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Significant northwest shift in suitable climate expected for North American bison by the year 2100

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Introduction: Many species are shifting their geographic ranges in response to changing climate, and identifying climate impacts on future species distributions will be critical for conservation success. North American bison (*Bison bison*) provide an exceptional study system for exploring the use of an interdisciplinary record of paleontological, archaeological, and historical data for conservation due to the plethora of past occurrences across a large geographic and temporal scale, in combination with their “near-threatened” designation by the IUCN Red List because of current small, fragmented populations following a near-extinction event in the 1880s. Moreover, the multiple identities of bison as free-roaming wildlife, as wildlife with limitations, and as captive semi-domesticated livestock introduce unique conservation concerns across the four sectors of the Bison Management System (BMS; Tribal, private, public, nonprofit-NGO).

Methods: To model bison climate suitability using “Bioclim”, we associated 1,774 bison occurrences over the last 21,000 years with three PastClim variables (warmest temperature of the warmest month, temperature seasonality, and precipitation of the coldest quarter) that were identified as the strongest predictors of past bison distributions using a variance inflation factor. The model was projected onto the WorldClim RCP4.5 and RCP8.5 future climate scenarios for the four remaining 20-year periods to 2100 CE and onto the WorldClim 2.1 version of current climate, to determine expected changes in climate suitability.

Results: The distribution of suitability scores changes rapidly, shifting significantly between each 20-year interval until the end of the century. By 2100, the centroid of suitable climate, using the standard 50% threshold, is expected to shift from its current location near the 49th parallel to the northwest and toward the northern border of Canada by 1,182 km under the RCP4.5 climate scenario and 2,254 km

under the RCP8.5 climate scenario. Suitability ranges above the optimal minimal threshold identified by the receiving operator characteristic (8.5%) are also predicted to shift to the northwest by 793 km under RCP4.5. and 1267 km under RCP8.5.

Discussion: With an anticipated geographic shift in the most suitable bison climate, it is necessary to prepare future management strategies for BMS sectors to maintain a sustainable relationship with bison.

KEYWORDS

anticipatory management, *Bison bison*, conservation paleobiology, species distribution model, species restoration

Introduction

Contemporary biological communities of large-bodied mammals have distributions largely modified by human impacts (Morrison et al., 2007; Ceballos et al., 2017). Natural ranges have been altered by land use, political conflicts, the introduction of invasive species, habitat destruction and degradation, fragmentation of the landscape, air and water pollution, and accelerated climate changes (Kinnaired and O'Brien, 2012; Suraci et al., 2021; Hesed et al., 2023). The combination of these impacts inhibit natural migratory movements of animals and adaptive range shifts in response to changing climate (Martin et al., 2021; Wendt et al., 2022). All over the world, species capable of dispersal have been documented expanding and shifting their ranges (Büntgen et al., 2017), while other species challenged by human interference are predicted to experience changes in their habitat ranges (Popov et al., 2024). North American climate predictions indicate increasing temperatures, aridity, and increasing interannual variability by the end of the century, leading to areas of severe drought, and more frequent extreme weather events (Klemm et al., 2020).

Human presence and the fruition of predicted climate changes could present significant challenges for the continued management and restoration of *Bison bison* (hereafter referred to as bison), particularly in the Great Plains. The Great Plains refers to a central region of North America consisting of widespread grasslands, which are where most privately owned and many public and Tribal bison herds currently reside (Hanberry, 2019; Martin et al., 2021; Vilsack, 2024). Although bison are considered native to North America, their ancestral species, *Bison priscus*, arrived from Eurasia via Beringia sometime between 190,000 and 135,000 years ago (Heintzman et al., 2016; Froese et al., 2017) and speciated into *B. antiquus*, the progenitor of *Bison bison*. As the largest surviving North American mammal (modern males body mass ranges 700–1100 kg and female body mass ranges 330–630 kg (Martin and Barboza, 2020a) following the late Pleistocene megafaunal extinction (Smith et al., 2003, p. 200; Wendt et al., 2022), bison were once widespread across North America,

especially in grassland habitats (McGuire et al., 2016; Littlefield et al., 2019; Martin et al., 2021, 2023; Wendt et al., 2022). Since the near extinction in the late 1800s as a result of westward colonial expansion (Lueck, 2002; Stoneberg Holt, 2018; Feir et al., 2024), bison populations have been on the rise with a total of approximately 400,000 head with the ongoing expansion of the Bison Management System (BMS) (Martin et al., 2021). However, bison remain classified as near-threatened by the IUCN and do not have the capability to naturally disperse, instead their distribution is defined by jurisdictional lines (IUCN, 2016; Martin et al., 2021).

