, and pCF in different combinations depending on the scenario) and Class 2: matrix of other land-cover classes, including other (mainly managed) forest areas. To assure sufficient difference in resistance between these two classes, we assigned the value 1 for the pCF clusters and the value 100 for the matrix. The resistance values were chosen to ensure contrast without influencing the connectivity distribution results, and we consider those values reasonable following, e.g., the "one-stage expert approach" (Zeller et al., 2012) and customary approaches to assign increasing resistance values when empirical data is unavailable (Koen et al., 2014).

The measure of connectivity was the cumulative current density (CCD) estimated for each pixel of the resistance surface raster. The estimated CCD values resulted from the current flow between all pairs of 24 focal nodes (552 combinations) placed at equal distance along the perimeter of a 50-km buffer zone around the study region. We used the same number and fixed locations of focal nodes for all scenarios to facilitate the comparison of the output CCD maps. To adjust to computational limits, we down-sampled the pCF-raster from a 50×50 m to a 500×500 m resolution prior to running the Circuitscape algorithm. As we were interested in global (study area) rather than local patterns and as coarsening the input grid usually brings results that closely approximate those generated at fine-scale resolution (see McRae et al., 2008), we foresaw no detectable effects of this coarser resolution on the final results. We applied the same procedure to all scenarios, including the baseline reference with non-forested area representing the matrix (cf. Class 2) and all forest lands representing potentially focal habitats (cf. Class 1). All maps were created with help of the open source software QGIS (QGIS Development Team 2017 Ver. 2.18) and GRASS GIS software (Neteler et al., 2012 Ver. 7.4.0).

We designed habitat suitability index (HSI) models (for review, see Edenius and Mikusiński, 2006; details provided in the **Supplementary Material**) for defined virtual species using two different selections of forest stands, i.e., (1) protected primary forest and (2) all primary forest delineated by GIS databases. The selection of virtual species should represent broad categories of species habitat demands, so they can function as a focal or umbrella/indicator species (Lambeck, 1997). Because forests are often composed of several tree species, classification of forest types in mapping is usually based on different mixtures of tree species expressed by ranges in their percentages. In the case of the boreal Sweden, Scots pine, Norway spruce, and collectively treated broadleaf trees (dominated by *Betula* spp.) may be considered as three main compositional components for forest-dependent species. For example, an organism specialized in old pines may find its habitat in both pure pine stands but also in mixed stands with, e.g., spruce, which simultaneously provide habitat for spruce specialists. Therefore, in our application of HSI models, five different forest classes originating from the high-resolution land cover dataset were used as a base for assessing the amount of habitat for three virtual species (**Supplementary Table A1**):

> *Pine dependent:* Pine forest + mixed coniferous forest + coniferous forest with an admixture of broadleaf trees corresponding to virtual species with natural pine-dominated forest as the main habitat.
>
> *Spruce dependent:* Spruce forest + mixed coniferous forest + coniferous forest with an admixture of broadleaf trees corresponding to virtual species with natural spruce-dominated forest as the main habitat.
>
> *Broadleaf dependent:* Broadleaf forest + coniferous forest with an admixture of broadleaf trees corresponding to virtual species with natural broadleaf-dominated forest as the main habitat.

Pine, spruce, and broadleaf forests were treated as optimal (habitat score = 1) for corresponding virtual species, and additional mixed tree species composition types (i.e., mixed coniferous forest and coniferous forest with an admixture of broadleaf trees) were treated as contributing with lower habitat value (habitat score = 0.5). The above habitat scores were used to calculate the effective habitat area for each virtual species.

Two contrasting levels of spatial requirements of virtual species were applied. These were based on the minimum habitat area and the amount of habitat at the landscape level (e.g., Manton et al., 2005; Orlikowska et al., 2020; **Supplementary Table A1**):

> *Low-demanding species* (LD): Small minimum habitat area (minimum 0.2 ha spatially connected pixels) and low landscape level requirements (minimum 5% in 1 $\text{km}^2 = 5$ ha).
>
> *High demanding species* (HD): Large minimum habitat area (minimum 2 ha spatially connected pixels) and high landscape level requirements (minimum 20% in 2 $\text{km}^2 = 40$ ha).

Hence, low-demanding species represent organisms that are able to colonize relatively small and isolated habitat patches, and high-demanding species represent organisms requiring larger contiguous patches of habitat and that are not able to exist in highly fragmented landscapes. In total, HSI models for six different virtual species (the two levels of habitat spatial demands and the three habitat types) were applied for both levels of conservation, i.e., securing just currently protected primary forests (low conservation level) or securing all existing primary forests (high conservation level; **Supplementary Table A1**). All spatial analyses in this part of the study were performed using the ArcGIS Focal Statistics tool (ESRI Inc., 2015) with a species-specific measure of neighborhood ("moving window") applied to assess landscape-scale requirements of the species. A more detailed description of the parameters and the entire modeling workflow is included in the **Supplementary Material**.

The resulting maps of habitat distribution for all defined virtual species were used to compare their habitat networks at the two different conservation levels. The HSI models provide (based on minimum habitat area, habitat type, habitat value, and landscape requirement) the total area of the networks. This area is composed of a number of spatially connected components, approximating a certain functional habitat area. To evaluate the different conservation levels (already protected primary forests vs. all primary forests), we report the total area of the habitat network as well as number and size distribution of the network components (**Supplementary Tables A2–A4**).

RESULTS

The share of pCF in total was higher in Norrbotten west (75%) and Västerbotten west (69%) and lower in Västernorrland and Gävleborg (both around 40%). There are consistently higher pCF-proportions in the inland mountain subregions, where the share increases northward. The proportion of pCF that does not overlap with HCVF decreases northward; however, eastern subregions have a generally larger proportion of pCF outside HCVF than the western. Consequently, the eastern and southern areas had only a low proportion (below 10%) of protected pCF (**Figure 2**). The highest level of pCF protection (50%) was found in Norrbotten west. In general, the proportions of unprotected HCVF are low across all subregions and lowest in the coast-inland subregions; i.e., a great majority of HCVF are actually protected in that part of the study region.

Our analysis of the structural connectivity showed divergent patterns both in the context of different levels of conservation ambition and concerning regional differences (**Figure 3**). We found low connectivity among protected forests with the exception of the mountain foothill forests. The connectivity pattern based on all protected and unprotected HCVF did not reveal any substantial connectivity increases. However, the connectivity map based on all primary forests demonstrates large connectivity improvement in the northern part of the study area and a clear strengthening of the connectivity in the southwest. Finally, given the high fraction of forestland in the region, the "baseline" connectivity map shows high connectivity across almost the entire study area.

The spatial distribution of suitable habitat for the virtual species based on protected primary forests and all primary forests are visualized in **Figure 4**. First, we found far more habitat area for low- than for high-demanding species. Second, the amount of suitable habitat based on all primary forests greatly exceeds the amount available based on protected primary forests, and this difference was more pronounced for low-demanding species. Third, the habitat networks of virtual species of different forest types were very dissimilar. For low-demanding species, all primary forests added a significant structural increase of habitat, and for high-demanding species, the structural increase associated with all primary forests is quite limited, particularly for broadleaf forest–dependent species. Broadleaf forests and the species that rely on such habitats are largely restricted to the alpine tree line mountain birch forest. The components of the habitat network of the high-demanding spruce specialist were concentrated to the Scandinavian Mountains foothills forest landscapes, and their equivalent for high-demanding pine specialists had concentrations in the north and southwest as well as along the coast.

The above regional differences for both the absolute (ha) and relative (percentage) increase of potential suitable habitat for the virtual species is presented in **Figure 5**. The increases were lower for the high-demanding species in the majority of the subregions. The largest increases in potential habitat area were observed for low-demanding pine species in Norrbotten east with 182 kha and in Dalarna with 176 kha. The proportional increase was highest for low-demanding pine species in Västerbotten east (2118%) and in Västernorrland (2058%), low-demanding spruce species in Västernorrland (2110%), and low-demanding broadleaf species in Norrbotten east (1989%).

The habitat networks of different virtual species varied concerning the size and number of their spatial components, i.e., spatially connected areas that fulfill habitat requirements of the virtual species (**Table 1**). As expected, the spatial components of habitat networks of low-demanding species were both more numerous and larger than those of high-demanding species regardless of whether protected or all primary forests are considered. The difference in the number of spatial components between low- and high-demanding species was particularly high in the broadleaf species network based on all primary forests (>12 times more in low-demanding species) and in total area of the pine species network based on all primary forests (>6 times more in low-demanding species). A great majority (>94%) of connected spatial components in all networks were more than 100 ha in size (**Table 1**). Corresponding figures for components with a size over 1,000 ha were between 48.8% (pine, high-demanding species, all primary forests) and 89.4% (pine, low-demanding species, all primary forests). Very large (>10,000 ha) spatial components of habitat networks encompassed from 10.7% (pine, high-demanding species, all primary forests) to 77.5% (pine, low-demanding species, all primary forests). The number and size distribution of the spatial components of habitat networks at the subregional level is presented in **Supplementary Tables A2–A4**.

DISCUSSION

Primary Forests as Providers of Habitat Networks

Functional habitat networks are the key feature of a green infrastructure (Liquete et al., 2015) with functionality implying the ability to support biodiversity conservation, landscape-scale ecological processes, and provisioning of a range of ecosystem services (Marini et al., 2019). Therefore, accurate

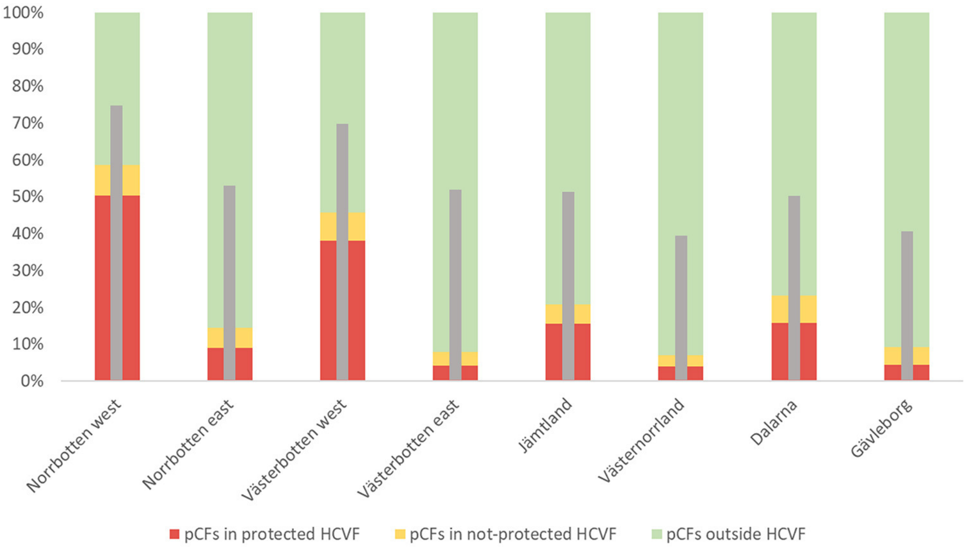

FIGURE 2 | Percentages of pCF located within high conservation value forests [protected HCVF (red), non-protected HCVF (yellow)], or outside HCVF (green), presented for the different subregions. The narrow gray bars depict the percentage of pCF in the total region's forest area (based on the Copernicus Land Monitoring Service data).

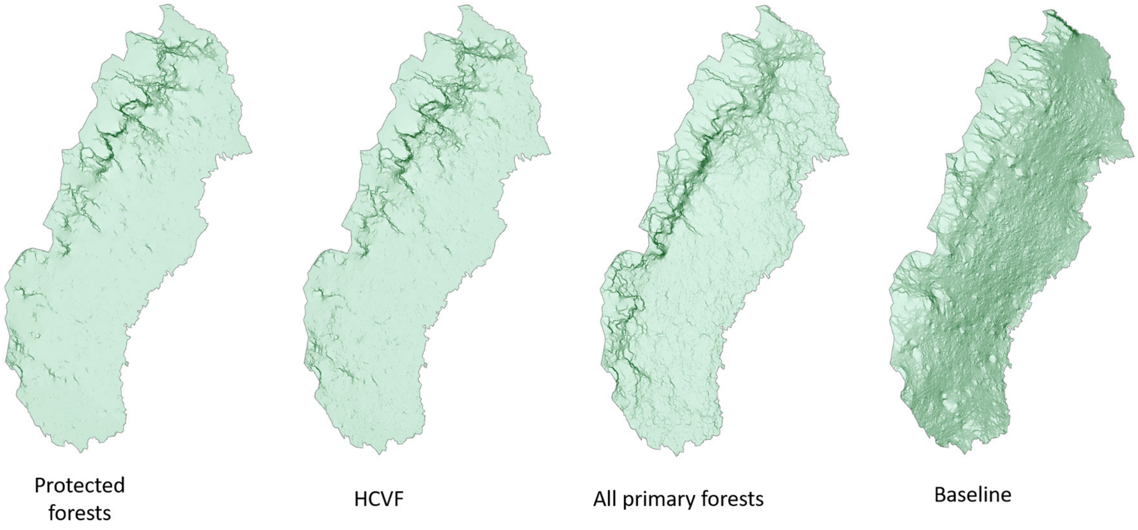

FIGURE 3 | Cumulative current density (CCD) mapping illustrating the global connectivity based for protected primary forests, protected and unprotected high conservation value forests (HCVF), all primary forest, and baseline (all forestland). The color scale from light to dark green depicts areas with subsequently higher current density, indicating better connectivity.

mapping and management of habitat networks is central to landscape planning (Opdam et al., 2001). Furthermore, with the extensive transformation of natural and semi-natural forest landscapes, which is the consequence of intensive industrial forest clearfelling, ecosystem and forest landscape restoration is needed with restoration actions to be applied preferentially in places where they are expected to generate a higher level of functionality (Angelstam et al., 2003, 2011, 2020). In this paper, we examined a considerable part of the European Union's boreal forest and northern subalpine biomes by analyzing the spatial distribution of forests with confirmed (i.e., validated) and potential, high conservation value as habitat networks for species with different ecological and spatial requirements. As for all planning, setting a target makes it possible to define the needed management and governance steps forward and the measures that have to be taken to reach the target. Thereby, this study generates a spatial target map that identifies challenges and opportunities for implementing functional green infrastructure

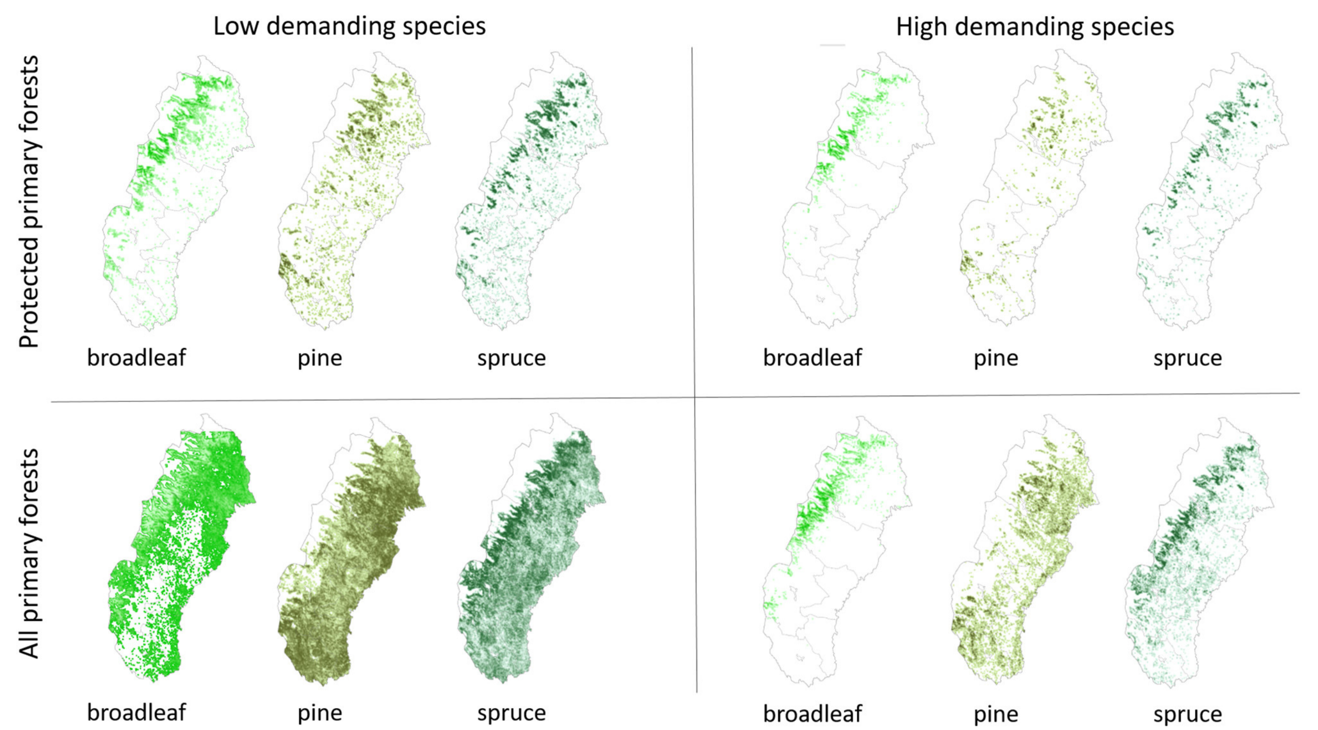

FIGURE 4 | The spatial distribution of suitable habitat for virtual species specialized in three forest types (broadleaf, pine, and spruce) and having two levels of habitat demands (low- and high-demanding species).

with respect to pine, spruce, and broadleaf forest-dependent species with low and high demands on habitat availability and its spatial configuration.

In our study, we first contrasted protected primary forests with all primary forests to assess the potential of unprotected areas to secure and strengthen functional green infrastructure. For generic landscape connectivity, the northwest part of the study area stands out as a largely functional network of protected valuable forest habitats, a fact that has been highlighted earlier (Jonsson et al., 2019; Svensson et al., 2019, 2020; Angelstam et al., 2020). Here, we add the information that currently unprotected primary forests in the southern part of the Scandinavian Mountains Green Belt could secure large-scale, overall north–south connectivity in the subalpine forests. This would increase the ecological resilience of this largely intact forest landscape in the face of climate change and other disturbances (Kuuluvainen et al., 2017). In the remaining part of the study area, the connectivity level of primary forests is drastically lower, particularly if only protected forests are considered. When including all primary forests, the overall connectivity clearly improves in parts of the study area, but it is still very far from a baseline situation with only natural fragmentation. Thereby, protecting all already known forests with high conservation values is not sufficient; their amount, density, and distribution do not provide even a basic large-scale structural connectivity. Hence, remote sensing and field-based inventories need to be intensified to identify and map remaining unknown areas of high conservation value and directed restoration operations need to be planned and executed in areas where there are gaps in forests with high conservation value. We argue that approaches comparing natural fragmentation with fragmentation caused by forestry is particularly needed in landscape planning, above all during mapping of places where restoration is needed to secure connectivity. Since green infrastructure studies on natural fragmentation of habitat appears to be rare (e.g., Haig et al., 2000; Gibson et al., 2017), we emphasize the value of providing a baseline connectivity map as a reference.

In the second step, we assessed primary forests through the eyes of habitat specialists, thereby exploring at a tactical level what is relevant for regional green infrastructure planning (Tittler et al., 2001). Our analysis of habitat networks for virtual species specializing in three different forest habitat types reveals large regional differences in both the available habitat area and the size distribution of components making up particular networks. The present distribution of habitat for species specialized in spruce, pine, and broadleaf forest habitats indicate the need for further protection of forest to increase the total area of the habitat networks and, thus, to improve both their structural and functional connectivity over a large scale. We found large numbers of single spatial components of habitat networks being small and isolated, particularly when including only protected primary forests. Angelstam et al. (2004) assessed the spatial needs for viable local populations of focal forest bird species (supporting 100 breeding females) in a landscape with a generally high amount of suitable habitat to be between 2,000 ha (woodlark *Lullula*

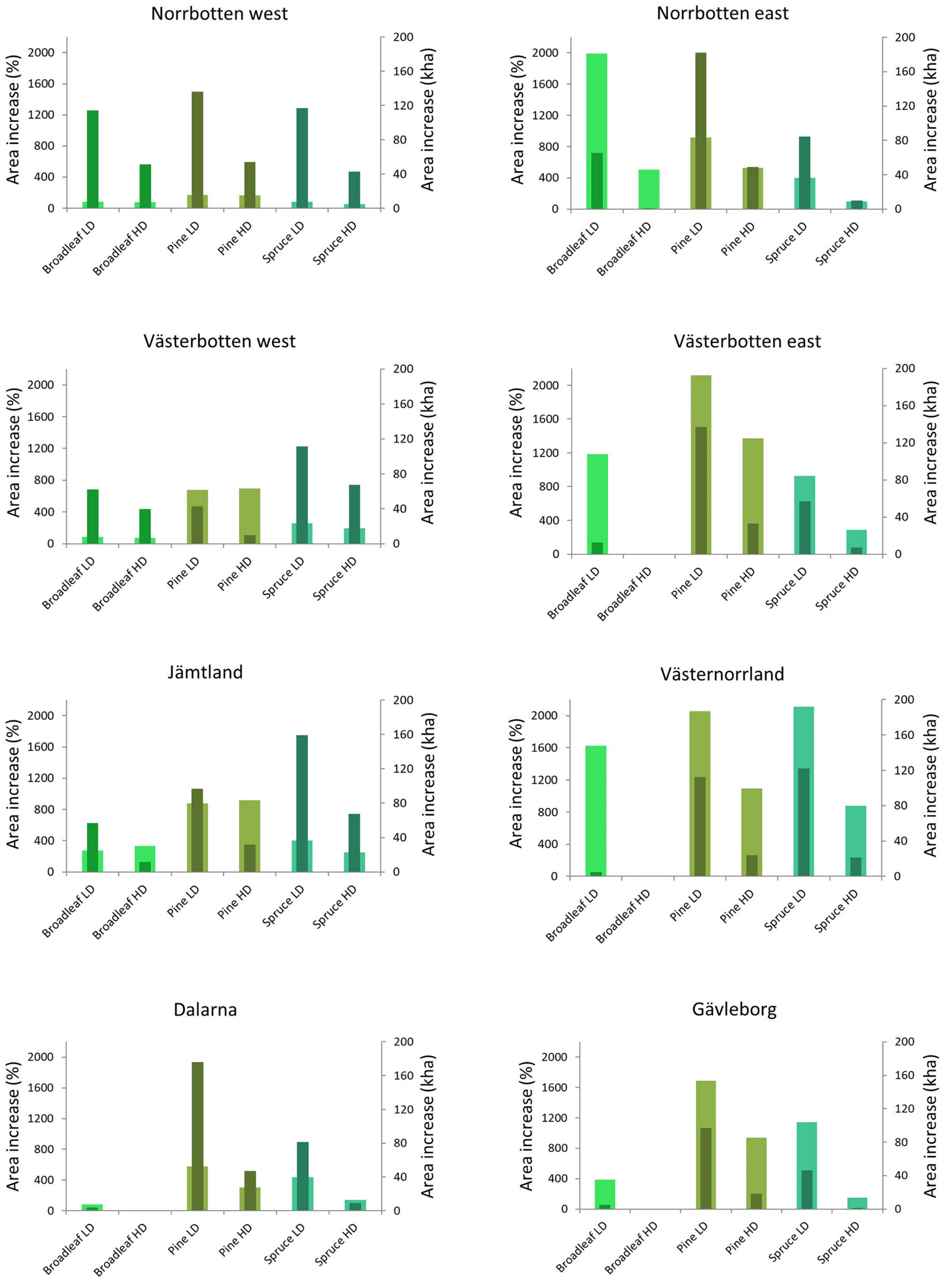

FIGURE 5 | The increase of habitat area when protected primary forests are compared with all primary forests. Wide columns refer to percentages (left axis) and narrow columns to increase expressed in hectares (right axis). LD concern low-demanding virtual species, and HD concern high-demanding virtual species.

TABLE 1 | Number, area, and size distribution of components of the habitat networks for different virtual species in the entire study region.

	Components (no)	Total area (kha)	> 100 ha (%)	> 1,000 ha (%)	> 10,000 ha (%)
Protected primary forests					
Broadleaf LD	3,165	1849.5	97.7	84.0	64.0
Broadleaf HD	864	561.5	97.9	81.6	61.3
Pine LD	3281	1435.5	96.5	69.4	23.4
Pine HD	836	327.0	96.7	53.9	11.7
Spruce LD	2,769	2000.6	97.4	80.4	55.1
Spruce HD	1,081	777.6	98.1	76.9	37.1
All primary forests					
Broadleaf LD	16,060	4808.0	95.0	79.0	62.8
Broadleaf HD	1,217	1016.1	98.2	83.6	63.0
Pine LD	17,600	11,951.0	98.2	89.4	77.5
Pine HD	7,053	1814.7	94.1	48.8	10.7
Spruce LD	23,067	10,506.1	96.9	80.4	61.2
Spruce HD	4,848	1965.5	96.1	68.9	38.7

LD, low-demanding species; HD, high-demanding species.

arborea) and 60,000 ha (black woodpecker *Dryocopus martius*). Corresponding figures for landscapes with low but still acceptable levels of habitat availability were found to be 50,000 and 300,000 ha, respectively, for the two species. In this perspective, the majority of the spatial components of habitat networks identified in our study are very much below these thresholds (see **Table 1** and **Supplementary Tables A2–A4**). This mismatch is clearly smaller if all primary forests are considered, but still, large gaps in networks are evident. This may lead to a situation in which many protected areas are unable to provide functional habitat for the species of conservation interest as demonstrated for several forest bird species (see also Orlikowska et al., 2020). This can be seen as the net result of an intensive forestry that has transformed a naturally dynamic boreal landscape into a heavily fragmented, managed production landscape (e.g., Kouki et al., 2001; Pohjanmies et al., 2017a; Jonsson et al., 2019).

Our large study region encompasses landscapes with different biogeographical conditions (topography, climate, soils, etc.) and with natural variation in forest types, particularly referring to the dominance of either Norway spruce or Scots pine (Nilsson, 1990). This may explain the presence of natural large gaps in habitat networks for virtual species linked to those tree species. Nevertheless, adding unprotected primary forest to our analysis improved the situation for species specialized in both pine and spruce forests quite substantially, particularly for less demanding species.

The situation is different in the case of species linked to broadleaf trees. On the one hand, habitat networks in subalpine landscapes dominated by mountain birch forest are abundant and very extensive for both types of habitat networks, i.e., based on protected primary forests and on all primary forests. Mountain birch forests and the coniferous-to-mountain birch transition zone in the Scandinavian mountain range have low tree-growth capacity, are not subject to forestry, and hence have a high level of naturalness (Jonsson et al., 2019; Svensson et al., 2020). On the other hand, a habitat network suitable for high-demanding species in broadleaf forests is largely absent from inland and coastal, representing a very large share of the study region (see **Figure 4**).

Broadleaf forest stands in naturally dynamic boreal landscapes are mostly linked to post-fire succession (Esseen et al., 1997). In addition to the current low frequency of wildfires in Fennoscandia in general (Rolstad et al., 2017), the intensive forest management applied in Sweden, aimed at maximizing production of coniferous timber and pulpwood, effectively limits the amount of mature stands with a large proportion of broadleaf trees (Bernes, 2011). Moreover, protecting forests does not ensure, in the absence of fire, the long-term maintenance of broadleaf trees in boreal forests (Bengtsson et al., 2003; Hardenbol et al., 2020). Stands rich in broadleaf trees are, except for the mountain birch forest, largely limited to the vicinity of settlements (Mikusiński et al., 2003) and different linear landscape features (e.g., riparian habitats) that cover relatively small areas and provide limited opportunities for forming effective habitat networks for different species (Ring et al., 2018).

Our analyses are based on the most recent national-scale data on protected and unprotected primary forests with known conservation value, with the pCF database treated as containing forests with the potential of being valuable due to the absence of recent clearfell-based harvesting (Svensson et al., 2019). Moreover, by stratifying these forests into three general types—pine-, spruce-, and broadleaf-dominated—based on the new detailed and high-resolution land cover data set and by analyzing their spatial distribution, we were able to further assess the spatial functionality of green infrastructure in boreal Sweden.

Nevertheless, we acknowledge the limitations in the data used and our approach as a whole. First, the pCF are somewhat overestimating the area of forests that have not been clearfelled, in particular, in the eastern inland and coastal part and along the river valleys, where forestry and other land use have a longer and more extensive history (Svensson et al., 2019). Therefore, the analysis based on all primary forests is optimistic; in reality, the habitat networks of our virtual species are probably less widespread and more fragmented; i.e., the situation is worse than we are able to show. Second, the virtual species used represent only two sets of spatial requirements and provide indicative rather than specific information on attributes for favorable conservation status. This calls for complementary species and species-group assessments. Moreover, and with the same limitations, distinguishing only three types of forests as habitat is also a simplification of the highly variable qualitative habitat preferences of the boreal and subalpine forest species occurring in Sweden (see, e.g., Berg et al., 1994). However, we argue that our evaluation of habitat networks is an important step toward improving our understanding of preconditions for securing functional green infrastructure in boreal Sweden.

Functional Green Infrastructure Based on Forests in Boreal Sweden

The EU strategy on green infrastructure (European Commission, 2013) aims at preserving and enhancing green infrastructure in order to preserve biodiversity and functional ecosystems and the provisioning of services and goods under climate change and ongoing forestry and other land use. It is understood that, with broader geographic scale, the greater the coherence and connectivity of the green infrastructure network, the greater are its conservation benefits. We demonstrate that the existing habitat networks represented collectively by both protected and unprotected pCF are able to support functional green infrastructure over sizable portions of the study region. However, as seen from the perspective of the three different forest types, there are obvious subregional differences in functionality. Thus, there are different habitat-type restoration needs in different regions.

We maintain that habitat distribution and density maps capturing the amount, spatial distribution (including the level of connectivity), and quality support large-scale green infrastructure planning. More detailed analyses of valuable forest networks could be applied at subnational or water catchment levels with the use of additional data concerning, e.g., distribution of species or habitats of conservation interest and available conservation planning software (Mikusiński et al., 2007; Snäll et al., 2016). Such detailed analyses should also include identification of local restoration needs that seem to be principally required for habitat networks based on broadleaf trees (e.g., Hof and Hjältén, 2018). Even if challenging, measures to create habitats dominated by broadleaf trees have been proven to be possible and successful (e.g., Hämäläinen et al., 2020).

Supporting biodiversity and ecosystem services through adding protected habitat is a central aspect in green infrastructure planning and implementation. Clearly, the most pressing green infrastructure challenge is the lack of broadleaf forest habitats, and restoration and re-creation is needed on a landscape scale throughout north Sweden. Although the potential for increasing functional connectivity of the already protected forests is large, it is unlikely to represent a realistic scenario for green infrastructure development. It has to be assumed that active forest management will continue into the future and that clearfelling will be a continued practice. It should be emphasized that the green infrastructure concept includes and does not exclude land use.

The approach taken in this study allows for identifying green infrastructure gaps to identify possibilities to restore certain types of habitat in certain places based on what is available and to define types and characteristics of missing habitats that need to be re-created. Thereby, our study contributes to direct green infrastructure planning and management guidelines with regional resolution. The increased capacity for each case assessed can be matched toward a green infrastructure target and included in regional green infrastructure plans to be reflected on the national plans.

The work on securing green infrastructure based on HCVF is evidently in conflict with other interests in boreal Sweden (Pohjanmies et al., 2017b; Jonsson et al., 2019). Simplified and intensively managed monocultures with timber, pulp, and biomass production as a main aim are not able to sustain biodiversity and multiple ecosystem services (Gamfeldt et al., 2013; Halme et al., 2013; Pohjanmies et al., 2017a). The current level of protection of HCVF in boreal Sweden, except for its northwestern part, is highly insufficient to support functional green infrastructure (Jonsson et al., 2019; Angelstam et al., 2020). Moreover, the level of protected area is far from the quantitative target #11 of the Aichi Biodiversity goals and does not satisfy the national Environmental Quality Objective "Sustainable Forests" (Swedish Parliament, 1998). As the conflict over the current and future use of Sweden's boreal forests intensifies (e.g., Sténs and Mårald, 2020), the current situation is at a value chain crossroad between strengthened nature conservation and intensified wood production in boreal forests.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

GM, JS, and BGJ delineated the general idea of the paper. GM provided the first draft. EHO and JWB performed all the spatial analyses. All authors contributed to the final text of the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

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A Step-by-Step Guide to Initialize and Calibrate Landscape Models: A Case Study in the Mediterranean Mountains

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The use of spatially interactive forest landscape models has increased in recent years. These models are valuable tools to assess our knowledge about the functioning and provisioning of ecosystems as well as essential allies when predicting future changes. However, developing the necessary inputs and preparing them for research studies require substantial initial investments in terms of time. Although model initialization and calibration often take the largest amount of modelers' efforts, such processes are rarely reported thoroughly in application studies. Our study documents the process of calibrating and setting up an ecophysiologically based forest landscape model (LANDIS-II with PnET-Succession) in a biogeographical region where such a model has never been applied to date (southwestern Mediterranean mountains in Europe). We describe the methodological process necessary to produce the required spatial inputs expressing initial vegetation and site conditions. We test model behaviour on single-cell simulations and calibrate species parameters using local biomass estimations and literature information. Finally, we test how different initialization data—with and without shrub communities—influence the simulation of forest dynamics by applying the calibrated model at landscape level. Combination of plot-level data with vegetation maps allowed us to generate a detailed map of initial tree and shrub communities. Single-cell simulations revealed that the model was able to reproduce realistic biomass estimates and competitive effects for different forest types included in the landscape, as well as plausible monthly growth patterns of species growing in Mediterranean mountains. Our results highlight the importance of considering shrub communities in forest landscape models, as they influence the temporal dynamics of tree species. Besides, our results show that, in the absence of natural disturbances, harvesting or climate change, landscape-level simulations projected a general increase of biomass of several species over the next decades but with distinct spatio-temporal patterns due to competitive effects and landscape heterogeneity. Providing a step-by-step workflow to initialize and calibrate a forest landscape model, our study encourages new users to use such tools in forestry and climate change applications. Thus, we advocate for documenting initialization processes in a transparent and reproducible manner in forest landscape modelling.

Keywords: calibration, Mediterranean area, LANDIS-II, PnET-Succession, forest landscape model, forest succession, initial vegetation map, forest inventory

INTRODUCTION

Forests are indispensable ecosystems for human societies. Due to their role as climate regulators, soil protectors and biodiversity hotspots, forests provide a multitude of ecosystem services and are fundamental elements in the world's economy (Krieger, 2001; Martínez Pastur et al., 2018). The potential adverse impacts of global change on forest ecosystems emphasizes the need to understand how to manage them in the future (Lindner et al., 2014; Hof et al., 2017; Mina et al., 2017).

In recent years, the use of computational models has been increasing in forest ecosystem research (Gustafson et al., 2017; Shifley et al., 2017). Although empirical studies are of fundamental importance for process understanding, simulation models are nowadays recognized as useful tools to assess our knowledge about the functioning of ecosystems as well as essential allies when predicting future changes (Seidl, 2017). Over the past decades, a large range of models were developed to describe future dynamics in forest ecosystems (Keane et al., 2015), from stand-scale empirical simulators to more complex process-based models operating at landscape scale (Fontes et al., 2010). Because of computational constraints, models integrating fine-resolution processes (e.g., photosynthesis, specific growth functions) at large scales in a spatially explicit framework were rare, and smaller grain processes were often strongly simplified (Elkin et al., 2012). However, these constraints are constantly being reduced by the increase in computational power, allowing for the flourishing of Forest Landscape Models (FLMs) which integrate physiologically based processes from stand to landscape level (Seidl et al., 2012; De Bruijn et al., 2014; Shifley et al., 2017; Petter et al., 2020).

According to Jorgensen and Fath (2011), ecological models comprise five elements: state variables, external variables, parameters, mathematical equations, and universal constants. The mathematical equations and universal constants are implicit within the model structure, while the initial conditions of the state variables (e.g., species biomass, species age), external variables and parameter values are usually provided as inputs by the user for each simulation study. In the case of FLMs, they represent forests across the landscape in a spatially explicit way. The landscape is depicted as a set of cells for which a series of state and external variables are defined. These variables are used to define the ecological processes taking place at cell level (e.g., growth, mortality among others) and at landscape level (e.g., seed dispersal, fire spread). For comprehensive reviews on the development, structure and recent applications of FLMs see Shifley et al. (2017); Keane et al. (2015), and He et al. (2017).

The above-mentioned structural elements are essential to set up a simulation in a specific landscape. This requires the user to obtain, prepare and organise comprehensive datasets to address the two first key steps in applying FLMs: model initialization (initial conditions of state and external variables) and calibration of model parameters. The initial conditions of the state variables describe the ecosystem at the beginning of the simulation. In turn, external variables are those forces affecting the ecosystem without being internal parts of it (Jorgensen and Fath, 2011). Most FLMs require initial values of at least certain state and external variables to start a simulation. As an example, the FLM LandClim requires elevation or browsing intensity for initialization (Petter et al., 2020). In addition to biophysical conditions (e.g., soil types, climate maps or regions), essential initial conditions for FLMs are vegetation maps describing which species are present in the landscape at the beginning of the simulation time. Decisions regarding the inclusion or exclusion of certain species can be highly relevant in certain ecosystems (e.g., shrubs in the Mediterranean area). Thus, these vegetation maps are a keystone within these experiments since forest dynamics and properties (biomass, available light, regeneration, etc.) are highly driven by initial conditions and structure (Duveneck et al., 2015; Scheller and Swanson, 2015). For example, most FLMs require information of tree species and their age classes across the landscape. This information can be very challenging to obtain and estimate for large spatial scales without necessarily combining multiple and complex datasets (Zald et al., 2014). The generation of input data for FLMs can therefore require significant time and skills, and often demands complementarity with experimental research from long-term field studies (Shifley et al., 2017; Scheller, 2018).

The calibration of model parameters has been defined as one of the greatest challenges in modelling under environmental changes (Keane et al., 2015; Scheller, 2018). Model parameters are values used in model equations which represent processes (Jorgensen and Fath, 2011). Most models simulating the succession dynamics of vegetation require parameters describing the behaviour of the species present in the landscape. These parameters may differ for each model, but commonly refer to species growth characteristics, fruit and seed dispersal, reproduction strategies and absolute or relative measures of tolerance to stress factors (Huber et al., 2018). A broad range of sources can be used to fulfil these parameters, ranging from empirical case-specific data collected by the modeller to values of standard variables stored in global databases. In either case, an evaluation of model outputs to identify appropriate parameter values is usually required to ensure that the model produces plausible outcomes at the local scale (Gutiérrez et al., 2016; Duveneck et al., 2017). This evaluation of parameter values is known as calibration (Mulligan and Wainwright, 2013). During this phase, the different model sensitivity to some parameters over others should be considered (McKenzie et al., 2019).

Successional processes and long-term projections in FLM are highly sensitive to initial conditions and model parameters (Scheller, 2018). Estimation of initial condition and calibration procedures are typically described in the method section in literature studies (e.g., Scheller et al., 2005; Boulanger et al., 2017), but often not on a level of detail to allow full reproducibility or with enough information to help non-modellers to setup a new landscape from scratch. Even fewer provide access to inputs, outputs and scripts in public repositories. The aims of this study are twofold. First, documenting the process needed to initialize and calibrate a FLM step-by-step, as an example for analogous uses. Fulfilling this goal would encourage the application of FLMs as scientific tools to assess future forest dynamics and management adaptation under global change. Second, we aim at testing different initialization data – with and without shrub communities – by assessing the model ability to project forest landscape dynamics in a biome where the model has not been applied so far (Euro-Mediterranean region).

MATERIALS AND METHODS

Model Description

In this manuscript, we chose LANDIS-II as our reference FLM. LANDIS-II[1] (Scheller et al., 2007) is a FLM designed to simulate forest dynamics at multiple spatial and temporal scales. It allows a wide degree of complexity depending on a set of extensions which can optionally be activated to simulate different processes such as succession, disturbances (fire, wind, herbivory, and pests) and management at different degrees of complexity (e.g., areas- and species-specific harvesting regimes, post-harvesting planting). The spatial scale (i.e., cell resolution) is defined by the user, which makes it very flexible and adaptable to a wide variety of simulation experiments. In LANDIS-II, the landscape is divided into ecoregions, which are subregions sharing similar climatic conditions and soil characteristics. Trees in each cell are represented as species-age cohorts, increasing the computational efficiency of the model (De Bruijn et al., 2014).

Particularly, we used the PnET-Succession extension v.3.4 (De Bruijn et al., 2014; Gustafson et al., 2015). This extension embeds the PnET-II ecophysiological model equations (Aber and Federer, 1992). PnET-Succession simulates forest succession in a more mechanistic way than previous approaches, representing an advantage for experiments where novel conditions such as climate change are being explored (Gustafson, 2013). In PnET-Succession, age is used to calculate cohort's biomass at the onset of the simulation (i.e., model spin-up) and cohorts with higher biomass are given priority access to light and water (Gustafson and Miranda, 2019). Cohort biomass is assumed to be homogeneously distributed in the cell and therefore shade conditions are also homogeneous within a cell (Scheller et al., 2007). Potential net photosynthesis rate is calculated as a linear function of foliar nitrogen (FolN) and biomass growth is a result of environmental conditions such as temperature, precipitation, photosynthetically active radiation (PAR), CO_2 concentrations and—optionally—ozone concentrations (De Bruijn et al., 2014). Biomass allocation depends on compartments turnover and fraction parameters. Mortality can occur at any time if carbon reserves become limiting (non-structural carbon <1%) or when age approaches species longevity (De Bruijn et al., 2014).

PnET-Succession requires a series of generic, ecoregion- and species-specific parameters. Although many default values have been made available by the model developers and in past application studies, most parameters require calibration according to the biogeographical location of the target landscape and the tree species included in the simulations (McKenzie et al., 2019; Mina et al., 2021).

Study Area

The simulated area considered in this study is located in the south eastern part of Iberian Peninsula and it covers approximately 390,000 ha (37.2° N, 3.1° W, **Figure 1**). The topography is mostly mountainous, including three mountain ranges. In the southern part of the study area, Sierra Nevada spreads from east to west and contains the highest peak in the Iberian Peninsula, Mulhacén (3,478 m). In the northern part of the study area, Sierra de Arana is located in the west, while Sierra de Baza-Filabres is in the east. More than half of the study area is under protection, either as National or Natural Park, and therefore a variety of exploitation and management regimes can be found in the study area.