The BMS sectors are distributed widely across North America and involve the stewardship and ownership of Tribal, non-profit NGOs, public, and private herds on landscapes both within (e.g., *in situ*) and beyond the animal's fundamental niche space (e.g., *ex situ*). Diverse conservation and production aims across the BMS have generated a multifaceted classification of bison as free-ranging wildlife, as wild-with-limitations, and as livestock, depending on jurisdiction and tenure (Martin et al., 2021). In some instances, hunting of publicly and tribally owned bison is permitted but often strictly regulated; privately owned bison, however, is regularly harvested for meat. The variability in the classification of bison poses unique challenges and opportunities for the continued revival of the population.

Anticipating widespread changes in the suitability of climate for bison is key to beginning to prepare and develop management strategies that can be used across the BMS system. Among the BMS sectors, bison provide significant ecological, economic, and cultural benefits (Martin et al., 2021; Shamon et al., 2022). For example, like many large mammals, bison act as ecosystem engineers and as a rangeland keystone species helping to regulate the flow of nutrients and support the creation of habitat for other organisms (Morrison et al., 2007; Nickell et al., 2018). Recent reintroduction of bison to areas of the Great Plains have resulted in a 103% increase in native plant species richness (Ratajczak et al., 2022; Eastman et al., In Press). However, by the end of this century, bison body size is predicted to decline by nearly 50% if climate trajectories follow the worst-case climate futures scenario (CFS) without emission mitigation and abatement (RCP/SSP 8.5) (Martin et al., 2018,

2021; Pörtner et al., 2022). Importantly, rapid and drastic decreases in body size may be consequential to fecundity and longevity of the animals (Martin et al., 2021). Lower forage quality, restricted water availability, and increasing temperature variability may contribute to heightened physiological stress and associated complications resulting in greater susceptibility to vector borne diseases and parasites (van Dijk et al., 2010; Rose et al., 2015; Martin and Klemm, In Press).

Conservation efforts to restore and sustain threatened and endangered species often employ various species distribution models to address future changes in habitat and climate suitability. These models leverage the known distribution of a species and the associated climate and environmental variables to understand preferred habitat. In constructing these models, we can predict the directional changes of the leading (expanding) edge and trailing (retracting or rear) edge of species habitat (Slaton, 2015). Although these studies can be useful in identifying regions of potential restoration for endangered and threatened species, many models only use the modern species distribution (Williams et al., 2009; Wilson et al., 2011; Smeraldo et al., 2017; Bellis et al., 2021). However, many modern species distributions have been heavily modified by anthropogenic influence. For example, all modern North American bison have drastically restricted dispersal abilities that prevent them from tracking their preferred climate and environment. There are no longer free-roaming bison herds in North America and very few herds are considered “wild”. In fact, the IUCN Red List distribution for bison is a small fraction of the species’ previous range, as only the “wild” herds are considered (Figure 1) (IUCN, 2016). Only considering the range of current “wild” herds vastly underrepresents the environmental, ecological, and climatic niche of bison. Moreover, human decision-making determines the placement of bison in fragmented landscapes and introduces applied management strategies to maintain healthy animals (e.g. vaccines, supplemental food and water) in areas in

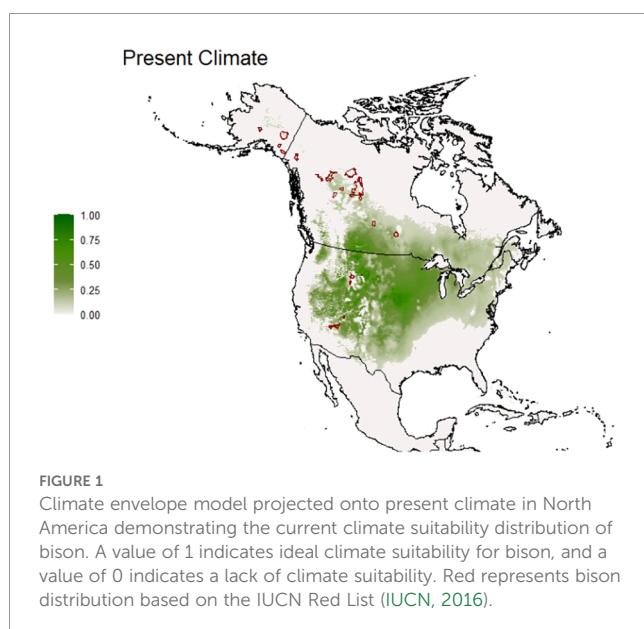
which they could not otherwise thrive (Huntington et al., 2019; USDA, 2022; Martin, 2023). Therefore, using the current range of bison would result in an incomplete interpretation of the species’ niche and the inability to accurately identify regions for long-term restoration. Utilizing paleontological and archaeological data across deeper time scales enables the study of species distributions across periods of past climate change to understand the full fundamental climatic niche of a species and how it may exist in the future, providing guidance for anticipatory management (Wingard et al., 2017; McGuire et al., 2023).

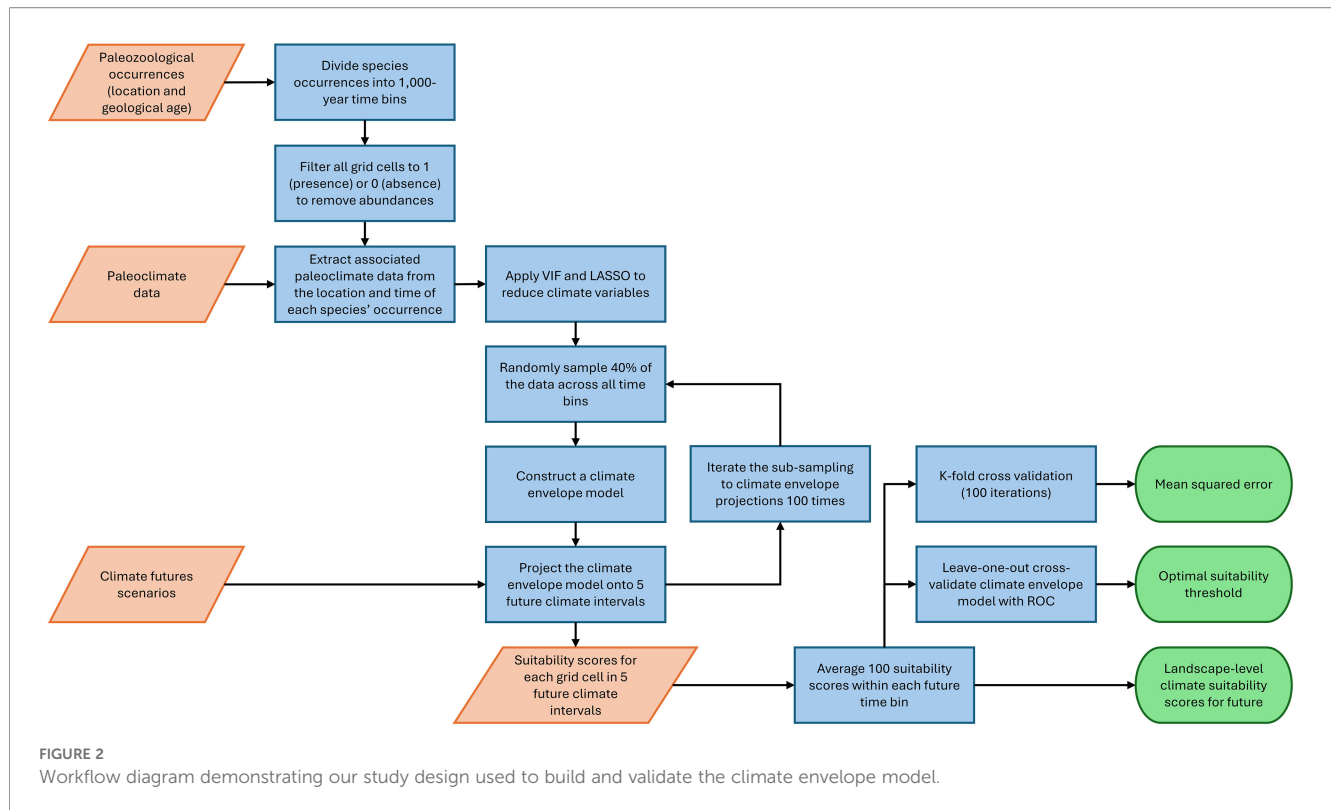
Here, we aim to support ongoing restoration and management of bison across the BMS by using 21,000 years of paleontological, archaeological, and historical data and the associated climate data to build a comprehensive climate envelope for bison in North America. We test climatic variables to identify which most effectively determine past bison distribution. We leverage the resulting climate envelopes to predict changes in climate suitability for bison in the United States, Mexico, and Canada across four future time intervals, extending to the end of this century. Our study identifies regions of North America where bison suitability will be lost and gained to anticipate regional challenges for the BMS sectors.