Several bioclimatic zones are found within the study area (Rivas Martínez, 1983; REDIAM, 2018). The supramediterranean zone (mean annual temperature 8–13°C) is the one covering most of the area, at low altitudes of Sierra Nevada and connecting with Sierra de Arana. An important proportion of the Sierra de Baza surface is also represented by this bioclimatic zone. Supramediterranean areas are mostly covered by a mosaic of conifer, mixed forests and sclerophyll shrubs. The highest areas represent the oromediterranean zone (mean annual temperature 4–8°C) and are covered by conifers, shrubs and sparse vegetation, except for the very high altitudes in Sierra Nevada, which encompass the cryoromediterranean zone (i.e., alpine tundra, mean annual temperature <4°C). These peaks are covered by scarce vegetation adapted to extreme climatic conditions. The rest of the study area, at altitudes commonly below 1,000 m, is mostly covered by mesomediterranean (mean annual temperature 13–17°C) and thermomediterranean zones (mean annual temperature 17–19°C). The precipitation follows a strong seasonal pattern, with dry summers and precipitation concentrated in a small number of events. Rainfall is the most common form of precipitation. Besides, snowfall at high altitudes is very important since slow melt down and subsequent infiltration into soil increases water availability for plants throughout the spring and summer season. Aspect also determines water availability due to different precipitation evapotranspiration patterns.

The study area is covered by diverse natural vegetation patches in combination with agriculture and *Pinus* forest plantations. Pine plantations are the dominant land use type, covering around

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[1] www.landis-ii.org/

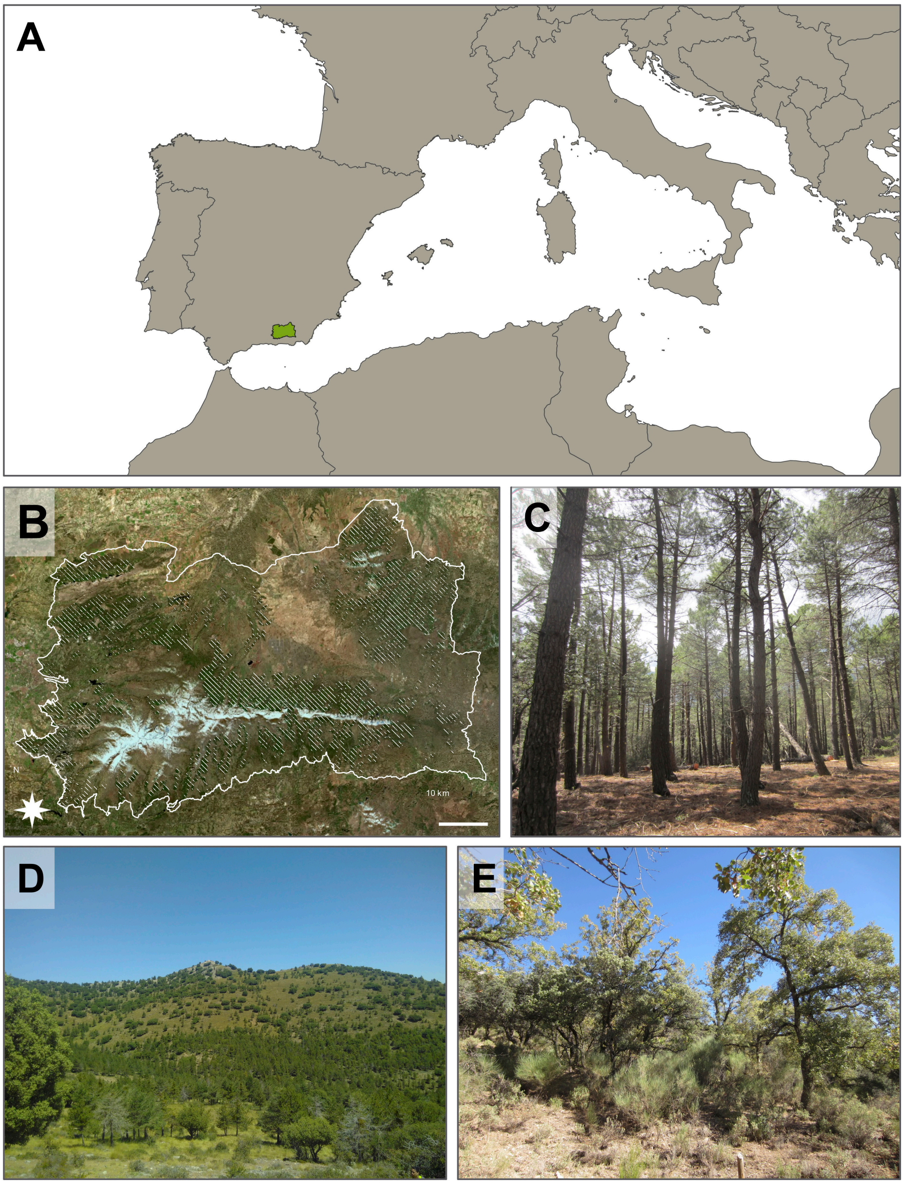

FIGURE 1 | Study area location **(A)**, orthophoto of the study area **(B)** and pictures of representative forest types: pine plantations **(C)**, mixed open forest **(D)**, oak-dominated stand **(E)**. Shaded area in panel **(B)** delimitates pine plantations.

20% of the study area, with a minor presence of natural pine forests. These plantations were mainly established between the 1950s and 1970s as means to halt soil erosion in recently abandoned agricultural areas. The main species are Maritime pine (*Pinus pinaster* Aiton), Aleppo pine (*Pinus halepensis* Miller.), black pine (*Pinus nigra* Arnold.) and Scotch pine (*Pinus sylvestris* L.) (Bonet García et al., 2009; Pemán García et al., 2017; Mesa Garrido, 2019). Pines were planted in high densities to drastically reduce soil loss. Afterwards, favourable climate conditions and lack of appropriate post-planting management have resulted in highly dense monospecific even-age stands. As a result, these forest plantations are nowadays under extreme risk by climate change and forest pests, which has resulted in decline and massive mortality processes (Sánchez-Salguero et al., 2010, 2012a).

Almost 40% of the study area is covered with shrublands and abandoned crops with sparse natural vegetation. Some of these areas host sparse trees (mainly *Quercus ilex* L.), which can be highly relevant seed sources at a local scale. Moreover, in a context of climate change and further abandonment of mountain agriculture activities, these sparsely vegetated systems can be highly important to understand the succession dynamics in pine plantations for two reasons: (1) Due to climate change, currently forested areas could suffer a decline and be replaced by shrublands as these areas become less suitable to sustain high levels of biomass; and (2) Tree species could expand to shrubland areas currently dedicated to marginal activities (mountain agriculture, livestock, fuelwood, and charcoal exploitation, etc.).

Model Initialization

In this section we describe the workflow followed to produce the necessary inputs required by LANDIS-II with PnET-Succession. We first focus on the generation of the initial vegetation conditions, followed by the methodological process to build biophysical inputs. The different sources of information used in this process are listed in **Table 1**.

Initial Vegetation Conditions

Most FLMs require estimates of initial conditions in the form of vegetation maps reporting the presence of tree species at the beginning of the simulations. Concretely, LANDIS-II requires a spatial representation of species cohorts by age classes (also called "initial communities"). To generate such vegetation maps, different information sources are often combined following a complex workflow that, if not exhaustively described, is often unreproducible. Even though such workflows can be model- and site-specific, three methodological steps can be defined: (1) Plot-level information (e.g., from national or regional inventories or permanent growth plots) is processed to extract tree measurements such as basal area, age or height; (2) Polygon-level information is processed to select stand-scale, spatially explicit variables which can be linked to plot-level information such as forest type, mean age, canopy cover, etc.; (3) A spatial imputation method is applied to produce a continuous map by assigning plot-level information to polygon-level information. In the following sections, we describe the methodological details for each of the three methodological steps of the workflow, which is summarized in **Figure 2**.

Plot-level information processing

Plot-level information is necessary to select the most common tree species and some of their demographic features in the area of interest. In our case, the Third Spanish National Forest Inventory (NFI) was used for this purpose (**Table 1**). The NFI contains homogeneous information about forest covers in Spain by reporting data collected in a systematic network of permanent sampling plots (Alberdi et al., 2017). The plots are evenly distributed on a 1 km^2 grid throughout the territory and contain plot- and tree-level information for each survey period. In addition to single-tree data (e.g., species, diameter, height, form, and health status), the plot is described in terms of the three most dominant tree species contributing to canopy cover. We selected the tree species to include in the model simulations based on the total coverage value of the species within the study area.

Tree age is often not available at single-tree level and its estimation is challenging as several factors influence growth rate of individual trees, leading to very different tree characteristics for the same age. Nevertheless, LANDIS-II uses cohort age-classes as a proxy for biomass, and therefore an estimated age is required for each species across the landscape. NFI provides estimated stand age for plots within even-aged stands. In our area, even-aged stands are composed by *Pinus* spp. Since these plots also have associated individual tree measurements (e.g., diameter, height), we calculated the average diameter per species and plot and joined it to the assigned stand age. In order to have as many observations as possible, we expanded the considered dataset to all plots within even-age stands from surrounding regions (provinces of Granada and Almeria). Since no estimated age was available for plots within uneven-age stands (mainly *Quercus* spp. and *Populus nigra*), a semi-quantitative method was applied. We used yield tables available from the literature

TABLE 1 | Information sources used in this study.

Information required	Source	References	Spatial scale
Plot-level vegetation information	Third Spanish National Forest Inventory (NFI)	Third Spanish National Forest Inventory (2007). Available as a Microsoft Access database at: https://www.miteco.gob.es/es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/cartografia_informacion_disp.aspx Source: Ministerio para la Transición Ecológica y el Reto Demográfico	1:50.000
Polygon-level vegetation information	Spanish Forestry Map (FM)	Map resulting from photointerpretation. Accessible as vectorial file at: https://www.mapa.gob.es/es/cartografia-y-sig/ide/descargas/desarrollo-rural/mfe_andalucia.aspx Source: Ministerio de Agricultura, Pesca y Alimentación	1:50.000
	Andalusian Vegetation Map (VM)	Map resulting from photointerpretation and field sampling. Accessible as vectorial file at: https://descargasrediam.cica.es/repo/s/RUR Source: REDIAM, Consejería de Agricultura, Ganadería, Pesca y Desarrollo Sostenible	1:10.000
Climate data	Reference data	Annual precipitation, mean, minimum and maximum annual temperature for the period 1971–2000. Accessible as raster files at: https://descargasrediam.cica.es/repo/s/RUR Source: REDIAM, Consejería de Agricultura, Ganadería, Pesca y Desarrollo Sostenible	100 m resolution
	Climate series	Maximum and minimum temperatures and precipitation for the period 1950–2005. Network common data files published by Karger et al. (2020)	0.049° resolution
		CO$_2$ concentrations times series for SSL station and period 1971–2018 published by Meinhardt and ICOS Atmosphere Thematic Centre (2020).	Point sampling: 47.9°N, 7.9°E
		Photosynthetically Active Radiation for the period 1950–2019. Network common data files published by Cornes et al. (2018) (Version 20.0).	0.25° resolution
Soil data	Regional soil maps	Sand, clay and silt soil content and soil depth. Raster files published by Rodríguez (2008).	250 m resolution

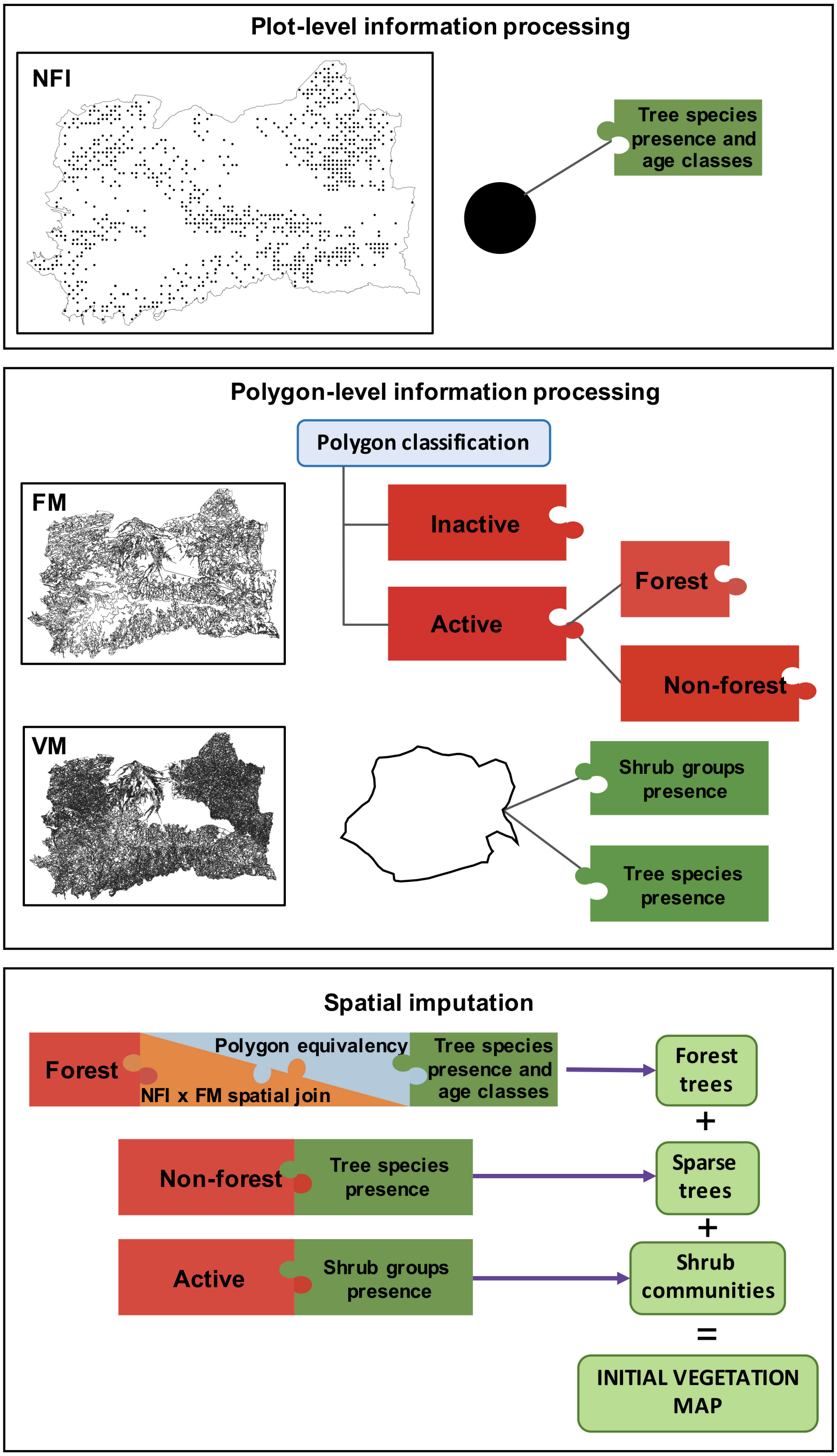

FIGURE 2 | Schematic view describing the workflow of the initial vegetation map generation. Tree species presence and age were extracted from plots of the Third Spanish National Forest Inventory (NFI) during the plot-level information processing phase. During the polygon-level information processing, the Spanish Forestry Map (FM) was used to classify polygons as active/inactive and no forest/forest. The Andalusian Vegetation Map (VM) was used to extract the presence of shrub communities and sparse trees. At the spatial imputation phase, plot- and polygon-level information was combined to generate a continuous map of vegetation.

(Teobaldelli et al., 2010). Then, we generated an age assignment table containing correspondence rules between tree age, diameter and height for each species under consideration. This table was validated based on expertise and observations in the study area. Finally, the age assignment table was used to attribute an age class to the species in each NFI plot (see **Supplementary Table 1** for more details).

Polygon-level information processing

Many government and private forestry organizations utilize cartographic products to support forest management. Polygon-level information usually contains forest variables at a landscape scale such as forest type, coverage or stand development stage. Here, we used the Spanish Forestry Map (FM) and the Andalusian Vegetation Map (VM) as the main source of spatially explicit landscape information (**Table 1**). The FM is a vectorial file generated by photointerpretation. It contains a series of attributes describing the forest vegetation for each polygon: polygon identifiers and surface; province and region; forest and land use characteristics (vegetation type, structural type, land use categories); name, coverage and state of the three most dominant species in dominance order; and tree and total coverage fraction. Based on these attributes, polygons were classified as active (those containing or potentially containing vegetation units useful for our purpose) or inactive (those where natural succession is hampered by human activities: crops, infrastructures, firebreaks, etc.). Active polygons were in turn classified as forest and non-forest. Forest polygons have an average size of 51 ha and a maximum of 357 ha.

The VM is also a vectorial file that contains an extensive list of attributes (140) describing the presence and characteristics of the tree species, shrubs and pastures present in each polygon (e.g., vegetation community, canopy coverage) at a higher resolution than the FM. Due to the importance of sparse trees and shrublands in our study area (see section "Study Area"), we used the VM to consider the occurrence of sparse trees in non-forest polygons in the initial vegetation map. Moreover, since the VM also provides information about shrubs, grasslands and pastures, we used a variable termed "life form" attribute to analyse the presence of shrubs within the study area. The life form attribute is based on the classification proposed by Raunkiaer (1934) and subsequently revised by Ellenberg and Mueller-Dombois (1967). According to this classification, plants can be: microphanerophytes ("*evergreen perennial plants that grow between 2 and 5 m, or whose shoots do not die back periodically to that height limit*"), nanophanerophytes ("*evergreen perennial plants that grow below 2 m tall, or whose shoots do not die back periodically to that height limit*"), chamaephytes ("*evergreen perennial plants whose mature branch or shoot system remains perennially within 25–50 cm above ground surface, or plants that grow taller than 25–50 cm, but whose shoots die back periodically to that height limit*"), hemicryptophytes ("*perennial plants with periodic shoot reduction to a remnant shoot system that lies relatively flat on the ground surface*"), geophytes ("*perennial plants with periodic reduction of the complete shoot system to storage organs that are imbedded in the soil*"), therophytes ("*annual plants whose shoot and root system dies after seed production and which complete their whole life cycle within 1 year*"). Shrub communities' size was extracted from this classification. Hemicryptophytes, geophytes and therophytes life forms were not considered for the analysis as they mostly refer to species with short life cycles. As a result, the presence of tall (2–5 m), medium (0.5–2 m), short (<0.5 m) shrub communities was extracted for each polygon in the study area. Each of these shrub communities was parameterized individually in PnET-Succession (see details below).

Spatial imputation

Spatial imputation is applied to combine plot-level to polygon-level information. To generate the initial vegetation map suitable for LANDIS-II, we combined plot- and tree-level information (NFI) with polygon-level information (FM and VM). The final aim of this step is to produce a forest composition map containing the species-age assemblage (species and age of each cohort) in every cell within the study area (see Duveneck et al., 2015 for the description of a similar approach in North America).

First, we performed a spatial join between the forest polygons from the FM and the plots from the NFI (**Figure 2**). FM polygons containing one single NFI plot were assigned the species-age assemblage of the surveyed plot. FM polygons with more than one NFI plot were assigned the species-age assemblage which results from merging all plots species-age assemblages. This only occurred in a small proportion of cases: 80 out of 789 forest polygons had two NFI plots in them, 3 polygons had 3 NFI plots in them and one polygon had 4 plots in it.

Forestry Map polygons without NFI plots were analysed to identify an equivalent polygon among those which have one or more intersecting NFI plots. Polygon equivalency was analysed at three levels: (i) Full equivalency: polygons matching vegetation type, species dominance, species development state, and total coverage fraction; (ii) Partial equivalency: polygons matching vegetation type, species dominance, and total coverage fraction; and (iii) Species equivalency: polygons matching species dominance and total coverage fraction. FM polygons were assigned the species-age assemblage of their equivalent polygon. If there were more than one equivalent polygon, the polygon was assigned the species-age assemblage resulting from the merge of all possible ones. FM polygons with no equivalent polygons were further analysed based on their species composition, without considering species dominance order. These polygons were assigned the species-age assemblage corresponding to the most common species-age assemblage containing the same species as the considered polygon in the whole study area. FM polygons containing species assemblages not occurring in the previously analysed polygons were assigned one cohort of each of the species present in it. The age of this cohort corresponded to the most common age for each species among all previously analysed polygons. This procedure resulted in the description of the forest trees within the study area.

Second, polygons labelled as non-forest by FM, were imputed to include sparse trees (**Figure 2**). We used VM to gather information for those polygons. Since VM does not report any variable describing the age of the species, VM polygons were imputed a species-age assemblage containing the reported species with the most common age for that species in the rest of the study area. By doing so, the description of the sparse trees within the study area was completed.

Third, we imputed shrub communities within the landscape by assigning the corresponding shrub community-age assemblage to each VM polygon (**Figure 2**). Shrubs were not allocated to different age classes but instead we arbitrarily assigned age 10 for all polygons. Since in LANDIS-II shrub biomass should not exceed tree biomass (see section "Model Description"), the role of shrubs in the model is mainly to compete for light and water in the understory (e.g., affecting establishment), thus we believe age class assignation for shrubs was not necessary.

Finally, we obtained the initial vegetation map by combining forest trees, sparse trees and shrubs communities. The map was rasterized at 100 m resolution (1 ha cells). Each cell was labelled with a code associated to a list of unique species-cohort assemblages.

Biophysical Inputs

The FLM LANDIS-II requires an input map of ecoregions as biophysical inputs. LANDIS-II ecoregions are continuous or discontinuous areas of the landscape which share climate conditions and soil texture (see section "Model Description"). To generate the map of ecoregions, we used a reference climate dataset and a regional soil map (**Table 1**). The reference climate dataset reports annual precipitation and mean, minimum and maximum temperature for the period 1971–2000 at a 100 m resolution. Firstly, an unsupervised k-means clustering was applied to the climate dataset to lump together cells with similar climate. MacQueen algorithm was used in this clustering (MacQueen, 1967). We evaluated different numbers of clusters and eventually ended up with four climate regions. The resulting ecoregions agree with our expectations considering topography and the bioclimatic zones found in the study area (**Figure 3**).

The resulting climate regions map was intersected with the soil texture map. The soil map reports the percentage of sand, silt and clay at a 250 m resolution. This map was derived by simply translating the percentages of sand, silt and clay to USDA soil texture categories. The final ecoregions map was therefore produced by overlapping the climate regions and the soil textures maps. This resulted in a total of 28 unique ecoregions defined by both a climate region and a soil type (**Figure 3**).

PnET-Succession also requires rooting depth for each ecoregion. Ecoregion rooting depth was calculated based on soil depth classes reported in the soil map (0–250 mm, 250–500 mm, 500–1,000 mm, 1,000–1,500 mm, >1,500 mm). The midpoint of each class was used to calculate the most frequent rooting depth for each ecoregion. Precipitation Loss Fraction and Leakage Fraction were given values of 0.6 and 1 for all ecoregions. All other PnET-Succession ecoregions parameters were given default values. A complete dataset containing model inputs is provided (see section "Data availability").

Calibration of Model Parameters

LANDIS-II and PnET-Succession require a set of parameter values for each species simulated in the landscape. Generic species parameters are required irrespective of the chosen succession extension (e.g., longevity, sexual maturity), while others are required by PnET-Succession (e.g., foliage nitrogen, foliage turnover, minimal, and optimal photosynthetic temperature). We firstly defined an initial set of parameter values from multiple sources. Then, we ran single-cell simulations to verify the species behaviour (e.g., growth, photosynthetic rates) under different conditions. On a single, empty 100 m cell, a single 10-years old cohort of each species was initialized and grown for 200 years preventing establishment of new cohorts. Five replicates were run for each simulation using static monthly averages of temperature, precipitation, PAR and CO_2 (**Table 1** and **Supplementary Figures 4–6**). Baseline climate conditions were used to avoid introducing variability due to fluctuating climate (Gustafson and Miranda, 2019).

The results of these simulations were compared with species biomass estimations for the study area and literature information. Biomass estimations were calculated for *P. halepensis*, *P. nigra*, *P. pinaster*, *P. sylvestris*, *Q. ilex*, and *Q. pyrenaica* based on forest inventory data and allometric equations published in Montero et al. (2005). Simulated versus observed Relative Growth Rates in relation to species biomass were used for comparison as this metric is independent from age, which has a high uncertainty degree in NFI data.

Following calibration guidelines for PnET-Succession (De Bruijn et al., 2014; Gustafson and Miranda, 2019) and evidences from a sensitivity analysis with the same model (McKenzie et al., 2019), we adjusted the most influential species-specific parameter values in an iterative process until the species showed the expected behaviour based on authors' expertise and observations.

We also evaluated the response of competing assemblages of species typical of the different forest types included in our landscape. These multi-species simulations allow the calibration in relative terms, as well-known competition effects can be assessed and species parameters can be adjusted accordingly. In these simulations, species are established in the cell at the same time and no new establishment is allowed, which is often not the case in natural ecosystems. Thus, the observed species development is the result of their growth traits and their different performance under competition and not due to different establishment strategies or other advantages.

Landscape Simulation

We simulated forest dynamics at the landscape scale incorporating the effect of spatial processes such as dispersal and climate and soil heterogeneity. We initialized the model with the biophysical inputs described above and with the parameters calibrated in the previous step. To verify the influence of shrub communities on simulated forest dynamics, we initialized LANDIS-II with two different vegetation datasets: (1) With shrub communities and (2) Without shrub communities. Since the aim of this study was to initialize the landscape for further experiments with LANDIS-II and PnET-Succession, neither natural nor human-driven disturbances (i.e., fire, harvest) were included in the experiment. We ran five model replicates using baseline climate for 200 years (**Table 1** and **Supplementary Figures 4–6**). We analysed model outputs in terms of temporal patterns of

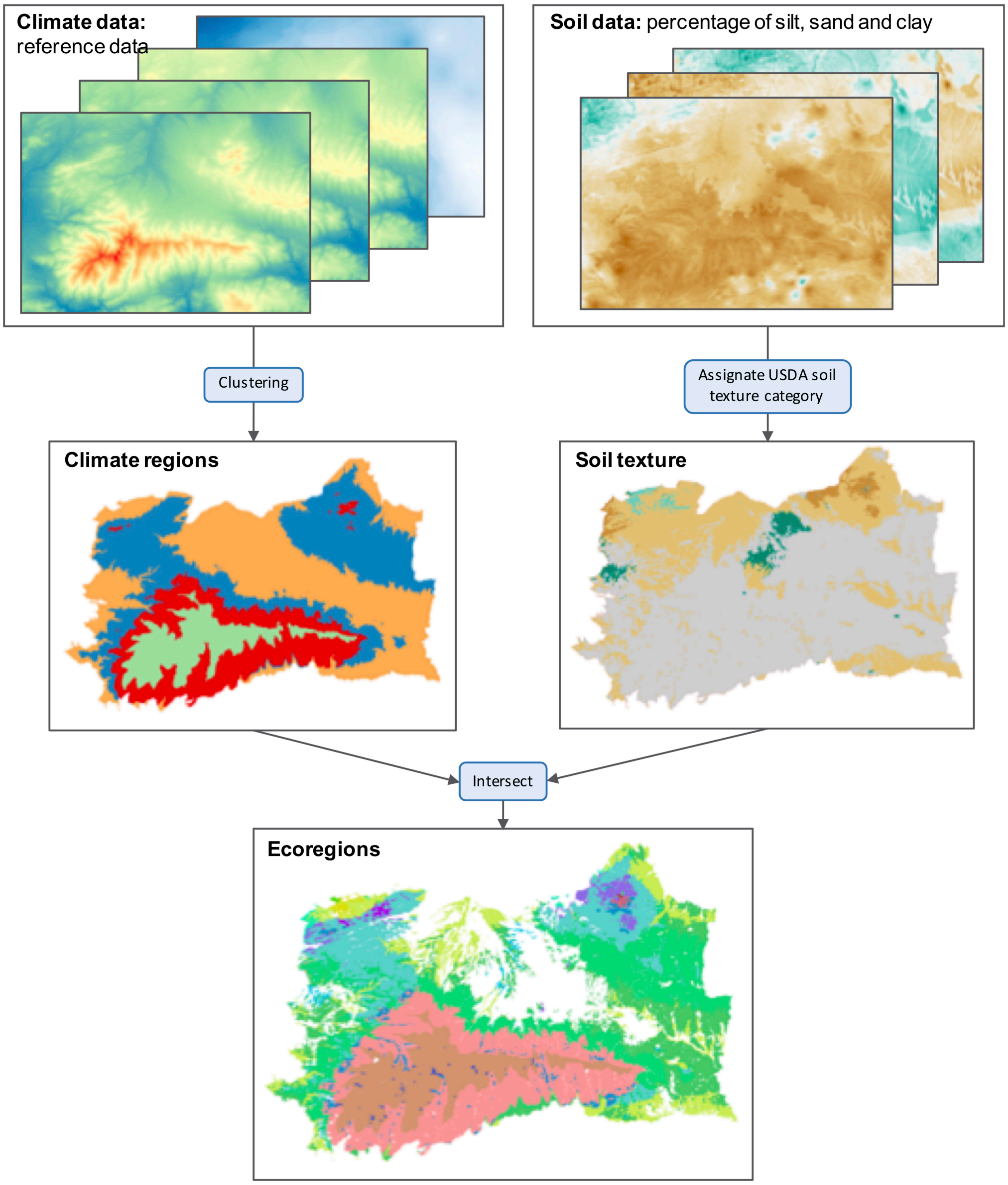

FIGURE 3 | Schematic view of workflow followed to produce the ecoregions map. Reference climate data consist of annual precipitation, mean, minimum and maximum annual temperature for the period 1971–2000 at 100 m resolution. Clustering of climate data resulted in four climate regions. Soil data consist of a percentage of silt, sand and clay at 250 m resolution. The intersection of climate regions and soil textures resulted in 27 ecoregions.

average biomass for each species. Moreover, we mapped and compared total aboveground biomass for selected simulation years across the landscape. All analyses were performed in R version 3.5.3 (R Core Team, 2020) and QGIS 3.10 (QGIS Development Team, 2020).

RESULTS

Spatial Imputation and Initial Vegetation Map

The analysis of 981 NFI plots falling within the study area resulted in eight species having a coverage value higher than 1%: *Quercus ilex* (25%), *Pinus sylvestris* (18%), *Pinus pinaster* (16%), *Pinus nigra* (16%), *Pinus halepensis* (16%), *Quercus pyrenaica* (2%), *Populus nigra* (1%), and *Juniperus oxycedrus* (1%). These species were selected to be included in the study. Besides, two extra species—*Quercus faginea* and *Juniperus communis*—were also included due to their importance in specific environments. *J. communis* covers vast areas above the tree line (cushion shape shrubs) (García, 2001) and *Q. faginea* is also locally abundant.

The analysis of the FM resulted in a classification of active versus inactive cells within the study area. Inactive areas cover 19% of the study area and mainly refer to crops and firebreaks (17.3%). Moreover, active cells were classified as forest and non-forest, which represent 41 and 40% of the study area, respectively.

The intersection of NFI plots and FM polygons defined the species-age assemblage of a total of 789 polygons within the study area. Out of 3,113 polygons with no NFI plot in them, 84% of them were imputed based on equivalent polygons (55% full equivalent, 22% partial equivalent and 7% species equivalent). The remaining 16% of polygons were imputed the species assemblage reported in the FM and the most common age for each of the species.

The use of the VM allowed a more detailed description of active non-forest areas. The analysis of sparse trees in non-forest polygons increased by 4% the surface of the study area where tree species are present. Even though it may seem as a small portion of the landscape, these sparse trees can represent important seed sources when long-term forest dynamics are simulated. Moreover, the VM analysis allowed the inclusion of shrub communities in the landscape's cells, which can affect the shade conditions as well as water availability.

Figure 4 shows the initial vegetation map as a result of combining the presence of forest trees, sparse trees and shrubs communities. Several portions of the landscape are covered by shrublands and *Juniperus* spp., surrounded by a mosaic of *Pinus* spp., *Quercus* spp. and mixed *Pinus-Quercus* forests, with a minor presence of *Populus nigra*.

Calibration of Model Parameters by Means of Site-Level Simulations

Estimating species parameter values was a complex task due to the amount of information sources required to cover all of them. **Table 2** reports the most important parameters required by LANDIS-II and PnET-Succession. A detailed explanation of all parameter values, sources and rationales for their adoption is provided in **Supplementary Table 2**.

Biomass estimations for *P. halepensis*, *P. nigra*, *P. pinaster*, *P. sylvestris*, *Q. ilex*, and *Q. pyrenaica* were compared with results from single-cell simulations initialized with individual species. Results of biomass and photosynthetic rates of species simulated individually on a single cell are reported in the **Supplementary Figures 1–3**. Simulated results are within the range of estimations, although estimations are highly variable among plots.

Among the more than 70 of single-cell simulations that were performed, we chose to show here two representing typical species assemblages of low and high altitude forest types (**Figure 5**). In the low altitude forest type, composed of two pine and two oak species, our results indicated a dominance of *Q. ilex* over *Q. faginea*, *P. halepensis*, and *P. pinaster* (**Figure 5A**). Cohorts of the two latter species were simulated to die by year 140 and 190, respectively, since they approached their longevity (pink and blue lines). *Q. ilex* clearly dominated *Q. faginea* but it did not fully outcompete it. The advantage of *Q. ilex* in this forest community seems to be related to its capacity to start photosynthesizing earlier in spring than the other species (**Figure 5B**).

In the high altitude forest type, *P. sylvestris*, *P. nigra*, and *Q. pyrenaica* coexisted along the simulation, although *P. sylvestris* built higher biomass compared to the other two species (**Figure 5C**). The advantage of *P. sylvestris* was related to its higher photosynthetic rate from the beginning of the season, while *Q. pyrenaica*, being a deciduous species, increased its photosynthesis more gradually after having built foliage biomass (**Figure 5D**). Generally, we found that PnET-Succession

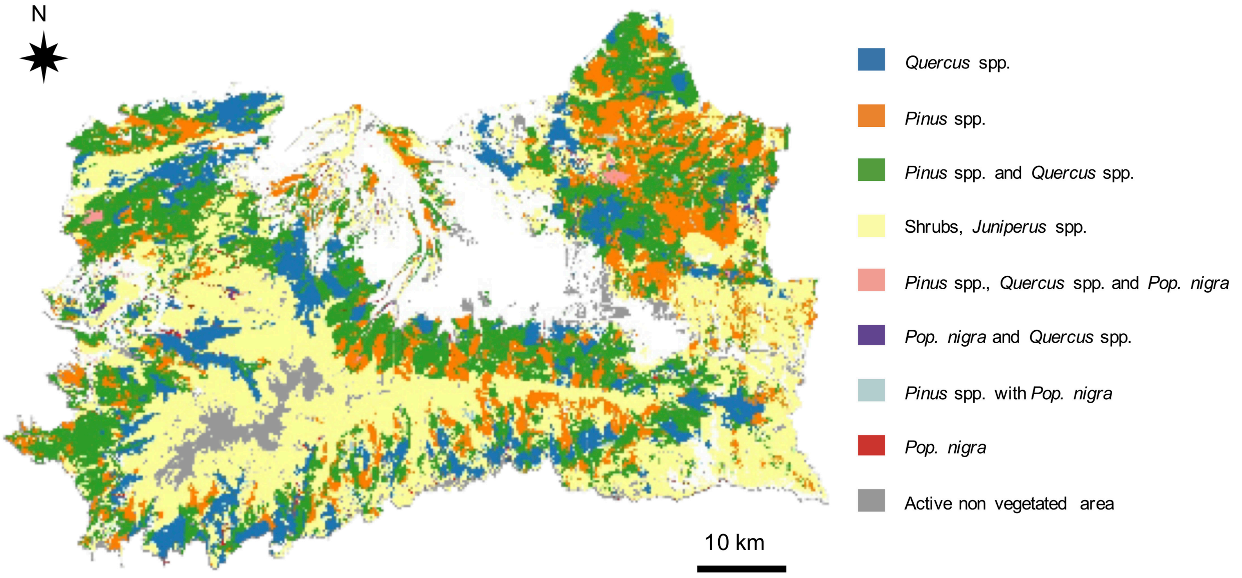

FIGURE 4 | Map of initial vegetation conditions including shrub communities. Each category represents a community dominated by one or more tree species, where shrubs and *Juniperus* spp. may also be present.

TABLE 2 | Species parameter values for LANDIS-II and PnET-Succession.

Species	Long.[1] (years)	FolN[2] (%)	SLW max (g m^{-2})	TOfol[2] (prop. year^{-1})	HalfSat[3] (μmol s^{-1})	H3[3] (m)	H4[3] (m)	PsnT Min[1] (°C)	PsnT Opt[1] (°C)
J. communis	600	0.85	200	0.50	264.5	115	155	3	21
J. oxycedrus	600	0.85	200	0.66	264.5	115	155	3	21
P. halepensis	150	1.19	240	0.34	282.5	118	160	3	26
P. nigra	400	1.02	240	0.26	245.0	115	155	2	23
P. pinaster	200	1.00	240	0.24	245.0	115	155	3	25
P. sylvestris	300	1.33	240	0.36	266.5	110	150	1	20
Pop. nigra	90	2.50	85	1.00	227.0	105	145	2	31
Q. faginea	300	1.92	110	1.00	224.5	115	155	3	26
Q. ilex	600	1.42	150	0.52	199.0	118	160	2	28
Q. pyrenaica	300	1.85	80	1.00	224.5	110	150	1	22
short shrubs	50	0.70	100	0.75	170.0	118	160	2	27
medium shrubs	50	0.75	100	0.75	175.0	118	160	2	27
tall shrubs	50	0.80	100	0.75	180.0	118	160	2	27

[1] *Serrada et al. (2008); Valladares Conde (2005)*, Montoya Oliver and Mesón García (2004). [2] *Kattge et al. (2020)* [3] *Niinemets and Valladares (2006); Pausas et al. (2004). FolN: Nitrogen foliar content; SLWmax: Maximum specific leaf weight at the top of canopy; Tofol: foliage turnover; HalfSat: Photosynthesis half saturation light level; H3, H4: Water stress parameters according to* Feddes et al. (1978)*; PsnTMin, PsnTOpt: photosynthesis minimum and optimum average daytime temperature (*Gustafson and Miranda, 2019*).*

reproduced reasonably well the bimodal growth patterns of Mediterranean tree species, mostly occurring during spring and fall instead of summer which is characterized by a lack of precipitations.

Landscape-Level Simulation

Both simulations with and without shrubs showed a trend to increase the average biomass of all tree species during the first years of the simulation and stabilization afterwards (**Figure 6**). In the simulation including shrubs, this increase was slower than in the simulation without shrubs, with a faster increase in the first 50 years. In both simulations the total average biomass at stabilization was around 100 tn ha^{-1}.

We found differences among species in terms of simulated biomass growth. Among pine species, *P. sylvestris* and *P. nigra* were those with a higher increase of average biomass in both simulations. Biomass of *P. halepensis* and *P. pinaster* increased during the first 50 years, followed by a decline and disappearance from the landscape toward the last decades of the simulation. Among oaks, biomass of *Q. ilex* increased notably, while *Q. pyrenaica* increased at lower rates and stabilized after about 100 years. Biomass of *Q. faginea* and *Pop. nigra* had similar trends, increasing slightly in the early years and declining afterwards, but still maintaining presence at low levels of biomass. Junipers slightly increased their biomass during the first 30 years and then strongly declined. These species show similar patterns in both simulations, but under the simulation without shrubs we observe a steeper increase of biomass during the first years. Shrub communities increased their average biomass during the first 40 years and declined afterwards.

Initial total landscape biomass (time 0) was similar in both simulations since shrub communities accounted for low levels of biomass (5.1% of total biomass). At time 50, the area with high biomass is wider in the simulation without shrubs (**Figure 7**). This pattern was observed at time 100 too, although the difference between the two simulations was smaller (see total biomass at each time step in **Figure 7**). At time 150 and 200, both simulations showed a similar quantity and distribution of the biomass across the landscape, with slightly higher values of biomass in the simulation without shrubs than in the one with shrubs. The biomass distribution within the study area followed the altitudinal gradient, with higher biomass found at medium elevations, specially at time step 150. At the beginning of the simulation, areas at high elevation (above c.a 2,000 m a.s.l.) show the smallest values of biomass relatively to the rest of the study area. This pattern remained by the end of the simulation in both cases.

DISCUSSION

We provide detailed step-by-step example to initialize, calibrate and set up a forest landscape model. Our work could help other potential users to better understand what is required to start applying such models. Thus, our fully documented methodological process represents a step forward toward the transparent application of forest landscape models in regions without prior application. We also made available a high-resolution map of vegetation conditions and calibration details for a large mountainous landscape in the European Mediterranean area, together with the input data and scripts used in the process. Our landscape level simulations reveal distinct dynamics among species according to their competitive potential and simulated intra-annual growth. These results also indicate that shrub communities shall be considered in forest landscape models as they have the potential to influence forest dynamics by delaying growth and expansion of tree species in Mediterranean ecosystems.

Spatial Imputation and Initial Vegetation Conditions

The selection of species to be included in modelling studies is typically done by analysing data from terrestrial plot

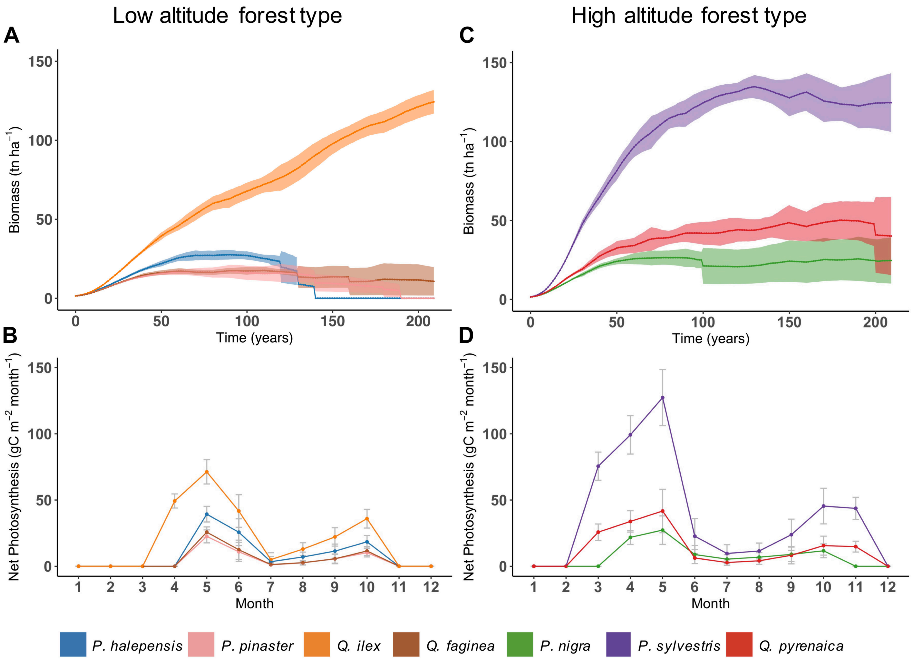

FIGURE 5 | Mean simulated annual total biomass (wood, roots and foliage) **(A,C)** and monthly net photosynthesis **(B,D)** for the two chosen forest types. Shaded area refers to standard deviation. Values of net photosynthesis are averages between years 50–75, with error bars indicating standard deviation. Note that lines connecting the points serve for illustrative purposes only, since PnET-Succession simulates photosynthesis at monthly time scale (not daily).

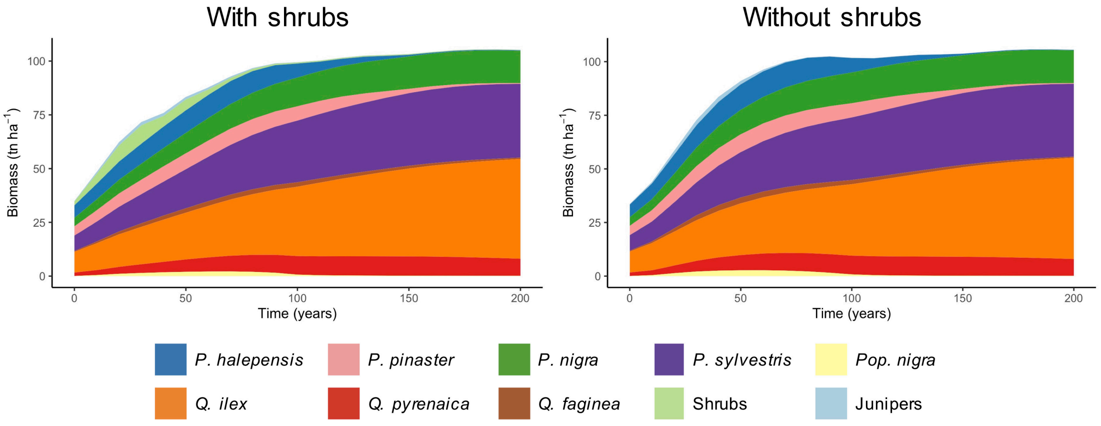

FIGURE 6 | Average biomass of species through time for the whole landscape. Note that Junipers (*J. communis* and *J. oxycedrus*) and shrub communities (short, medium, and tall) have been grouped together.

measurements such as forest inventories (e.g., Wang et al., 2019). However, for certain ecosystems, limiting this inspection to forest inventories has some disadvantages. Forest inventory data commonly report information on tree species, neglecting important functional groups (in our case, *J. communis* and shrubs communities). Moreover, selection is usually based on variables such as basal area or stand coverage. This selection may result in the exclusion of species that may not be abundant at the landscape level but whose presence is crucial at the local scale. For example, *Q. faginea* would have been initially excluded from our study since its coverage falls below the 1% of the study area (0.03%). However, this species is found at high abundance in some locations and has a higher susceptibility to summer drought than *Q. ilex*. Therefore, the dynamics and distribution of *Q. faginea* are expected to be highly affected by climate change (Quero et al., 2006). Similarly, *J. communis* was included due to its importance in areas above the treeline. In these areas, *J. communis* is susceptible to interact with tree species under climate change conditions by limiting or facilitating uphill migration of tree species. Therefore, even though forest inventory data are important resources for generating inputs for FLMs, we recommend combining such datasets with other information

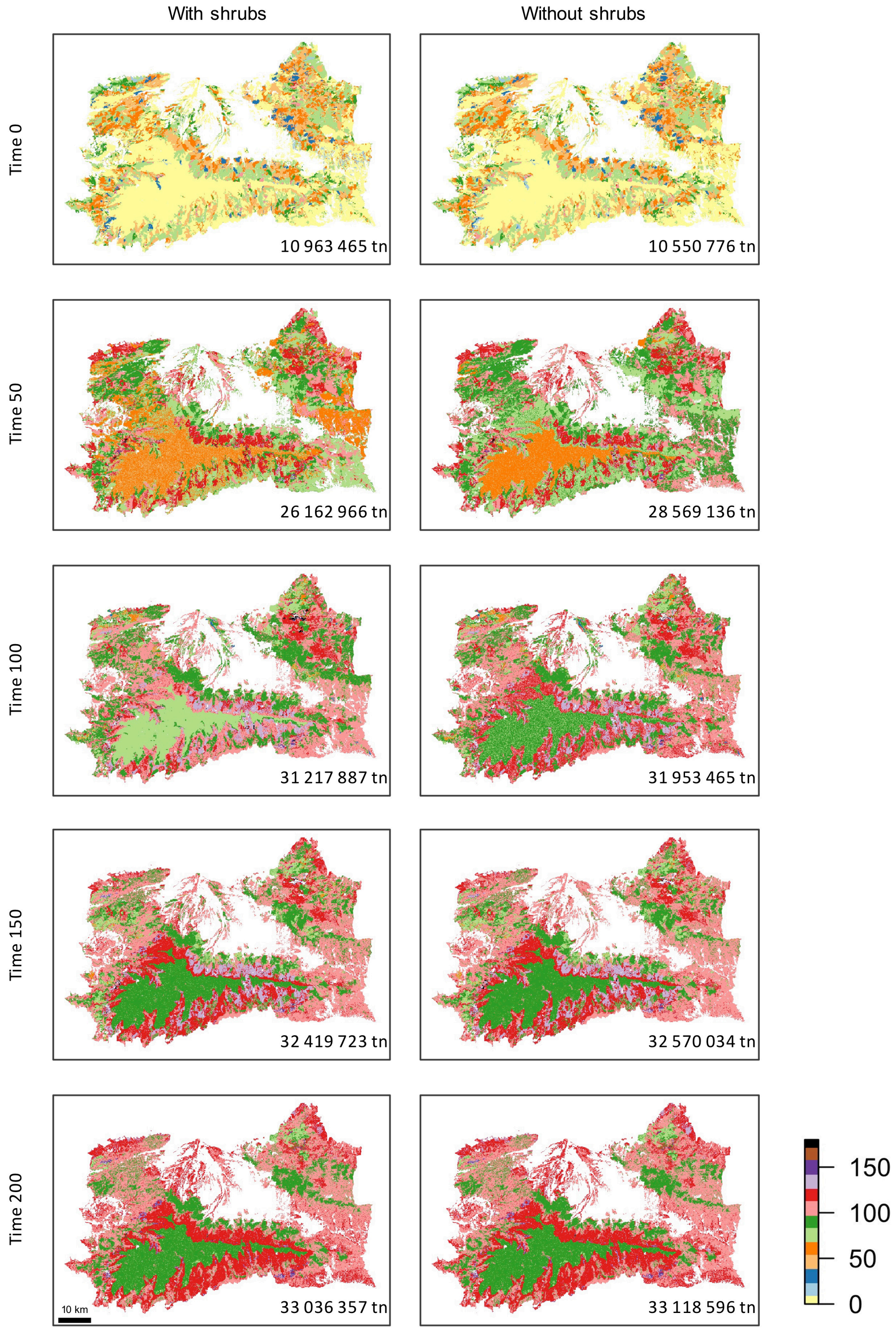

FIGURE 7 | Total aboveground biomass (tn ha-1) at years 0, 50, 100, 150, and 200 for the two simulations, as indicated in the scale bar on the right. Number in each panel indicates the total aboveground biomass (Tg) for the whole landscape at each time step.

sources (e.g., vegetation maps, local studies) according to the forest ecosystem under consideration and study focus—in our case, climate change applications—. Considering factors such as relevance in specific habitats or cultural importance (e.g., Lucash et al., 2019) may result in inclusion or exclusion of some species.

Our method, which combined multiple information sources allows the inclusion of fine-coarse information such as the presence of sparse trees and shrub communities. The inclusion of sparse trees in the initial vegetation map is important in the Mediterranean mountains, since we simulate succession in pine plantations, artificially created stands where regeneration is highly affected by seed dispersal from adjacent patches of native vegetation (González-Moreno et al., 2011; Navarro-González et al., 2013). Although shrubs' biomass is generally low, they can shade the forest floor and therefore influence simulated light and soil water dynamics, as well as affect establishment (further discussion below). Moreover, shrubs play a key role in other processes such as fire dynamics due to their role as fuel in forest fires (Syphard et al., 2006).

In this study, we have used a categorical methodology for the spatial imputation, contrary to commonly used methods based on geographic or data space distance (e.g., Wilson et al., 2012; Ohmann et al., 2014; Duveneck et al., 2015). Our study area is a highly anthropized mosaic of different land uses and management regimes, and therefore imputation based solely on distance might not have been an appropriate criterion, as indicated by Duveneck et al. (2015). For example, the most common forest type in our landscape, pine plantations, are the result of past forestry policies which were applied almost simultaneously all over the region. Therefore, a high similarity is expected between stands, regardless of the physical distance between them. This is a common situation in other Mediterranean ecosystems (European Environmental Agency [EEA], 2016), and therefore this approach could also be used in such cases.

The uncertainties of this methodology are inherently related to the uncertainties of the information sources. Besides, an additional source of uncertainty in the initial vegetation conditions map is related to the assignation of age to cohorts. Tree age data is rarely available at single-tree level in forest datasets, as reliable tree age estimations are resource-consuming and often invasive (Fazan et al., 2012; Rohner et al., 2013). Thus, modellers are commonly forced to assign each tree (or cohort) to an age class inferring it from available measurements (e.g., diameter, height, average stand age; Abrams, 1985; Rozas, 2003). In the case of LANDIS-II, a cohort's age determines simulated biomass, which in turn influences light and water availability at cell-level. Therefore, assumptions in the age assignation process may not be so relevant as long as the relative difference between species reflects real conditions. Considering this, we created correspondence rules between tree age and diameter and height for each of the simulated species and age classes. Thus, the growth pattern assigned to each of the species is relative to the other species, reflecting the differential access to water and light by each species-age. This methodology could be further improved by considering additional local yield tables and observations. Nevertheless, by documenting such correspondence rules the model inputs generation is significantly more transparent and reproducible than other LANDIS-II studies (e.g., Mina et al., 2021).

Our goal was to increase the reproducibility of model input generation by ensuring high transparency and detail in the process description. The methodology presented in this study does not necessarily introduce new methods compared to previous studies (e.g., He et al., 1998) but rather it highlights all aspects of the process, which we believe could be of great benefit for beginner modellers to set up applications in new landscapes. Firstly, considering multiple information sources at plot- and polygon-level may be necessary. In our case, multiple vegetation maps were required to consider forested areas, dispersed trees and shrub communities. Secondly, the collected information likely requires processing and transformation, which may introduce assumptions (e.g., age assignation). Thirdly, the selection of the appropriate spatial imputation method should consider the study area characteristics (e.g., coetaneous patches of pine plantations) and available information.

Calibration of Model Parameters and Site-Level Simulations

Calibration of model parameters was performed by running simulations and testing long-term species dynamics and competitive interactions at site-level. The obtained results were iteratively assessed to adjust parameter values until the species showed their expected growing patterns. Experiments at site scale using landscape models have also been used before to analyse the influence of different factors on model outputs by avoiding the high complexity resulting from large landscapes simulations (Gustafson et al., 2017, 2018).

During the calibration phase, species parameters were adjusted to ensure that the model simulates realistic species biomass estimations. Species biomass data derived from field observations (e.g., growth-and-yield sites, inventories and permanent plots) are usually highly variable as they differ depending on multiple factors (e.g., location, stand development, site index). Moreover, biomass values often have a high degree of uncertainty, since they are commonly estimated based on general allometric equations from other measured variables (e.g., diameter, height, wood density) (Forrester et al., 2017). Therefore, such comparisons should be interpreted with caution. In this study we used such estimations to ensure that the simulated biomass falls within realistic ranges rather than adjusting parameter values to match the exact values (see **Supplementary Figure 3**). With this approach, we calibrated the most relevant species for this study (*P. halepensis*, *P. nigra*, *P. pinaster*, *P. sylvestris*, *Q. ilex*, and *Q. pyrenaica*).

Besides, we review here other studies which provide biomass estimations for some of our species. The dynamics of *Q. pyrenaica* stands have been studied by Santa Regina (2000), who estimated its biomass in four plots in north-western Spain. Our simulations have a high degree of agreement for foliage biomass, while certain overestimation remains for wood biomass. This difference, nevertheless, can be justified as in the plots studied by Santa Regina (2000) the presence of shrubs could be reducing *Q. pyrenaica* productivity. Río and Sterba (2009) studied the productivity of mixed stands of *P. sylvestris* and *Q. pyrenaica*. They found that although *P. sylvestris* is less productive when growing in mixed stands, the reduction in productivity is smaller than the reduction in occupied area. Accordingly, our simulations show a decrease in productivity of *P. sylvestris* when growing together with other species such as *Q. pyrenaica*, but it remains as a highly productive species.

Other methodologies have been applied for model calibration (e.g., Duveneck et al., 2017; Cassell et al., 2019; Mina et al., 2021). As an example, Duveneck et al. (2017) used data from flux towers within New England (United States) to calibrate PnET parameters. The application of some methodologies over others usually responds to the availability of data for the simulated area. In this sense, the lack of available biomass accumulation curves limited the application of more exhaustive calibration methodologies. Our calibration could therefore be improved if additional data sets become available, such as high-resolution biomass measurements or growth rates based on flux towers measurements.

Our results clearly show that PnET-Succession reproduces the characteristic bimodal growth observed in Mediterranean species (Larcher, 2000). This growth pattern is the result of dry summer conditions, which impose a limitation for growth to numerous species. Thus, Mediterranean species often show two peaks of productivity through the year, in late spring and fall (Camarero et al., 2010; Gutiérrez et al., 2011). *Q. ilex* bimodal growth has been studied in detail by Gutiérrez et al. (2011). They report asymmetrical radial increment peaks in May and September for a coastal location in north-eastern Spain, with high plasticity dependent on climatic conditions and most of the growth occurring during the first growing phase. The simulated growth of *Q. ilex* reproduces this pattern both when the species is simulated growing alone or in association with other species. Modelling such growth interannual variability remains a challenge for forest models, for which improvements are proposed to include such processes (Mina et al., 2016). In the case of PnET-Succession, the high temporal resolution (monthly scale) and mechanistic approach allows reproducing such patterns and therefore makes this model highly suitable for applications in Mediterranean systems.

Distinct dynamics were observed according to the species competitive potential and simulated intra-annual growth. Species leaf habits is one of the factors influencing species competitiveness. Among the simulated species considered in this study, only *Q. faginea*, *Q. pyrenaica,* and *Pop. nigra* are deciduous while all other species are evergreen. Deciduous species have a higher potential for net photosynthesis in PnET-Succession (De Bruijn et al., 2014) but they are generally less shade and drought tolerant and need to spend more energy in building foliage biomass than evergreen species. The trade-off between benefits and losses caused by different leaf habits explains the coexistence of species with different strategies (Escudero et al., 2017), as it is clearly observed in the growth patterns of *Q. ilex* and *Q. faginea*.

The calibration of non-tree species—junipers and shrubs—was particularly challenging. Although we believe including both junipers (*J. communis* and *J. oxycedrus*) in the initial vegetation map was important in our target ecosystem, the lack of information and reliable data on these species limited a finer calibration. As a result, both species were assigned with very similar parameter values, their simulated behaviour was almost identical and thus they were grouped together. In the case of shrub communities, since they represent functional groups rather than single species, calibration was achieved mostly by extrapolation, comparison with similar studies (e.g., Cassell et al., 2019) and tuning according to expected simulated behaviour relatively to tree species. Their ecological role, for the sake of this study, was mainly as shade providers and competitors for establishment, and therefore our main objective in this sense has been oriented to ensure survival and growth beneath the tree canopy. For further applications where the role of non-tree species is more relevant (e.g., fire dynamics, facilitation), their parameterization shall be improved to better reflect differences between shrubs species or functional types.

Landscape-Level Simulation

Our results show that the shrub communities influence the forest dynamics by delaying the growth and expansion of tree species. In our simulations, we found that shrubs reduce tree species establishment. However, shrubs are known to serve as nurse plants, favouring tree seedling growth by amelioration of adverse dry conditions and protection against herbivory (Castro et al., 2004; Gómez-Aparicio et al., 2005; Prévosto et al., 2020).

Modelling the role of understory in forest succession has also been investigated by Thrippleton et al. (2016) with the LandClim model. Similarly to our results, they found delayed establishment of trees when herbaceous understory was abundant. Moreover, both Thrippleton et al. (2016) and our results show that shrubs are unable to establish under dense canopies, eventually declining and even disappearing from the landscape. This agrees with field observations: weak regeneration of shrubs and tree species under dense canopies biomass even when the sapling bank is present (Mendoza Sagrera, 2008). Also, the decline of shrubs in our simulations was likely not realistic, since small-scale perturbations creating patches where light availability increases and shrub communities thrive (e.g., due to fire, Leverkus et al., 2014) were not included in our experiment. However, the interactions occurring between trees and non-trees species and abiotic factors such as fire justify the need to include these communities in these kinds of applications (e.g., Loudermilk et al., 2013).

The increase of forest biomass observed in our simulations at landscape level was somewhat expected, since we did not include harvesting or natural perturbations (e.g., fire, pest outbreaks). Additionally, simulations were run with the same climate inputs used for calibration (baseline climate), thus potential impacts of changing climate (e.g., higher temperatures, extended drought, CO_2 fertilization) were not considered. At medium altitudes, where most forest stands are found, the growing tendency in biomass was likely a result of pine plantations being relatively young at the beginning of our simulations. Pine plantations in Sierra Nevada and Sierra de Baza have been showing in latest years signs of decay as a result of increasing drought stress and intense interspecific competition (e.g., Sánchez-Salguero et al., 2010, 2012a,b). These mortality events could not be observed in our study since increasing drought was not considered in our climate inputs.

Even though there was a general growing trend in biomass, the dynamics among species differed. *P. halepensis* and *P. pinaster* biomass declined as they approached longevity and seemed unable to regenerate beneath the canopy, while *Q. ilex* kept growing. *P. sylvestris* and *P. nigra*, however, were able to coexist with *Q. pyrenaica*, and therefore they remained present in the landscape and even increased their biomass through time. Factors influencing the establishment of pines and oaks in Sierra Nevada and Sierra de Baza have been profusely studied (e.g., Mendoza et al., 2009a,b; Gómez-Aparicio et al., 2009; Herrero Méndez, 2012), showing limitations to recruitment mainly due to high post-dispersal seed predation rates and dry summer conditions. Our simulations also reflect poor establishment of some species, probably related to dry summer conditions and species shade tolerances being higher than in reality. In the case of junipers, they are probably limited by a short growing season due to their minimum and optimal photosynthesis temperatures and low biomass levels which prevents them from accessing light and water.

Modelling Aspects, Limitations and Future Research

The selection of the model used in this study was based on the flexibility and potentiality of this model. LANDIS-II is a well-documented model supported by an active scientific community, which ensures help and support for new modellers. Moreover, several model extensions are available for a wide variety of future applications (e.g., harvest, fire, wind, biological agents). To simulate forest dynamics, we specifically chose PnET-Succession as it simulates ecological succession with a more mechanistic approach than past extensions. As mentioned above, by simulating growth at monthly resolution, intra-annual growth variability can be properly captured, which is of crucial importance for simulations under climate change and applications in the Mediterranean area.

However, the model is still limited in some aspects which could be further improved. First, the need to provide cohort age certainly adds uncertainty to the initial conditions. Given that PnET-Succession uses age to determine initial cohorts' biomass, other variables such as diameter, basal area or height—often available from field observations—could be used instead, reducing uncertainty. Even though latest PnET-Succession version allows providing initial biomass, this variable often needs to be estimated with allometric equations. Besides, since cohort's biomass is highly dependent on tree density, tree density could also be incorporated into the model in some way to improve model representation of competition effects (but see Wang et al., 2014). This would be especially relevant in ecosystems such as pine plantations, where extremely high tree densities cause inter- and intraspecific competition to be an important factor explaining vegetation dynamics.

The grouping of cells into homogeneous climatic conditions (ecoregions) prevents a fine-coarse capturing of topographic influence on climate, which is a relevant issue in mountainous areas. The definition of such ecoregions is commonly done by clustering average climate information to define homogeneous climate regions. These homogeneous regions are assigned with climate time series typically obtained as the average among all cells within the ecoregion. By doing so, the influence of topography on climate is not well captured and extreme conditions, such as the ones found in the mountain peaks, are smoothed down. In our case, the increase in biomass at high altitudes was probably due to the fact that temperature was not limiting enough the establishment of species beyond their natural treeline. In a large model comparison study, Petter et al. (2020) also found that no clear treeline emerged from LANDIS-II simulations, in which the area above vegetation was binned into a single ecoregion, compared to other models in which each cell has its own climatic condition. The use of continuous maps for climate conditions (i.e., each cell assigned its own environmental and climate condition) could improve how PnET-Succession simulates the effect of topography on climate and thus on vegetation changes. Other forest landscape models developed for mountain environments already make use of continuous maps explicitly accounting for topography (e.g., LandClim; Schumacher et al. (2004)). This feature is currently under development for LANDIS-II, which was initially designed to efficiently simulate large landscapes (more than 1 million interacting cells).

Even considering the above-mentioned limitations, the model showed a great potential for a wide range of applications in the Mediterranean area. The transparent initialization of the model and the documented calibration can serve as a guide for new users, encouraging the application of forest landscape models. Besides, testing different initialization data has allowed us to confirm the importance of shrub communities in the forest dynamics within the study region. Further experiments will analyse the vegetation dynamics under natural perturbations such as fire or defoliators. Moreover, the inclusion of climate change and silviculture will allow us to explore future forest dynamics, and, by doing so, deliver management recommendations to promote ecosystems adaptation to global change.

DATA AVAILABILITY STATEMENT

The datasets and scripts generated for this study can be found in https://doi.org/10.5281/zenodo.4584475.

AUTHOR CONTRIBUTIONS

MS-M: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, software, visualization,

writing – original draft, writing, review, and editing. MM: conceptualization, methodology, supervision, validation, writing, review, and editing. PS: formal analysis, writing, review, and editing. RN-C and JQ: validation, writing, review, and editing. FB-G: conceptualization, resources, writing, review, editing, supervision, methodology, and funding acquisition. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.653393/full#supplementary-material

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Forecasting the Cumulative Effects of Multiple Stressors on Breeding Habitat for a Steeply Declining Aerial Insectivorous Songbird, the Olive-sided Flycatcher (*Contopus cooperi*)

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To halt ongoing loss in biodiversity, there is a need for landscape-level management recommendations that address cumulative impacts of anthropogenic and natural disturbances on wildlife habitat. We examined the cumulative effects of logging, roads, land-use change, fire, and bark beetle outbreaks on future habitat for olive-sided flycatcher (*Contopus cooperi*), a steeply declining aerial insectivorous songbird, in Canada's western boreal forest. To predict the occurrence of olive-sided flycatcher we developed a suite of habitat suitability models using point count surveys (1997–2011) spatially- and temporally-matched with forest inventory data. Flycatcher occurrence was positively associated with small (∼10 ha) 10- to 20-year-old clearcuts, and with 10–100% tree mortality due to mountain pine beetle (*Dendroctonus ponderosae*) outbreaks, but we found no association with roads or distance to water. We used the parameter estimates from the best-fit habitat suitability models to inform spatially explicit state-and-transition simulation models to project change in habitat availability from 2020 to 2050 under six alternative scenarios (three management × two fire alternatives). The simulation models projected that the cumulative effects of land use conversion, forest harvesting, and fire will reduce the area of olive-sided flycatcher habitat by 16–18% under Business As Usual management scenarios and by 11–13% under scenarios that include protection of 30% of the land base. Scenarios limiting the size of all clearcuts to $\leq$10 ha resulted in a median habitat loss of 4–6%, but projections were highly variable. Under all three management alternatives, a 50% increase in fire frequency (expected due to climate change) exacerbated habitat loss. The projected losses of habitat in western boreal forest, even with an increase in protected areas, imply that reversing the ongoing population declines of olive-sided flycatcher and other migratory birds will require attention to forest management beyond protected areas. Further work should examine the effects of multiple stressors on the demographic mechanisms driving change in aerial insectivore populations, including stressors on the wintering grounds in South America, and should aim to adapt the design of protected areas and forest management policies to projected climate-driven increases in the size and frequency of wildfires.

Keywords: aerial insectivore, bark beetle outbreak, clearcut logging, climate change, cumulative effects, habitat suitability, landscape simulation, wildfire

INTRODUCTION

Over the past half century, steep population declines in terrestrial birds have coincided with changes in climate and land-use patterns across North America (Butchart et al., 2010; Northrup et al., 2019). Climate-driven increases in the frequency and intensity of natural disturbance events, such as fire and insect outbreaks, may compound or ameliorate the negative effects of human-induced habitat loss on bird populations (Vitousek, 1994; Betts et al., 2017). Over the 50-year period from 1966 to 2006, birds that feed on flying insects, or aerial insectivores, showed the strongest declines of any songbird group in North America, with long-distance migrants (to South America) showing the most acute negative trends (Nebel et al., 2010; Smith et al., 2015; Rosenberg et al., 2019). To halt these widespread declines, we need policies that identify and minimize loss of critical habitat, account for climate change, and fully integrate biodiversity goals (Butchart et al., 2010; Favaro et al., 2014; Nebel et al., 2020). Such policies can be developed quantitatively by using avian habitat models in landscape simulations to project future habitat conditions under a range of land-use scenarios and natural disturbance events (Mahon et al., 2014).

There is strong evidence that natural and anthropogenic disturbances drive changes in bird populations, especially in systems that experience large-scale natural disturbance events, such as boreal and hemi-boreal forests (Drapeau et al., 2000; Schmiegelow and Mönkkönen, 2002; Norris and Martin, 2010). It has been hypothesized that boreal birds are adapted to large-scale natural disturbances, such as insect outbreaks and fire, making them more resilient to human-caused fragmentation (e.g., forest harvesting, roads, and/or oil and gas pipelines) relative to species occupying habitats with less frequent natural disturbances (Schmiegelow and Mönkkönen, 2002; Schmiegelow and Villard, 2009). Indeed, some species and even entire communities show positive population-level responses to some levels of forest harvesting in the boreal and hemi-boreal forests of Canada (Lemelin et al., 2007; Drever and Martin, 2010). However, recent evidence suggests that forest harvesting, in the presence of other disturbances such as those associated with oil and gas extraction, can have compounding negative effects for many boreal bird species (Mahon et al., 2019). Furthermore, climate change is likely to exacerbate negative population-level responses to harvesting in boreal forests (Cadieux et al., 2020). In addition to current and significant industrial activity in northern and western forests, climate change is projected to increase the frequency and severity of fires and insect outbreaks (Wootton, 2010; Cohen et al., 2019). In British Columbia, the area burned annually by wildfires was three times higher in 2017 and 2018 compared with the previous decade (Government of British Columbia, 2019a), after years of major outbreaks of mountain pine beetle (*Dendroctonus ponderosae*). Thus, to understand and reverse population declines of birds breeding in severely climate-impacted western boreal forests, there is a need to evaluate the cumulative, additive, and/or interactive effects of multiple natural and human-induced disturbances (cumulative effects; Schmiegelow and Villard, 2009; Duinker et al., 2012; Mahon et al., 2014).

To assess cumulative effects of multiple disturbances on boreal migratory birds, Mahon et al. (2014) modeled future habitat supply and population size for a suite of species under various landscape change scenarios. They found that population objectives set for these species (Government of Canada, 2013) would not be met under the current climate and current management prescriptions. The study provided a robust framework for assessing cumulative effects, developed habitat-based objectives required to restore or maintain populations, and highlighted the need to incorporate population-specific habitat requirements in regional cumulative effects assessment processes to simulate future habitat availability in other parts of the boreal forest where habitat associations likely differ.

Here, we assess the cumulative effects of multiple stressors on habitat suitability for the steeply declining olive-sided flycatcher (*Contopus cooperi*), across multiple spatial and temporal scales in boreal forest in the southern Peace River region of northeastern British Columbia (**Supplementary Figure 1**). Pressed against the east side of the northern Rocky Mountains (North America's continental divide), the southern Peace River region is part of a major avian migration route and home to one of Canada's most diverse avian assemblages (Campbell et al., 1997), but is under intense development pressure from hydroelectric dams, mining, agriculture, forestry, and oil and gas production (Nitschke, 2008). It therefore represents an important location to examine the cumulative effects of multiple stressors on avian habitat. We chose to study the olive-sided flycatcher because it is a broadly distributed, elevational generalist, aerial insectivorous bird species, undergoing steep population declines across the Americas, including a decline of approximately 70% in Canada between 1970 and 2017 (Smith et al., 2019). Olive-sided flycatchers are typically associated with small forest gaps created by fire and/or tree mortality in disturbance-driven forested ecosystems, and ∼40% of all individuals that occur in Canada breed in British Columbia (Haché et al., 2014; Altman and Sallabanks, 2020; Boreal Avian Modelling Project, 2020).

Our objective was to assess the cumulative effects of multiple human-induced and natural environmental stressors on olive-sided flycatchers, using a stepwise approach. First, we built Bayesian generalized linear mixed-effects models that predicted occurrence of flycatchers in point count surveys from spatially- and temporally-matched forest inventory data, to determine how multiple environmental factors influence habitat suitability. Second, we used spatially explicit state-and-transition simulation models to project future land use, forest harvesting and regrowth, fires, and insect outbreaks, under six scenarios representing the combination of three management alternatives and two fire alternatives (**Table 1**). The management alternatives included (1) Business As Usual, (2) Increased Protected Area (protect from harvest 30% of the land base by adding protection to publicly managed forest with a stand older than 75 years and affected by mountain pine beetle), and (3) Reduced Cutblock Size (restrict timing and size of cutblocks to match optimal habitat conditions as defined by habitat suitability models). The fire alternatives were (1) Baseline Fire (current conditions) and (2) Increased Fire [fire frequency increased by 50% compared to current conditions, following projections for British Columbia under the Intergovernmental Panel on Climate Change (IPCC)-A2 emissions scenario; Wootton, 2010]. Third, we used our best-supported habitat suitability models to predict habitat suitability for olive-sided flycatcher at baseline (current conditions) and under each future scenario. Based on previous research (Haché et al., 2014; Bale et al., 2019; Westwood et al., 2019), we expected that olive-sided flycatcher densities would be highest in forest stands with small openings, such as wetlands and roads, but show thresholds in response to disturbances such that larger clearcuts would have negative effects on abundance. We further expected that land cover change (from forest to other uses, e.g., cropland or urban), clearcut logging, and fire would exacerbate habitat loss over the coming decades under Business As Usual scenarios, but that conservation measures represented in the Increased Protected Area and Reduced Cutblock Size scenarios would mitigate habitat loss.

MATERIALS AND METHODS

Study Area

The southern Peace River region of northeastern British Columbia (Dawson Creek Timber Supply Area) covers about 2.6 million ha of boreal forest between the boreal plains in the east and the central Canadian Rocky Mountains in the west (Government of British Columbia, 2013; **Supplementary Figure 1**). The climate is characterized by cold, prolonged winters and warm, short summers, and the area includes four biogeoclimatic zones: Boreal White and Black Spruce, Engelmann Spruce-Subalpine Fir, Sub-Boreal Spruce, and Alpine Tundra (Pojar et al., 1987). The primary tree species are white spruce (*Picea glauca*), black spruce (*Picea mariana*), lodgepole pine (*Pinus contorta*), subalpine-fir (*Abies lasiocarpa*), trembling aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*); mixed coniferous/broadleaf stands are common. The mean allowable annual cut within the 758,335 ha available for harvest in the Dawson Creek Timber Supply Area was 1.81 million m^3 for the study period between 1998 and 2011 (Government of British Columbia, 2014).

Olive-sided Flycatcher Data

We acquired point count datasets from the Breeding Bird Atlas compiled by Birds Canada (2008–2011; BC Breeding Bird Atlas, 2008) and from the Wildlife Species Inventory provided by the BC Ministry of Environment and Climate Change Strategy (1993–2011; Government of British Columbia, 2020a). We included only point counts conducted by a stationary observer over a fixed length of time and geo-referenced within the Dawson Creek Timber Supply Area between 54.5 degrees and 56.5 degrees latitude (**Supplementary Figure 1**). All point counts were conducted in forested ecosystems (**Supplementary Table 1**). Some points were missing the spatial coordinates of the observer's location, but included coordinates for each bird detected. In these cases, we took the centroid of all bird coordinates as the point count location. Combining datasets resulted in some repeated points (same day, location within two point count radii), and these were removed by eliminating the corresponding Breeding Bird Atlas points. Because point count surveys were designed to capture abundance and diversity of multiple species of resident and migratory birds, many were conducted before olive-sided flycatchers arrived from wintering grounds or after their main period of vocal activity. We therefore constrained the dataset to points between 31 May (earliest detection of olive-sided flycatcher) and 29 June (1 day after penultimate detection of 28 June; latest detection was 19 July) for all years (**Supplementary Figure 2**).

All point counts were conducted between 0400 and 1000 h, but protocols varied with respect to point count radii (80 m, 100 m, 200 m, or unlimited distance) and duration (3, 5, 8, or 10 min per point count). The probability of detecting birds during any given breeding bird survey (detectability) is the

TABLE 1 | Landscape simulation scenarios applied to current landscape in the southern Peace River region of British Columbia, Canada.

Scenario	Management	Fire probability
Business As Usual, Baseline Fire	Cut size and land conversion follow historic rates	Historic rates
Business As Usual, Increased Fire	Cut size and land conversion follow historic rates	50% increase
Increased Protected Area, Baseline Fire	Protect 30% of land base >75 years old and affected by mountain pine beetle	Historic rates
Increased Protected Area, Increased Fire	Protect 30% of land base >75 years old and affected by mountain pine beetle	50% increase
Reduced Cutblock Size, Baseline Fire	Restrict clearcut size to ≤10 ha	Historic rates
Reduced Cutblock Size, Increased Fire	Restrict clearcut size to ≤10 ha	50% increase

product of the singing rate of individuals (availability) and the probability of the observer receiving the cue (perceptibility; Diefenbach et al., 2007). We calculated an offset correction factor (QPAD) by applying previously published estimates of singing rate and effective detection radius for olive-sided flycatcher from a Canada-wide study (Boreal Avian Modelling Project, 2020) to correct our occurrence data according to the survey duration and radius of each count in the R package "qpad" (Sólymos et al., 2013; Sólymos, 2016). We calculated the probability of detection, $p = 0.788$, and the effective detection radius, EDR = 121 m. Singing rate for this species can decline during the day (i.e., from dawn to afternoon) and as breeding stage advances (i.e., from female arrival through nest building and care of young; Wright, 1997). It is possible that some individuals were missed due to point counts occurring late in the morning or after pair formation; however, we were unable to account for these factors due to limitations in the data.

Land Cover Data

Georeferenced land cover data were acquired from multiple sources and matched to point count locations using the North American Datum 1983 and BC Environment Albers coordinate reference system, in the program ArcGIS (Environmental Systems Research Institute [ESRI], 2015). We used data from the Freshwater Atlas of British Columbia (Government of British Columbia, 2016d) to determine the planar distance from each point count location to the nearest body of water (wetland, lake, or river). We used annual aerial insect surveys (Government of British Columbia, 2020b) to determine the presence and severity of mountain pine beetle infestation at each point count location: zero if no recently killed trees were detected in the polygon, light if 0–10% of trees were recently killed; moderate to very severe if 11–100% of trees were killed (severity classifications; Government of British Columbia, 2019b). We used data from the British Columbia Digital Road Atlas (Government of British Columbia, 2016c) to determine the type of any roads within a 50-m radius of the point count (paved or unpaved road vs. no roads). Trails were not considered as roads. Using British Columbia forest cutblock and fire perimeter data (Government of British Columbia, 2016a,b), we determined size and time since cutting or fire for any cutblock or burned area occurring within a 50-m radius of the point count. Median cutblock size where point counts were conducted was 47 ha and cuts occurred a median of 6 years prior to the point count survey. We had no point counts in recent burns (<15 years old), and thus we were unable to model the direct effects of fire on habitat suitability. Therefore, we assumed that olive-sided flycatchers would respond to forest gaps created by fire in the same way as they responded to gaps created by clearcuts (Altman and Sallabanks, 2020; see *Simulation of Future Habitat*, below).

Habitat Suitability Models

We analyzed data following the protocol described in Zuur et al. (2010). Since olive-sided flycatcher populations likely vary year-to-year at a regional scale, we included year as a random effect in habitat suitability models. All predictor variables were checked for pairwise correlations before including in the same models, and no pairs exceeded a Spearman's rank correlation coefficient of 0.5. Habitat suitability models were created and evaluated in RStudio running R version 3.5.3 (R Core Team, 2019). We applied the QPAD offset correction factor to the olive-sided flycatcher occurrence data, so that the response variables produced the probability of occurrence per hectare, while accounting for detection error. Although we had a large sample of point counts ($n = 1134$), detections of olive-sided flycatcher were sparse ($n = 43$), and initial attempts to model presence (1) or absence (0) of flycatchers using Generalized Linear Models resulted in complete or quasi-complete separation of the data, with most models failing to converge. We thus employed penalized regression by using the bglmer command in the blme package (Chung et al., 2013) to model presence/absence of olive-sided flycatcher using Bayesian Generalized Linear Models (binomial family, logit link), imposing zero-mean Normal priors (with a standard deviation of 3) on the fixed effects (Bolker, 2015). A standard deviation of 2.5 or 3.5 gave very similar results (**Supplementary Figure 3**). We specified optimization by quadratic approximation (BOBYQA) with 200,000 iterations.

We were unable to include all potential predictors in a single habitat model because some variables of interest were mutually exclusive (e.g., if a site was uncut there could be no time-since-cut or cut size). We thus divided the dataset according to whether points were located within 50 m of a cutblock (Post-cut) or not (Uncut), and analyzed each subset of the data using a separate set of models. We had no point count data from 1998, 2000, 2001, or 2003–2005, and within each data subset we removed years that had no detections of olive-sided flycatcher, so the resulting post-cut dataset included 5 years (1997, 2002, 2007, 2008, 2010) and the uncut dataset included 6 years (2006–2011). We compared models within each model set using an information theoretic approach, to find combinations of habitat factors that best explained variation in olive-sided flycatcher occurrence. We scaled continuous variables to have a mean of 0 and a standard deviation of 1. In both model sets we included models with fixed effects of roads and distance to water. The first model set, Post-cut, additionally included cut size, time since cut, and their quadratic effects. We restricted these data to points in cutblocks <300 ha, to avoid undue influence of extremely large cutblocks where olive-sided flycatchers were never detected, and to reflect the natural range of variation in cutblock size found in areas with high densities of olive-sided flycatchers (the species occurs in cutblocks ranging in size from 0.005 to 284 ha; Norris and Martin, unpublished data). Restricting the data to cutblocks <300 ha did not impact the sign or significance of the coefficient of cut size on the probability of detection, but reduced the magnitude of the coefficient; further restricting the data to cutblocks <150 or <100 ha had little effect on the results (see **Supplementary Figure 4**). The second model set, Uncut, included mountain pine beetle as a fixed effect (in addition to roads and distance to water). Within each set, we compared models using Akaike's Information Criterion corrected for small sample size (AICc) and Akaike weights, and considered models to be plausible if they fell within two AICc points of the lowest AICc model. We calculated the area under the curve of the receiver operating characteristic (AUC) using the performance command in the

ROCR package to evaluate classifier performance independent of cutoff values (Sing et al., 2005). AUC ranges from 0 to 1, where a value of 1 indicates perfect prediction, and a value of 0.5 indicates prediction no better than random; we considered models with AUC > 0.7 to have acceptable predictive ability (Hosmer et al., 2013).

Parameter estimates in our models were the natural logarithm of the odds ratios. The odds ratio for each parameter indicates the change in odds of occurrence of olive-sided flycatchers associated with a one unit increase in the (scaled) predictor variable (Crawley, 2007). We examined odds ratios and their 90% Wald confidence intervals for all parameters in all models. For prediction of olive-sided flycatcher occurrence, we looked within the subset of plausible models (ΔAICc < 2) with acceptable predictive ability (AUC > 0.7) for each set, and chose the simplest model that included all of the parameters (from the model set) whose odds ratios had confidence intervals that did not overlap 1.

Landscape Simulation Models

To forecast the future cumulative effects of multiple stressors on habitat, we first developed a spatially explicit model of land use and land cover change for the study area. We then processed the spatial model projections through the habitat models described in the previous section to produce spatial habitat projections. We used the ST-Sim package (version 3.2.21) for SyncroSim (version 2.2.27; ApexRMS, 2021) to construct a state-and-transition simulation model (Daniel et al., 2016) that simulated future land use and land cover change within the study area from 2020 to 2050. The simulation study area encompassed a landscape just under three million hectares in size, subdivided into nearly 3.7 million 90 × 90-m simulation cells. We stratified the landscape according to both ecological characteristics (British Columbia Biogeoclimatic Ecosystem Classification zone and subzone; Government of British Columbia, 2011) and jurisdiction (private, protected, or land managed primarily by the provincial government; Government of British Columbia, 2020d). Both types of stratification affected transition rates in the model. Ecological and jurisdictional strata were static in their location within each model simulation, although the location of jurisdictional strata varied among simulation scenarios (i.e., the location of protected areas). In addition to stratification, the landscape was classified according to eleven possible dynamic state classes: cropland, developed (urban or industrial), grassland, barren (i.e., rock, ice), water, wetland and five classes of forest (**Figure 1**). The five forest classes were: forest stands having recently experienced a moderate to very severe mountain pine beetle outbreak (classified as pine), pine stands having recently experienced a clearcut or burn, undisturbed pine stands, non-pine stands having recently experienced a clearcut or burn, and undisturbed non-pine stands. Pine stands are those vegetated polygons defined as having experienced, at any time, a moderate to very severe mountain pine beetle outbreak or where >10% of trees are pine (Government of British Columbia, 2018). To simulate transitions between state classes, the state-and-transition simulation model included the following transition types: clearcut logging, wildfire, urbanization, and agricultural expansion.

State variables for each simulation cell were initialized for 2020 by extracting land cover class (**Figure 1**) from The Agriculture and Agri-Food Canada 2010 Land Use Map

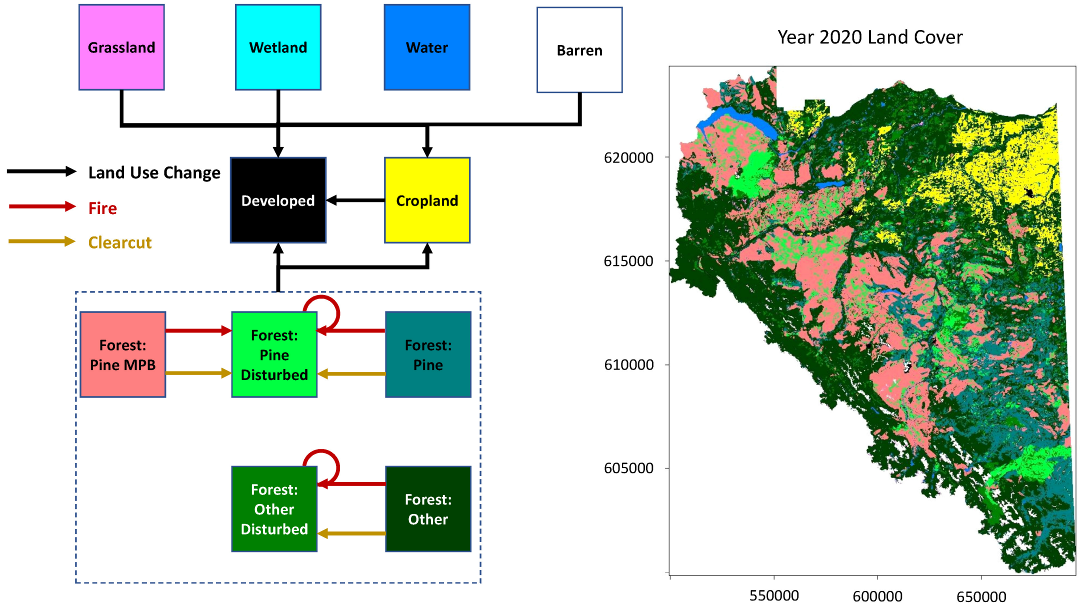

FIGURE 1 | Transition diagram for state-and-transition simulation model for the Dawson Creek Timber Supply Area in the southern Peace River region of British Columbia, Canada. Squares indicate states, and arrows indicate possible transitions between states. Broken rectangle encompasses all forest states, all of which can transition to developed land or cropland via land use change. Map of study area shows land cover in 2020.