Materials and methods

Figure 2 provides a workflow diagram of our study design. First, North American bison occurrences were sourced from the Martin et al. (2022, 2023) dataset ($n = 6440$). We filtered the data to retain *Bison bison* and the closely related *B. occidentalis* and *B. antiquus* while removing *B. latifrons* and *B. priscus* (Heintzman et al., 2016; Froese et al., 2017; Martin et al., 2023). *B. latifrons* and *B. priscus* are ancient relatives of the modern bison and were removed from the study because they may exhibit different climate preferences, altering the results of our climate envelope model (Shapiro et al., 2004; Wilson et al., 2008). We restricted the data to those with dates: (1) less than 21,000 years ago to remove early occurrences with poor temporal resolution and (2) more than 250 calibrated radiocarbon years before present (i.e., older than 1700 CE) to avoid bison distributions more heavily influenced by the presence of European settlers. Ages are from Martin et al. (2023), which applied the IntCal20 calibration for the radiocarbon dates initially reported for each locality (Reimer et al., 2020).

We obtained climate data for the past 21,000 years as well as 100 years into the future to determine changes in climate suitability. The 21,000 years of North American paleoclimate data were downloaded from the ‘pastclim’ R package (Beyer et al., 2020; Leonardi et al., 2023). Beyer et al. (2020) assimilated 17 global climate variables matching those used by WorldClim into 1,000-year time intervals at a 5-minute spatial resolution (9 km) (Supplementary Table S1). Current climate was obtained from WorldClim version 2.1 using the ‘geodata’ R package (Hijmans et al., 2024). Two future emissions scenarios (RCP4.5, RCP8.5) from the Hadley Centre Global Environment Model version 3 — that were derived from the IPCC AR5 (Kuhlbrodt et al., 2018) — were downloaded from the ‘geodata’ R package (Hijmans et al., 2024) at a





5-minute spatial resolution (9 km) to be used to predict the presence of *Bison* in North America for four future 20-year intervals: 2021–2040, 2041–2060, 2061–2080, and 2081–2100. RCP4.5 emission scenario reflects changes in climate based on mitigated human emissions, while RCP8.5 is climate without any emission mitigation, or also called “business as usual” (Tebaldi and Wehner, 2018).

Climate suitability model

Due to the temporal extent of the bison occurrences, we needed to account for sampling biases across the 1,000-year intervals. To avoid over-representing the climate of a single geographic 5-minute grid cell, we did not use abundances. Instead, each grid cell was identified by presence or absence of bison, regardless of the frequency of occurrences in that grid cell (1 or 0, respectively) (Watling et al., 2013). Ultimately, 1,775 bison occurrences were used to build the climate envelope model. We further chose to use a presence-only approach because we cannot confidently know if absences in the pre-modern record are true absences or a result of preservation bias. Inclusion of absences could produce a model that substantially underrepresents the extent of the bison climatic niche (Supplementary Figure S1). Finally, because 50% of bison presences occurred in the last 2,000 years, climate envelopes were constructed using a random subsampling approach to assemble 100 iterations of the climate envelope model. The subsampling method randomly pulled 40% of the bison presences from the whole 21,000-year

dataset and replaced the randomly sampled occurrences between each of the 100 iterations.

To avoid over-fitting the model, the climate variables were tested for multicollinearity using a variation inflation factor (VIF) in the ‘car’ R package (Fox et al., 2001). Any variables with the common conservative VIF score >5 were excluded from the model to simplify projections and better identify areas impacted by future climate (Park et al., 2021; Doxa et al., 2022). A total of 12 variables were identified as having high multicollinearity and were removed, leaving five predictor climate variables for further analysis.

We used the bioclim function in the ‘dismo’ R package to build climate envelope models based on the subsampled bison occurrences (Beaumont et al., 2005). Bioclim generates a distribution of values for each climatic variable that is compiled from all grid cells where bison were present across all time intervals and extracts the median value. Across the landscape, the closer that the climatic variable value is to the median, the higher the suitability score, such that the suitability score decreases as the value deviates from the median value. While bioclim can analyze up to 35 climatic parameters in a single model, the disadvantage is that a larger number of parameters can decrease the ecological realism of the results because of the negative correlation with the size of potential species distributions (Beaumont et al., 2005). However, we used multiple methods to reduce the number of parameters and identified those with stronger predictability of bison occurrences to avoid this issue. Moreover, bioclim is advantageous for our study because it does not require absences or background points to build the model; presence-only models are ideal when using fossil data

(Beaumont et al., 2005). We tested several other modeling approaches that used absences or background points (i.e., Maxent, GLM, Random Forest, ensemble models). We encountered two critical issues: 1) inclusion or absences resulted in a drastically reduced climate envelope that suggested little to no suitability for bison in North America due to the large number of absences across all 1,000-year intervals in comparison to the relatively smaller number of bison occurrences, and 2) because we are working with the fossil record and time intervals with variable preservation biases, grid cells without bison specimens cannot be confidently determined as true absences (Supplementary Figure S1).