(Government of Canada, 2010); Biogeoclimatic Ecosystem Classification subzone, forest age, and forest composition from The Vegetation Resources Inventory (Government of British Columbia, 2018); jurisdiction class (private, protected, or other provincially managed land) from The British Columbia Parcel and Conservation Lands Maps (Government of British Columbia, 2020c); beetle-attack status from the annual aerial insect surveys (Government of British Columbia, 2020b); burned status from the British Columbia Historical Fire Perimeters Map (Government of British Columbia, 2016a); and cut status from the Consolidated Cutblocks Map (Government of British Columbia, 2016b). Simulation cells having experienced a clearcut in any year were classified as clearcut when initializing the landscape for 2020. Wildfire events, which tend not to affect all trees in a stand, were not considered in our 2020 landscape initialization if the burn was >40 years old. Finally, simulation cells having previously experienced both fire and a mountain pine beetle infestation of moderate or greater severity were initialized using the most recent of the two disturbance events.

Historic urbanization and agricultural expansion rates (ha per year) were estimated using the difference between the Agriculture and Agri-Food Canada 2010 and 2000 Historical Land Use Maps (Government of Canada, 2010). In our simulations, these annual rates were assumed to continue from 2020 through 2050. Urbanization and agricultural expansion transitions were constrained within the model to only occur on cells adjacent to the developed (urbanization) and cropland (agricultural expansion) state classes. The probability of these transitions increased linearly with the number of neighboring cells in the destination state class.

Historic logging rates (ha per year) were estimated using the Consolidated Cutblocks Map from the year 2000 to 2018 (Government of British Columbia, 2016b). Area logged was stratified by Biogeoclimatic Ecosystem Classification subzone and jurisdiction (private, protected and provincially managed). For each model realization and time step, we sampled a year between 2000 and 2018 and then applied the historic logging rate for that year to that future simulation time-step according to Biogeoclimatic Ecosystem Classification subzone and jurisdiction. In this way, we maintained within-year correlations in the amount of logging across Biogeoclimatic Ecosystem Classification subzones and jurisdictions.

Annual fire probabilities (stratified by Biogeoclimatic Ecosystem Classification subzone) were estimated using the British Columbia Historical Fire Perimeters Map (Government of British Columbia, 2016a) using the ratio of area burned to area available to burn each year and averaged across all years in the fire history. In addition, we calculated the historic normalized area burned each year across the landscape for each historic year and sampled from this distribution as a multiplier against the base fire probability for each model time-step and realization, thus including a level of variability in our projections that is comparable to what was observed historically.

Fires and clearcuts were both simulated as spatial events using size distribution estimated using the corresponding historic perimeters. For fire sizes, we sampled from the entire historic distribution of fire size. For clearcut sizes, we sampled from historic cutblock sizes starting in the year 2000. We also simulated two scenarios where cutblocks were constrained to a maximum size of 10 ha. Because mountain pine beetle outbreaks are expected on a ∼50-year cycle, and the most recent outbreak occurred after 2000, we did not simulate new outbreaks before 2050. Forests classified as beetle-attacked in 2020 remained as beetle-attacked forests until they transitioned to cleared forest through clearcutting or wildfire.

Simulation Scenarios

We ran six simulation scenarios representing the combination of three management alternatives ("Business As Usual," "Increased Protected Area," and "Reduced Cutblock Size") and two fire alternatives ("Baseline Fire" and "Increased Fire"). The Business As Usual scenarios applied historic rates and spatial patterns of land use and logging. The Increased Protected Area scenarios increased protected areas from 13% to 30% of the land base by adding provincially managed land that was unprotected in 2020, and was covered by forest older than 75 years of age having experienced a moderate to very severe mountain pine beetle infestation. We considered older forest and forest affected by mountain pine beetle to be high quality habitat for insectivorous forest birds (Mahon et al., 2014; Saab et al., 2014). The protected area figure reflects Canada's goal of protecting 30% of habitat by 2030 (Government of Canada, 2019). The Reduced Cutblock Size scenarios constrained clearcuts to a maximum size of 10 ha but maintained the historic distribution of area logged. We applied fire probabilities at the historic rate (**Supplementary Table 2**) for the Baseline Fire alternative, and at 150% of the historic rate for the Increased Fire alternative, according to likely future scenarios of climate-induced fire frequencies (Wootton, 2010). Each model scenario was replicated with 100 Monte Carlo realizations.

Simulation of Future Habitat

Once simulations were complete, we created 600 maps projecting habitat suitability for olive-sided flycatcher in 2050 (six scenarios × 100 Monte Carlo realizations) by processing the spatial model projections through the top-ranked habitat suitability models for cut and uncut sites, respectively (**Table 2**). For each realization, we sampled from the distribution estimated for the parameters of the selected habitat suitability model to account for uncertainty around model parameters. Thus, variation in the results of projected habitat suitability reflects both uncertainty in the simulations of land cover, and uncertainty in the parameters of habitat suitability models for olive-sided flycatcher. We were unable to include fire history as a predictor in our habitat models, so we assumed that the probability of olive-sided flycatcher occurrence in burned areas was equivalent to the probability of occurrence in a clearcut of the same size and age (i.e., olive-sided flycatchers tend to be associated with forest gaps created by fire and/or tree removal; Altman and Sallabanks, 2020). Habitat suitability (ha) was calculated as the sum product of cell area and probability of occurrence for each year and Monte Carlo realization. Percent change in habitat suitability was calculated as the difference between habitat suitability in 2020 vs. 2050, divided by habitat suitability in 2020 and multiplied by 100. Simulated habitat suitability in

2020 varied slightly across scenarios (**Supplementary Table 4**) because for each Monte Carlo realization we sampled the habitat model parameters from their estimated distributions to calculate habitat at the start (2020) and end (2050) of that realization. We then calculated the habitat change from 2020 to 2050 for each Monte Carlo realization before summarizing percent change in habitat (**Supplementary Table 4**). Information on accessing model datasets is available in the **Supplementary Materials**.

RESULTS

Habitat Suitability for Olive-sided Flycatcher

In the first set of habitat suitability models (Post-cut models), plausible models included clearcut size and a quadratic effect of time since cut as predictor variables for which the 90% confidence intervals on the odds ratios did not overlap 1 (**Table 2** and **Supplementary Table 3**). According to the top-ranked model in this set, the probability of olive-sided flycatcher occurrence declined with increasing cutblock size (**Table 2** and **Figure 2A**), an effect that was robust across candidate models (**Supplementary Table 3**) and also robust to the exclusion of extreme values of fixed effects (cut size and time since cut; **Supplementary Figure 4**). Probability of olive-sided flycatcher occurrence was highest for mid-aged clearcuts (10–20 years old); confidence intervals on the odds ratio were large but did not overlap 1 (**Table 2** and **Figure 2B**), and again this effect was robust across candidate models and robust to the exclusion of extreme values of fixed effects (**Supplementary Table 3** and **Supplementary Figure 4**). Year (random effect) had a small effect on olive-sided flycatcher occurrence (SD = 0.53, vs. parameter estimates of −1.74 for cut size, 0.75 for time since cut, and −1.11 for [time since cut]^2; **Supplementary Figure 5**). Among the models in the second set (Uncut), mountain pine beetle was the only parameter for which the confidence intervals on the odds ratio did not overlap 1 (**Supplementary Table 3**). According to the top-ranked model in this set, points with moderate to very severe mountain pine beetle had 8.9 times the odds of olive-sided flycatcher occurrence, compared to points with no or light amounts of mountain pine beetle; again, confidence intervals on the odds ratio were large but did not overlap 1 and the effect was robust across candidate models in the set (**Table 2**, **Figure 2C**, and **Supplementary Table 3**). Year (random effect) had an effect on olive-sided flycatcher occurrence of similar magnitude to the fixed effect of mountain pine beetle (SD = 1.83 for year, vs. parameter estimate of 2.19 for beetle; **Supplementary Figure 5**).

Landscape Conditions and Projected Change

Within the study area, Vegetation Resources Inventory data (Government of British Columbia, 2018) were available for three million ha, of which approximately 2.6 million ha were forested in 2020. Historic logging rates (2000–2018) were 7744 ± 566 ha/year (mean ± SE) with a mean cutblock area of 30 ± 0.61 ha (range: <1–405 ha). Mean annual historic fire probability varied by subzone within the Biogeoclimatic

TABLE 2 | Plausible (ΔAICc < 2) habitat suitability models (Bayesian Generalized Linear Mixed Models) for olive-sided flycatcher in two sets: (1) Post-cut, and (2) Uncut.

Model	ΔAICc	W_i	AUC	Parameter	Odds ratio
Set 1. Post-cut Models, n = 316					
C08	0	0.33	0.82	Intercept	0.019 [0.0073, 0.048]
				Cut size	**0.176 [0.071, 0.435]**
				Time since cut	2.11 [0.915, 4.86]
				Time since cut^2	**0.328 [0.126, 0.858]**
C20	1.47	0.16	0.79	Intercept	0.0098 [0.0043, 0.023]
				Cut size	**0.205 [0.089, 0.474]**
C03	1.94	0.12	0.82	Intercept	0.019 [0.007, 0.047]
				Cut size	**0.218 [0.0823, 0.575]**
				Cut size^2	1.24 [0.645, 2.38]
				Time since cut	2.11 [0.916, 4.86]
				Time since cut^2	**0.318 [0.120, 0.847]**
Set 2. Uncut Models, n = 536					
U05	0	0.47	0.72	Intercept	0.024 [0.0053, 0.106]
				Beetle	**8.91 [1.29, 61.6]**
U02	1.73	0.20	0.71	Intercept	0.026 [0.0059, 0.117]
				Beetle	**8.66 [1.29, 58.0]**
				Road	0.75 [0.271, 2.09]

*Models were compared only within sets. Akaike weights (W_i) and model performance (AUC) are indicated for each model, and odds ratios [90% Wald confidence intervals] are indicated for each fixed effect. All continuous variables were scaled to have a mean of 0 and standard deviation of 1. Odds ratios >1 and <1 indicate an increase and a decrease, respectively, in the odds of olive-sided flycatcher occurrence associated with an increase in the predictor variable. Where the 90% confidence interval of the odds ratio does not overlap 1, the parameter (in bold) is considered a significant predictor of olive-sided flycatcher occurrence. Models C08 and U05 were selected for prediction of olive-sided flycatcher occurrence at cut and uncut sites, respectively. All models included year as a random effect. See **Supplementary Table 3** for a complete list of all habitat suitability models with odds ratios and their confidence intervals for each parameter.*

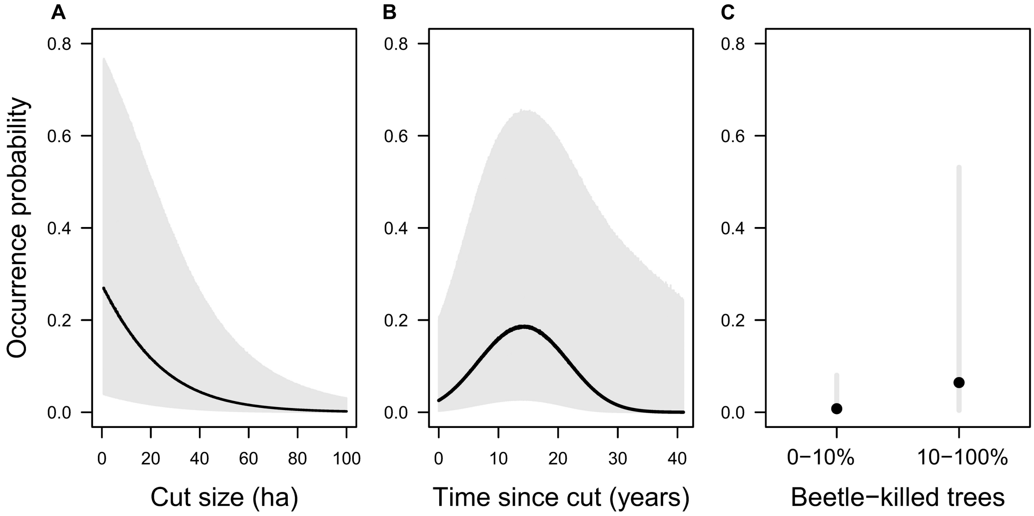

FIGURE 2 | Probability of olive-sided flycatcher occurrence (black) with 90% prediction intervals (gray) according to top-ranked models. **(A,B)** Top ranked model in the first set (Post-cut), for points within 50 m of a clearcut: Occurrence ∼ Cut size + Time since cut + Time since cut^2 + 1| Year. **(C)** Top-ranked model in the second set (Uncut), for points >50 m from a clearcut: Occurrence ∼ mountain pine beetle + 1| Year). We allowed **(A)** cut size, **(B)** time since cut, and **(C)** mountain pine beetle, to vary, while holding the other fixed effects near their optima (**A:** time since cut = 15 years, **B:** cut size = 10 ha). The predicted value and prediction interval for each value of the predictor variables represents the mean of 50,000 simulations using the predictInterval command in the merTools package of R, and includes the uncertainty related to residual variance, the uncertainty in the fixed coefficients, and some of the uncertainty in the variance parameters for the random effect of year (Knowles and Frederick, 2020).

Ecosystem Classification, from 0.00005 (fire every 20,000 years) in the Engelmann Spruce Subalpine Fir wet cold parkland zone to 0.0029 (fire every 345 years) in the Boreal White and Black Spruce moist warm zone; **Supplementary Table 2**). Twelve percent of the land was under private jurisdiction, 13% was in protected areas, and 75% was land managed primarily by the provincial government.

On average, our scenarios projected that a cumulative area of ∼405,000 ha (16% of current forest) would be burned or cut between 2020 and 2050, if historic levels of fire are maintained, versus ∼462,000 ha (18% of current forest) under the alternative of a 50%-increased fire probability (**Supplementary Table 4**). The Business As Usual with Baseline Fire scenario resulted in the smallest cumulative area of forest burned or cut (median 387,434 ha, 95% CI: 311,425, 523,908), and the Reduced Cutblock Size with Increased Fire scenario led to the largest cumulative area of forest burned or cut (median 493,264 ha, 95% CI: 329,357, 570,488; **Supplementary Table 4**).

Projected Change in Olive-sided Flycatcher Habitat

Overall, probability of olive-sided flycatcher occurrence was highest in the forests surrounding the Rocky Mountains, where much of the forest was affected by mountain pine beetle (**Figure 3**). Estimated habitat suitability across the landscape was 182,473 ha in 2020 (see **Supplementary Table 4** for details), and by 2050 it was projected to decrease by 16.4% (median of 100 Monte Carlo realizations) under the Business As Usual scenario with Baseline Fire, and by 18.1% under the Increased Fire alternative (**Figures 3**, **4**). Under the Increased Protected Area alternative, median habitat suitability was projected to decrease by 10.6% with Baseline Fire, and by 12.5% with Increased Fire (**Figures 3**, **4**). Almost all Monte Carlo realizations for the Business As Usual and Increased Protected Area scenarios projected declines in habitat suitability (**Figure 4**). Results of the Reduced Cutblock Size scenarios were highly variable among Monte Carlo realizations, resulting in confidence intervals for change in habitat suitability that overlapped zero, but, for most realizations, large declines in habitat suitability were not projected under these scenarios (median habitat loss of 4.0% under the Baseline Fire alternative, and 5.6% under the Increased Fire alternative; **Figures 3**, **4**). Uncertainty in the projected change in habitat suitability was greatest for the Reduced Cutblock Size scenarios (**Figure 4**).

Within each scenario, the direction of change in suitable habitat (increase or decrease) was consistent across subzones within the Biogeoclimatic Ecosystem Classification (**Supplementary Figure 6**). When we examined habitat changes according to jurisdiction, we found that the Reduced Cutblock Size scenarios reduced habitat loss (compared to other scenarios) primarily on land managed by the provincial government (**Supplementary Figure 7**). Within protected areas, there were no major differences across scenarios, and overall projected loss in future habitat was less than the loss projected for private and provincially managed land.

DISCUSSION

We assessed current and future habitat suitability for declining populations of olive-sided flycatchers considering the cumulative

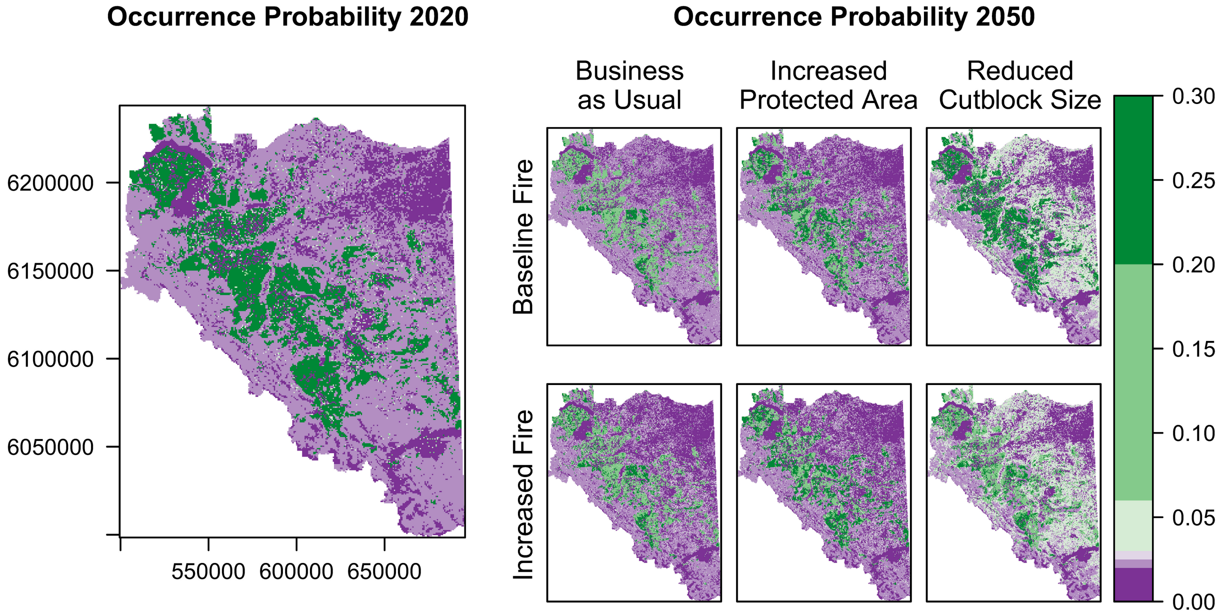

FIGURE 3 | Occurrence probability of olive-sided flycatchers across the southern Peace River region of British Columbia, based on habitat suitability indices derived from parameter estimates of top-ranked habitat suitability models C08 and U05 (**Table 2**). Values closer to 1.0 (green) indicate the most suitable habitat and values closer to 0 (purple) indicate the least suitable habitat. The 2020 map shows probability of olive-sided flycatcher occurrence under current conditions, including recent mountain pine beetle outbreaks. The 2050 maps show future expected probability of olive-sided flycatcher occurrence, given projected forest harvesting, wildfires, urbanization, and agricultural expansion, under six scenarios that combined three management alternatives with two wildfire alternatives. Management alternatives were: Business As Usual, Increased Protected Area (protected areas increased from 13% to 30% of land base), and Reduced Cutblock Size (size of clearcuts limited to 10 ha). Wildfire alternatives were: Baseline Fire (fire frequency maintained at historic levels) and Increased Fire (50% increase over historic levels). Results are limited to three million ha for which data were available. The Rocky Mountains run northwest to southeast across the study area.

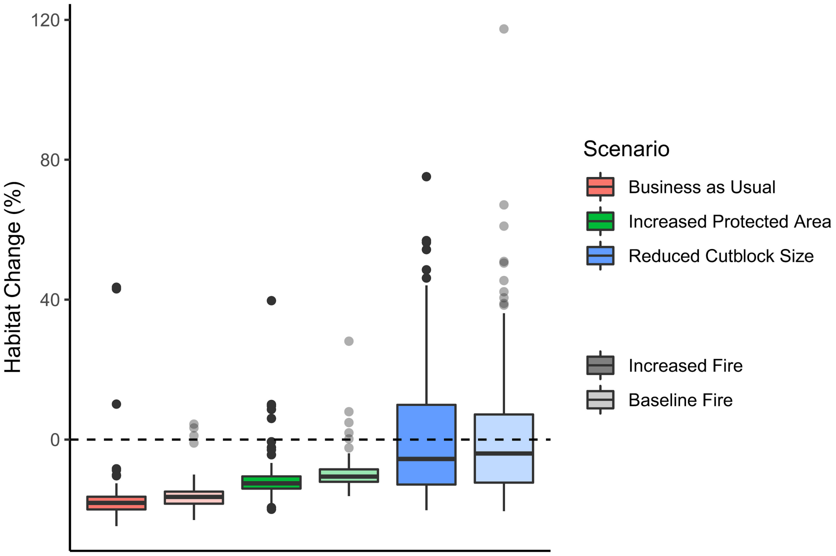

FIGURE 4 | Percent change in habitat suitability for olive-sided flycatchers from 2020 to 2050 across the southern Peace River region of British Columbia under six scenarios of landscape change. Habitat suitability was calculated for 2020 and 2050 by multiplying the projected probability of olive-sided flycatcher occurrence (per ha) for each simulation cell by the area of the cell (0.81 ha) then summing over all cells. Percent change in habitat suitability was the difference between suitable habitat in 2020 vs. 2050, divided by suitable habitat in 2020 and multiplied by 100. Thick black bars indicate the median % habitat change from 100 Monte Carlo realizations, boxes indicate the 1st and 3rd quartiles, whiskers extend to the maximum and minimum values within 1.5× the interquartile range, and points indicate the results of simulations that fell outside of this range. Variation in the projected change in habitat suitability within each scenario reflects both uncertainty in the simulations of land cover, and uncertainty in the parameters of habitat suitability models for olive-sided flycatcher. Darker shades of color indicate Increased Fire scenarios (50% increase in fire frequency), and lighter shades indicate Baseline Fire scenarios (fire frequency remained at the historic average).

effects of multiple stressors in the southern Peace River region of British Columbia. The quantity of suitable habitat for olive-sided flycatchers is likely to decline in the next 30 years, in the absence of changes to current forest management policies. Consistent with our predictions, olive-sided flycatcher occurrence was correlated positively with small, 10- to 20-year-old clearcuts and moderate to very high severity mountain pine beetle outbreaks. Contrary to our predictions, olive-sided flycatcher occurrence was not correlated with distance to roads or wetlands. State-and-transition simulation models projected declines in suitable habitat if current management continues (Business As Usual alternative), and even if protected areas are increased to 30% (Increased Protected Area alternative). Increased wildfire under current Business As Usual and Increased Protected Area scenarios would amplify these declines in habitat suitability. Many static conservation approaches for at risk species spend limited conservation dollars to increase the size of protected areas, potentially increasing the intensity and scope of forest harvesting outside of protected areas. Our results suggest that in this portion of the olive-sided flycatcher's range, changes to forest management outside of protected areas will also be critical, and require implementation of harvesting alternatives such as restricting clearcut size to ≤10 ha to help limit projected declines in habitat suitability under baseline fire conditions. While we found considerable variability in the projected habitat change under the Reduced Cutblock Size scenario, significantly reducing clearcut size could function as an 'other effective area-based conservation measure' (OECM) to help stem the steep continental declines of this neotropical migrant (Rosenberg et al., 2016; Watson et al., 2016).

Cumulative Effects of Stressors on Availability of Suitable Habitat

Our result that olive-sided flycatchers were associated with small clearcuts and mountain pine beetle is consistent with other studies, in which olive-sided flycatchers were associated with forest openings, where they may find increased foraging opportunities (Robertson and Hutto, 2007; Bale et al., 2019; Westwood et al., 2019; Altman and Sallabanks, 2020). Olive-sided flycatchers can adapt to, and likely select for, small-scale human-induced changes such as small patch forest cutting and/or small-scale fires (Altman and Sallabanks, 2020) as were traditionally applied by Indigenous peoples before European colonization of the southern Peace River region (Gillies, 2015). However, the amount of habitat suitable for olive-sided flycatcher was projected to decline under both Business As Usual and Increased Protected Area scenarios, especially if fire frequency increases, indicating a cumulative effect of larger-sized clearcutting and climate change on habitat loss.

The best scenario for reducing habitat loss was limiting cutblock size to 10 ha, while fire was maintained at historic levels. However, assuming environmental stability when designing conservation networks and developing individual site-management strategies is inappropriate (Hole et al., 2011) and projections assuming baseline historic fire conditions may be overly optimistic, considering future climate projections (Wootton, 2010). Further, we simulated future fire frequencies using only the IPCC-A2 emissions scenario, which was predicted to be the most likely climate scenario. Habitat projections would differ if emissions are less than, or surpass expected levels, and fire frequency is subsequently higher or lower than anticipated in our models. To optimize the future effectiveness of a conservation network, planning frameworks must address the long-term value of individual sites and resilience of the network as a whole to climate change (Hole et al., 2011). In a cumulative effects assessment for northeastern Alberta, olive-sided flycatchers were associated with recently burned forest and were projected to increase slightly in abundance over 50 years under harvesting scenarios that resulted in an overall increase in forest age; however, consistent with our findings, the projected increases were lessened by increased fire frequencies expected as a result of climate change (Leston et al., 2020). As the frequency of fires increases across the western boreal forest, maintaining suitable habitat for olive-sided flycatchers in the southern Peace River region seems possible only by reducing allowable annual cut in the Dawson Creek Timber Supply Area. Future work should include scenarios that reduce the total allowable annual cut, to determine the amount of area that is required to compensate for the losses in forest habitat due to expected climate-induced wildfires. Future management of breeding habitat for olive-sided flycatchers should support efforts to reduce greenhouse gases that contribute to climate change, restrict the size of clearcuts, and incorporate the traditional Indigenous land-use practices of creating small forest openings (Gillies, 2015).

Conservation Prospects

Canada-wide population declines of olive-sided flycatcher have slowed recently, from 80% decline between 1973 and 2009, to 19% between 2006 and 2016 (Committee on the Status of Endangered Wildlife in Canada [COSEWIC], 2018). The greatest regional-level decreases occurred west of the Rocky Mountains, in British Columbia, where breeding densities are highest (Committee on the Status of Endangered Wildlife in Canada [COSEWIC], 2018; Boreal Avian Modelling Project, 2020). However, following IUCN criteria of ≤30% decline across three generations (10 years for birds) across Canada, olive-sided flycatcher was recently recommended for down-listing from "Threatened" to "Special Concern" (Committee on the Status of Endangered Wildlife in Canada [COSEWIC], 2018). Although its legal status has not yet changed under the Canadian federal Species at Risk Act (Government of Canada, 2002), a down-listing to Special Concern removes the requirement to identify critical habitat for federal protection. The current short-term population objective for olive-sided flycatcher in Canada is to halt the national decline by 2025 while ensuring the population does not decrease more than 10% over this time, and the long-term (after 2025) population objective is to ensure a positive 10-year population trend (Government of Canada, 2016). Our simulations of breeding habitat indicate that current management practices are not likely halting population declines in Northeastern British Columbia, and it will be difficult to reverse declines in breeding habitat over the next 30 years, even under the best-case scenarios. Given the steep declines west of the

Rocky Mountains and our projected negative trends in habitat suitability on the east slope of the mountains, our results support a decision to assess olive-sided flycatcher population trends by management units matched to bird conservation regions, to ensure that declines are detected and critical habitat is identified and protected where needed. In addition, we recommend that landscape simulations be applied in areas where the dates and locations of point counts are closely matched with the dates and locations of land cover data so that disturbance thresholds, such as limits to cutblock size, can be identified. Given the removal of protections associated with down-listing species in Canada, we suggest that for bird species with sufficient data, declines should be assessed over a longer timescale than a single decade, and should take into account the probability of future recovery.

Our landscape simulations indicated that current forest management in western Canada may be contributing to observed declines in olive-sided flycatcher populations, and that changing the management of breeding habitat to limit clearcut size could potentially reduce population declines. However, such measures should be accompanied by efforts to understand and address additional stressors across their full annual life cycle, including prolonged heat events that increase energetic demands of thermoregulation; exposure to contaminants; collisions with buildings and other infrastructure; direct nest loss due to forestry and other industrial activities; and phenological mismatches and declines in high quality insect prey (Calvert et al., 2013; Wilson et al., 2018; Spiller and Dettmers, 2019; Andreasson et al., 2020). Outside of the breeding season, Rodewald et al. (2019) estimated that 10.7% of olive-sided flycatchers winter in mining concessions in the northern Andes, where a transition to active mines is expected to result in habitat loss, fragmentation, and pollution. Additional non-breeding records across the Brazilian Amazon, Cerrado and Atlantic Forest (Willis, 1993; de Lima-Pereira, 2016) occur in regions already subject to high levels of forest loss; for example, 88% of the original Brazilian Atlantic Forest and 46% of the Cerrado have already been cleared, and large-scale agriculture is projected to replace 31–34% of the remaining Cerrado by 2050 (Ribeiro et al., 2009; Strassburg et al., 2017). If researchers can obtain data on non-breeding habitat use by olive-sided flycatchers and other aerial insectivores, they can use landscape simulations to assess cumulative effects of multiple stressors on wintering grounds. An important next step is to integrate full life-cycle population models (e.g., Wilson et al., 2018) into landscape simulations to identify specific management practices in each part of the annual life cycle that can have the greatest effect on reversing population declines.

Caveats

Our study uses the best available data to project suitable habitat for olive-sided flycatcher in the southern Peace River Region of British Columbia, taking into account the cumulative effects of multiple disturbances, but with several caveats. First, although olive-sided flycatchers often show positive numerical responses to fire (Hutto, 1995; Kotliar et al., 2002; Haché et al., 2014; Altman and Sallabanks, 2020), we were unable to test directly for effects of fire on occurrence, and had to assume that fires would have a similar effect as clearcuts (positive effect of small gaps; negative effect of large gaps). Second, we do not know the fitness consequences of breeding in clearcuts or burned areas: in some studies, nest survival was lower in harvested areas and burned areas, and in others, nest survival was higher in burned areas (Kotliar et al., 2002; Robertson and Hutto, 2007; Altman and Sallabanks, 2020). Before-after-control-impact studies are necessary to determine how burning influences habitat suitability relative to other important disturbance factors such as clearcuts and insect outbreaks. Further, we did not examine how climate-related variables, such as weather during breeding, influenced annual variation in populations and habitat associations. Therefore, we cannot evaluate the relative importance of breeding habitat factors in the face of increasing climate change pressures. Third, we used Biogeoclimatic Ecosystem Classification zones to stratify our landscape simulation because forest managers use these zones in planning, but the detections in our point count data were too sparse to stratify habitat suitability models by the same zones. Olive-sided flycatchers occur across forested zones, and our preliminary inspection of the data did not suggest that detections were correlated with Biogeoclimatic Ecosystem Classification zone, soil moisture, elevation, crown closure, or spatial coordinates. Fourth, 72% of the point counts in our dataset were within 100 m of a road. Although we did not find a relationship between the occurrence of olive-sided flycatchers and the presence of roads in the southern Peace River region, roadside surveys can under-sample certain habitats in boreal forest, and under-represent bird densities (Sólymos et al., 2020). Simulations of future habitat availability would be best suited to areas with higher densities of the target species (which can, however, be difficult for species that have experienced steep declines) and more comprehensive land cover and point count data, and subsequently, lower error in habitat suitability models. To better align with forest planning objectives, the design of point count surveys should take into account regional forest classifications (such as Biogeoclimatic Ecosystem Classification in British Columbia), attempt to cover off-road areas, and encompass a wider variety of disturbances, including smaller cutblocks, areas exposed to recent wildfires and insect outbreaks, and areas exposed to both insects and cutting (specific recommendations in Mahon and Pelech, in press). Collecting a minimum of habitat data (tree species, stand age, severity of disturbances) during point count studies would improve resolution and reduce the problem of missing land cover data.

CONCLUSION

Our simulation study highlights potential avenues to explore in adaptive management or with experiments on the ground. We suggest testing the generality of our scenarios as prescriptions for management of olive-sided flycatcher habitat, especially outside the study area. Moreover, management for olive-sided flycatcher and other birds associated with small forest openings will need to balance the benefits of limiting cut block size with the cost of increased road infrastructure and increasing forest fragmentation, which can affect other wildlife populations at risk (e.g., woodland caribou *Rangifer tarandus caribou*; Johnson et al., 2015). Our landscape simulations highlight the importance of integrating disturbance thresholds (such as clearcut size) into land-use planning, when protected areas alone are insufficient to halt or reverse population declines.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because the study used existing datasets and did not involve handling of animals.

AUTHOR CONTRIBUTIONS

ARN, KLD, LF, and AR conceived the idea. ARN, JT, and AL sourced and curated the data. ARN, CD, KLC, and LF performed the analyses. ARN, KLC, and LF wrote the manuscript with suggestions from other authors. All authors contributed to the manuscript and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.635872/full#supplementary-material

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Assessing Pathways of Climate Change Effects in SpaDES: An Application to Boreal Landbirds of Northwest Territories Canada

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Distributions of landbirds in Canadian northern forests are expected to be affected by climate change, but it remains unclear which pathways are responsible for projected climate effects. Determining whether climate change acts indirectly through changing fire regimes and/or vegetation dynamics, or directly through changes in climatic suitability may allow land managers to address negative trajectories via forest management. We used SpaDES, a novel toolkit built in R that facilitates the implementation of simulation models from different areas of knowledge to develop a simulation experiment for a study area comprising 50 million ha in the Northwest Territories, Canada. Our factorial experiment was designed to contrast climate effects pathways on 64 landbird species using climate-sensitive and non-climate sensitive models for tree growth and mortality, wildfire, and landbirds. Climate-change effects were predicted to increase suitable habitat for 73% of species, resulting in average net gain of 7.49 million ha across species. We observed higher species turnover in the northeastern, south-central (species loss), and western regions (species gain). Importantly, we found that most of the predicted differences in net area of occupancy across models were attributed to direct climate effects rather than simulated vegetation change, despite a similar relative importance of vegetation and climate variables in landbird models. Even with close to a doubling of annual area burned by 2100, and a 600 kg/ha increase in aboveground tree biomass predicted in this region, differences in landbird net occupancy across models attributed to climate-driven forest growth were very small, likely resulting from differences in the pace of vegetation and climate changes, or vegetation lags. The effect of vegetation lags (i.e., differences from climatic equilibrium) varied across species,

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resulting in a wide range of changes in landbird distribution, and consequently predicted occupancy, due to climate effects. These findings suggest that hybrid approaches using statistical models and landscape simulation tools could improve wildlife forecasts when future uncoupling of vegetation and climate is anticipated. This study lays some of the methodological groundwork for ecological adaptive management using the new platform SpaDES, which allows for iterative forecasting, mixing of modeling paradigms, and tightening connections between data, parameterization, and simulation.

Keywords: landscape simulation, ecological forecasting, vegetation, fire, decision support, forest management, reproducibility, reusability

INTRODUCTION

The North American boreal forest represents approximately 48% of the continent's forests (Smith et al., 2018), and it provides breeding habitat for half of North American bird species (Wells and Blancher, 2011). In recent decades, the southern boreal forest has seen rapid economic development from forestry, agriculture, oil, bitumen and gas, with attendant consequences for the region's biodiversity (Hebblewhite, 2017; Mahon et al., 2019; Stewart et al., 2020). However, in the northern parts of the boreal forest, climate change is perhaps the greatest threat to biodiversity (Price et al., 2013). The region is warming at twice the global average rate (Masson-Delmotte et al., 2019), which is expected to increase the frequency, extent, and severity of droughts and wildfires (Boulanger et al., 2014; Gauthier et al., 2015; Masson-Delmotte et al., 2019). An overall decrease in tree productivity and total biomass may be expected in these northern regions (Boulanger et al., 2017), with projected shifts from mid- and late-successional conifers (*Picea* spp.) to fire-adapted pioneer species of genus *Populus* and *Pinus*. Major vegetation transitions of this nature have been documented (Wang et al., 2020), with a combination of frequent fire and drought (Whitman et al., 2019) as well as permafrost thaw (Helbig et al., 2016) potentially playing major roles. As a result, climate change may alter the diversity and abundance of many terrestrial taxa (Dawson et al., 2011), including landbirds (Stralberg et al., 2015a; Cadieux et al., 2020).

More than half of boreal landbird species have shown declines in abundance over the last five decades (Rosenberg et al., 2019) and climate change may exacerbate these trends. According to Stralberg et al. (2015a), projected changes in end-of-century breeding habitat for boreal landbirds range from an average 40% change based on bioclimatic models alone (with 45% of species decreasing), to a projected 20–60% contraction when considering vegetation lags due to climate change (70–100% of species decreasing). Similarly, Bateman et al. (2020a) estimated that 98% of 48 modeled boreal landbird species were at moderate to high risk of range size contraction due to climate change, based on bioclimatic niche models. Climate change may cause range and/or population changes through several mechanisms, with different implications for management. Climate change might act indirectly, through climate-induced changes to vegetation or wildfire and resulting change to habitat, or directly, through non-vegetation mediated climatic effects. The relative importance of these pathways has important implications for management. For example, if climate-caused declines are indirect, land managers can use tree-planting, vegetation restoration, or fuel limitation as on the-ground adaptation strategies to reduce the system's vulnerability to the effects of climate change (Bauduin et al., 2020), and consequently improve conservation. If climate-caused declines are direct, more drastic adaptation actions such as species translocation, as well as mitigation strategies that can change climate trajectories in the short-term may be needed to meet conservation objectives. Quantifying the relative importance of these alternate pathways is a matter of urgency given current and projected declines in boreal landbirds (Tremblay et al., 2018; Stralberg et al., 2019; Cadieux et al., 2020).

Separating direct from indirect pathways of climate effects poses a significant challenge for standard statistical modeling approaches to both predicting and forecasting wildlife distribution. Interactions and feedback loops (or simply "feedbacks") among different drivers of change are not yet fully understood, but have the potential to greatly influence outcomes (Bush and Lemmen, 2019; Wilcox et al., 2019; Turetsky et al., 2020). It has been shown, for example, that the forecasted direction of species' movements under climate change in some cases suggests northern retractions rather than the expected expansions (e.g., Clason et al., 2020). Our current ability to forecast how the various pathways of climate may affect landbird occupancy in boreal forests is limited. Landbird projections to date have been mostly based on statistical correlations between landbird abundance and climate and vegetation covariates, without including feedbacks between climate, habitat, and disturbance regimes (but see Tremblay et al., 2018; Cadieux et al., 2019, 2020). More realistic near-term forecasts can come from dynamic simulations where ecological elements can interact during the forecast period. Interactions and feedbacks could allow, for example, annual vegetation changes to affect annual wildfire forecasts, which in turn affect subsequent vegetation (Marchal et al., 2017a,b, 2019). Absent this, forecasts may diverge too greatly from the upcoming future, potentially resulting in ineffective management actions and misapplication of scarce conservation resources. To address such challenges in the field of predictive ecology (Peters, 1982; Clark, 2001; Dietze et al., 2018; Yates et al., 2018; Dietze and Lynch, 2019; White et al., 2019) and conservation biology (Travers et al., 2019), and improve both uncertainty assessment and conservation resource allocation, the ability to integrate dynamic simulation models such as of forest growth and mortality, wildfire, and wildlife distribution is essential. Spatial Discrete Event Simulation (SpaDES) has been developed with such purposes in mind (Chubaty and McIntire, 2021; McIntire et al., 2021).

Spatial Discrete Event Simulation is a platform that facilitates the use of the PERFICT approach, which stands for **P**redictive **E**cology that is built on the concepts of **R**eusability, **F**ree availability, and **I**nteroperability of models, which are built around a **C**ontinuous workflow, and **T**ested automatically (McIntire et al., 2021). In a nutshell, the SpaDES platform allows wrapping models (typically implemented in R scripts) into *modules* and schedules the execution of these modules, allowing for different models (e.g., from siloed areas of knowledge) to interact through their shared inputs and outputs. For example, both forest age and species composition influence the estimation of wildfire parameters (i.e., ignition, escape, and spread probabilities), which in turn, are used to simulate landscape burning modifying both the forest age and its composition (i.e., via serotiny). Continuing the simulation, the new forest composition and age modify the following year's fire parameter probabilities. Species distribution models are then influenced by the forest composition and potentially other parameters for each simulation year, and can eventually also play a role in modifying both forest growth and wildfire regimes if biological processes such as seed dispersal are modeled. Because SpaDES is implemented in R, it allows tight coupling of data import, processing, modeling, and analyses with simulation components.

Focusing on the Taiga Plains ecozone within the Northwest Territories, Canada, we used this novel and dynamic simulation platform to (i) begin teasing apart the individual effects of direct and indirect climate-change pathways, and (ii) forecast the combined direct and indirect effects of climate pathways, including their interactions and feedbacks, on landbirds. To answer such complex ecological forecasting questions, we developed a simulation experiment of climate sensitive/non-climate sensitive models for (i) forest growth, (ii) wildfire, and (iii) landbird densities. We used existing modules for forest growth and wildfire and wrapped the landbirds' statistical models into a module, as described below. Considering the large simulated effects of climate on both vegetation (Boulanger et al., 2017) and wildfire regime in several boreal regions (Boulanger et al., 2014; Gauthier et al., 2015; Masson-Delmotte et al., 2019; Cadieux et al., 2020), we anticipated that all pathways would contribute substantially to the effect of climate on landbird species forecasted occupancy. Using SpaDES allowed us to integrate statistical and geospatial simulations to generate tightly coupled data-simulation forecasts covering large spatial and temporal extents (McIntire et al., 2021) to begin investigating the pathways through which climate change will affect boreal landbird species.

MATERIALS AND METHODS

Study Area and Species

The Taiga Plains ecozone within the Northwest Territories is located in northwestern Canada, and encompasses approximately 50 million ha (**Supplementary Appendix I Figure A1**). This vast area is primarily composed of upland (50%) and lowland (15%) boreal forests, intermixed with many lakes and small waterbodies (15%), with the remaining 20% land cover composed mostly of low vegetation (i.e., shrubs, herbs, barren ground), ice, and human development (Ecosystem Classification Group, 2007). The predominant tree species are black spruce (*Picea mariana*), white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and tamarack (*Larix laricina*) (Ecosystem Classification Group, 2007).