We used a least absolute shrinkage and selection operator (LASSO) to evaluate climate models built on the five remaining ‘pastclim’ variables following the VIF analysis. LASSOs are commonly used as a preferred Akaike Information Criterion-based computational efficiency method to identify the best predictor variables for a model, as well as reduce the number of predictors to avoid overfitting (Ranstam and Cook, 2018). A corrected Akaike Information Criterion (AICc) determined the model that best detected the presence of bison [$\Delta AICc < 2$; (Guthery et al., 2003; Burnham et al., 2011)]. We used the bioclim suitability predictions to cross-validate 80% of the past occurrences (Watling et al., 2013).

We then used a nonparametric area under the curve (AUC) of the receiving operator characteristic (ROC) (Pepe, 2004) of the selected climate suitability model predictions of past occurrences against a “gold standard” of documented presence occurrences. Higher ROC values, on a 0–1 scale, reflect a greater predictability power to locate true presences (Pepe, 2004). To translate the model’s continuous probability scores into a binary classification of suitable versus unsuitable habitat, an optimal threshold was identified using the Liu cutpoint method (Liu, 2012) to maximize the product of sensitivity and specificity. We also determined the model sensitivity, specificity, and correctly classified metrics of three other commonly applied thresholds of 25%, 50%, and 75%. A bootstrap analysis with 1,000 replications was performed to assess threshold stability, and we report the partial AUC for the false positive rate of each threshold.

We report the results of the optimal threshold as well as 25%, 50%, and 75% thresholds. We focus largely on the ROC-derived optimal threshold because it is statistically justified. However, the optimal threshold is low enough that it may not fully facilitate anticipatory management. By using multiple and larger thresholds, we can address a wider range of areas that can expect to encounter management implications.

Climate futures scenario data and spatiotemporal averaging techniques

Each of the 100 climate envelope models was projected onto climate futures scenarios (CFS) using four 20-year intervals: 2021–2040, 2041–2060, 2061–2080, 2081–2100, resulting in a total of 400 projections. For each of the four-time intervals, the 100 iterations of suitability scores, ranging from 0 (low) to 1 (high), were assigned to 448,355 raster grid cells across North America and then averaged to

generate future landscapes of suitability scores. The standard error of the suitability scores was used to provide confidence values for each grid cell. We defined changes in climate suitability using four thresholds and evaluated the directional shift of climate suitability by calculating the location of the centroid of climate suitability thresholds and for each emission model (Figure 1).

To validate the ability of the model to predict future suitable climate ranges of *Bison* based on the selected climatic variables, a random past time interval (2,000 – 1,000-year) was chosen and the occurrences within that time bin were removed from the data set. We ran the subsampling routine without the occurrences of the removed time bin and generated a new climate envelope model that could be used to assign suitability scores for the 2,000 – 1,000-year time bin. We rescaled the suitability scores into deciles representing the frequency and distribution of suitability scores (Gormley et al., 2011; Rauniyar and Power, 2023). To determine the model’s predictability strength for identifying the presence of bison across the grid cells, we calculated the number of true presences that had a suitability score above the 50% decile because that is the traditional default threshold used in binary models (Freeman and Moisen, 2008). A $k_{(5)}$ -fold validation approach was also applied to validate the accuracy of our climate envelope model in predicting climate suitability of bison. Twenty percent of bison occurrences across all time bins were randomly selected to build a testing dataset, while the remaining 80% of occurrences were used as a training dataset. We created a generalized linear model using occurrences and the three climate variables used to build the climate envelope model (BioClim04, BioClim05, BioClim19). A mean squared error was calculated to evaluate the accuracy of our model. This analysis was reiterated 100 times and the mean squared errors were averaged across all iterations.

Software and analyses

All climate envelope models and analyses were run in R version 4.1.2 (2021-11-01), except for the ROC and AUC tests, which were performed in Stata/SE (v19.0; StataCorp LLC., College Station, Texas). All maps use WGS84 coordinate system with Albers Equal Area Conic projection.