The Northwest Territories hosts nearly 300 breeding landbird species (Lepage, 2019), with twenty of these considered Species at Risk (SAR) at the federal and/or territorial government levels (GNWT, 2019). Our present analysis focused on 64 of these landbird species (**Table 1**), including two SAR. The species selected for modeling were chosen primarily based on the availability of survey data within the Northwest Territories and the availability of density offsets (Sólymos et al., 2013) to standardize point-count survey estimates (see section "Landbird Models").

Simulation Experiment

We developed statistical and simulation models for boreal landbirds, wildfire, and forest growth using the SpaDES modeling framework (Chubaty and McIntire, 2021; **Figure 1**), implemented as a suite of packages in R (R Core Team, 2019). Even though many of the drivers used in the geospatial simulation models (specifically LandR-Biomass and FireSense; see below) have been estimated using statistical approaches, we distinguish "simulation models" as iterative, dynamic models whose subsequent iteration depends on the previous state. This describes the vegetation and fire models, but not the "statistical" landbird models, for which predictions are derived solely from the covariates, which may or be dynamic or static, at the time of prediction (e.g., as "simulated" by the fire and vegetation models).

We developed or adapted three types of ecological models: (i) forest growth and succession (simulation model); (ii) wildfire (simulation model); and (iii) landbird species densities (statistical models). We developed pairs of each of these three model types: "climate-sensitive" (CS) variants in which climate covariates are explicit, and "non-climate-sensitive" (non-CS) variants where climate covariates are excluded (although climate may act implicitly, e.g., via vegetation covariates), for a total of six models: two forest growth succession models (CS and non-CS), two wildfire models (CS and non-CS), and two landbird density (CS and non-CS). To disentangle climate pathways, we developed a fully factorial simulation experiment involving the three model types with two levels each (CS and non-CS), resulting in 2 × 2 × 2 = 8 treatment combinations (labeled I to VIII; **Table 2** and **Figure 2**). By developing six unique models, we are implementing a "best-in-type" approach to forecasting. Such a novel approach involves building two distinct models (CS and non-CS) for each model type (tree growth, wildfire, and landbird) rather than one "full" model of each type where the non-CS forecast is simply the full model with fixed climate covariates at their mean. The best-in-type

TABLE 1 | Landbird species code, common and scientific names, and the number of records (number of individuals detected in point count surveys) per species in the dataset used to build the landbird statistical models.

Species code	Common name	Scientific name	No. records
ALFL	Alder Flycatcher	*Empidonax alnorum*	21,766
AMCR	American Crow	*Corvus brachyrhynchos*	25,672
AMRE	American Redstart	*Setophaga ruticilla*	17,689
AMRO	American Robin	*Turdus migratorius*	34,825
ATSP	American Tree Sparrow	*Spizella arborea*	354
BAWW	Black-and-white Warbler	*Mniotilta varia*	5,963
BBWA	Bay-breasted Warbler	*Setophaga castanea*	4,048
BBWO	Black-backed Woodpecker	*Picoides arcticus*	421
BCCH	Black-capped Chickadee	*Poecile atricapillus*	8,258
BHCO	Brown-headed Cowbird	*Molothrus ater*	9,092
BHVI	Blue-headed Vireo	*Vireo solitarius*	6,358
BLPW	Blackpoll Warbler	*Setophaga striata*	1,132
BOCH	Boreal Chickadee	*Poecile hudsonicus*	2,567
BRBL	Brewer's Blackbird	*Euphagus cyanocephalus*	5,643
BRCR	Brown Creeper	*Certhia americana*	3,196
BTNW	Black throated Green Warbler	*Setophaga virens*	9,318
CAWA	Canada Warbler	*Cardellina canadensis*	3,715
CHSP	Chipping Sparrow	*Spizella passerina*	41,075
CORA	Common Raven	*Corvus corax*	14,733
COYE	Common Yellowthroat	*Geothlypis trichas*	14,935
DEJU	Dark-eyed Junco	*Junco hyemalis*	17,901
EAKI	Eastern Kingbird	*Tyrannus tyrannus*	895
EAPH	Eastern Phoebe	*Sayornis phoebe*	1,407
FOSP	Fox Sparrow	*Passerella iliaca*	2,302
GRAJ	Gray Jay	*Perisoreus canadensis*	9,999
HETH	Hermit Thrush	*Catharus guttatus*	25,251
HOLA	Horned Lark	*Eremophila alpestris*	300
LCSP	Le Conte's Sparrow	*Ammodramus leconteii*	6,727
LEFL	Least Flycatcher	*Empidonax minimus*	26,990
LISP	Lincoln's Sparrow	*Melospiza lincolnii*	23,225
MAWA	Magnolia Warbler	*Setophaga magnolia*	10,868
NOFL	Northern Flicker	*Colaptes auratus*	5,012
NOWA	Northern Waterthrush	*Parkesia noveboracensis*	4,675
OCWA	Orange-crowned Warbler	*Oreothlypis celata*	5,245
OSFL	Olive-sided Flycatcher	*Contopus cooperi*	1,575
OVEN	Ovenbird	*Seiurus aurocapilla*	57,723
PAWA	Palm Warbler	*Setophaga palmarum*	4,709
PISI	Pine Siskin	*Spinus pinus*	12,022
PIWO	Pileated Woodpecker	*Dryocopus pileatus*	1,757
PUFI	Purple Finch	*Haemorhous purpureus*	1,183
RBGR	Rose-breasted Grosbeak	*Pheucticus ludovicianus*	14,546
RBNU	Red-breasted Nuthatch	*Sitta canadensis*	10,964
RCKI	Ruby-crowned Kinglet	*Regulus calendula*	20,671
REVI	Red-eyed Vireo	*Vireo olivaceus*	51,564
RUGR	Ruffed Grouse	*Bonasa umbellus*	4,214
RWBL	Red-winged Blackbird	*Agelaius phoeniceus*	28,540
SAVS	Savannah Sparrow	*Passerculus sandwichensis*	19,748
SOSP	Song Sparrow	*Melospiza melodia*	16,415
SWSP	Swamp Sparrow	*Melospiza georgiana*	5,945
SWTH	Swainson's Thrush	*Catharus ustulatus*	48,944
TEWA	Tennessee Warbler	*Oreothlypis peregrina*	68,503
TRES	Tree Swallow	*Tachycineta bicolor*	6,375
WAVI	Warbling Vireo	*Vireo gilvus*	10,734
WCSP	White-crowned Sparrow	*Zonotrichia leucophrys*	1,965
WETA	Western Tanager	*Piranga ludoviciana*	9,671
WEWP	Western Wood-Pewee	*Contopus sordidulus*	2,657
WIWA	Wilson's Warbler	*Cardellina pusilla*	1,324
WIWR	Winter Wren	*Troglodytes hiemalis*	9,391
WTSP	White-throated Sparrow	*Zonotrichia albicollis*	86,333
WWCR	White-winged Crossbill	*Loxia leucoptera*	6,778
YBFL	Yellow-bellied Flycatcher	*Empidonax flaviventris*	2,202
YBSA	Yellow-bellied Sapsucker	*Sphyrapicus varius*	13,672
YEWA	Yellow Warbler	*Setophaga petechia*	24,564
YRWA	Yellow-rumped Warbler	*Setophaga coronata*	59,281

approach proposed here partitions more of the variance to non-climate covariates in the non-CS model than it does in its climate-sensitive counterpart, since there is likely some degree of collinearity between these covariates. While some of the extra partitioned variance will be noise, some of it will be a signal incorrectly attributed to the climate covariates in the CS models. This results in a more informative non-CS model than a single "full" model type. A caveat to this approach is that the "control" model (in the present work, the non-CS) is not merely a simplified version of the "experimental" model (in the present work, the CS model with no climate covariates): they are alternative fits to data with different assumptions. As discussed below, we focused on assessing the pathways of climate change effects on landbirds (i.e., differences between models) rather than exploring forecasted climate-sensitive landbird occupancy (i.e., forecasts of one model). In this case, using a "full control model" that would only include factors that are not changing over time (i.e., our non-CS model I with included static climate variables) would result in mostly unchanging predictions, which are not relevant for the purpose of this study. Therefore, while our control model could include climate variables, it would not present different outcomes from the one used. Our used approach has the advantage of allowing researchers to reuse models from any arbitrary source, regardless of the area of research and method used, e.g., computer simulation or machine learning, in this case.

We ran 90-year simulations at an annual time step from 2011 through 2100. We used a common spatial resolution of 250 m across all models to align with the resolution of the input stand biomass layers. For each of the eight treatment combinations, we ran 10 replicate simulations to incorporate the inherent stochasticity of the wildfire and vegetation dynamics models. Finally, for each component of this study we have selected, to our knowledge, the best available models given the available data and process models, and our objectives.

Climate Data

We obtained historical climate normals (1981–2010) from ClimateNA (Wang et al., 2016) and https://adaptwest.databasin.org/ to match as closely as possible the years of data in each

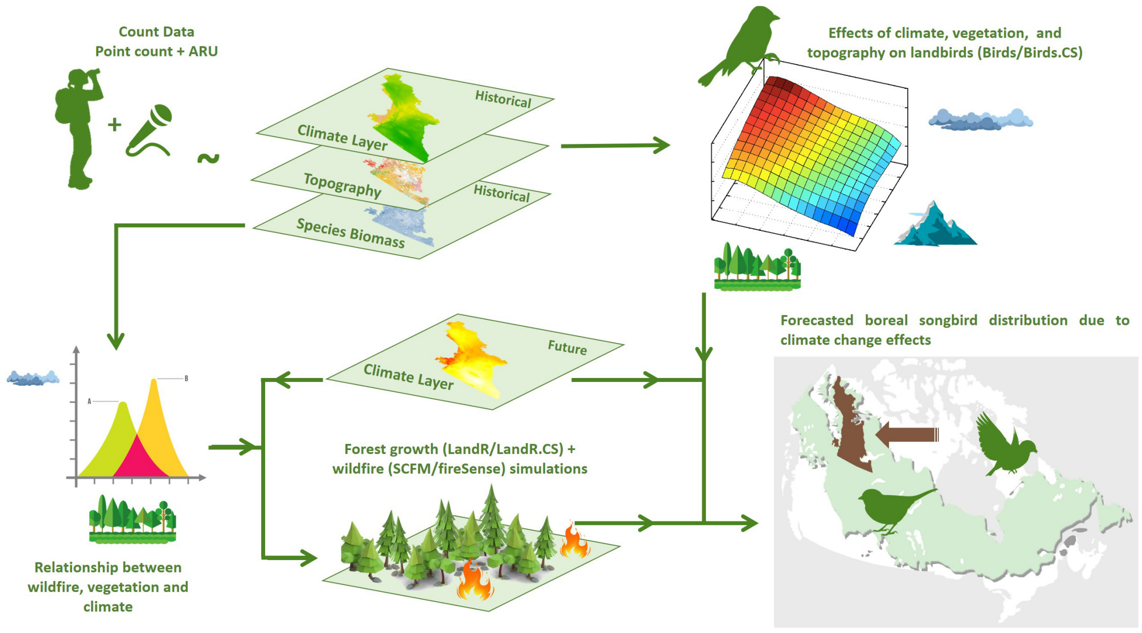

FIGURE 1 | Study framework connecting boreal landbird model (Birds/Birds.CS) fitting, forest growth (LandR/LandR.CS), and wildfire (SCFM/FireSense) simulation and landbird occupancy forecasting. Point-count data to generate landbird models was compiled from the database of the Boreal Avian Modelling Project (Barker et al., 2015), supplemented with data from Automated Recording Units (ARUs; WildTrax, 2019).

of the vegetation, fire and bird databases and used these for parameterizing each of the climate-sensitive components of the respective models. We obtained annual (2011–2100) climate projection layers, downscaled to a 1-km grid cell resolution using the ClimateNA software, from forecasts of the Community Climate System Model version 4 (CCSM4) general circulation model from the U.S. National Center for Climate Research. CCSM4 is a coupled climate model that simulates earth's climate system. It was chosen due to its high spatial resolution (0.9424° latitude, 1.2500° longitude) and because it has shown good overall performance in other regions when compared to other climate models with available annual forecasts (Ahmed et al., 2019) and its averaged precipitation and temperature changes are is the closest to the ensemble model for our study region (Fajardo et al., 2020). We used climate forecasts under Representative Concentration Pathway (RCP) 8.5, which may be considered as a worst-case scenario of climate change for 2100 based on a continuation of current policies and economic incentives (Hausfather and Peters, 2020). We chose RCP 8.5 as evidence suggests that the average increase in temperature in the present century will likely exceed RCP 4.5 (Sherwood et al., 2020), supporting instead the use of RCP 8.5 for forecasts (Schwalm et al., 2020). We focus our current work on assessing uncertainty due to climate effect pathways, rather than other sources of uncertainty, such as choice of climate model or emissions scenario. The climate data was post-processed to match the resolution of the vegetation layers by applying a bilinear interpolation using the function *postProcess* from the reproducible R package (McIntire and Chubaty, 2021).

TABLE 2 | Wildfire, forest growth and landbird models used in a factorial simulation experiment to explore the pathways through which climate change might drive responses and forecast the net effect of climate change on different boreal landbird species.

Short code	Wildfire model	Forest growth model	Landbird model
I	SCFM	LandR	Birds
II	**FireSense**	LandR	Birds
III	SCFM	**LandR.CS**	Birds
IV	SCFM	LandR	**Birds.CS**
V	**FireSense**	**LandR.CS**	Birds
VI	**FireSense**	LandR	**Birds.CS**
VII	SCFM	**LandR.CS**	**Birds.CS**
VIII	**FireSense**	**LandR.CS**	**Birds.CS**

Each model type ($n = 3$) presented two possible formulations ($n = 2$; climate-sensitive and non-climate-sensitive). The factorial experiment used all eight possible combinations of these models ($2^3 = 8$). Climate sensitive model variants are indicated in bold.

Models

Forest Growth and Succession Models

For non-CS and CS forest growth and succession models we used the LandR Biomass and LandR.CS model suites, respectively. The LandR Biomass ("LandR" hereafter) model (**Supplementary Appendix II**), is an implementation of the LANDIS-II biomass succession model (v3.2.1; Scheller and Mladenoff, 2004) in R. LandR has some minor model algorithm differences compared to LANDIS-II, notably simultaneous within-year growth across cohorts, rather than sequential. As with LANDIS-II, there are many tree species-level traits to parameterize. We parameterized

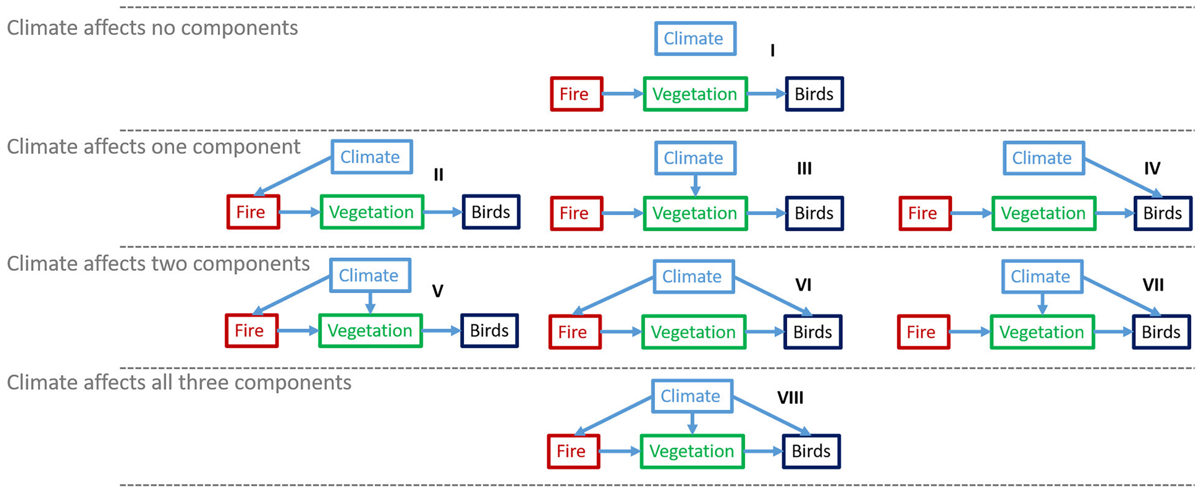

FIGURE 2 | Framework of the factorial experiment of vegetation (green), wildfire (red), and landbird (black) models. This factorial experiment covers the eight possible combinations of the two forms of the three models. The arrows represent the pathways via which climate might affect landbirds ("Birds"). Each graphical representation of the model combinations used can be matched with the model numbers (roman numbers) in **Table 2**.

tree species' *growth curve* and *mortality shape* based on permanent sample plot data (**Supplementary Appendix II** and Acknowledgments Section). For other species-level traits (*longevity*, *sexual maturity*, ability to *resprout*), we used the best available estimates from the literature and trait values used in LANDIS-II applications (**Supplementary Appendix II**). Briefly, during simulations using LandR, one or more cohorts (defined as the biomass of a given tree species with a given age in a pixel) is created and maintained as a non-linear function of growth and mortality equations (i.e., growth curves and within-pixel competition), dispersal dynamics, and responses to disturbances, such as wildfire (i.e., mortality, serotiny, and resprouting; more details in **Supplementary Appendix II**). The main output from LandR consists of annual tables and maps of the biomass and age of every tree species cohort in every pixel with at least one cohort.

To create the CS version of LandR, we modified cohort growth and mortality equations following the statistical approach developed in Luo et al. (2019). Rather than using their simultaneous multivariate approach, from which we could not correctly predict without developing our own custom statistical routines, we fit two separate univariate models for plot-level biomass growth increment (t/year) and biomass mortality (t/year) as functions of spatially explicit climate variables. Specifically, we first calculated the annual growth and mortality from permanent sample plots (**Supplementary Appendix II**) located in the Boreal and Taiga Plains ecozone. Even though there are permanent sample plots in the Northwest Territories, the (i) minimum three repeated measurements to fit a statistical model for growth and mortality are still lacking, (ii) there are not enough sampling plots to be modeled without supplementation from other portions of the ecoregion, and most importantly, (iii) there are concerns regarding the time disparity between repeated measures for these permanent sample plots and the reference years from other permanent sample plots. Therefore, we used data from across the southern part of the ecoregion in Alberta and Saskatchewan to be able to model the climate effects on growth and mortality. This also allowed us to encompass some of the warmer future climates that might characterize our study area in the future. We then related plot-level biomass growth increment and mortality to annual temperature anomalies (ATA) and an annual Climate Moisture Index (CMI; Hogg, 1994), accounting for cohort age (*sensu* Chen et al., 2016). We used a Generalized Linear Mixed Model (GLMM) and a Generalized Additive Model specifying the Location, Scale, and Shape of the data distribution (GAMLSS; gamlss R package; Rigby and Stasinopoulos, 2005), for growth increment and mortality, respectively. We then calculated CMI and ATA using historical monthly temperature and precipitation for summer months (**Supplementary Appendix I Figure A2**). For each driver (tree growth or tree mortality), we calculated the annual "climate effect ratio" (CER), which is the ratio of the growth (or mortality) under each annual future climate and the growth (or mortality) under the averaged historic climate, for each pixel. We finally multiplied the LandR-derived growth and mortality by this CER. This gives, for example, no change in growth (or mortality) when a future year has the same climate as the historical average, because the ratio is 1. As future climate changes, this ratio can go above or below 1, resulting in deviations from the non-CS stand-level growth (or mortality). We did not apply the CER to cohorts under 20 years of age because they were not represented in the permanent sample plots, lacking information on their climate sensitivity. We, therefore, determined their growth and mortality using the default LANDIS-II equations. We also placed upper and lower limitations on this ratio (1.66 and 1/1.66 = 0.6, respectively, which allows for up to a 66% increase or decrease in growth and mortality) in an attempt to balance two opposing sources of forecasting error: minimizing cases where we deemed that the extrapolation would be too great and not allowing for future climate to have unrealistically severe effects on growth and mortality. In other words, we used a percentile to estimate the effect of climate on growth/mortality for climate sensitive forest growth models, where we divided the current climate effects by reference climate effects. We used these upper and lower limits to circumvent problems caused by very small denominators as well as constraining predictions outside the data range used to generate the model. We selected these thresholds to be slightly outside the range of the most extreme predictions made within the first few decades of projected climate values. We attempted to extract tree species-specific CER, but there were insufficient sample sizes for most species. As a result, we used plot-level growth increment and mortality.

We ran the above dynamic forest growth models for all "treed" pixels, including treed wetlands. Land cover classes modeled were the ones classified as "treed" by Latifovic and Pouliot (2005), i.e., 1–15, 20, 32, 34, 35, and 39. Even though 34 and 35 are classified as burned, we converted those to the nearest-neighbor's forested class to allow for forest regeneration. We used Beaudoin et al. (2014) dataset as our starting layers for biomass (for details, please refer to **Supplementary Appendix II**). Data were not supplemented with the Northwest Territory's forest inventory data due to the small spatial coverage of this dataset in comparison to the size of our study area. We did not simulate dynamic vegetation changes for non-treed locations: non-vegetated, non-treed wetlands, shrublands, herb dominated, grasslands, croplands, and lichen dominated land cover classes, which summed to 35% of the total landscape cover. These were held static during simulations as we did not have access to a sufficiently fine-grained dynamic forest growth model within the study area.

Wildfire Models

We used two landscape fire models, SCFM and FireSense to represent non-CS and CS fire models, respectively. SCFM is a three-stage landscape fire model (Cumming et al., 1998; Armstrong and Cumming, 2003). It simulates wildfire as a process of ignition (fires that ignited at a given time period), escape from ignition pixels to neighboring cells (the binary probability of escaping or extinguishing), and spread from escaped pixels across a rasterized landscape (if a fire escapes, what is the probability it will burn the neighboring cells). This approach is a variant of percolation models (Hargrove et al., 2000). Fires are extinguished when no further spreading occurs. Each of the three stages is probabilistic, and the probabilities were estimated from historical fire data between 1965 and 2016 (Canadian Forest Service, 2019). We considered lightning-caused fires only, as human-caused fires have been negligible within our study area (Canadian Forest Service, 2019). We estimated ignition rate (fires per 100 km^2 yr^{-1} – translated to pixel-level probability of ignition) from all known fires of all sizes. We estimated the pixel-level escape probability as the ratio of fires >1 pixel to the number of fires. We calculated the mean size of escaped (i.e., realized) fires (>1 pixel area burned) from historic fire data obtained from the Canadian National Fire Database (Canadian Forest Service, 2019). We estimated the spread probability using a calibration approach whereby we simulated approximately 100,000 fires with different landscape-constant spread probabilities. We fitted a shape-constrained Generalized Additive Model (Pya and Wood, 2015) to the scatterplot of spread probabilities simulated fire sizes. From this curve, we determined the landscape-specific, pixel-level spread probability that reproduces the historical mean fire size for the landscape. All pixels were either flammable with their given ignition, escape, and spread probabilities (not only treed land cover classes, but also lower vegetation ones) or non-flammable (water bodies, ice and snow, rocks and non-vegetated areas such as human development). The model simulates stand-replacing fires only, and the only influence of climate and vegetation on SCFM is indirect through their influence on the historical fire regime.

FireSense also simulates fires through percolation as described for SCFM, but with ignition, escape, and spread probabilities that vary spatially and temporally as a function of annual fire weather and vegetation. We developed statistical models to predict the simulation parameters from these covariates, using methods adapted from Marchal et al. (2017a,b, 2019). We used Monthly Drought Codes from annual Global Climate Model projections (*sensu* Bergeron et al., 2010) as annual fire weather covariates. For ignition and escape, we classified the historical and projected landscapes based on land cover classes (Latifovic and Pouliot, 2005), while for spread, the most complex model of the three, we classified the historical and projected landscapes into one of the four land cover classes, following this order: (i) **young** (<15 years since disturbance), (ii) **deciduous** leading, (iii) **conifer** leading, and (iv) **other**; the pixel "leading" tree species or land cover class is that accounting the largest proportion of total species biomass.

Landbird Models

We used landbird density models fit by the Boreal Avian Modelling (BAM) project (Cumming et al., 2010; Barker et al., 2015) with avian point count data from the Boreal and Taiga Plains ecozone [as represented by Bird Conservation Region 6 (Bird Studies Canada and NABCI, 2014; **Supplementary Appendix I Figure A1**)]. Data were compiled as part of the BAM project and include data from both publicly available and independent projects within the boreal and hemi-boreal regions of North America. These human-based avian point-count surveys were conducted between 1993 and 2018. The BAM database was supplemented with point-count data from autonomous recording units (ARU) deployed in the Northwest Territories and Alberta between 2012 and 2018 by the Canadian Wildlife Service and the University of Alberta Bioacoustic Unit (WildTrax, 2019). The final database used to fit the bird models comprised 126,621 point-counts (5.5% of which were from ARUs), from a total of 42,612 sampling stations. This resulted in 975,527 individual bird records (**Table 1**) for the species modeled in this study. Of these point-counts, 63% took place in Alberta, 9% in British Columbia, 11% in Manitoba, 6% in Saskatchewan, and 11% in the Northwest Territories. Even though there is unbalanced spatial coverage due to the challenging nature of data collection in remote Northern forests, the data coming exclusively from the Northwest Territories still comprised almost 4,700 unique sampling stations. To minimize the influence of this spatial data imbalance on the landbird models, we weighted individual point-count observations (counts) according to the inverse of the number of surveys conducted within a 5 km × 5 km window around the survey station (including repeat visits to the same station), thereby down-weighting the influence of individual surveys in heavily sampled areas.

For each landbird species (n = 64; **Table 1**), we developed two species density models: non-CS (vegetation and terrain covariates only) and CS (vegetation, terrain, and climate covariates). Even though we recognize that the non-CS model is not necessarily insensitive to climate, its effect would be mostly indirect, and we chose to use a consistent naming convention (CS vs. non-CS) for our factorial experiment. These count models were fit as boosted regression trees (BRT) with a Poisson distribution using the *gbm.step* function in the dismo package (Hijmans et al., 2011), following methods outlined in Stralberg et al. (2015b). We used ten-fold cross-validation to assess model robustness to sampling bias. The covariates (**Table 3**) used for the bird model fitting were either: (i) assumed static over the simulated period and not allowed to change, e.g., water bodies, wetland, urban/agriculture, water proportion, human development proportion (Latifovic and Pouliot, 2005); (ii) static, i.e., topographic ruggedness (Sappington et al., 2007); or (iii) dynamic and allowed to change, e.g., tree species, biomass, age, and climate covariates. Tree species biomass covariates for fitting the bird models were derived from predicted biomass layers for 2001 or 2011 (Beaudoin et al., 2014, 2017). Pre-2006 sampling events were associated with the 2001 biomass data, whereas events from 2006 and up were associated with the 2011 biomass data. Tree species used for biomass covariates included the main tree species present in the study area: paper birch, tamarack, white spruce, black spruce, jack pine, and trembling aspen.

To standardize the landbird density models, we accounted for differences in sampling protocol and covariate effects on landbird species detectability using statistical offsets. This included the effects of time of day and day of year on the probability of availability given presence, and the effects of tree cover and land-cover type on the probability of detection given availability (Sólymos et al., 2013). Offsets were calculated based on removal and distance-sampling models (Sólymos et al., 2018). The adjustments appeared as offsets in the BRTs so that expected values represented species density. We assumed that ARU detectability rates were similar to those of human observers (after Van Wilgenburg et al., 2017; Yip et al., 2017). We assessed potential correlation between predictors using Pearson correlation coefficients between climate, topographic, and vegetation covariates. We did not include covariates that presented stronger correlation than 0.9 with other covariates (*sensu* Stralberg et al., 2015b).

We also summed relative importance of vegetation and climate variables (i.e., predictors) to assess the combined relative importance of climate vs. vegetation (and assumed-static covariates) in each species' model. The summed relative importance for climate predictors was compared with the net effect on occupancy (see below) using linear regression.

TABLE 3 | Type of covariates, covariate acronyms, definitions, and range of possible values for the covariates used to build the landbird models.

Type	Covariate acronym	Definition	Possible values
Naturally dynamic, but held static	wat	Sample point is defined as water	Binary variable, 1 or 0
	wet	Sample point is defined as wetland	Binary variable, 1 or 0
	led25	Water proportion within 5 × 5 moving window	Continuous variable, from 0 to 0.04
	dev25	Development proportion within 5 × 5 moving window	Continuous variable, from 0 to 0.04
Naturally static	vrug	Topographic ruggedness	Continuous variable, between 0 and 0.165
Naturally dynamic and simulated	Species_Betu_Pap_v1	Total biomass of paper birch	Integer variable, from 0 to 5599
	Species_Lari_Lar_v1	Total biomass (t/ha × 100) of tamarack	Integer variable, from 0 to 4364
	Species_Pice_Gla_v1	Total biomass (t/ha × 100) of white spruce	Integer variable, from 0 to 12822
	Species_Pice_Mar_v1	Total biomass (t/ha × 100) of black spruce	Integer variable, from 0 to 11257
	Species_Pinu_Ban_v1	Total biomass (t/ha × 100) of jack pine	Integer variable, from 0 to 8476
	Species_Popu_Tre_v1	Total biomass (t/ha × 100) of trembling aspen	Integer variable, from 0 to 14572
	Structure_Stand_Age_v1	Stand Age	Integer variable, from 0 to 298
	AHM	Annual heat-moisture index (MAT+10)/(MAP/1000))	Continuous variable, between 5 and 33
	CMD	Hargreaves climatic moisture deficit (mm)	Continuous variable, between 0 and 311
	eFFP	The day of the year on which frost-free period ends	Continuous variable, between 224 and 266
	EMT	Extreme minimum temperature over 30 years	Continuous variable, between −54 and −39
	FFP	Frost-free period	Continuous variable, between 49 and 125
	MAP	Mean annual precipitation (mm)	Continuous variable, between 217 and 839
	MAT	Mean annual temperature (°C)	Continuous variable, between −9 and 3
	NFFD	The number of frost-free days	Continuous variable, between 75 and 162
	PPT_wt	Winter precipitation (mm)	Continuous variable, between 28 and 164
	SHM	Summer heat-moisture index [(MWMT)/(MSP/1000)]	Continuous variable, between 18 and 111
	Tave_sm	Summer mean temperature (°C)	Continuous variable, between 8 and 18
	TD	Temperature difference between MWMT and MCMT, or continentality (°C)	Continuous variable, between 21 and 44

Land cover model covariates were derived from the Commission for Environmental Cooperation (CEC) North American Land Cover 2005, vegetation biomass was derived from Beaudoin et al. (2014, 2017) and climate covariates representing the 1981–2010 normal period were derived from Wang et al. (2016).

Quantifying Direct and Indirect Climate Effects on Landbird Occupancy

Our analyses were based on changes in mapped predicted densities within the study region, over the course of a simulation. Predicted densities in 2011 included large areas of very low (effectively zero) densities, outside of species' known distributions (BirdLife International, 2021), as well as very small areas with very high densities (up to three orders of magnitude higher densities than average). This increased the complexity of the estimation of density changes between scenarios. To address this, we converted species' density maps into occupancy maps by applying species-specific density thresholds defined by historically identified high density areas, i.e., areas where predicted densities exceeded the mean predicted density within the model-building area (*sensu* Stralberg et al., 2015a). Although the thresholds used to define occupancy may affect pixel-level changes, the relative magnitudes of direct, indirect, and net climatic effects are likely insensitive to the choice of threshold. Changes in thresholds used to define occupancy would likely modify the magnitude of change in occupancy, but not the qualitative differences in change observed among the three pathways. We generated these occupancy maps for 2011 and 2100, for each species, treatment, and replicate resulting in 160 maps per species (2 years × 8 treatments × 10 replicates).

For each landbird species, treatment and replicate, we subtracted the 2011 occupancy map from the 2100 occupancy map. The resulting 80 maps representing the changes in occupancy for each of the 64 species had pixels coded 1, −1, or 0, depending whether a pixel changed from 0 to 1 (gain of the given species in that pixel), changed from 1 to 0 (loss of the given species in that pixel), or did not change, respectively. For each pathway effect (direct, indirect via vegetation, indirect via fire), we stacked the 80 maps into two groups (CS and non-CS), resulting in 40 maps per pathway effect of the CS model versions, and 40 per pathway effect of the non-CS versions (i.e., vegetation pathway – CS group = III, V, VII, VIII and non-CS group = I, II, IV, VI; fire pathway – CS group = II, V, VI, VIII and non-CS group = I, III, IV, VII; direct pathway – CS group = IV, VI, VII, VIII and non-CS group = I, II, III, V; see **Table 2** and **Figure 2**). For estimating the net effect of climate, i.e., cumulative and additive effects of climate change pathways, we only used the full CS (Scenario VIII) and the full non-CS (Scenario I) models, which resulted in two groups of 10 maps per species. We then estimated the per-pixel probabilities of gain and loss for each of these groups (two additional maps), separately:

P_{gain} = *number of replicates with gain/total number of replicates* (i.e., either 40 if individual pathway effects, or 10 for the net effects)

P_{loss} = *number of replicates with loss/total number of replicates*

This resulted in 16 maps per species: one gain and one loss of occupied area maps for each of the two climate grouping, CS and non-CS, for each of the four pathway and net effects [(i) direct, (ii) indirect via vegetation, (iii) indirect via fire, and (iv) net effect, i.e., 2 × 2 × 4]. For each species, we multiplied probabilities by pixel area to estimate the mean areas (in ha) of species gain and loss per pathway. Then, for each species we subtracted areas of species loss from areas of species gain, to estimate the total climate effect on occupancy for each pathway. A schematic representation of this process is found in **Figure 3**. Information regarding code and data to reproduce the analysis can be found in a GitHub repository[1]. Finally, we mapped the change in the number of species (i.e., species turnover) between 2100 and 2011 due to net climate effects by calculating the difference in occupancy between the full CS (VIII) and full non-CS (I) models across species (**Figure 2**).

RESULTS

Landbird Model Performance and Variable Importance

Model performance varied widely across landbird species and models. Pseudo-R^2 values ranged from 0.02 (WIWA) to 0.459 (SAVS) for non-climate sensitive models, and from 0.079 (NOFL) to 0.705 (ATSP) for climate-sensitive models (**Supplementary Appendix III**). The total relative importance of vegetation variables averaged 59% in non-climate-sensitive models (with a mean *pseudo-*R^2 of 0.21) and 24% in climate-sensitive models (with a mean *pseudo-*R^2 of 0.25; **Supplementary Appendix III**). Climate-sensitive landbird models showed widely varying relative importance of climatic variables, ranging from 19% (OVEN) to 91% (WCSP) across species (**Supplementary Appendix I Figure A3** and **Supplementary Appendix III**).

Climate Effects on Forest Growth and Mortality and Wildfire

The CS forest growth simulation model showed a net increase in tree biomass of 400 kg/ha (15.4%; **Figure 4**) compared to results from the non-CS simulation model. CS fire simulations alone resulted in a net increase in tree biomass of 100 kg/ha, representing a 13% increase across the whole study area compared to results from the non-CS fire simulations (**Figure 4**). Another 100 kg/ha increase can be accounted for by interactions between fire and vegetation in the combined CS models. Thus, the net climate effect on tree biomass was an increase of 600 kg/ha in 2100 (**Figure 4**). Net climate effects on biomass changes can be spatially seen in **Supplementary Appendix I Figure A4**. The distribution of pixel-level leading tree species showed fairly modest changes, with higher deciduous conversion in the southeastern portion and more conversion to conifer in the central and eastern portions (**Supplementary Appendix I Figure A5**), with small increases in black-spruce dominated mixed stands, and small decreases in mixed stands dominated by white spruce and trembling aspen (see **Supplementary Appendix I** for detailed results).

Comparing CS to non-CS fire simulations, mean annual area burned increased by 280 thousand ha in 2100 (**Figure 5**). This represents a climate-driven increase of almost 90% relative to historical conditions (1965–2016). Given the modest changes in

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[1] https://github.com/tati-micheletti/NWT/tree/FEE

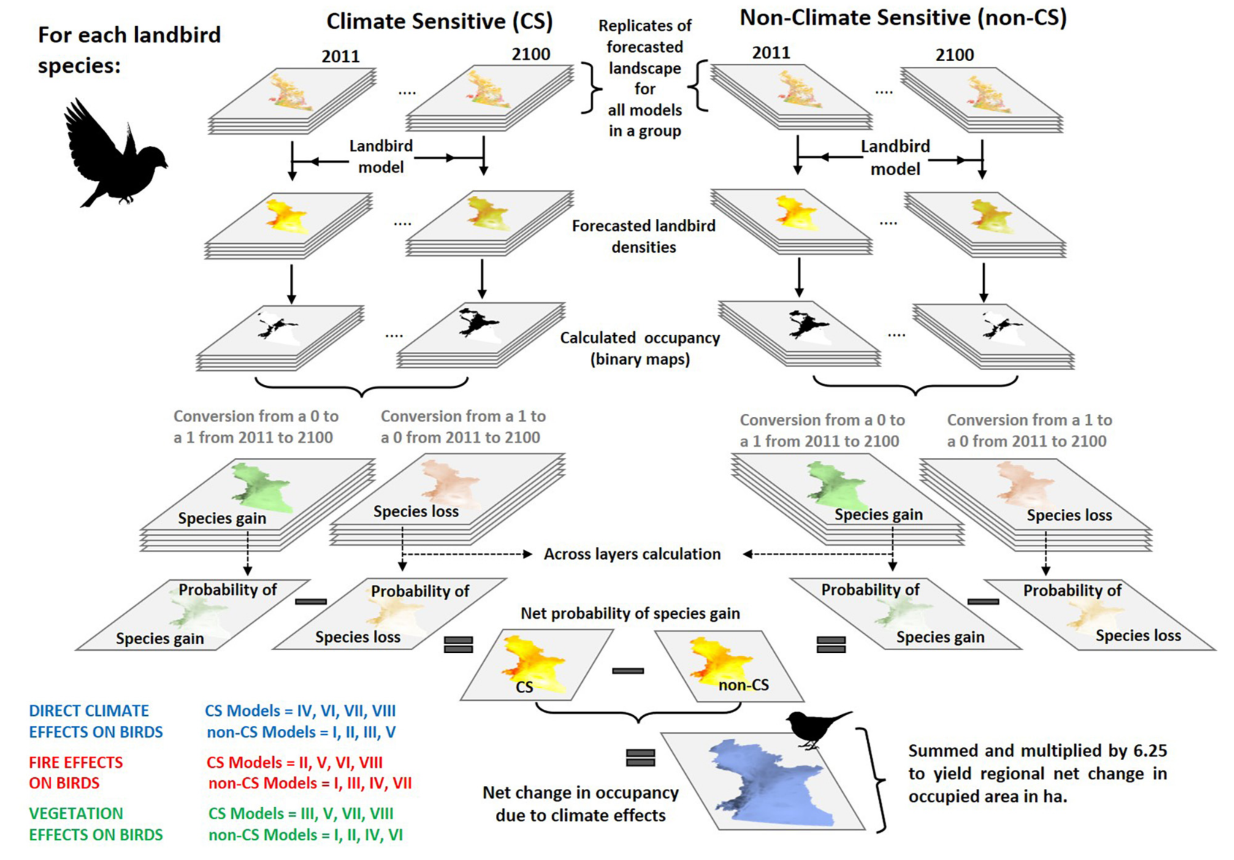

FIGURE 3 | Scheme describing the steps taken to calculate change in occupancy of landbird species by direct and indirect climate effects (summarized in **Figure 6**) from the forecasted landscape.

fuel type abundances reported above, this increase is attributable to the direct effects of climate warming on fire activity.

Climate Effects on Landbird Distributions

Climate change was projected to positively affect average landbird occupancy area in the Northwest Territories by about 7.39 million ha. This area represents approximately 15% of the Taiga Plains ecozone within the Northwest Territories (**Figure 6A** and **Supplementary Appendix IV**). Over all species, we forecasted a positive mean difference of 7.49 million ha exclusively due to the direct effects of climate change (dashed blue vertical line on **Figure 6B**), which were partially offset by a negative mean difference of 97 thousand ha due to indirect effects of climate via fire (dashed red vertical line on **Figure 6B**). Effects of climate via changes in forest growth and mortality were negligible (a positive mean difference of 4,250 ha; dashed green vertical line on **Figure 6B**). Overall, the direct effect of climate on landbirds was almost two orders of magnitude greater than the indirect effects, based on simulated changes in landbird distributions (**Figure 6**). We reiterate that results presented here are not simulated forecasts of future occupancy but instead represent the difference between forecasted occupancy with CS and non-CS models. Even though in some cases the present results might match forecasted occupancy (for example, if the forecasts of non-CS models are unchanging through time) the present results (**Figure 6**) should not be interpreted as future distribution shifts or range expansions and contractions without careful consideration of the control model (model I).

Approximately 19% of the landbird species showed both positive and negative direct effects of climate as measured by the gained and lost areas (blue bars on **Figures 6A,B**). Most species (75%) showed a net area gain to direct effect of climate when comparing variants CS vs. non-CS (**Figure 6A**), while for 25% there was a net area loss due to direct effects of climate, when making the same comparison. The indirect effect of climate acting through fire or vegetation on landbird distribution varied considerably among species, generating important spatial variation in local gain and loss of occupied area (**Figures 6**, **7**). The net climate effects across species were not correlated with the relative importance of climate variables in the CS models (**Figure 8**).

The forecasted effect of climate (CS vs. non-CS variants) suggested a net reduction in richness of up to 12 and seven species in the south-central and northeastern regions, respectively (**Figure 7**). In contrast, the western regions of the study area showed an increase of up to 20 species when comparing the CS vs. non-CS variants. Species turnover was highest in the

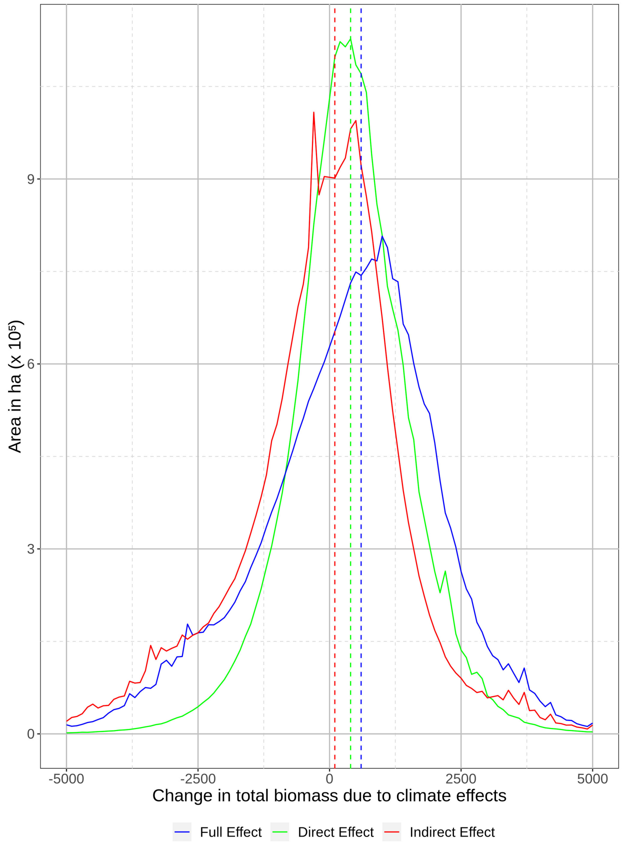

FIGURE 4 | Distribution of area (number of pixels multiplied by resolution) difference of simulated tree species biomass (kg/ha) across models and replicates within the study area in 2100. Dashed lines represent median of biomass differences due to direct climate effects on vegetation (+400 kg/ha; green), indirect effects via fire (+100 kg/ha; red), and the total net effects (+600 kg/ha; blue).

northeastern, south-central (higher species loss) and western regions (higher species gain) of the study area (**Figure 7**).