Results

Temperature-related variables facilitate a northwestern shift of the leading edge of suitable climate into Canada and Alaska and a retraction of the trailing edge from Mexico and the southern contiguous US under both climate future scenarios (CFS; RCP4.5 and RCP8.5).

Selected climate variables and model performance

The LASSO identified temperature seasonality (BioClim04), maximum temperature of the warmest month (BioClim05), and

TABLE 1 Summary statistics of five thresholds from ROC analysis.

Suitability threshold ($\geq\%$)	TPR (%)	TNR (%)	FPR (%)	Correctly classified (%)	Partial AUC of the FPR (%)
0.0001	100.00	0.00	100.00	0.91	78.53
8.47	73.39	70.86	29.14	70.88	13.45
25.00	49.94	86.79	13.21	86.45	3.40
50.00	11.16	97.28	2.72	96.50	0.16
75.00	0.28	99.91	0.09	99.01	0.00

TPR, true positive rate (sensitivity); TNR, true negative rate (specificity); FPR, false positive rate (100% - TNR); percent correctly classified; and partial area under the curve (AUC) of the FPR.

precipitation of the coldest quarter (BioClim19) as the best combination of climatic variables to maximize the true positive rate and limit the false positive rate of predicting the presence of *Bison* over the last 21,000 years in North America.

The ROC analysis revealed that this model achieves an AUC of 0.7853 (95% CI: 0.7750 - 0.7956) at a threshold of ≥ 0.0001 (Table 1). A test of equality of ROC area against a gold standard yielded an optimal threshold of 0.0847 (95% CI: 0.0553 - 0.1141) with a sensitivity of 73.4%, specificity of 70.9%, and a correct classification of 70.9% (Table 1). With increasing threshold value, the model exhibits increasingly correct classifications with increasing specificity at the expense of decreasing sensitivity (Table 1).

Our model validation process provides confidence in the predictability strength of our climate envelope model under RCP4.5 and RCP8.5 climate future scenarios. Our validation approach demonstrated adequate predictability strength with over 98% of the grid cells with true *Bison* occurrences scoring greater than the 50% decile value (0.05). Over 73% of the grid cells where bison were present had a suitability score greater than the 80% decile value (0.17). Moreover, we found that 99.91% of the raster cells with bison present had a climate suitability score greater than the optimal threshold identified by the ROC (~8.5%). The k-fold cross-validation analysis resulted in an average mean squared error value of $1.11e-27$. We also demonstrated the consistency of the suitability scores with minimal standard errors of climate suitability across all grid cells (min = 0, mean = 0.001, max = 0.005), with the highest values occurring in the regions with the greatest suitability scores (Supplementary Figure S2).