DISCUSSION

Understanding the relative importance of key pathways through which climate change affects ecosystems is important for informing potential adaptation and mitigation measures. The abundance and distribution of landbirds – and wildlife in general – are affected by climate change through the effects of climate on their habitat, more specifically on vegetation, i.e., indirect climate effects (Wisz et al., 2013), but also directly through, e.g., physiological responses to temperature and precipitation (Riddell et al., 2021). Understanding the relative influence of direct and indirect effects enables wildlife managers to identify opportunities to address negative effects of changing climate on valued ecological indicators (Bauduin et al., 2020). We present a novel evaluation of the relative influences of three potential climate-change pathways (vegetation, wildfire, and climate) on future landbird distributions in Northwest Territories, Canada. Direct climate effects were approximately two orders of magnitude more important in explaining predicted changes in landbird occupancy than the indirect pathways. Despite a 90% simulated climate-driven increase in annual area burned by 2100, this did not translate into major vegetation changes across our large study area. Models simulated an average increase of 600 kg/ha in tree biomass, but with only modest changes in leading tree species due to climate change. These results suggest that actions directed at indirect pathways such as wildfire suppression or forest management may not be enough to effectively mitigate landbird species distributional changes under climate change.

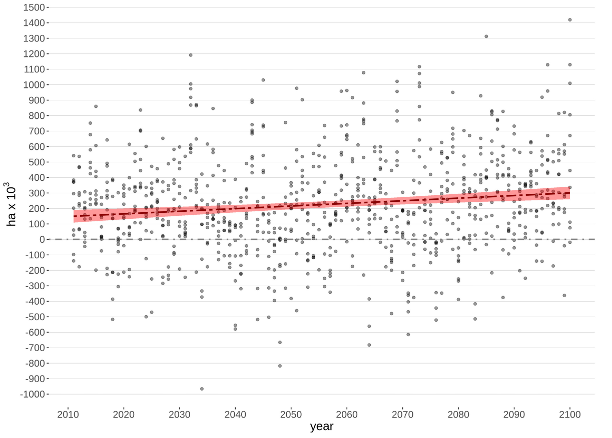

FIGURE 5 | Difference in mean area burned from 2011 to 2100 when simulating landscape change and wildfire between with climate-sensitive and non-climate-sensitive models [Scenarios (II, V, VI, VIII) – (I, III, IV, VII)] for the Taiga Plains Ecozone within the Northwest Territories (dots). The red line represents the fitted linear regression of values through time ($y = 1.7x - 3258.2$; $p = 0.00003$).

In our models, climate drives both forest growth and mortality (i.e., via climate-affected modifiers to these parameters), as well as the probabilities of wildfire ignition, escape and spread. Yet, the indirect effects of climate change on species distribution were still marginal compared to direct effects. This might be explained by vegetation lags. Rapid climate change, accompanied by a relatively slow vegetation change, could result in a state of disequilibrium between climate and vegetation (Wu et al., 2015). Stralberg et al. (2015a) drew attention to the importance of considering lags in vegetation responses to changes in climate when evaluating the effects of climate change on the distributions of boreal landbirds. In theory, the more important the vegetation lag, the more landbird species are likely to experience important range contraction, due to reductions in suitable habitat (Stralberg et al., 2015a). Still, based on the simulated changes in forest growth, mortality, and wildfire regime, our results suggest that vegetation lags may be longer than the simulation time span used in this study, and that direct and/or indirect effects of climate will not necessarily impose important range contractions to most of the 64 species we studied, as previously proposed. Farther south, in Alberta, Cadieux et al.'s (2019) projections suggest larger changes in species composition, reflecting shorter lags in vegetation response to climate change.

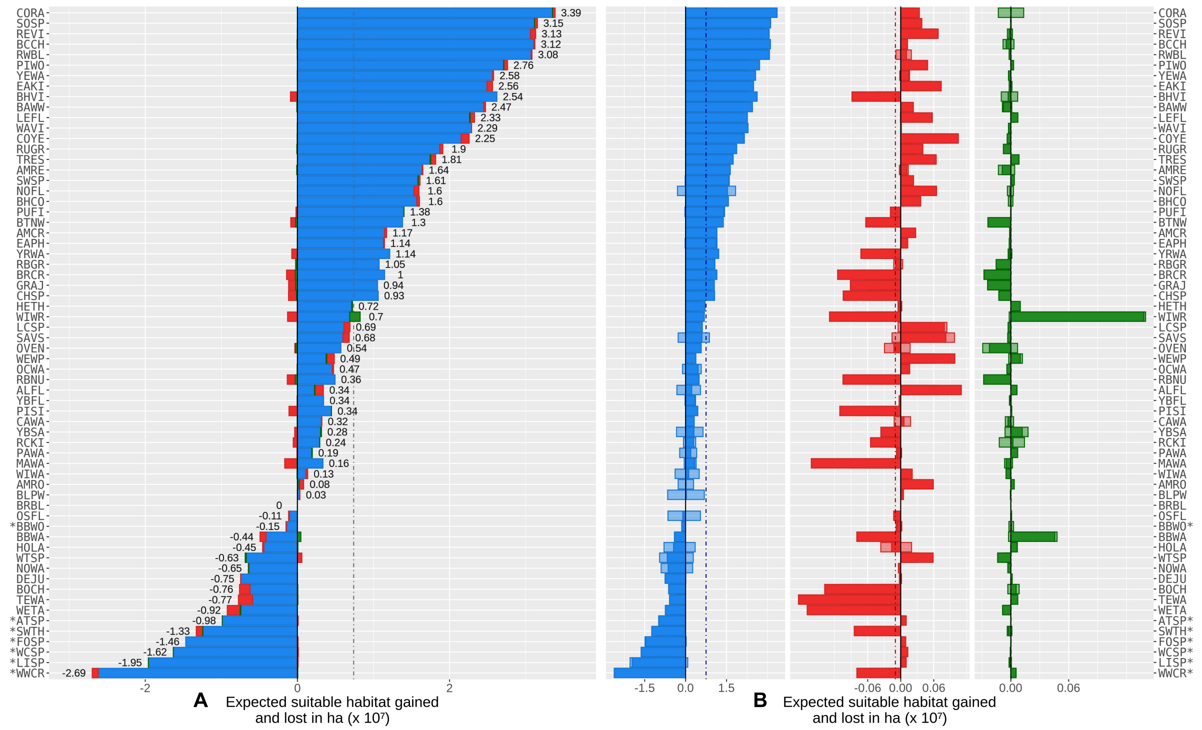

FIGURE 6 | Direct and indirect effects of climate change on the distributions of 64 landbird species within the study area (**Supplementary Appendix I Figure A1**). Effects are measured as the absolute or relative differences between paired climate-sensitive and non-climate sensitive models (**Table 1**) in the changes in pixel occupancy between 2011 and 2100, in terms of probabilities calculated over replicates. Left to right, **(A)** the net direct effects (Scenarios [IV, VI, VII, VIII] – [I, II, III, V], **Table 2**); blue), and indirect effects via fire (Scenarios [II, V, VI, VIII] – [I, III, IV, VII], **Table 2**; red) and via forest change (Scenarios [III, V, VII, VIII] – [I, II, IV, VI], **Table 2**; green). Net effects are the difference between the climate sensitive model and non-climate sensitive model predictions, after calculating the total net area (gained minus lost); **(B)** light colored bars represent mean expected areas gained (positive) and lost (negative) for each one of the bird species due to direct (blue) and indirect effects of climate (red via fire, green via forest change). Full color bars depict the net effect (gained minus lost) of each of these pathways. The dotted lines represent the average across species. Species for which the net differences in abundance between paired climate-sensitive and non-climate sensitive models (i.e., losses higher than gains) were higher than 90% are marked with an "*".

Projected shifts in climate and habitat resulted in species distribution patterns with 47 of 64 (73%) of species projected to show an increase in the area they occupy and 16 of 64 (25%) of the species projected to show a decrease in the area occupied within the study area by 2100 when comparing CS vs. non-CS variants. Of the 47 species which net climate effects would increase the occupied area, 72% (34 species) currently have their range centroid south of our study area, supporting previous results projecting northward range shifts of migratory birds (Hitch and Leberg, 2007; Langham et al., 2015; Bateman et al., 2020b; McCaslin and Heath, 2020). Interestingly, these results might point to slower rates of change in mountain ranges, as well as the ability for species to move up slopes to suitable habitats. Species whose models project increases in its habitat extent generally have diverse habitat associations; however, species with the largest net gains ("winners") are primarily associated with deciduous forests, e.g., Black-capped Chickadee (*Poecile atricapillus*), Yellow Warbler (*Setophaga petechia*), Black-and-white Warbler (*Mniotilta varia*), Least Flycatcher (*Empidonax minimus*), Warbling Vireo (*Vireo gilvus*), and Ruffed Grouse (*Bonasa umbellus*). Species whose models project the largest net losses ("losers") are species associated with: (1) conifer forest, such as White-winged Crossbill (*Loxia leucoptera*), Boreal Chickadee (*Poecile hudsonicus*); (2) non-forested habitats, such as Lincoln's Sparrow (*Melospiza lincolnii*), Fox Sparrow (*Passerella iliaca*); or (3) treeline-tundra habitats such as American Tree Sparrow (*Spizelloides arborea*), Horned Lark (*Eremophila alpestris*). These outcomes align with other simulation studies in the western boreal forests (Mahon et al., 2016; Cadieux et al., 2020), and highlight the importance of simulating landscape change with climate sensitive components when forecasting potential future species distributions. Still, two important caveats should be considered when interpreting these results. First, only forested habitats were simulated by the forest growth and mortality model which might influence expected changes in non-forested habitat, and consequently, on landbird species associated with these environments. Second, the extent of current range of landbird species could also influence expected gains and losses for species with narrow ranges within the data set, for example White-crowned Sparrow (*Zonotrichia leucophrys*). Although this species occurs within the Northwest Territories, it is uncommon across all of the northern region of Alberta, from which much of the data to fit the landbird statistical models was collected.

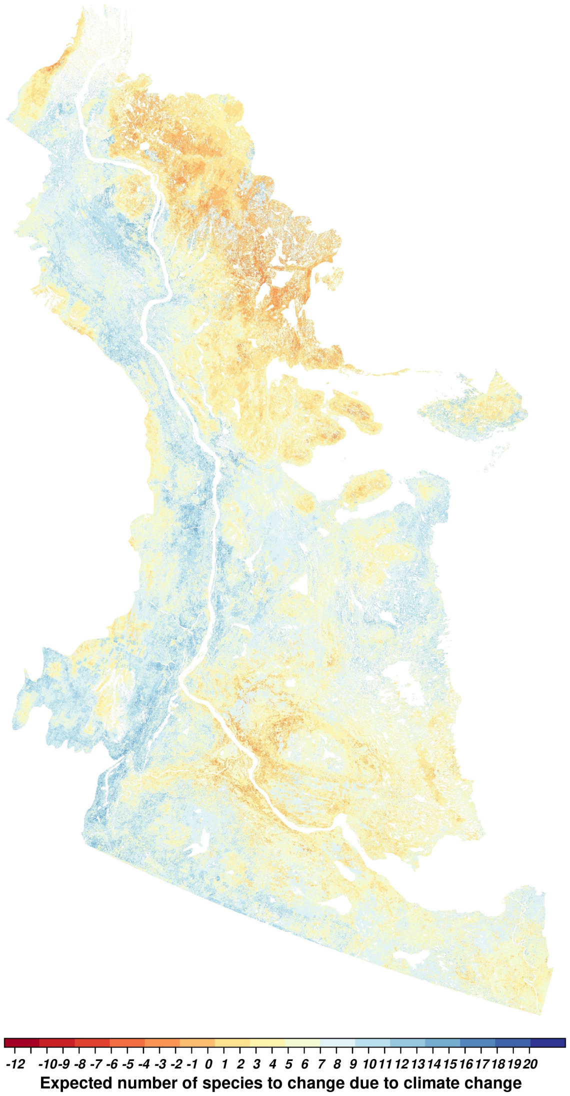

FIGURE 7 | Expected change in the number of species due to net effects of climate change (difference of the change from 2011 to 2100 between full climate-sensitive models and full non-climate-sensitive models) in the Taiga Plains ecozone within the Northwest Territories, Canada. Yellow to red values represent species losses, and yellow to blue values represent species gains.

In light of the highly variable magnitudes of potential vegetation change in the North (e.g., Rehfeldt et al., 2012), further studies should aim to better understand temporal response of both forested and non-forested habitats, and wildfire regime to climate change, including lag responses of vegetation to climate change, and further assess the implications of climate and landscape change on landbird communities.

The lack of a relationship between importance of climate variables in the species distribution models and the net climate change effects in simulation (**Figure 8**) implies that our forecasted changes in landbird occupancy are not simply a consequence of the strength of climate variables in the CS models. It may be explained by the fact that the predicted densities from a species distribution model are the *product* of the magnitude of the covariate effect (i.e., the importance of climate variables combined with the explanatory power of the model and the underlying simulated landscape covariates). This result (**Figure 8**) emphasizes the importance of actually *performing* forecasts (i.e., simulating landscape changes and forecasting species concurrent changes in occupancy) to understand plausible future outcomes (Dietze et al., 2018); it is not sufficient to infer possible futures directly from coefficients of species distribution models.

We recognize that there may be mismatches between the specific vegetation changes simulated and those captured by the landbird models, and that our results are a direct outcome of the particular forest growth and mortality, and wildfire models used. Our models also do not account for important ecological processes such as permafrost thaw or changes in surface hydrology (Helbig et al., 2016), nor do they capture or simulate extreme weather events (Tanner et al., 2017), that are likely to change with climate. We also could improve our models and obtain more refined landbird forecasts if including other explicit biological processes such as landbirds' dispersal capacity and potential changes in species interactions due to future climate change (i.e., mismatches in ecological networks). These processes could all alter avian habitat quantity and quality through direct and indirect mechanisms. Our choice of occupancy thresholds for landbirds may also have resulted in over- or under-estimation of species gains, losses, and turnover. However, this should not have influenced the overall patterns observed or our main finding, i.e., relatively small effects of indirect vs. direct climate pathways on landbird occupancy across our study area.

To our knowledge, this study represents the first example of a fully reproducible and reusable modeling workflow, covering every step from acquisition and assimilation of raw data, through the parameter estimation of all statistical models, the specification of simulation experiments, and their execution to generate the samples of forecasts. This study highlights the platform's ability to actually perform (i) yearly simulation of ecological processes (i.e., forest growth and wildfire) with (ii) existing feedbacks when forecasting species (i.e., landbird) distribution, in contrast to using a scenario based approach for forecasting, which neglects the effects ecological feedbacks among ecological processes, and (iii) on the same platform, as opposed to using one platform for the landscape simulation and another for wildlife modeling (*sensu* Regos et al., 2018), which improves both model reusability and nimbleness. This study also (iv) allowed us to account for direct effects of climate on both wildfire regimes and forest growth, and (v) represents both the vegetation component with a high level of details (i.e., several species cohorts per pixel), both of which have been previously identified as a limitation of other platforms and models (De Cáceres et al., 2013). Our workflow, using the SpaDES platform, allows for frequent updates and revisions, even to input datasets far upstream from the simulations. Further, at every step, we were able to include expertise of multiple subject experts to update and correct components of different models. We mixed numerous statistical modeling tools (e.g., BRTs, GAMLSS, GLM, GAMS, non-linear mixed effects models) and simulation paradigms

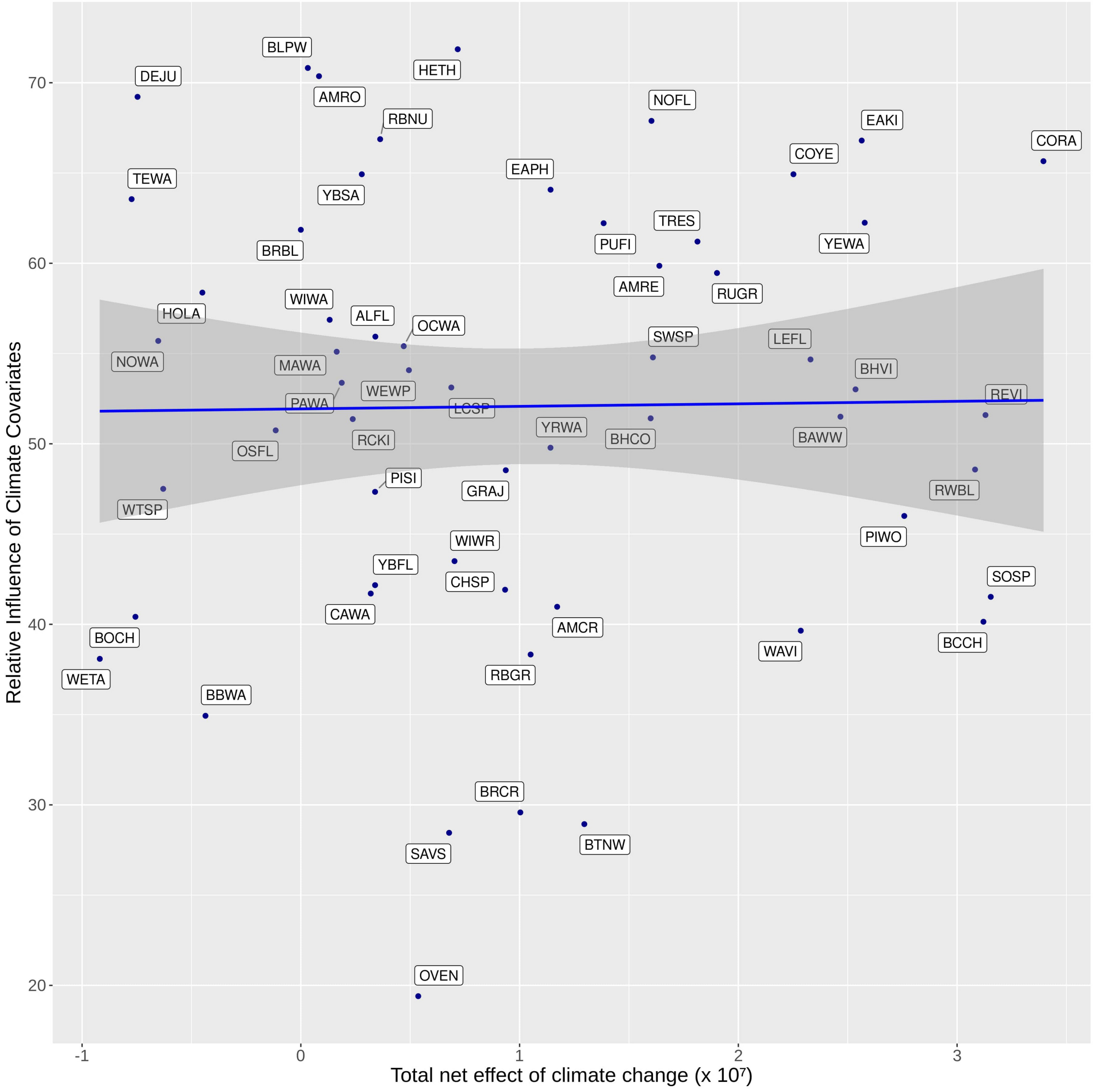

FIGURE 8 | Non-significant correlation (blue line) between relative importance of climate covariates in the climate-sensitive avian species distribution models and total net effect of climate change in terms of area – calculated as the difference of the area affected by climate change calculated between climate-sensitive and non-climate-sensitive predictions in 2100 – for 64 boreal landbird species within the Bird Conservation Region 6 within the Northwest Territories.

(e.g., percolation processes, continuous tree propagule dispersal, forest stand growth modeling), using the best science currently available from each discipline. The SpaDES platform allowed us to integrate these diverse tools in a single data-driven paradigm with reusable modular components (Chubaty and McIntire, 2021; McIntire et al., 2021). This platform is especially well suited to address the new generation of the ecological forecasting paradigm (Dietze et al., 2018; Stall et al., 2019; Bodner et al., 2020) and the implementation of the PERFICT approach (McIntire et al., 2021). This approach can, for example, help reduce model overfitting by enabling faster and iterative re-evaluation and updating of models and model fit. This can also be done, not only by the original model creators but also other researchers, when new data becomes available, speeding up scientific advances. This nimble approach can improve science-based decision making processes, where increasingly complex ecological processes and management objectives can be addressed (McIntire et al., 2021).

This study, and the use of the SpaDES framework, sets the stage for continued testing and development of models and hypotheses to inform land management. The two avian model variants used for this experiment, although not necessarily state-of-the-art models, were appropriate for forecasting because they only required external climate inputs, and tree species composition and age. This made these models particularly well suited for integration with ecological process forecasting, as they did not include covariates for which forecasted data is not available. As with most forecasting studies, there were a large number of ecological processes that were held static or not included in our simulations (e.g., wetland dynamics, permafrost change, extreme events, and anthropogenic disturbances), each of which may have impacts on our estimates of direct versus indirect climate effects on landbirds. A crucial element of our simulation system was the close connection between data and models, and between statistical data analysis and the parameterization of the ecological process models used in the simulation. SpaDES is the only platform, to our knowledge, that could handle our entire workflow. This study – and the models used and developed here – will become part of an iterative, continuously improving forecasting process (*sensu* Dietze et al., 2018; White et al., 2019). Future development will weave in forecast validation and integrate ecological processes (mentioned above), improving the capacity of these and other models to forecast likely impacts of climatic change and other processes of management concern.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

TM worked on the integration of models and development of the analysis. EM worked on the development of the analysis. DS, RP, SV, ML, CM, EB, SH, JT, and FSc worked on the development and assessment of the landbird-associated components. EM, SC, and IE worked on the development and assessment of wildfire-associated components. EM, CB, IE, and AC worked on the development and assessment of vegetation-associated components. All authors worked on the design, concept, and writing of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.679673/full#supplementary-material

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Understanding and Modeling Forest Disturbance Interactions at the Landscape Level

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Disturbances, both natural and anthropogenic, affect the configuration, composition, and function of forested ecosystems. Complex system behaviors emerge from the interactions between disturbance regimes, the vegetation response to those disturbances, and their interplay with multiple drivers (climate, topography, land use, etc.) across spatial and temporal scales. Here, we summarize conceptual advances and empirical approaches to disturbance interaction investigation, and used those insights to evaluate and categorize 146 landscape modeling studies emerging from a systematic review of the literature published since 2010. Recent conceptual advances include formal disaggregation of disturbances into their constituent components, embedding disturbance processes into system dynamics, and clarifying terminology for interaction factors, types, and ecosystem responses. Empirical studies investigating disturbance interactions now span a wide range of approaches, including (most recently) advanced statistical methods applied to an expanding set of spatial and temporal datasets. Concurrent development in spatially-explicit landscape models, informed by these empirical insights, integrate the interactions among natural and anthropogenic disturbances by coupling these processes to account for disturbance stochasticity, disturbance within and across scales, and non-linear landscape responses to climate change. Still, trade-offs between model elegance and complexity remain. We developed an index for the degree of process integration (i.e., balance of static vs. dynamic components) within a given disturbance agent and applied it to the studies from our systematic review. Contemporary model applications in this line of research have applied a wide range process integration, depending on the specific question, but also limited in part by data and knowledge. Non-linear "threshold" behavior and cross-scaled interactions remain a frontier in temperate, boreal, and alpine regions of North America and Europe, while even simplistic studies are lacking from other regions of the globe (e.g., subtropical and tropical biomes). Understanding and planning for uncertainty in system behavior—including disturbance interactions—is paramount at a time of

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accelerated anthropogenic change. While progress in landscape modeling studies in this area is evident, work remains to increase model transparency and confidence, especially for understudied regions and processes. Moving forward, a multi-dimensional approach is recommended to address the uncertainties of complex human-ecological dynamics.

Keywords: compound disturbance, linked disturbance, feedback effects, resilience, forest landscape model (FLM), landscape legacy, cross-scale interaction (CSI)

INTRODUCTION

Reciprocal interactions between disturbances and forested landscapes have been a cornerstone of landscape ecological research and modeling for decades (Baker, 1989; Mladenoff and Baker, 1999; Seidl et al., 2011; Perera et al., 2015). A current frontier in this line of research is the spatially explicit investigation of disturbance interactions across spatial scales (Buma, 2015; Burton et al., 2020; Canelles et al., 2021). Within forested ecosystems, natural disturbances, anthropogenic disturbances, and climatic and anthropogenic drivers interact across a range of spatial scales to shape forested landscapes in term of patterns, processes, and functions (**Figure 1**) (Turner, 2010). Modeling disturbance interactions can be particularly challenging when and where the cumulative effects of such interactions, including non-linear and threshold behavior, result in catastrophic mega disturbance (Millar and Stephenson, 2015). Hence, a combination of empirical and modeling studies is needed to understand forest ecosystem dynamics that emerge from the interactions of multiple disturbances as well as biophysical and demographic drivers within forested landscapes (Fraterrigo and Rusak, 2008; Johnstone et al., 2016; Davis et al., 2018).

Natural disturbances (e.g., wildfire and insect outbreaks) have traditionally been investigated separately within different sub-disciplines of ecology (fire ecology and entomology, respectively) and further separated from the effects of human disturbances, focusing therefore on the properties of "disturbance regimes" (patch size distributions, severity, frequency or rotation length; **Figure 2**) and with an emphasis on stochasticity. Despite the apparent stochastic nature of natural disturbances, disturbance regimes generally emerge from feedbacks between internal system processes and external drivers across scales in time and space (Peters et al., 2011). Comparatively, anthropogenic disturbances (e.g., harvesting; **Figure 2**) have been traditionally viewed as deterministic (i.e., under human control). Yet, human systems are subject to analogous uncertainty and surprise caused by economics, social pressures, and political change that directly impact our ability to implement harvest and other land use plans at the temporal scale of forest rotations (Messier et al., 2019). Interactions among natural disturbances, human disturbances, and vegetation responses to those disturbances further influence system predictability. Proactive and adaptive management practices that embrace system uncertainty are therefore needed to respond to emerging "surprises" in disturbance regimes (Foley, 2005; Peters et al., 2011; Parrott and Meyer, 2012; Allen et al., 2014).

Several conceptual advances have been proposed to help disentangle the emergent properties of disturbance interactions (Foley, 2005; Fraterrigo and Rusak, 2008; Turner, 2010; Peters et al., 2011; Buma, 2015; Messier et al., 2016; Kane et al., 2017; Davis et al., 2018; Ratajczak et al., 2018). These conceptual advances underscore the interplay between pattern and process in natural disturbance dynamics, deterministic and stochastic elements of anthropogenic disturbance, and uncertainty due to climate change that need to be accounted for in modeling frameworks of processes and disturbances across scales (Keane et al., 2015; Urban et al., 2016). Here, we review the conceptual advances and empirical approaches that help disentangle the apparent complexity of disturbance interactions. We further conducted a systematic review of forest landscape simulation modeling studies including more than one disturbance type published since 2010. A class of models known as forest landscape models (FLMs) dominated this field of study. We therefore overview the general design of FLMs, showing how recent developments have shifted from statistically-based disturbance regimes (i.e., static) to process-based methods where disturbance regimes and ecosystem responses are emergent behaviors (i.e., dynamic), and further expanded the ability to choose the degree of system feedbacks depending on the question at hand (Seidl et al., 2011; Keane et al., 2015; Perera et al., 2015). Studies were then categorized according to the specific disturbance interaction questions investigated (as clarified by recent conceptual advances) and the relative balance of static to dynamic model components across disturbance types. We argue for minimum standards in documentation – particularly as model complexity increases – for increased transparency and confidence in model results. We conclude highlighting the current limitations, frontiers, and directions in the understanding and modeling of disturbance interactions at landscape levels.

CONCEPTUAL ADVANCES

Disturbances act upon the components of an ecosystem in a way that changes the structure defining the system (Pickett and White, 1985; Rykiel, 1985; Lindenmayer et al., 2017; Newman, 2019). Within forested ecosystems, a disturbance typically disrupts the functioning of its dominant life form (trees) via physical or chemical damage impacting growth and survival. The effects of disturbance can range from "pulse" disturbances that are concentrated in space and time and lead to abrupt change (Jentsch and White, 2019) to "press" disturbances that are diffuse in space and time and lead to cumulative system stress (Bender et al., 1984). The intensity of a disturbance is measured in terms of force, energy, or analogous quantity (e.g., density of insects), while the severity of the disturbance is the consequence

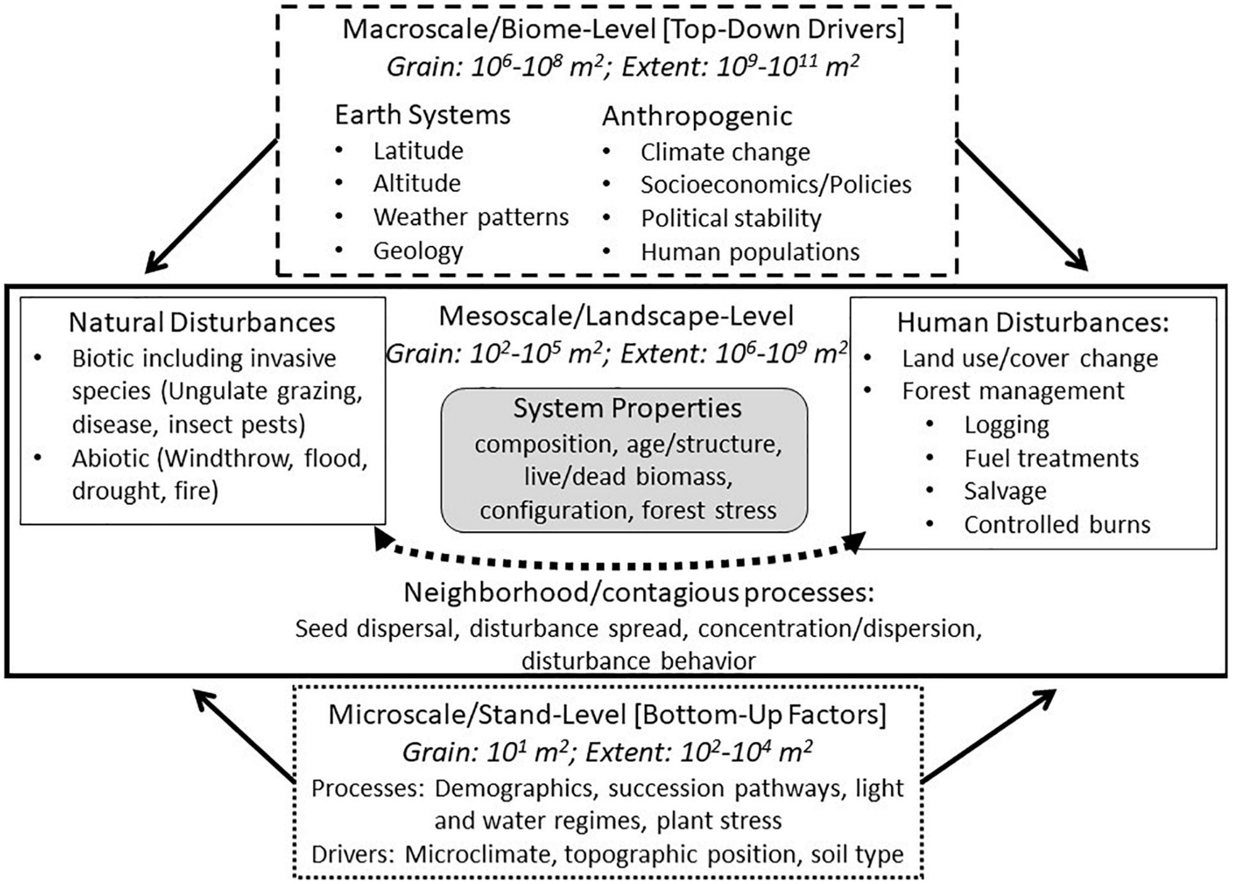

FIGURE 1 | Disturbances at the mesoscale (landscape-level) are affected processes and drivers (bottom-up) at the microscale (stand-level) and higher-order drivers (top-down) at the macroscale (biome-level). Landscape disturbances interact in space and time with reciprocal feedback evident at the landscape level (double-arrow dotted lines). Cross-scale interactions occur where either both bottom-up processes and/or top-down drivers amplify or attenuate disturbance processes within landscapes via threshold behavior in time and space.

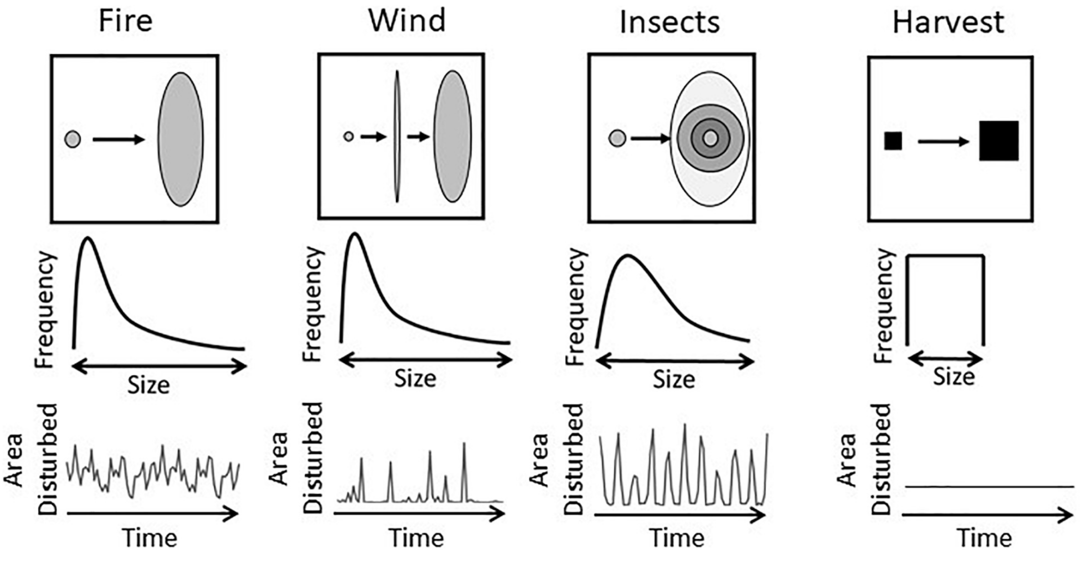

FIGURE 2 | Disturbance regimes are traditionally characterized according to size distributions, shapes (e.g., wind), degrees of intensity (e.g., grayscale under insects), and temporal patterns.

of that disturbance intensity on the state of the system (Keeley, 2009). Diversity in life history traits among tree species and other life forms mediate the relationship between disturbance intensity and severity via adaptation (Noble and Slatyer, 1980). Defining characteristics of a disturbance also depend on the scale of observation (Allen and Hoekstra, 2015). For example, a disturbance may be locally abrupt and severe (e.g., killing individual trees) but broadly diffuse and mild if killed trees are thinly dispersed across a large area. Once disturbed, forest system traits such as crown closure, height, and composition can take a long time to recover via the processes of recolonization, growth, and succession, respectively. Disturbances therefore affect landscape spatial heterogeneity including tree-species composition, age structure, and configuration (e.g., James et al., 2011b; Sturtevant et al., 2014).

Disturbance Interaction Process and Terminology

The opportunity for disturbance interaction occurs when one event follows another. Kane et al. (2017) observed that the likelihood of such occurrence depends on both the frequency and size of each disturbance, where opportunities for disturbance interactions increase by chance alone as their respective frequency and size increase. The nature of the specific interaction may be determined by a range of factors such as the disturbance mechanisms at play, the precise sequence, extent, and arrangement of the overlap, and the time since the previous disturbance (Kane et al., 2017; **Figure 3**). Interactions may include one or more types defined by the constituent components of the disturbance event—its incidence/extent, its intensity, and (or) its effects (Kane et al., 2017). Any of these components may be positively or negatively affected, or otherwise unaffected by the previous event. The nature of the interaction can also take multiple forms—for example the effect of one disturbance on another, or the combined effect of two disturbances on an ecosystem property or function.

From a disturbance-interaction standpoint, the legacy from one disturbance becomes the new system state for the subsequent disturbance (Peterson, 2002). A "linked" disturbance interaction occurs when the legacy of one disturbance is a critical driver for another, affecting the likelihood, extent, or severity of the second disturbance (Buma, 2015). As elaborated by Kane et al. (2017), the specific components underlying the interaction are important to the nature of that interaction. For example, logging disturbance does not generally affect either the incidence (frequency and extent) or intensity of windstorms. In this regard, a wind event following logging disturbance might be considered a "random co-occurrence" (sensu Burton et al., 2020). However, the severity (i.e., effects) of a given wind event can be strongly linked to logging practices – for example, taller trees (generally older) tend to be more susceptible to wind damage than shorter (generally younger) trees, hard edges created by specific logging practices can increase the susceptibility of trees along that edge, and tree species with different rooting habits or wood densities can have differing responses to winds of a given intensity (Quine et al., 1995). Hence, patterns of wind effects may well be linked to the legacy of logging practices. Conversely, if salvage logging is a commonly applied practice, then the incidence and extent of salvage logging will be linked to the disturbance patterns created by wind events.

The occurrence, relative strength, direction, and duration of linked disturbance interactions are mediated by both internal ecosystem processes and external drivers. For example, insect disturbance leading to tree mortality can create pulses of heavy fuels that can set the stage for higher severity fire once the new fuels become combustible, but the period over which that legacy persists as a factor affecting fire depends on fuel decomposition rates (Fleming et al., 2002; but see Section "Empirical Approaches, Challenging Long-standing Dogma"). In some boreal systems, harvesting can transition highly flammable conifer forests to fire-resistant deciduous forest (Carleton and Maclellan, 1994; Cumming, 2001)—a legacy mediated by internal ecosystem recovery processes. Opportunities for disturbances to interact at a given location are therefore sensitive to the timing and sequence of when and where a given disturbance event overlaps a subsequent one, contingent on any relevant time-lag effects (Burton et al., 2020). For example, while tree-killing disturbances can influence soil stability underlying the likelihood of landslide disturbances, this linked disturbance interaction is constrained by topography (i.e., slope angle and position) (Carabella et al., 2019).

Certain disturbances are more sensitive to forest composition or age structure than others, and this sensitivity will determine the relative strength of the feedback between vegetation, the specific disturbance, and (by extension) linked interactions with other disturbances. For instance, most outbreaking insects are limited to a few host tree species, leading to relatively strong feedbacks between vegetation and insect disturbance impacts across all three interaction types (incidence, intensity, and effects; **Figure 3**) (Ohmart, 1989; Hennigar et al., 2008; Bentz, 2019). When landscape spatial pattern is shaped by the cumulative effects of one disturbance (e.g., logging; Sturtevant et al., 2014), the consequent spatial pattern can either enhance or limit subsequent disturbances in terms of their intensity, duration, and size (e.g., insect outbreak; Robert et al., 2018). Such disturbance "legacies" often accumulate across space and time, producing "landscape memory" (Peterson, 2002) with important consequences for future disturbance regimes and consequent landscape dynamics (Foster et al., 1998; Buma and Wessman, 2011).

"Looped disturbances" form a subset of linked disturbance interactions in the form of recurrent disturbances with feedbacks that create a metastability of the system (Burton et al., 2020). Classic looped disturbances are often associated as a component of disturbance regimes supporting a systems' historic range of variability (HRV; Landres et al., 1999). For example, boreal conifers with fire-dependent life-history traits (e.g., serotiny) are both adapted and conducive to infrequent but extensive crown-fire events. Likewise, many temperate pine systems once dominant across much of the southern United States (Hanberry et al., 2020) are adapted (e.g., thick bark, high canopy) and conducive (e.g., grassy flammable understory) to frequent surface fire events (**Figure 4**). Looped disturbances of the same

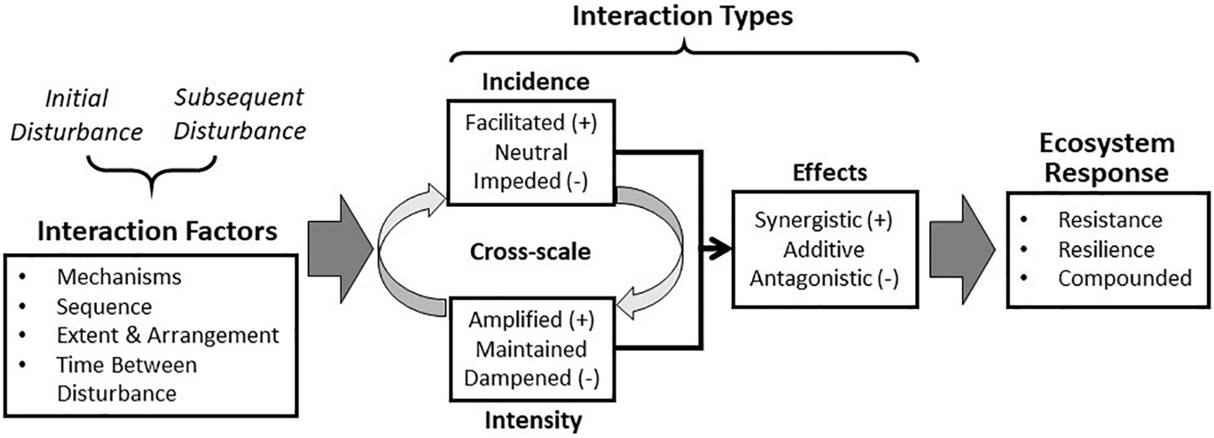

FIGURE 3 | The factors and processes specific to disturbance interactions. A series of *interaction factors* define the degree and strength of the disturbance interaction, which may manifest through one or more interaction types any of which may be positive, negative, or neutral. Feedback between interaction types (and also drivers; **Figures 1**, **5**) may manifest as *cross-scale interactions*. Ultimately, the effects of the disturbance interaction determine the ecosystem response (**Figure 5**). Reprinted from Publication: Forest Ecology and Management Vol 405, Characterizing interactions between fire and other disturbances and their impacts on tree mortality in western U.S., p188–199, 2017, with permission from Elsevier.

type can occur wherever life history traits of the primary vegetation are adapted to given type of disturbance so that it replicates itself – such as the build-up of fir regeneration in the understory that is released by the periodic defoliation by eastern spruce budworm (*Choristoneura fumiferana* Clemens) in the North American boreal forest (Baskerville, 1975). More complex looped disturbances across disturbance types are also possible when those types help reinforce each other in sequence (as illustrated by Burton et al., 2020).