Suitable climate for bison will shift northwest

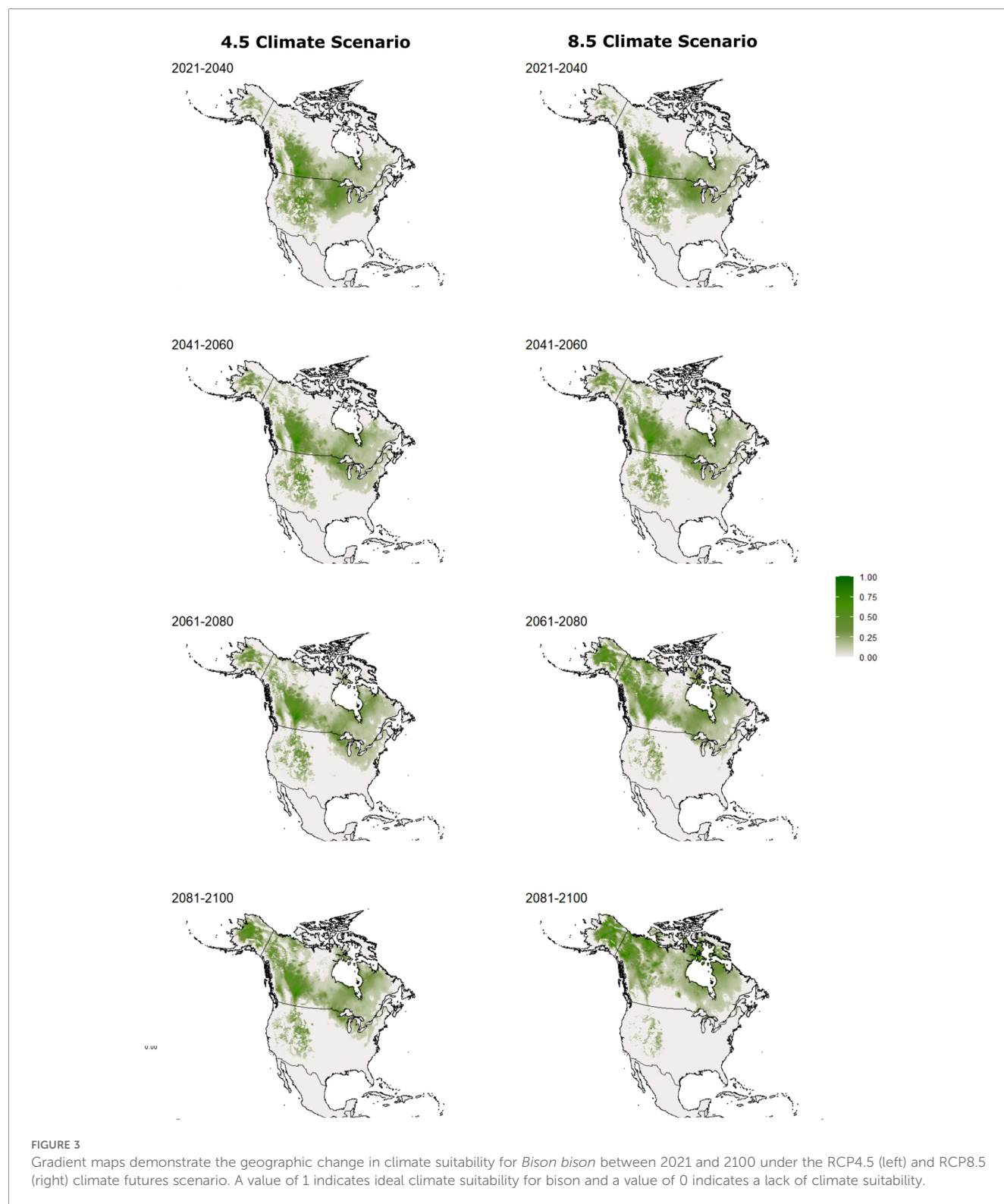
The northwestern shift is apparent across all thresholds (8.5%, 25%, 50%, 75%) and across the four future intervals (Figures 3–5). Moreover, under both the RCP4.5 and RCP8.5 CFS, the range of climate suitability expands its area under the 8.5% and 75% thresholds (Figure 6; Table 2). North American grid cells with increasing suitability between present climate and the year 2100 are widespread across Canada and Alaska, while grid cells with decreasing suitability are largely concentrated in the central region of the 48 contiguous states (Figure 4). In fact, the change in climate suitability across North America is so rapid that the

distribution of suitability scores is significantly different between each time interval under both climate futures scenarios (Supplementary Table S1).

Under the RCP4.5 CFS, the centroid of suitable climate shifts to the northwest by the year 2100 (8.5% = 793 km, 25% = 1071 km, 50% = 1876 km, 75% = 485 km), moving from near the border of the contiguous U.S. and Canada to the border of Alaska and Canada (Figure 5). Over the century, the 50% suitability threshold experiences the greatest centroid shift. The centroid undergoes the greatest geographic change between the 2061–2080 and 2081–2100 intervals (Figures 3, 5). However, under the RCP8.5 CFS, the greatest centroid shift occurs earlier between 2041–2060 and 2061–2080. From the present to 2100, the RCP 8.5 centroids of the various thresholds shift more dramatically to the northwest region of North America (8.5% = 1267 km, 25% = 1773 km, 50% = 2254 km, 75% = 2394 km) than do the centroids under RCP4.5 (Figures 3, 5). In fact, the geographic shifts that occur at the 50% and 75% thresholds are so great that nearly none of the present range has any overlap with the 2100 range (Table 2).

From the present to 2100 and under both the RCP4.5 and RCP8.5 CFS, the area of suitable climate increases in North America at the 8.5% and 75% thresholds (Figure 6; Table 2). The 8.5% threshold range initially increases in size following the present climate but remains relatively consistent until 2081–2100 under the RCP4.5 scenario. At the 75% threshold, the range is nearly cut in half by the 2021–2040 interval but expands dramatically between the 2061–2080 and 2081–2100 intervals. Under the RCP8.5 scenario, the area above the 8.5% threshold initially increases following the present but slowly decreases at each future interval. The area above the 75% threshold declines rapidly twice: first, after the present climate interval and into the 2021–2040 interval and second, from 2041–2060 to 2061–2080. However, the area increases by the 2081–2100 interval as suitability expands into Alaska, similar to what is found under the RCP4.5 CFS.