"Compound" disturbance interactions occur when the combination of two or more disturbances have a multiplicative effect over the state of the system (Buma and Wessman, 2011), often via the recovery processes affecting ecosystem resilience (Buma, 2015; Coop et al., 2020). In the above example for boreal conifers, two fires in rapid succession can burn the tree regeneration of a serotinous species before they have sufficient time to produce new seeds—dramatically delaying subsequent system recovery (**Figure 4**). Indeed, starkly different vegetation communities resulted from different combinations and sequences of fire and wind in Minnesota as the life history strategies of different tree species were affected quite differently by each disturbance type and their compound disturbance effects (Johnstone et al., 2016). By contrast, regeneration failure due to more frequent fire is a feature of pine savannah (**Figure 4**) (Hanberry et al., 2020). Decreasing fire frequency enhances regeneration success, leading to increased stem density and canopy connectivity that make the systems more susceptible to catastrophic disturbances such as bark beetles, crown fire, or both in combination (Negrón and Fettig, 2014; Clarke et al., 2016). The consequence of the restriction of a fundamental structuring agent in this example (frequent surface fires) is therefore a bifurcation of the system to the extremes: either closed canopy forest or grassland (**Figure 4**). Analogous patterns have been observed in many regions (e.g., western North America; Coop et al., 2020). The potential for compound disturbance is likely increasing as climate change can directly and indirectly affect disturbance processes (Soranno et al., 2014; Becknell et al., 2015), human land use intensification is disrupting natural disturbance regimes on a global scale (Foley, 2005), and increasing mobility and transportation increases novel introductions of pests and disease (Liebhold et al., 2017). Such broad-scaled changes can have non-linear "cascading effects" resulting in disturbance regime shifts and transforming the system to alternative states (Buma and Wessman, 2011; Buma, 2015; Johnstone et al., 2016; Ramsfield et al., 2016; Burton et al., 2020).

The effects of the disturbances and their interactions depends on a larger context of system dynamics. This larger context includes (1) external drivers operating at regional scales [e.g., biome constraints (Burton et al., 2020), anthropogenic pressure (Turner, 2010)] (**Figure 1**), (2) states of the system (e.g., vegetation composition, age structure, soil conditions, etc.) that determine the behavior and effects of (3) disturbance mechanisms (e.g., defoliation, stem breakage, and combustion) that in turn determine the new state of the system (Peters et al., 2011; **Figure 5**). The new state is considered the legacy of the disturbance, upon which internal ecosystem processes (e.g., recolonization, growth, and succession) enable subsequent system recovery (Peterson, 2002, Johnstone et al., 2016). The type of ecosystem response, as defined by Kane et al. (2017; **Figure 3**), depends upon how the disturbance legacy relates to the internal processes of the system. If the essential structure (i.e., tree density, size, and composition) remains effectively intact, the ecosystem response is one of *resistance*. If the system requires a longer recovery period but remains within the natural variability of the broader ecosystem, the ecosystem response to the disturbance interaction is one of *resilience*. If the recovering system falls outside that natural variability the disturbances *compounded* to result in an alternate system state (**Figure 5**). External drivers such as climate and climate change interact with disturbances via three pathways (Seidl et al., 2017) – *directly* via its effect on a

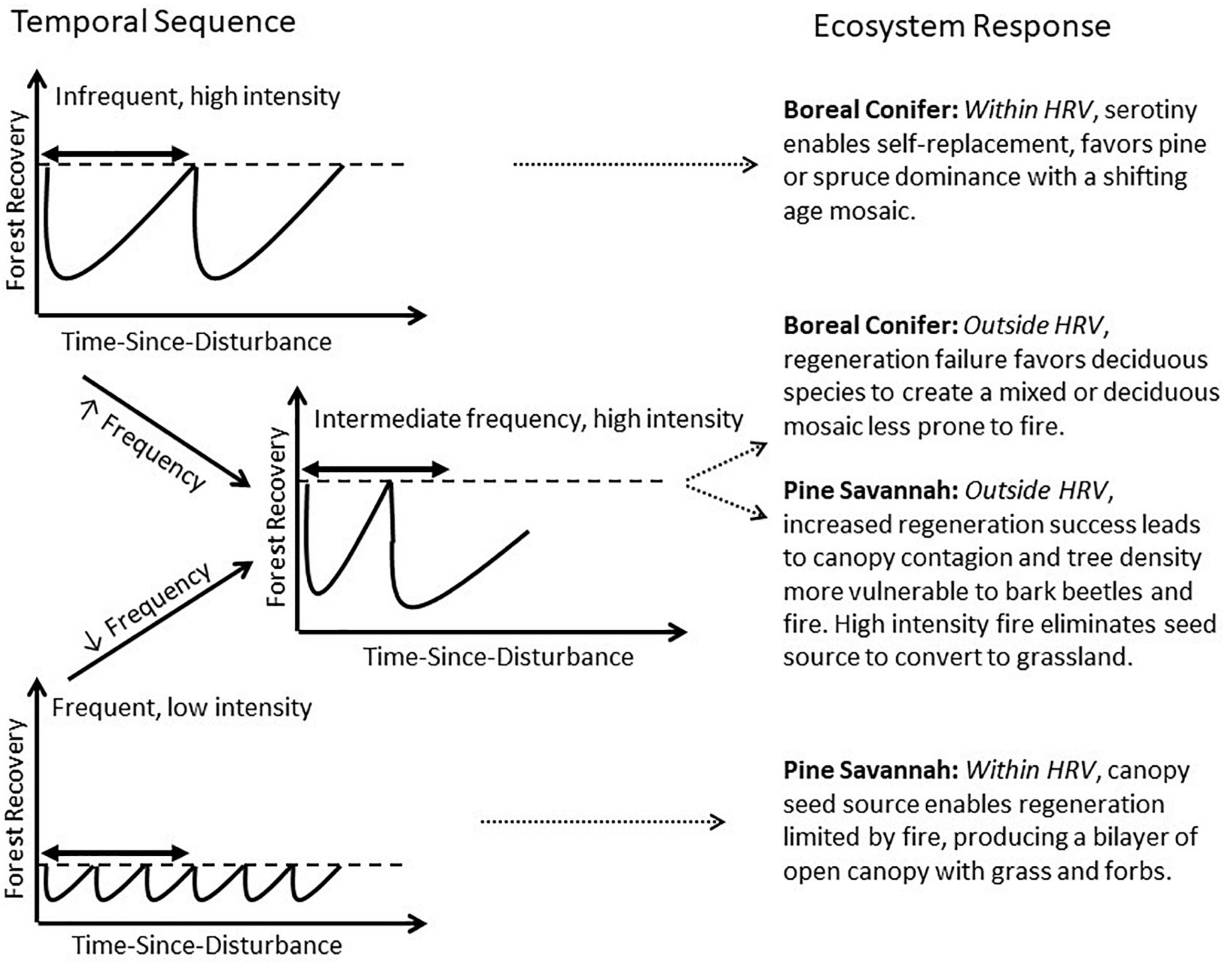

FIGURE 4 | Compound disturbances are those affecting system recovery (i.e., resilience), where the Historic Range of Variability (HRV) serves as the context for ecosystem resilience. By example, serotinous boreal conifers are adapted to high intensity crown fire but require sufficient time to develop a canopy seed bank. Non-serotinous pines often require frequent fire to dampen regeneration to maintain open savannah structure. Fire frequencies intermediate to these extremes can consume the seed producing potential in either system, leading to a conversion to new systems (see text for references).

disturbance property such as incidence or intensity, *indirectly* via effects on internal processes that modify system properties that in turn affect the disturbance process, and through a *secondary interaction* with another disturbance process that in turn affects the focal disturbance (i.e., the focus of this paper).

Cross-Scale Interactions

To understand processes affecting multiple disturbances and their interactions, integration of processes and disturbances operating at more than one scale is needed (O'Neill et al., 1996; Wu and David, 2002; Peters et al., 2007; Soranno et al., 2014) (**Figure 1**). Living and non-living elements of a system tend to interact most strongly with other elements that have characteristic process rates and spatial scales similar to their own (Allen and Hoekstra, 2015), leading to more closely-linked feedbacks within a single domain of scale (Messier et al., 2016). For example, at tree and stand-levels, life history traits of tree species affect demographic (mortality and recruitment), ecosystem (nutrient cycling), and disturbance (e.g., flammability, plant defense, etc.) processes that can include neighborhood effects that may also be self-reinforcing (Frelich and Reich, 1999). Nonetheless, the statistical properties of disturbance regimes (i.e., **Figure 2**) are not defined by processes at any one scale, but rather they emerge from the interactions of processes across scales (**Figures 1**, **5**). So while compartmentalizing system dynamics into scale-specific components is a useful way to disentangle system complexity (Allen and Hoekstra, 2015), cumulative changes at one scale can either amplify or attenuate system behaviors across scales—a phenomenon known as a "cross-scale interaction" (Peters et al., 2004, 2007; **Figure 3**). For example, when local fuels become interconnected across landscapes to the point that firestorms (fire events that create their own weather) are possible, then discontinuities that previously served as fuel breaks may become irrelevant (Peters et al., 2004).

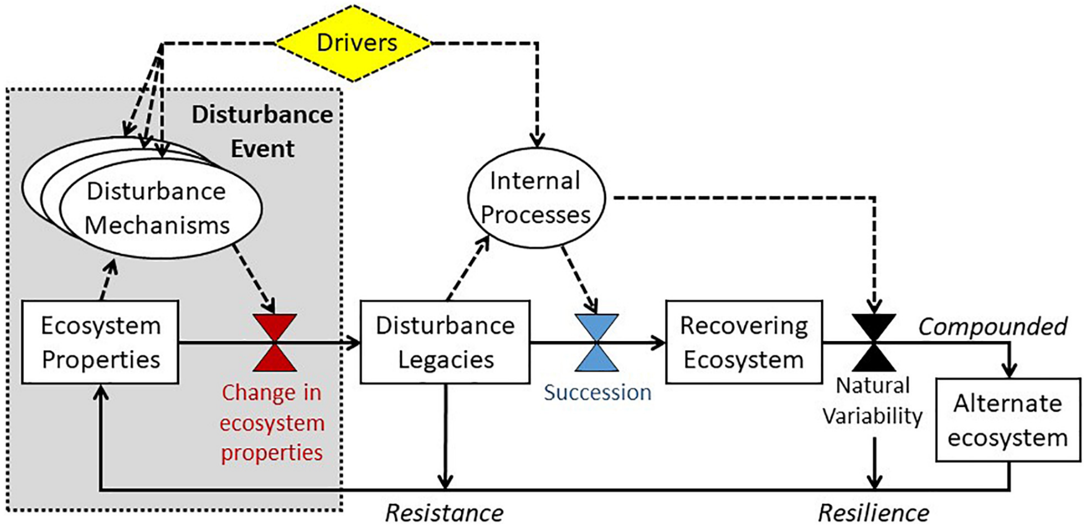

FIGURE 5 | Disaggregating disturbance mechanisms, drivers, and internal processes affecting ecosystem response to disturbance interactions. Drivers (yellow) refer to the microscale and macroscale factors affecting mesoscale dynamics in **Figure 1**. Hourglass symbols represent system changes that can either be abrupt (red – rapid disturbance effects), gradual in time (blue – succession), or gradual in space and time (black – natural variability in local system states). Depending on the degree of change in system properties, the legacies that remain, and the recovery processes, the mesoscale ecosystem response can be one of resistance, resilience, or (if overlapping disturbances compound to impede recovery processes) transformation to an alternative system. (Adapted from Peters et al., 2011).

Cross-scale interactions often underlie dramatic change as a system shifts from a strong negative effect to a strong positive one. More precisely, different processes operating at different scales can work synergistically to amplify disturbances across scales. For example, tree-killing bark beetles subject to strong, non-linear and density-dependent feedbacks (e.g., Raffa et al., 2008) are often linked to other disturbance types. Under low-density endemic situations, individual healthy trees easily defend against attacking beetles. Outbreaks are generally triggered by drivers that enable beetle populations to grow sufficiently to overwhelm the resources of healthy trees. In Europe, windstorm events provide a pulse of food resources in the form of weakened or fresh-killed trees (i.e., a disturbance legacy) that enables European spruce bark beetle (*Ips typographus* L.) populations to increase to the point they can overcome adjacent healthy tree defenses, such that a strong negative feedback (strong defense) changes to a strong positive feedback (ample food) (Kausrud et al., 2012). Such an effect can be further amplified if wind events overlap periods of drought, where trees are already stressed and defenses weakened (Kausrud et al., 2012). Climate warming in central Europe serves as a common driver increasing the frequency and intensity of windstorms, the frequency and intensity of drought events, and decreasing generation time of *I. typographus* to dramatically increase population growth potential (Senf and Seidl, 2018, **Figure 6**). Climate-driven synergies underlying explosive outbreaks of this insect have been further exacerbated by a long history of spruce plantation establishment in the region (Jansen et al., 2017), leading to relatively continuous food resources (Seidl et al., 2016b, **Figure 6**). While this example appears like a “perfect storm” event, it is a pattern replicated across many forest insect systems across the globe, particularly in bark beetle systems subject to similarly strong non-linear feedback processes (Burton et al., 2020; Kneeshaw et al., 2021).

Insights From Conceptual Advances

Current conceptual advances in disturbance interaction investigation include formal disaggregation of disturbances into their constituent components, embedding the disturbance process into system dynamics affected by both external drivers and internal processes (**Figure 5**), and explicitly recognizing the interaction factors, types, and ecosystem responses (**Figure 3**). While early modeling investigations of disturbance interactions focused only simple binary interactions (**Figure 7**; Mladenoff et al., 1996), the desire to include more processes structuring landscapes has spurred development and application of more complicated and complex models including many interacting disturbances having direct and indirect effects (**Figure 7**) – a theme we will return to in Section “Modeling Approaches.” Furthermore, under the Anthropocene, socio-economic drivers are crucial to include as well in forest disturbance models (e.g., **Figure 6**).

Importantly, the same drivers affecting disturbance mechanisms may also influence the internal processes affecting ecosystem response (**Figure 5**). The sum total of the drivers’ effects on disturbances, internal processes, and their interactions can lead to changes in system properties and system behaviors that can be either gradual or abrupt, depending on the direction and form of the effect (Ratajczak et al., 2018). Empirical disturbance interaction studies (see Section “Empirical Approaches”) should therefore take care to define the nature and form of the interaction explicitly, while models (see Section “Modeling Approaches”) should effectively capture the form,

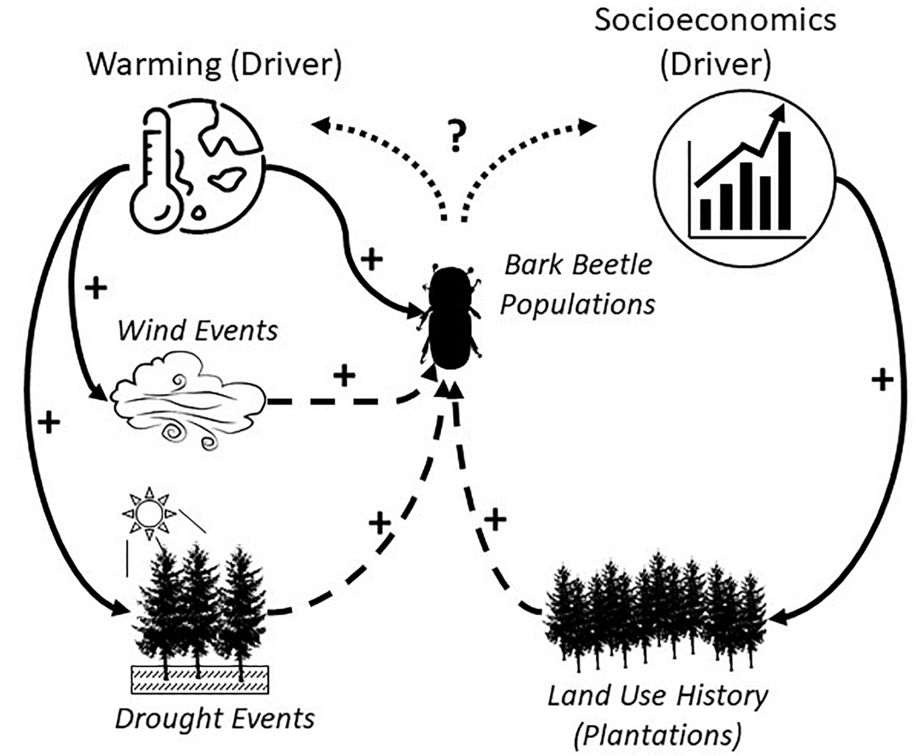

FIGURE 6 | Direct and indirect interactions of disturbances and drivers contributing to the amplification of a disturbance agent, illustrated using the European spruce beetle example from central Europe (see Section "Cross-Scale Interactions").

direction, and magnitude of interaction processes, including accounting for processes that transcend spatiotemporal scales.

EMPIRICAL APPROACHES

In the last decade, there have been several excellent papers reviewing interactions among disturbances. For example, Kleinman et al. (2019) reviewed compound disturbance interactions reported in nearly 300 journal articles, finding that such studies tended to be concentrated in North America, and focused primarily on fire, wind, and salvage logging. Salvage logging interactions have been more extensively reviewed by Leverkus et al. (2018) and Thorn et al. (2018), demonstrating a concentration of such studies in North America and Europe. Kane et al. (2017) reviewed fire interactions with other disturbance types concentrating on studies from the western United States (**Figure 3**). Kolb et al. (2016) reviewed the responses of biotic disturbances (insects, disease, and parasitic plants) to drought in the United States. Emerging from their review was a series of observed trendlines between different classes of insects and disease and their impact response to drought severity. Canelles et al.'s (2021) systematic review focused on disturbance interactions between insect disturbance and other forest disturbance types, and included a synthesis revealing different processes underlying those interactions. Seidl et al. (2017) performed a meta-analysis of the direct, indirect, and interaction effects of climate change on disturbance processes. Among the commonalities of these different synthesis articles is the geographic concentration of studies primarily in North America and Europe, an emphasis on certain disturbance types, with important knowledge gaps in mass-movement disturbances such as avalanches and landslides, meteorological events beyond wind and drought (e.g., ice storms), and disease. The reviews further noted an emphasis on the amplifying effects of disturbance interactions, with fewer empirical examples of the buffering effects of such interactions. While most of these reviews contained landscape modeling studies, they were not the primary focus of the research. Here, we present different empirical approaches to investigating disturbance interactions as a fundamental source of knowledge underlying the conceptualization and implementation of disturbance interactions within landscape models (**Table 1**).

Serendipitous Studies

The study of disturbance interactions in forested ecosystems has unique challenges because it is nearly impossible to manipulate for the overlap of two (or more) disturbances in the field. Consequently, there are many serendipitous correlational studies in the disturbance interaction literature. For example, the extensive bark beetle epidemics affecting western North America in the last two decades, coincident with both widespread drought (Raffa et al., 2008), and highly active fire seasons (Hart et al., 2015) enabled a broad range of opportunistic

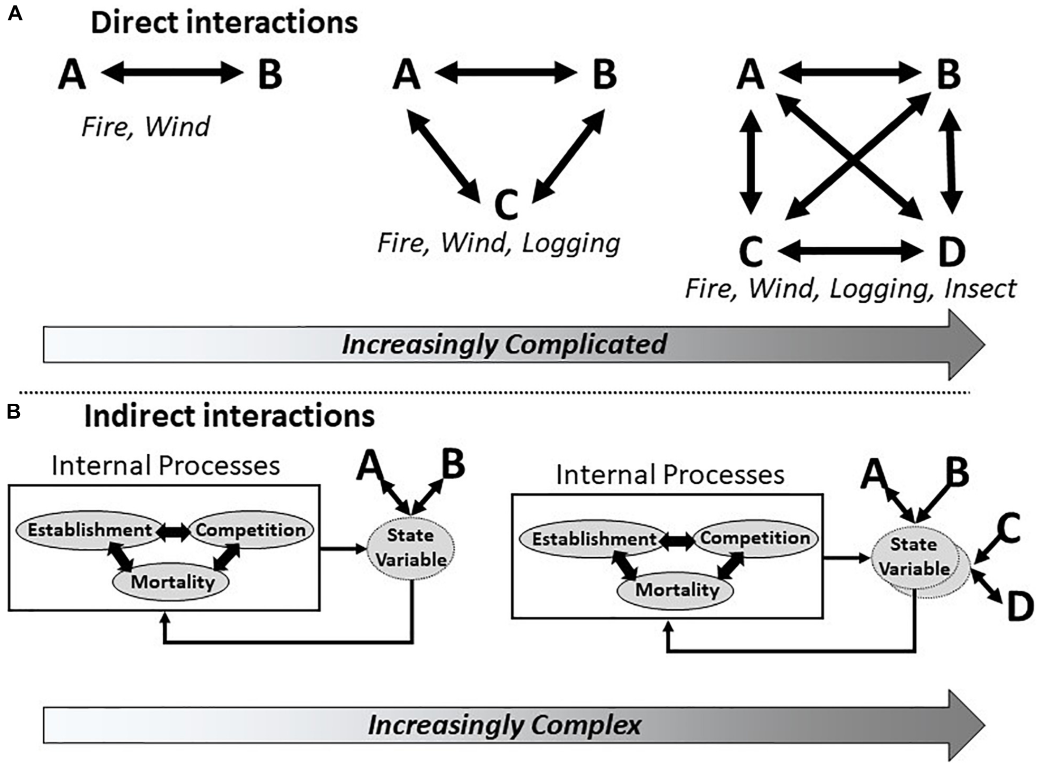

FIGURE 7 | Challenges and approaches to simulating multiple disturbance interactions. When disturbance interactions are simulated as *direct* **(A)**, the number of interactions can multiply quickly to become increasing complicated, especially if the interactions are bidirectional (i.e., double-arrows). *Indirect* interactions are those mediated through ecosystem state variables, such as composition or fuel **(B)**. Depending on model design, it may be more elegant (i.e., fewer interactions) to explicitly model the indirect processes affecting disturbance processes, but such models may also be more *interdependent* and therefore more *complex*.

disturbance-interaction studies (Kulakowski and Veblen, 2007; Kulakowski et al., 2012; Stevens-Rumann et al., 2015; Agne et al., 2016; Millar and Delany, 2019), including the widespread study of salvage logging and its effect on ecosystem response and recovery (Leverkus et al., 2018). Such studies are often descriptive in nature, documenting patterns rather than understanding the processes producing them. Nonetheless, as the Anthropocene increasingly enhances disturbances under climate change, such disturbance overlap may become increasingly frequent (Seidl et al., 2016b; Burton et al., 2020; Kim et al., 2020).

Retrogressive and Prospective Studies

One common approach for investigating disturbance interactions is "retrogressive" (sensu Simard et al., 2011), where investigators reconstruct disturbances over a longer period of time, using a variety of data sources such as archived satellite imagery, air photos, dendrochronology, and disturbance records (e.g., Bebi et al., 2003; Howe and Baker, 2003; DeRose and Long, 2012; Sturtevant et al., 2014; Hart et al., 2015; Meigs et al., 2015; Robert et al., 2018, 2020). A challenge facing retrogressive approaches is that the quality of data defining underlying drivers, such as forest composition or age structure, generally degrades the further back in time one investigates (McKenzie and Perera, 2015; Robert et al., 2020) (**Table 1**). Conversely, empirical data defining a given disturbance legacy (e.g., fuel) are often used to drive models to infer future disturbance behavior (e.g., flame length) (DeRose and Long, 2009; Simard et al., 2011; Meigs et al., 2015; Seidl et al., 2016a). Such "prospective" studies, including those referenced above, typically apply models at the plot or stand scale as their method to infer consequent system behavior.

Experimental

A number of recent manipulative experiments have focused on disturbance mechanisms and their interactions on a variety of ecosystem responses. For example, Royo et al. (2010) examined the interactive effects of canopy gaps, ungulate browsing pressure, and fire via girdling, fencing, and prescribed fire, respectively. The authors found substantial synergistic effects leading to greater herbaceous diversity under the combined disturbances relative to any one disturbance alone. Quentin et al. (2012) applied a combination of irrigation and mechanical defoliation to investigate the interactive effects of water supply and leaf consumption on eucalyptus (*Eucalyptus globulus* Labill) plantations in Tasmania. Sparks et al. (2018) investigated the interactive effects of drought stress and fire on western larch (*Larix occidentalis* Nutt.) seedlings and found that severely drought-stressed seedlings had higher survival following fire relative to moderately drought-stressed seedlings, in part due to the physiological response to drought. Cannon et al. (2014) simulated windthrow disturbance by the static winching of

TABLE 1 | Strengths and weaknesses of alternative empirical approaches for investigating disturbance interactions (DI).

Category	Description	Strengths	Weaknesses/Challenges	Examples
Serendipitous	Opportunistic data collection in regions where disturbance events overlap in space—either in sequence or simultaneously.	Space for time substitution, may or may not contain a wide breadth of severities and ecosystem states.	Predisturbance data are often missing or incomplete; Inference of causal relationships not possible.	Kulakowski and Veblen, 2007; Kulakowski et al., 2012; Stevens-Rumann et al., 2015; Agne et al., 2016; Millar and Delany, 2019
Retrospective	Disturbances reconstructed over longer time frames from either archived spatial data (remote sensing, air photos) or disturbance surrogates (tree-ring data).	Can more directly address temporal factors, may or may not contain a wide breadth of severities and ecosystem states.	Data quality and quantity degrade as one goes back in time; Inference of causal relationships not possible.	Bebi et al., 2003; Howe and Baker, 2003; DeRose and Long, 2012; Sturtevant et al., 2014; Hart et al., 2015; Meigs et al., 2015; Robert et al., 2018, 2020
Prospective	Empirical data used to parameterize models of disturbance mechanisms to make DI inferences.	Data quality and quantity can be high (present day); enables insight into underlying process.	Availability of supporting process-based models can be uneven among disturbance types; aspatial.	DeRose and Long, 2009; Simard et al., 2011; Meigs et al., 2015; Seidl et al., 2016a
Experimental	Controlled manipulative studies that focus on mechanisms underlying DI and ecosystem response.	Control for external factors to get at causation; replication; repeatability.	Limited scope, scale, and tree size/life stage.	Royo et al., 2010; Quentin et al., 2012; Sparks et al., 2018; Cannon et al., 2014; Westlake et al., 2020
Holistic syntheses	Combine lines of evidence from multiple data sources, scales, and models to holistically infer underlying process and consequence of DI.	Comprehensive; big picture enables detection of threshold behavior and cross-scaled interactions.	Case studies may be limited in scope to a system and/or location; generalizations are qualitative.	Allen, 2007; Raffa et al., 2008; Anderegg et al., 2015; Soranno et al., 2014; Cobb and Metz, 2017; Ratajczak et al., 2018
Advanced statistics	Advanced statistics such as Bayesian hierarchical modeling as well as data-mining techniques (e.g., machine learning) applied to large and complex data sets (remote sensing and time series).	Scope, scale, and range of severities and system states can be very broad; detection of patterns (including threshold behavior) not possible through traditional methods.	Risk of overfitting, patterns may or may not correspond with underlying process; "black-box" data mining may limit interpretation.	Fleming et al., 2002; Sturtevant et al., 2014; Seidl et al., 2016b; James et al., 2017; Mezei et al., 2017; Candau et al., 2018; Itter et al., 2019; Robert et al., 2018; Brice et al., 2020; Robert et al., 2020

trees to investigate consequent fire behavior, burn intensities, and consequent effects of those intensities related to elevated fuels on vegetation composition. Such studies can support the development of more process-based models enabling the simulation of disturbance interactions based on first principles (**Figures 3**, **5**). The challenges in their application relate to their inherent limitations, such as the extrapolation of disturbance or stressor responses across tree life stages (Máliš et al., 2016; Dayrell et al., 2018), or the scale or intensity of experimental vs. natural disturbances (Cannon et al., 2014) (**Table 1**). Indeed, it is often the spatial dynamics of disturbances and their interactions that simulation models are designed to investigate, precisely because empirical measurement of such processes are difficult to quantify explicitly in space. Nonetheless, experimental studies can inform even spatial processes, such as the spatial concentration of ungulate herbivory associated with burned locations, and the cascading effects on plant species diversity across space (Westlake et al., 2020).

Holistic Syntheses

Despite the value of process identification and quantification, a whole systems approach is often necessary to fully understand the nature and behavior of disturbance interactions. For example, Anderegg et al. (2015) offered a data-driven conceptual model to capture the processes underlying interactions between temperature, precipitation, tree stress, and the different physiological, chemical, and ecological constraints influencing herbivory by bark beetles and defoliators that can lead to widespread mortality under climate change. Likewise, Cobb and Metz (2017) adapted the heuristic "disease triangle", traditionally applied to forest and plant pathology, to understand the landscape ecology of tree diseases. The disease triangle consists of the pathogen, its host, and the environment conducive to the infection of the host by the pathogen. From the perspective of disturbance interactions, past disturbance events from various agents might contribute to the "environment" point of the triangle that can either facilitate or impede infection rates. Such syntheses can serve as the foundation for process-based landscape simulation models.

Case study syntheses further enable the investigation of disturbance interactions from a more holistic systems perspective. Evidence for the relative strength of specific interactions are built from diverse data sources—often at widely different scales—and gaps in knowledge may be addressed through a combination of prospective modeling and speculation based on systems and scaling theory (Peters et al., 2007). For example, Allen (2007) investigated cross-scaled interactions among drought, bark beetles, fire, and erosion in northern New Mexico based on a conceptual model that included non-linear dynamics that could either amplify or ameliorate the propagation of the different disturbances at play. Synthesized data sources spanned seven distinct studies ranging in spatiotemporal scale from weekly dendrometer (i.e., physiology) measurements to regional maps of inter-annual forest dieback developed via remote sensing. Such syntheses may be uniquely poised to address the sharp non-linearities associated with cross-scaled disturbance interactions that can lead to fundamental disturbance regime shifts. However, broader inference from such case studies will remain limited until the greater body of underlying theory can be rigorously tested (Allen et al., 2014) (**Table 1**).

Advanced Statistics

Analysis of ecological data in recent decades has shifted from the use of analytically tractable statistical methods constrained by parametric assumptions, such as ordinary least-squared regression and analysis of variance, to more advanced but computationally intensive methods such as mixed effects models, Bayesian inference, and machine learning techniques (Touchon and McCoy, 2016; Holmes and Huber, 2018). Such recent methods are better able to address the complexities of ecological datasets that are rapidly accumulating, including data collected via remote sensing and other automated sensors, as well as time-series data from long-term monitoring and experiments.

The combination of advanced statistical techniques and rich data resources enabled the modeling of underlying processes, legacy interactions, and driver roles related to disturbance interactions in time and space. For example, For example, Mezei et al. (2017) examined temporal patterns in disturbance rates of the European spruce beetle as a function of wind disturbance, prior beetle disturbance, and climatic variables affecting brood frequency. The authors used generalized additive models to allow detection of non-linear relationships, and applied multi-model inference (Burnham et al., 2011) to select from a set of candidate models reflecting plausible alternative hypotheses of underlying processes. Hierarchical and hidden process modeling better accommodate the variability and uncertainties inherent in ecological research (Gimenez et al., 2014), as well as non-linear responses due to the interactions among disturbances and climatic drivers (Brice et al., 2020), leading to more complete understanding of complex phenomena like disturbance interactions. As such, Itter et al. (2019) applied Bayesian hierarchical modeling to tree ring data in eastern and western regions of boreal Canada to evaluate the separate and combined impacts of tree defoliation and drought on tree growth patterns. They found a synergistic effect of defoliation plus drought on the "ecological memory" of the disturbances in terms of their temporal recovery period. Thus, advanced statistical modeling techniques can be applied to complex datasets to determine the relative importance of disturbance types and factors that affect the state of forest ecosystems.

Similarly, machine learning techniques are often more appropriate to modeling complex and non-linear relationships (Olden et al., 2008). For example, Candau et al. (2018) applied random forest methods to define spatial domains in central Canada where fire and eastern spruce budworm defoliation were likely to interact, based on compositional (i.e., host) and climatic gradients (i.e., moisture). Deep learning methodologies such as convolutional neural networks have been applied to extract useful patterns from complex data, such as imagery and LiDAR, although their application has focused on extracting patterns rather than understanding the processes underlying those patterns (Brodrick et al., 2019). Machine learning techniques are both diverse and evolving, and do have limitations such as propensity to over fit models and (particularly in the case of neural nets) lower transparency in the model-building process (Olden et al., 2008; Liu et al., 2018). Nonetheless, such methods may detect relationships or domains of scale that are poorly understood and worth more explicit attention.

Challenging Long-Standing Dogma

Regardless of the empirical approach, a critical role of empirical studies is to challenge long-standing assumptions of disturbance interactions that often find their way into landscape models. For example, the persistent dogma of "insect disturbance increases fuel load and therefore fire risk"—has been confronted with conflicting empirical evidence. Analysis of spruce eastern budworm outbreaks suggested that they increased forest fire probability in the first 20 years post-outbreak (Fleming et al., 2002), while Meigs et al. (2015) found that fire probability was lower after a western spruce budworm (*Choristoneura freemani* Razowski) event. These two studies were similar in that they were retrospective studies that evaluated whether the area burned increased during periods of budworm outbreaks, using a range of lag periods (i.e., time since outbreak). By contrast, James et al. (2017) investigated a similar question for spruce budworm in a similar geographic area to that of Fleming et al. (2002) but included weather drivers as covariates in the analyses. They found that the magnitude of defoliation effects was lower than those associated with weather. Likewise, a literature review of bark beetle-fire interactions in western North America concluded the effects of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) disturbance on fire occurrence and severity were ambivalent (Simard et al., 2008). A subsequent study applied prospective modeling to focus on a particular fire process (i.e., probability of active crown fire; Simard et al., 2011). The authors considered the changes in fuel characteristics with time since disturbance (i.e., dead needles in canopy, deposited needles, fallen trees, and understory development), weather characteristics affecting fire behavior (wind speed and moisture) and interactions between the disturbance legacy and weather drivers (e.g., micrometeorology below canopy). As in Simard et al. (2011), James et al. (2017) found that the potential amplifying effects of the fuel disturbance legacy from the outbreak were constrained by fire weather conditions. Hicke et al. (2012) found that categorizing studies according to a conceptual model of expected lags in different fuel components as they related to different stages of bark beetle outbreaks led to more consistency in results and consequent fire implications across studies.

Insights From Empirical Studies

Empirical study of processes and drivers governing disturbance interactions are prerequisites of plausible models that simulate their dynamics. The different empirical approaches to the investigation of such interactions each have their role to play in the development and application of such models. Empirical study should justify when and where the added complexity of disturbance interactions is warranted, and confront persistent dogma based on perception rather than data. While interest in this line of research has increased in recent decades, disturbance interactions remain complex and challenging to quantify. Recent conceptual advances (see Section "Conceptual Advances") are helping to refine the questions and terminology to channel empirical research, while advances in statistical methods, coupled with increasingly detailed data sources, provide additional tools to probe the characteristically messy data for useful insights. As evidenced by a series of recent reviews, research in this area is active but also unevenly distributed across geography, biomes, and disturbance types. By extension, such deficiencies limit the scope of landscape modeling in this line of research.

MODELING APPROACHES

The application of landscape models with multiple disturbances has exploded with the availability of advanced landscape models and increasing accessibility to computing power. We systematically reviewed the literature using the online search engine ISI Web of Science. Our initial review (access date August 15, 2020) applied the keywords "forest*", "landscape*," "simulation*," and "disturbance*"; where we searched abstracts for landscape simulation studies including least two simultaneous disturbance agents. Landscape simulation studies were identified as those falling within the range of spatial scales falling within the landscape to regional extent (i.e., $5.0 \times 10^1 - 5.0 \times 10^7$ ha) defined by Seidl et al. (2017), with model designs that allowed for spatial interactions among finer-scaled entities (i.e., grid cells or polygons). We further limited our review to papers from 2010 forward to focus on the most recent studies with the latest technology. Our initial search yielded 81 papers, however, we found it missed a number of relevant studies. We therefore repeated the literature review of the same search engine, using the names of the modeling software identified in the first review as keywords. This second review, with a final access date of June 06, 2021, identified an additional 66 papers meeting the above criteria (total = 146). The full details of the systematic review and the resulting citation list are provided in **Supplementary Materials**.

We note that our review methodology had consequences for the final set of papers included in the review. Landscape simulation studies that included more than one disturbance agent were included regardless of whether the investigation of disturbance interactions was stated as an explicit objective. In reality, investigators include multiple disturbance types for a wide diversity of questions that fall along a spectrum of explicit to implicit attention to the interactions of those disturbances within the simulations. Conversely, we did not include studies focused on a single disturbance agent, such as the fire frequency interactions illustrated in **Figure 4**. Doing so would retain all landscape simulation studies that simulated single disturbance regimes. However, we did retain studies investigating interactions between different agents of the same type, for example, between multiple insect species, or between wildfire and prescribed burning practices. Further, certain classes of models were excluded that have relevance to the broader question of disturbance interactions, but were not landscape models *per se*. Prospective modeling studies (**Table 1**) of disturbance interaction were commonly investigated using plot or stand level models (e.g., Simard et al., 2011). Many such studies covered a large geographic extent (e.g., Jain et al., 2020), but could not account for contiguous spatial processes fundamental to landscape ecology. Similarly, aspatial forest optimization models aggregate local dynamics across broad spatial units without spatial interaction within or between units. This is also the case for dynamic global vegetation models (DGVMs) that aggregate disturbance processes within course-resolution cells without any spatial interactions within or between cells. We also identified a couple fine-resolution land surface model applications that lacked spatial processes. All such aspatial model applications were excluded from our review. It is also possible that the initial use of the term "landscape" may have neglected models from some disciplines (e.g., hydrology) that use alternative terms (i.e., watershed, basin, etc.) to define their geographic extent.

Human land management was included in most of the disturbance interaction studies surveyed (79%), though only 7 studies included land use/land cover (LULC) change as a disturbance agent. By comparison, the most frequently investigated natural disturbance type from our review was fire (65%), followed by wind (38%) and insects (37%). Less frequently investigated disturbance types included water balance (drought or flooding; 15%), mammalian browsing/grazing (10%), and mass movement (i.e., erosion, debris flows, landslides, avalanche; 7%). Only two interaction studies included a simulated disease, perhaps due to a lack of empirical studies (Cobb and Metz, 2017).

Consistent with past reviews of disturbance interactions more generally (see Section "Empirical Approaches"), studies identified by our systematic review were unevenly distributed across continents and biomes (**Table 2**). Nearly two thirds of the studies were from North America, primarily from the United States and Canada, including nearly all of the boreal examples. Close to a quarter of the studies were from Europe, focused on temperate and alpine systems, but also including some Mediterranean examples. Studies from Asia accounted for about 10 percent of the total, distributed a little more evenly across biomes, including several studies from China. We found only 3 studies from Australia, one from South America, and none from Africa. Clearly there are underrepresented regions of the world within this field of research, most notably within tropical and subtropical systems. However, some of this uneven distribution may be attributed to our search methodology. We suspect the inclusion of the keyword "savanna*" would have expanded the geographic scope a bit further. Searching on formal model names, while clearly essential in terms of the numbers of studies identified, may have biased the results to regions of the world where those models are applied. Custom models implemented in more generic software such as R were identified within the first search, but not the second name-specific search; this method may have also missed studies from under-represented regions. Nonetheless, our systematic review represents a strong cross-section of the landscape modeling investigations of disturbance interactions.

Forest Landscape Models

A specific class of models known as forest landscape models (FLMs) dominated the literature of landscape

TABLE 2 | Geographical distribution of disturbance interactions studies covered by the systematic review (**Supplementary Materials**).

Study biomes	North America	Europe	Asia	Australia	S America	Africa	Subtotal
Boreal	21		3				**24**
Temperate coniferous	33	23	8				**64**
Temperate broad-leafed/mixed	47	11	3	2			**63**
Mediterranean		4			1		**5**
Temperate grassland/savanna/shrub	2						**2**
Deserts and xeric shrublands	4						**4**
Subtropical/tropical (combined)	1		2	1			**4**
Subtotal	**94**	**33**	**15**	**3**	**1**	**0**	**146**

TABLE 3 | Summary of the software applied to address disturbance interactions from the systematic review (**Supplementary Materials**).

Forest landscape model	**Forest dynamics**	**Land mgmt.**	**LULC**	**Fire**	**Wind**	**Insects/ disease**	**Browse/ graze**	**Mass movement**	**$H_2$0 balance**	**# studies**
LANDIS	Tree species cohorts	4		**3**,4	3	4				8
LANDIS-II	Tree species cohorts (optional biomass, ecophysiology, or biogeochemistry)	2,3,**4**	(4)	3,4,5	3	3,**4**	2,3,4,5	(4)	(3),4,5	77
LandClim	Tree species cohorts (size/density)	3,4,5	(5)	3,**4**	3	5–6	3		4	11
LANDIS Pro	Tree species cohorts (size/density)	4	(4)	3,4						6
FireBGC	Hybrid gap, ecophysiology and biogeochemistry	4,5		5		5			5	3
iLAND	Individual-based ecophysiology	4,**6**		5	4,5	4,**6**		**1** (6)	5	16
SELES	State and transition/growth and yield	4,**5**,6		3,4,5		4		1		6
CHANS (envision)	State and transition	4–5		5						2
ST-SIM	State and transition	(5)		3						1
VDDT/TESLA	State and transition	4		3	3	4				3
R	Forest type/age	4		4						1
Spatial hydrology model										***2***
RHESSys/FVS	Empirical growth and yield	3		4						2
Stand model + GIS										***4***
FVS	Empirical growth and yield			Input		1				1
PICUS	Individual-based tree/patch	4,5				6	4	1		3
Down-scaled DGVM										***2***
MC2/envision	Downscaled via state and transition probabilities	4		4						1
MC1/VDDT	Downscaled via state and transition probabilities	4		3						1
Spatialized physical or dispersal models										***4***
Phoenix rapid fire	Spatial inputs			6						1
Hydrologic/land movement	Spatial inputs			Input				6	6	1
SIBERIA	Spatial inputs				3			6	6	1
R (Bark beetle IBM)	Spatial inputs				Input	6				1

*Numbers under each disturbance type reflects the different levels of process integration applied for each type (**Table 4**). Note that the absence of a value under a given disturbance type does not mean the software is not capable of simulating that type, it simply was not present in the pool of studies from our review. Bold underscore indicates dominant mode in applications. Numbers in parentheses indicate an external coupled model.*

disturbance interactions, representing 92% of studies from our systematic review (**Table 3**). FLMs were first developed in the late 20th century (Baker, 1989; Mladenoff and Baker, 1999; Gustafson, 2013) and have greatly diversified since then (He and Mladenoff, 1999; Schumacher et al., 2004; Lischke et al., 2006; Scheller and Mladenoff, 2007; Keane et al., 2011; Seidl et al., 2012; Wang et al., 2014, among others). Landscape modeling software (Fall and Fall, 2001;

e.g., Bolte et al., 2007) further enabled the rapid development of customized FLMs. Despite this diversification, a common FLM structure has emerged integrating vegetation dynamics (succession, growth, mortality, senescence, etc.) with spatially-explicit disturbances affecting those dynamics. In some fashion, both vegetation and disturbance dynamics may be influenced from the "bottom up" by biophysical drivers such as soil characteristics and terrain, and from the "top down" by climatic drivers such as precipitation and temperature patterns, and in some cases atmospheric conditions (e.g., CO_2 concentrations, flux of photosynthetically active radiation). Model development during the last two decades improved the architecture of the models, in terms of modular design and scaling methodologies, the relative balance between phenomenological patterns and simulated processes, and the diversity of disturbance agents that can affect system dynamics. Active development and widespread application of FLMs precipitated several reviews in the last decade (Seidl et al., 2011; Keane et al., 2013, 2015; Shifley et al., 2017).

Disturbance processes simulated within FLMs and other landscape models share common elements of initiation, spread or contagion, intensity, and effects, where opportunities for interaction can occur within each of these processes (**Figure 3** and **Table 3**). Direct interactions between disturbances are often approximated through some surrogate for underlying process. For example, time since fire may serve as a proxy the process of fuel build-up. Indeed, Mladenoff et al. (1996) extended this approximation to enable one of the first formal disturbance interactions within an FLM, where a recent wind event increases the intensity of a subsequent fire event. Such logic becomes increasingly *complicated*, however, as one simulates multiple overlapping disturbances or other disturbance types, such as harvesting or insects (**Figure 7**). To what degree does the surrogate (in this case, either time since fire or time since disturbance) approximate the process (fuel accumulation) when multiple disturbances are at play? There is the potential for compounding error as additional direct disturbance interactions are added (**Figure 7**). This issue relates to any of the interaction types that can occur within a system (**Figure 3**). The complexity of state and transition models, for example, multiply with the number of disturbance processes that are included, because transition probabilities must be specified for every combination of possible disturbance sequences (James et al., 2011a; Daniel et al., 2017).

The solution to the increasing intractability of "direct" interactions via surrogates is to model the underlying process, such as fuel dynamics, as a state variable. Here, the interaction becomes indirectly mediated by the internal processes underlying the dynamics of the state variable, that in some cases, may be more elegantly modeled than attempting to keep track of overlapping surrogate variables (**Figure 7**). Such methods have other benefits, such as allowing for external drivers such as climate to further mediate the interaction (**Figure 5**), and to model the lagged effects appropriate for a given process and location (Burton et al., 2020). Simulation of multiple interacting disturbances is likely related to the decline of the state and transition model approach within FLMs in favor of tracking individual tree species that can respond individualistically to a wider range of disturbance types and their various combinations. Only 10 percent of the studies in our review applied the state and transition model approach (**Table 3**). A more recent innovation in FLMs is the simulation of tree stress via carbon balance (e.g., Keane et al., 2011) or even more explicitly in the form of non-structural carbohydrate reserves (Seidl et al., 2012; DeBruijn et al., 2014). Such innovations enable trees to respond to the accumulation of multiple stressors that include both disturbances and environmental drivers.

A related model design choice relates to trade-offs in "static" versus "dynamic" disturbance regimes. A static disturbance regime is one parameterized according to its statistical properties (e.g., rotation, event size distribution, intensity distribution, etc.; **Figure 2**). The focus of such applications is typically the response of the system to a given disturbance regime, without feedback to the regime itself. A fully dynamic disturbance regime is one where the statistical properties of the regime are an emergent property of the system dynamics (Perera et al., 2015). In practice, any of the individual components of a given disturbance type (i.e., **Figure 3**) can be simulated as either static or dynamic. Most contemporary FLMs simulate disturbance effects dynamically, where mortality is contingent on the relative susceptibility of forest types, tree species, age classes, or some combination of these variables. Many introduce stochastic elements that may be related to process (e.g., likelihood of insect damage or fire ignitions related to vegetation characteristics). Some models offer different options where the user can specify the relative balance of static vs. dynamic components (e.g., Sturtevant et al., 2009; Keane et al., 2011; DeJager et al., 2017).

We developed a classification scheme to address the degree of process integration (i.e., balance of static vs. dynamic components) within a specific disturbance agent within a given landscape disturbance application (**Table 4**), and then applied that scheme to the different disturbance agents simulated across the studies identified by our systematic review (**Table 3**). While the classification scheme was both logical and readily applied given proper documentation – we found this supporting documentation was sometimes lacking within individual studies. Many referenced earlier model applications, or original model publications, requiring more extensive review to fully understand the nature of the disturbance interactions simulated. Other applications required assumptions on our part where the documentation was insufficient, including vague descriptions of the specific model options applied, or references to model code requiring literacy of the underlying programming language. Nonetheless, we were able to document ranges of process integration across disturbance types and model software platforms (**Table 3**), including dominant modes of process integration, and instances where more detailed process integration was possible via the coupling of models (see Section "Coupled Models"). We found that while the trend in disturbance modeling is toward more explicit modeling of disturbance processes and their emergent effects on system dynamics and landscape structure (Gustafson, 2013; Keane et al., 2015), static disturbance regimes are still commonly applied. The relative balance of static vs. dynamic components in application was also unevenly distributed across different disturbance types and model approaches – including non-FLM applications (**Table 3**).

Some contemporary FLMs are better described as model *frameworks*, where different trade-offs in process vs. surrogates, static vs. dynamic disturbance regimes, and the number and types of disturbance mechanisms simulated may be customized according to both the question addressed and the available supporting data. The most frequently applied model software from our review was LANDIS-II, an FLM model framework accounting for 59% of all studies (**Table 3**). A case study pair of applications of this model in north central Minnesota (United States) illustrates the framework approach (Lucash et al., 2017, 2018) (**Figure 8**). The authors applied a highly mechanistic succession option (Scheller et al., 2011a) where tree-species cohorts respond individualistically to different disturbance types and compete for above and belowground resources (light, water, nitrogen) via a set of life history traits and parameters. The first study focused on how the combination of climate change and forest management affected forest resilience following wind events (i.e., forest recovery rates), applying a factorial experiment that crossed climate scenarios with forest management scenarios (Lucash et al., 2017). The second study focused on the degree to which multiple disturbance regimes affected tree mortality rates (i.e., effects). Results of the latter supported antagonistic interactions, where total tree mortality caused by multiple disturbance regimes applied simultaneously was less than the sum of the mortality from each of the respective disturbance types applied independently. Closer examination of the simulation methods reveals a combination of process integration methods were applied to different disturbance types (Lucash et al., 2018). Wind disturbance was simulated as "mostly static" regimes with characteristic size, shape, and rotations of three classes of wind patterns (microburst, tornado, and derecho), each with species and age-specific impact patterns. Such static regimes are consistent with the lack of feedback between vegetation and wind event frequency or intensity, but cannot address spatial factors such as the effect of forest edges on tree susceptibility to windthrow (see Section "Disturbance Interaction Process and Terminology"). Fire regimes were simulated as mostly dynamic functions of the vegetation, fuel dynamics, and climate-related fire weather. Limitations of this approach in terms of emergent fire behavior are shared across virtually all FLMs: rules governing fire spread do not account for critical feedbacks between fire behavior and weather that fundamentally change those rules (such as long-distance dispersion of fire embers) (see Section "Cross-Scale Interactions"). Recent wind or insect disturbance could modify fuel attributes as direct interactions (**Figure 7**). The three different insect disturbance agents included intermediate blends of dynamic and static regime elements, where the extent of each disturbance was directly related to availability of vulnerable host, but the frequency and intensity of outbreaks was predefined. The exception was the patterns of mortality in oak (*Quercus* spp.) species by the two-lined chestnut borer (*Agrilus bilineatus* Weber) that occurred in instances where forest tent caterpillar (*Malacosoma disstria* Hübner) defoliation overlapped in time with drought events, reflecting a surrogate for tree stress defined by direct interactions with defoliation and climate, respectively (**Figure 8**).

Questions and Approaches Across Disturbance Types

We summarized the class of explicit disturbance interaction questions addressed across the different disturbance types (**Table 5**), using the conceptual advances summarized in **Figures 3**, **5**. Frequencies of studies across questions and disturbance types were limited to those who either quantified the effect via their experimental design, or explicitly defined the nature of the simulated interaction within their methods. "Ecosystem response" was the one exception (see below). Linked disturbance interactions were specified according to which disturbance types were affected by another type. While looped disturbance types of the same disturbance (e.g., the effect of fire frequency on future fire likelihood) were not included in **Table 5**, instances where disturbance of a given type included multiple agents of that type (e.g., more than one insect agent) were included in the tabulation. Linked disturbances generally related to questions of disturbance resistance (Buma, 2015), but some studies aggregated responses across multiple disturbance types. In these cases, we tallied the study under "resistance (general)" (**Table 5**). Articles addressing resilience interaction questions were defined as studies that quantified the rates of return to a reference condition, shifts to alternative vegetation states, direct comparisons with HRV, or some combination of these responses. Climate-mediated disturbance questions refer to those studies where a given disturbance type was either modified to be consistent with future climate, or dynamically linked to climate. In the case of land management, climate-mediated disturbance involved some form of intentional climate adaption, such as assisted migration via planting. Cross-scaled disturbance frequencies refer to those studies that quantified cross-scaled interactions via their experimental design. Ecosystem response frequencies refer to those studies quantifying state variables other than those expressly linked to the disturbance interaction questions above (e.g., compositional trends). We note that most studies, whether self-identified as disturbance interaction studies or not, have an interest in capturing system dynamics under multiple interacting disturbance regimes. Frequencies of ecosystem responses in **Table 5** therefore reflect the number of studies that included ecosystem responses regardless of whether the specific effect of a given disturbance type could be quantified in those response variables via the experimental design.

The most commonly investigated linked disturbance was fire (**Table 5**), with most investigations focused on how land management actions such as fuel treatments or logging affected fire severity or extent. Far fewer studies investigated fire as linked to insect disturbance. Insect disturbance was investigated as linked to a broad range of disturbance types in half the studies for which it was included. Wind was less often investigated as linked to other disturbances, with the largest exceptions from studies in central Europe. Studies including the major disturbance types (management, fire, wind, and insects) investigated questions related to system resilience in roughly a quarter of their respective

TABLE 4 | An index reflecting the relative degree of process integration applied for a given disturbance type and more complete description, with index values corresponding to the numbers applied within disturbance type columns in **Table 3**.

Degree of Integration	Description (see text for details)
(1) Susceptibility index	Surrogate variable such as host abundance or fuel distributions
(2) Fully static regime	All components predetermined, may be applied stochastically
(3) Mostly static regime	Most components predetermined/stochastic, but with dynamic effects
(4) Intermediate static-dynamic	Intermediate mix across incidence, extent (spread), and intensity components. Can include simple climate constraints.
(5) Mostly dynamic regime	Dynamic across all disturbance components, but without explicit mechanisms for cross-scaled interactions. Climate or weather often a driver of behavior.
(6) Fully dynamic regime	Reserved for spatialized physics models and/or individual-based models that enable emergent behavior based on simulated state variables and human and environmental drivers. Explicit cross-scaled interactions may be simulated.

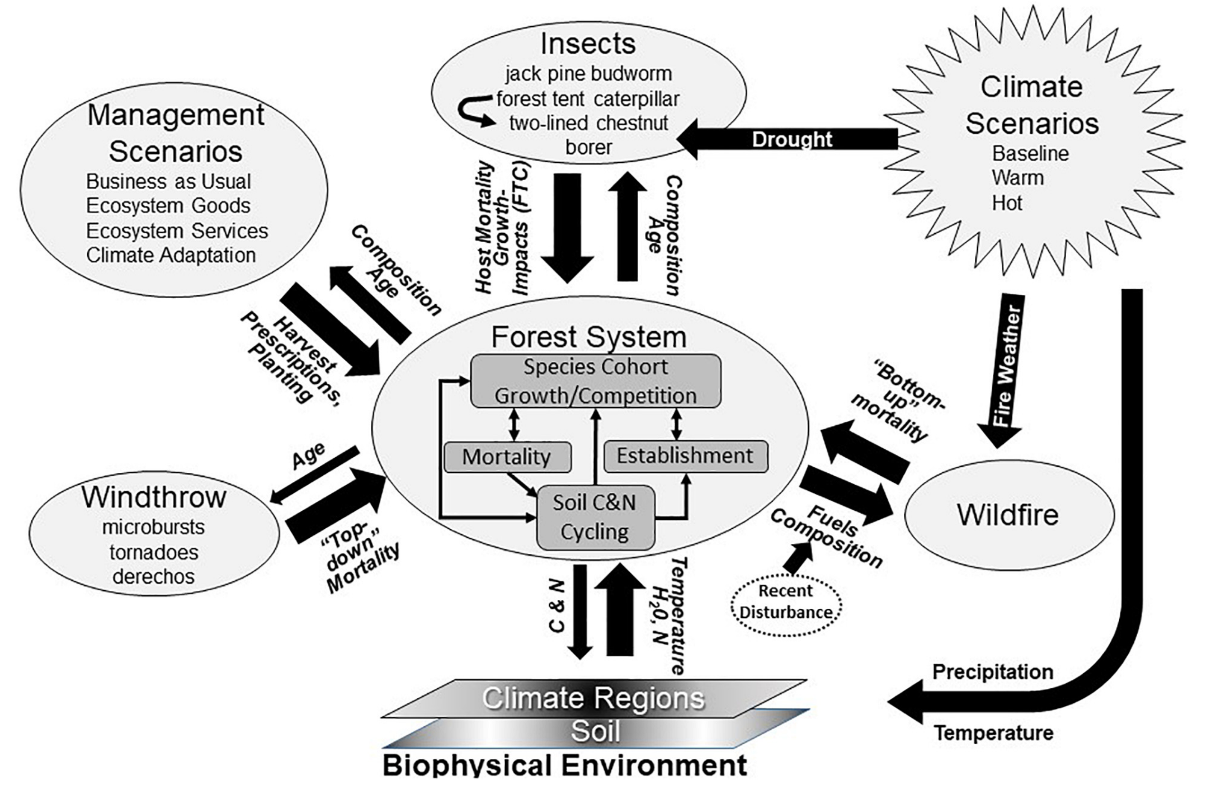

FIGURE 8 | Example modeling study investigating multiple disturbance interactions, where disturbance interactions are primarily indirect via site-level state variables such as composition, age structure, and fuel loading. Climate drivers directly affect just small subsets of disturbances directly, but indirectly affect state variables that can lead to emergent system behavior as a function of two scenario factors (i.e., climate and management). (Adapted from Lucash et al., 2018).

cases. For less-studied disturbance types, questions addressed varied widely, though the sample size was low. Drought was primarily investigated as a climate-mediated disturbance (16 of 22 studies) and related questions of forest resilience (6 of 22 studies). Six of 15 studies including mammalian browse investigated questions of ecosystem resilience, often related to the loss of forest cover. Almost all of the studies including mass movement disturbances focused on linkages to other disturbance types that either removed forest cover or otherwise destabilized soil in steep terrain.

Half of the studies from our review included some form of climate mediation of disturbance regimes (**Table 5**). Of those, 61 studies evaluated the degree to which forest management scenarios could mitigate the less desirable effects of climate change, such as elevated mortality (i.e., resistance) or transition to alternative system states (i.e., resilience). For example, Cadieux et al. (2020) investigated how projected climate change interacted with logging and fire disturbance to affect bird species habitat in the boreal forests of Alberta, Canada. In this case, the focus was on the vegetation response rather than on disturbance processes. They therefore applied mostly static fire and drought regimes parameterized differently for each climate scenario, based on empirical studies (Boulanger et al., 2014; Chen et al., 2016, respectively). The combined effects of climate change in combination with the associated elevated fire and drought mortality resulted in transitions from conifer-dominated

TABLE 5 | Frequency of explicit disturbance interaction questions addressed by studies in the systematic review (**Supplementary Materials**).

Question				**Disturbance type**				**# studies**
Linked to type	**Land management***	**Fire**	**Wind**	**Insects/disease**	**Browse/graze**	**Mass movement**	**H_20 balance**	**70**
Land management	1	29	5	10		6		46
Fire	6			5		2		13
Wind	8		1	11	3	4		24
Insects/disease	8	6	1	3		6		20
Browse/graze						2		2
Mass movement								0
H_20 balance	2	1		6		1		8
Resistance (general)	3	3	5	3	2		1	**7**
Resilience	30	25	14	12	6	1	6	**37**
Climate-mediated	14	42	13	21			16	**72**
Cross-scaled	2		3	4			3	**4**
Ecosystem response	93	74	42	44	13	1	18	**116**
Total	**116**	**95**	**55**	**54**	**15**	**10**	**22**	**146**

**Includes land use/land cover (LULC) change.*

*Linked disturbance interactions specify which disturbance types (columns) were affected by another type (rows). Disturbance questions relate to the framework defined by **Figures 3**, **5**. See text (Section "Questions and Approaches Across Disturbance Types").*

*** Frequency of studies in bold italics text refer to the subtotal for the question type (rows) or disturbance type (columns). Subtotals are generally less than the sum of the respective column or row due to inclusion of multiple disturbance types and questions within individual studies.*

forests to either deciduous forest or open habitats, with important implications for bird habitat. How this change to alternative forest states might interact with the fire regime itself could not be quantified using this approach. Keane et al. (2019) explicitly focused on emergent fire dynamics related to climate change, and how such behavior might be mitigated via either fire suppression or fuel treatment rates. In this study, they used simulations under historic climate and without human intervention to define the multivariate HRV for three contrasting landscapes in the northern Rocky Mountains (United States). This approach, combined with their process-based modeling framework (Keane et al., 2011), enabled them to draw inferences with regards to tipping points in system behavior that indicated loss of system resilience relative to the benchmark HRV, and the degree to which human action might affect system resilience in the face of climate change.

The relative balance of static to dynamic process in disturbance agents define the degree to which reciprocal interactions among those agents may be investigated, and therefore must be specified carefully with regard to the questions asked and addressed. For example, Chen et al. (2011) investigated the effects of larch caterpillar (*Dendrolimus superans* Butler) defoliation of different intensities on fire regime. However, key assumptions governing the fire regime, such as whether fire size and rotation was an input or an output of the model, were not provided, making it impossible to evaluate their results regarding insect effects on response variables such as fire frequency. Sturtevant et al. (2012) investigated reciprocal interactions between spruce budworm and fire disturbance and demonstrated that budworm defoliation disturbance reduced live ladder fuels, and therefore decreased fire extent over long time scales (centuries), despite increasing fire spread and intensity at shorter (decadal) scales. Specifically, the authors examined how an intermediate static-dynamic insect disturbance regime affected a mostly dynamic fire regime. While they could directly address the question of budworm effects on fire regimes, they could not fully address the reciprocal question (i.e., how does fire influence the insect disturbance regime?). Temperli et al. (2015) coupled a spatially-explicit bark beetle model with the LandClim FLM (Schumacher et al., 2004) to investigate interactions among spruce bark beetles (*Dendroctonus rufipennis* Kirby), fire, wind, and climate. In this case, wind disturbance was simulated as a mostly static regime, fire was intermediate (i.e., ignitions and size distributions were static inputs, but spread and effects were dynamic), drought stress was linked to climate inputs, and beetles responded dynamically to vegetation, drought, host abundance, and windthrown host resources. Analogous to Sturtevant et al. (2012), the authors could address the effects of wind and fire on bark beetle disturbance behavior, but not the reverse. They found that climate change-driven drought events would promote beetle outbreaks, but the combination of the two mortality agents progressively reduced long-term susceptibility to bark beetle outbreaks. As a final example, Seidl and Rammer (2017) simulated emergent dynamics of bark beetles responding to wind disturbance and climate change in the Austrian Alps, concluding that climate change amplified the outbreaks initiated by wind events, in large part by shifting the optimal development rates of the beetles to higher elevations where its spruce host was more concentrated. Since the authors applied disturbance agents that each responded dynamically to both climate drivers and ecosystem state variables, they could make inferences about reciprocal interactions among disturbance agents, as well as the mediating role of climate.

Some of the constraints on the types of disturbance interaction questions that may be addressed via landscape modeling are imposed by the design constraints of the selected model software (e.g., **Table 3**). Nonetheless, model designs are ultimately constrained by supporting knowledge and data. In the insect examples above, there is greater consensus on the landscape factors controlling bark beetle dynamics than there are for defoliator dynamics (Kneeshaw et al., 2021). Indeed, bark beetles were included in all four of the disturbance interaction studies that explicitly addressed cross-scaled interactions (**Table 5**). Of those, one approximated non-linear responses of bark beetles to host abundance via percolation theory (Seidl et al., 2016a). The remaining three explicitly modeled emergence and spread of bark beetle agents as they interacted with environmental drivers such as temperature, food resources including both pulses provided by windthrow and host concentrations impacted in part by drought stress (Temperli et al., 2015; Dobor et al., 2020; Honkaniemi et al., 2020) (see **Figure 6**). While a few model designs may have allowed for cross-scale interactions in other studies (**Table 3**), they were not explicitly quantified so their importance cannot be evaluated.

Modeling Anthropogenic Forest Disturbance

Forest management was frequently investigated as a linked factor affecting other disturbance types, however, the reverse (effects of natural disturbance on land management) was far less common (**Table 5**). Eleven of the studies linking management to other disturbances included explicit salvage logging and/or sanitary logging, representing post-disturbance harvest of felled trees and preventative treatments to reduce insect impacts, respectively. Given the quantity of empirical studies investigating salvage logging, it is somewhat surprising this process is less investigated via landscape modeling.

FLMs most often model forest management practices as partially dynamic functions of landscape conditions (**Table 3**). Harvest locations are often selected via ranking algorithms such as oldest harvested first or biased toward species or forest types of interest (Gustafson et al., 2000). Harvest intensity and effects can likewise be defined to reflect a wide range of management prescriptions. However, the rates (i.e., extent) of any given treatment is generally predefined within scenarios. By contrast, forest planning models represent a different class of models that approach the question of how much to harvest dynamically based on the temporal changes and sometimes spatial distribution in the timber resource (Pukkala, 2013). Disturbance interaction questions from a forest optimization point of view often revolve around accounting for natural disturbances that can add uncertainty to the optimization process (Savage et al., 2011). There is a well-developed literature on spatial forest planning models that focus on the drivers of timber management such as growth and yield, access, road-building, and especially cost-benefit trade-offs that FLMs generally lack (Baskent and Keles, 2005; De Pellegrin Llorente et al., 2017). Nonetheless, such approaches have struggled with the stochastic and contiguous nature of natural disturbances, and therefore either simplistically account for such processes as aspatial rates of disturbance or ignore them altogether (De Pellegrin Llorente et al., 2017). Occasionally these divergent approaches have been blended to account for both human and ecological drivers of disturbance interactions. For example, forest optimization models have been used to define harvest rates for scenarios implemented in an FLM (e.g., Daniel et al., 2017). Raulier et al. (2014) used the SELES modeling platform to apply an iterative harvest optimization process – one that included spatially contagious processes such as road building and salvage logging where existing roads enabled rapid access. They used the model to simulate reciprocal interactions between fire and timber harvest to better quantify risk to timber supply under climate change in boreal Canada.

More recent methods for integration of socioeconomic drivers that contribute to both reciprocal interactions with forest landscape systems include demand and allocation models and also agent-based models (An, 2012; Egli et al., 2019). Developers recently incorporated agent-based logging and salvage logging within the iLAND model (Rammer and Seidl, 2015). Such development enabled simulation experiments examining reciprocal interactions among wind, European bark beetle, and forestry practices in the face of climate warming (e.g., Dobor et al., 2020) as illustrated in **Figure 6**, and account for the studies linking land management to wind and insect disturbance in **Table 5**. Agent-based forest management approaches are now being implemented in other FLM platforms (Spies et al., 2017; Sotnik et al., 2021). Land-use intensification and other anthropogenic disturbance activities have profound effects on landscape legacies and disturbance regime shifts (Watson et al., 2014). An emerging hotspot of research activity therefore lies in the investigation of reciprocal interactions between human activities and ecosystem processes—falling broadly under the scope of coupled human and natural systems (Wimberly et al., 2015). Anthropogenic and natural disturbance interactions might be modeled using integrated modeling platforms (Verburg and Overmars, 2009), where the combined effects of disturbance events and climate change can be explored via experimental designs that include either contrasting or a range of climatic and land-use intensification scenarios (Becknell et al., 2015). While six studies from our review used outputs from human land use change models to drive land cover change within FLMs (e.g., Duveneck and Thompson, 2019), none coupled land used change dynamically with forest harvest or natural disturbances to investigate their reciprocal interactions. One study applied an FLM to estimate forest productivity under alternative climate change scenarios and coupled those outputs with that of yield models from other economic sectors (agriculture and livestock) to drive an economic land allocation model to simulate land conversions under the twin drivers of climate change and human incentives (Briner et al., 2012). This example represents the closest approximation to the complete system portrayed in **Figure 1** of any included in our review.

Coupled Models

As illustrated by the coupling of FLMs with land cover change models in the previous section, some authors of articles in our review extended the capabilities of a given model by coupling them with one or more additional models. Different models may be linked via a "loose coupling," where the output of one model is used as input for another (i.e., the most common form, see Section "Modeling Anthropogenic Forest Disturbance"), or "tight coupling", where the dynamics of one model interact with the dynamics of another (Sturtevant et al., 2007). Loose couplings of models are widely used as a scaling technique, for example by deriving the input parameters of a coarse-scaled model from a finer-scaled process model (Urban et al., 1999; Xu et al., 2012; Boulanger et al., 2018; Huang et al., 2018) or down-scaling vegetation or disturbance behavior from coarse-scaled models such as DGVMs (Halofsky et al., 2014; Turner et al., 2015) (**Table 3**). FLM outputs are also commonly used as inputs for wildlife habitat or viability models that may be considered a dimension of ecosystem response to disturbance interactions (e.g., Longru et al., 2010; Scheller et al., 2011b; Nitschke et al., 2020).

Apart from human factors such land cover change or forest optimization, use of coupled models to address disturbance interactions centered on better representation of hydrologic and mass movement processes currently lacking within FLMs (**Table 3**). Research by Saksa et al. (2020a,b) coupled an ecohydrology model with a stand growth and yield model (for vegetation dynamics) and a fire behavior model to evaluate the integrated effects of fuel treatment patterns on fire risk and hydrologic outputs from small watersheds of the Sierra Nevada Mountains in the western United States. A planar surface model was used to define the flood disturbance regime for an FLM application to a Mississippi floodplain system in the central United States (DeJager et al., 2019). The combination of forest cover, disturbances, and impervious surface outputs from a coupled land cover change and FLM model system were used to project flood risk via a simple hydrologic model (Thompson et al., 2016). Scheidl et al. (2020) used the projections of an FLM to drive a physically-based spatial hydrologic model coupled with a slope-stability model to evaluate the integrated effects of climate change, forest management, and natural disturbance processes on shallow landslide frequency within the eastern Alps of Austria.

Hybrid Empirical-Simulation Modeling

Hybrid empirical-modeling studies leverage the synthetic knowledge within process models to relate data representing measurable system components to processes underlying disturbance interactions that are either difficult or impossible to measure directly. For example, McGuire and Youberg (2019) empirically investigated the effects of repeat burns on both soil water infiltration rates and the occurrence of debris flow disturbances in dry montane forests of southeastern Arizona, United States. They then coupled remote sensing and terrain inputs with a high-resolution hydrologic model to demonstrate that differences in soil infiltration between once and twice burned soils were sufficient enough to affect threshold rain intensities necessary to generate debris flows. Similarly, Hancock et al. (2012) measured windthrown trees and consequent erosion patterns following a cyclone impacting northern Australia. They then used this data within the geomorphic landform model SIBERIA (Willgoose et al., 1991) to investigate ecohydrological controls (including windthrow patterns) on long-term erosion and catchment evolution. Økland et al. (2016) investigated a critical transition in bark beetle outbreak dynamics where beetle populations move from trees injured or killed by wind events to attack healthy trees (i.e., windfall-driven to patch-driven dynamics). They compared alternative models representing different hypothesized drivers within an individual-based model framework and found that the model driven by beetle aggregation was the most consistent with their empirical data on the spatial progression of an outbreak in Tatra National Park in Slovakia. Analogous hybrid modeling by Seidl and Rammer (2017) now serves as the foundation for the individual-based model of beetle disturbance contained within the iLAND FLM.

Model Transparency, Uncertainty, and Confidence

A primary challenge to conducting a systematic and consistent review of landscape models featuring disturbance interactions was the lack of standards by which to classify the implementation of a given disturbance agent in terms of its relative degree of process integration - or for that matter, documentation standards for FLMs more generally. There is an increasing call for standardization of methods in analogous classes of models, including agent-based model designs (Grimm et al., 2010) and species distribution models (Zurell et al., 2020). **Table 6** represents a partial example of how documentation standards relevant to disturbance interactions can convey the nature of the interactions being simulated and investigated. Minimum standards should include the disturbance interaction type simulated (**Figure 3**), the response variable quantifying its effect, and the dynamic components of a given disturbance agent that dictate which interaction types are justifiably investigated. This documentation would facilitate a rapid classification – like that in **Table 4** – so that the nature of the simulated interaction is transparent to the reader. Other essential documentation should include a clearly articulated study design and basic information such as the spatial and temporal grain and extent of simulated processes (**Table 6**). The latter is coming increasingly important to clarify as the temporal and spatial resolution (grain) has become more specific to individual processes as model designs become more refined (**Table 6**). Additional relevant documentation includes the level at which disturbance effects are applied (patch/cell, age class, species, cohort, tree, etc.), the spatial implementation of the disturbance agents (spread, dispersion, etc.), and how the various disturbance agents are interspersed in time. All such documentation should be specific to the model application at hand, rather than the potential capabilities of a given model software, as this was sometimes conflated in the articles we reviewed. Outputs from spatial models are complex enough without confusing artifacts of modeling assumptions with emergent behavior based on underlying process.

We do not assert that complex models are better than simple models. Rather, that one should account for the processes underlying the question being investigated to the extent that data and knowledge can support them. The contemporary argument for design of models based on first principles is that such models should make more robust predictions under the increasingly novel conditions of changing climate, atmospheric composition, and disturbance agents (Cuddington et al., 2013; Gustafson, 2013). We note also that many landscape modeling

TABLE 6 | Representative studies reviewed in the "Modeling Approaches" Section, including disturbance interaction type(s), response variable(s), disturbance classes, characterization of disturbance components*, study design, and scale.

				Spatial (ha)		Temporal (yr.)	
Citation	**Interaction type (response)**	**Disturbance classes***	**Design**	**Grain**	**Extent**	**Grain**	**Extent**
Lucash et al., 2018	Effects (tree mortality), ecosystem response (composition), climate-mediated (fire/insect extent)	Logging, wind, *Insects*, ***Fire***	Single vs. combined disturbances × climate (3)	4	$3.4*10^{7}$	1–10	100
Cadieux et al., 2020	Ecosystem response [bird habitat, forest (biomass, composition, age)], resilience (forest area), climate-mediated (fire and drought)	Logging, *Drought*, fire	Logging (3) × climate (3)	6.25	$6.4*10^{6}$	10	200
Keane et al., 2019	Extent (area burned), Resilience (basal area, fuel, composition, and biomass relative to HRV), climate-mediated (area burned)	**Logging**, ***Fire***, fire suppression	Fire suppression (10) × fuel treatment (4) × climate (2) × location (3)	$9*10^{-2}$	$4.8*10^{5}$	1 day	200
Sturtevant et al., 2012	Extent (burned area, defoliated area), intensity (fire "severity"), ecosystem response (composition)	***Fire***, *Insects*, wind	Forest and fire (modern vs. HRV) × insects (2)	1	$4.3*10^{5}$	10	300
Temperli et al., 2015	Ecosystem response (composition), extent (burned area), effects (beetle-caused mortality), climate-mediated (fire, insects, and drought)	*Drought*, ***Fire***, ***Insects***, wind	Insect × fire × climate (4)	$6*10^{-2}$	$4.0*10^{3}$	1–10	200
Seidl and Rammer, 2017	Extent (blowdown area, insect-impacted area), Climate-mediated (wind and insects)	***Insects***, *Wind*	Insect × fire × climate [temp (3) vs. precip (3) vs. wind speed (3)]	$1*10^{-2}$	$9.3*10^{3}$	1 month	8
Briner et al., 2012	Extent (LULC, logging), climate-mediated (LU productivity), ecosystem response (crop yield and profitability)	*Drought*, ***Logging***, ***LULC***	Economic change (3), climate scenarios (3), vs. all combined	$6*10^{-2}$	$4.4*10^{4}$	1–10	70
Scheidl et al., 2020	Extent (landslide and salvage logging), climate-mediated (wind and insects), eosystem response (tree species)	***Insects***, ***Wind***, ***Landslide***, ***Logging***	Logging (2) × wind + beetles (2) × climate (5)	$1*10^{-2}$	$4.8*10^{3}$	1 min 1 day	200
McGuire and Youberg, 2019	Incidence (likelihood of debris flow)	Fire, ***Debris flow***	Burn severity (3) × burn history (2) × rain event (8)	$1*10^{-4}$	$2.4*10^{4}$	1 min	Hours
Økland et al., 2016	Incidence (number of infestations), extent (size of infestations)	***Insects***, wind	Beetle dispersal vs. beetle dispersal + aggregation	1.2	$2.5*10^{3}$	1	5

Static (predetermined) vs. dynamic (emergent) components are indicated by text type: effects (all examples),* ***Incidence*, *Extent, Intensity*

All examples except the final two were applications of forest landscape models.

studies did not explicitly investigate disturbance interactions *per se*, but rather included multiple disturbance agents to simply account for all the relevant structuring processes within their forest system. Regardless, it is important to acknowledge and account for the cumulative effects of model error propagation as the number of interacting components increase and from one scale to another (Rastetter et al., 1992). To be more explicit about the relative importance of multiple processes and errors, Cressie et al. (2009) promoted the use of hierarchical statistical modeling that allows the quantification of the relative importance of uncertainty stemming from the data model (i.e., data error), the process model (i.e., model specification error), and the parameter model (i.e., parameter estimation error). There are, however, multiple additional sources of uncertainties—ranging from the data, models, processes, knowledge of the processes, and climate scenarios—that will affect the precision and accuracy of model projections.

To quantify the relative importance of these various types of uncertainty, one could compare the outcomes of several models (Cheaib et al., 2012). A recent comparison of four "state of the art" FLMs demonstrated wide divergence in model outcomes, in large part due to design choices affecting vegetation response to disturbance (Petter et al., 2020). This result suggests a certain degree of humility when reporting the results of landscape models – particularly where interactions by multiple disturbance agents may compound error associated with cumulative vegetative responses.

Scheller (2018) suggested that parameterization and "model confidence" are twin challenges facing contemporary landscape modeling studies. The increased burden of input parameter specification that generally comes with replacement of simple statistical relationships with more mechanistic detail may potentially undermine the perceived robustness of process-based models if those parameters are either poorly understood or quantified (McKenzie et al., 2019). Relevant knowledge acquisition necessary for parameter estimation will require multidisciplinary research crossing different domains in scale, integrating experimental research, monitoring of earth systems, advanced statistical analyses, and next generation models assembled from these insights to determine process-based responses to future climatic conditions. Knowledge gaps may further require more novel hybrid modeling frameworks (e.g., Talluto et al., 2016) that integrate process-based and statistical models to include both bottom-up processes and drivers and top-down drivers and account explicitly for feedbacks across scales (**Figure 1**). Such integrative models require knowledge about ecological responses based on targeted experiments in the field and carefully designed data analysis of existent data (Poisot et al., 2016).

Model confidence refers to the degree to which independent readers trust the utility of the model results – in this regard independent validation data remains a fundamental issue underlying confidence in FLMs (Shifley et al., 2017; Scheller, 2018). Validation issues may be particularly acute in the area of disturbance interactions given system sensitivity to the timing and order of disturbance mechanisms and the individualistic responses of the vegetation. While there were examples within our review that evaluated their results using empirical observations (Henne et al., 2013; Karam et al., 2013; Schwörer et al., 2014; Thom et al., 2018), these examples were rare. Validation of model components in combination with targeted uncertainty and sensitivity analyses may also improve model confidence (Cressie et al., 2009; Xu et al., 2012; Scheller, 2018; McKenzie et al., 2019). More specifically, model uncertainty refers to the degree to which model inputs are known as well as their associated measurement error, whereas sensitivity analyses focuses on the degree to which model inputs have influence on the model outputs (McKenzie et al., 2019). Guidance on effective uncertainty and sensitivity analyses can be found across disciplines for simulation modeling more generally (e.g., Saltelli et al., 2006; Wagener and Pianosi, 2019).

Synthesis: New Insights

We found a broad spectrum of questions related to disturbance interactions in forested landscapes have been addressed by an equally diverse range of modeling approaches (**Tables 3**, **6**). Notably, it is the more intractable of these questions that are also the most challenging to quantify empirically, and these require the support of simulation models to investigate. Integration of recent conceptual advances (i.e., linked disturbances, compound disturbances, cross-scaled interactions, and cascading effects) often require more detailed processes to simulate. Among the most important are non-deterministic tree-species competitive interactions and disturbance responses via life history traits, explicit modeling of stand structural characteristics, physiological traits of tree species that enable dynamic responses to climate and biophysical variables, and various integrations of these factors (Keane et al., 2011; Scheller et al., 2011a; Seidl et al., 2012; DeBruijn et al., 2014; Wang et al., 2014). Depending on the questions asked, modeling disturbances require ecological detail necessary to effectively capture their incidence, extent, intensity, and/or effects (see examples within Section "Questions and Approaches Across Disturbance Types"). We are approaching a point where some of the most process-based disturbance models, such as physical fire models, individual-based insect models, and agent-based human disturbances are possible either within FLMs or coupled model architectures (Rammer and Seidl, 2015; Bentley and Penman, 2017; Seidl and Rammer, 2017). Nonetheless, trade-offs between model elegance and complexity remain (McKenzie and Perera, 2015). For example, the parameter demands of highly complex models may exceed the data available to parameterize them (Scheller, 2018) (see also Section "Model Transparency, Uncertainty, and Confidence"). We also observe that the most mechanistic examples reviewed here were comparatively limited in the extent at which they were applied (e.g., thousands versus millions of ha, years versus centuries), illustrating practical trade-offs between ecological detail and scope remain despite advances in computing power (**Table 6**).

The study of disturbance interactions through landscape modeling reflects the asymmetry in systems and disturbance agents of the empirical studies (see Section "Empirical Approaches"). Studies were concentrated primarily and temperate, boreal, and alpine regions of North America and Europe (**Table 2**) and were almost absent from the southern hemisphere. Perhaps it is no coincidence that the prevalent disturbance regimes of subtropical and tropical regions (e.g., mass movement, hurricane/cyclones, mammalian grazers; Burton et al., 2020) were less commonly investigated in the context of disturbance interactions (**Table 5**). We found that human disturbance – by far the most commonly simulated disturbance type – was primarily simulated as a driver rather than an interactive component of the simulations. Cross-scale interactions remain an important concern that are particularly challenging to model and quantify. Each of these deficiencies suggests fruitful areas of future research. Finally, we echo the plea made by previous authors to improve model transparency – perhaps via documentation standards such as that developed for other classes of models.

FUTURE DIRECTIONS

Our review demonstrates substantial progress in the study of disturbance interactions necessary to model their effects on forested landscapes. We now have far greater clarity in the conceptual underpinnings of disturbance interactions, a wealth of empirical studies to draw from, and more advanced model frameworks capable of simulating multiple disturbance types across a range of complexities, relative to what was available at the turn of the millennium when such questions were gaining traction. Questions asked by ecologists are becoming increasingly more ambitious, in part due to the expanding data resources and tools available, and in part due to urgently expanding needs for reliable forecasts of natural and managed ecosystems under increasing anthropogenic stressors. Multiple disturbances and drivers as well as their interactions increasingly insert uncertainty and surprise as forested systems adjust to novel conditions (Urban et al., 2016), complicating our ability to project their behavior. It is therefore paramount to unravel the cumulative effects of multiple disturbances and factors (e.g., edaphic, environmental, and climatic) on vegetation change, with the understanding that as the number of interactions increases, so does the uncertainty associated with ecosystem responses. Such complexity underscores the need to include both conceptual advances and empirical approaches in a review that is ultimately about effective modeling of forest landscape disturbance interactions. As so eloquently stated by Seidl (2017), "to model or not to model, that is no longer the question…". Conceptual understanding, empirical study, and simulation modeling should continually reinforce one another if we are to unravel the complexities of disturbance interactions in time and space.

The "art" of modeling landscape disturbance interactions calls for balanced approaches and scales: while macroscale, empirical models are used to approximate processes, the integration of micro- and mesoscales mechanisms into process-based models is the way to adapt and plan for the novel conditions of the "Anthropocene" (Bodner et al., 2020). The simulation studies cited in this review demonstrate a broad range of modeling approaches that reflect the diversity of ways investigators balance trade-offs in scale, scope, and ecological complexity when modeling disturbance interactions (e.g., **Tables 3**, **6**). Given the importance of transparency to model confidence (Scheller, 2018), it is critical that modelers be explicit about basic assumptions and methods. We note that many landscape simulation studies in the literature cite the *potential* capabilities of a given modeling platform while glossing over the *specifics* of the options they applied. We further caution against loading simulation studies with multiple disturbance types simply because a given model platform allows it. Careful consideration of how the disturbances interact within the context of the model design and the questions being addressed are recommended to avoid compounding model artifacts that can produce misleading results. Furthermore, computing technology may enable modeling of processes that lack the empirical studies necessary to parameterize them—hence the need for a multi-dimensional research agenda.

Turner (2010) emphasized the importance of explicitly accounting for human-induced changes and societal land-use intensification demands, as well as societal responses to disturbance regime shifts and rapid land cover changes. The effects of landscape change resulting from disturbance regime shifts can be investigated by comparing alternative scenarios of plausible system states (Titeux et al., 2016; Urban et al., 2016). By contrast, the more human-focused modeling studies tend to focus on a single ecological response variable (Egli et al., 2019). Blending the state-of-the-art in coupled human natural systems modeling and FLMs remains a current frontier, leveraging the advances in each respective discipline (e.g., Briner et al., 2012).

To sum, modeling disturbance interactions across scales epitomizes the broader challenges plaguing ecological research more generally. The dynamic nature of earth systems makes a strong argument for process-based modeling grounded in a mechanistic understanding of the dynamics of individual system components (Cuddington et al., 2013; Gustafson, 2013). Yet the compounding uncertainty of the interactions between system components—including disturbance processes—that can be both non-linear and scale-dependent lie at the heart of the intractability of complex human-ecological systems (Turner, 2010). Clarity in concepts (knowledge), an empirical foundation (data and analysis), and model designs (synthesis and software) will ultimately enhance understanding of complex systems, but the choice of which processes to model explicitly and which processes to aggregate remains a fundamental challenge of our time.

AUTHOR CONTRIBUTIONS

BS and M-JF jointly developed the theme and content of the manuscript. BS led the literature review and the writing of the manuscript. M-JF provided literature review support, helped shape the flow of ideas, and edited several versions of the manuscript through its current form. Both authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

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