In contrast, there is a decline in area of suitability at the 25% and 50% thresholds, with the greatest decline in area occurring at the 50% threshold under the RCP4.5 (-94%); however, there is also a major decline under the RCP8.5 scenario (-89%) (Figure 6; Table 2). Under both scenarios, the size of the area decreases from the present climate to the 2021–2040 interval but has little variability in size from 2021–2040 to 2100. The loss of area at the 25% threshold is minimal (<5%) under both scenarios with a consistent increase in area from 2041–2060 to 2061–2080; however, under the RCP8.5, the area decreases in size again by 2081–2100.



Discussion

We predict a northwest shift of suitable climate for bison into northern Canada and Alaska by 2100. The geographic center of suitable climate is currently near the 49th parallel border between the contiguous United States and Canada, but by 2100, it will be

located near the border of Canada and Alaska (Figures 4, 5). By the end of the century, we find a geographic expansion in the overall area of suitable climate above the 8.5% and 75% thresholds under the RCP4.5 climate scenario (Figure 6; Table 2). In contrast, there is a decrease at the 25% and 50% thresholds by as much as 94%. Similarly, under the RCP8.5 climate scenario, we find an increase in

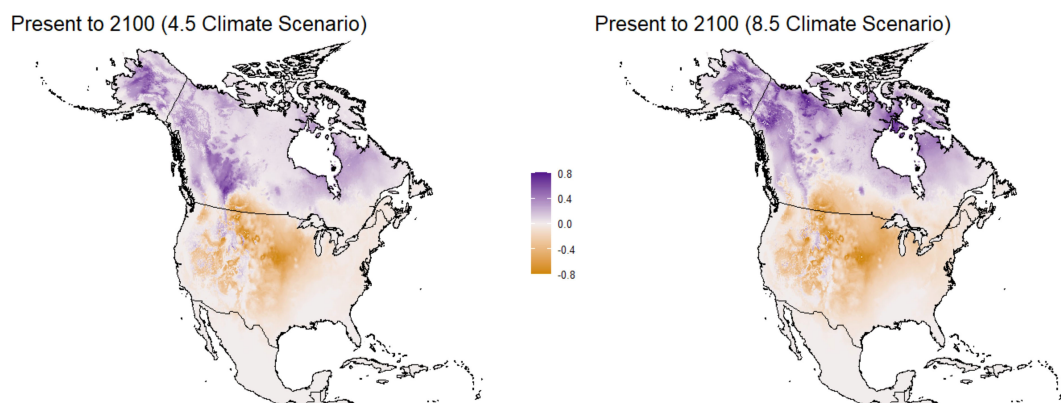


FIGURE 4

Anomaly map showing the relative change in climate suitability across North America between 2021–2040 and 2081–2100 for RCP4.5 (left) and RCP8.5 (right) climate futures scenarios. Positive values represent areas with a gain in climate suitability between the present and 2100. Negative values represent areas with a loss in climate suitability between the present and 2100.

range size for 8.5% and 75% suitability thresholds and a decline in range for 25% and 50% thresholds, with the greatest loss again under the 50% suitability threshold (Figure 6; Table 2).

Impacts of suitability changes vary across leading and trailing edges

North America is predicted to experience substantial warming by the end of the century, with regional variability in seasonal precipitation and temperature (Polley et al., 2013). Impacts of the impending climatic changes in North America by 2100 will likely affect bison management strategies by altering forage quality and water availability. Furthermore, water-holding capacity of the soil, phenological responses, and primary productivity of vegetation may all be altered (Polley et al., 2013). However, the effects of changes in precipitation and temperature can depend on the vegetative

community composition and soil characteristics of a region (Polley et al., 2013).

Under both climate futures scenarios (RCP4.5 and RCP8.5), we demonstrate that the leading edge of suitable bison climate will extend into northern regions of Canada by 2100 under all thresholds (Figures 3, 5), although nearly half of current suitability based on the optimal threshold (8.5%) will be maintained (Table 2). The largest centroid shift will occur earlier under the RCP8.5 scenario than it will under the RCP4.5 scenario, influenced by the more rapid shift in climate predicted for RCP8.5. During the final time interval (2081 – 2100), the area of suitable climate increases above the optimal threshold and 75% threshold, expanding into central Alaska and across northern Canada (Figures 3, 6; Table 2). The most suitable climate for bison (>75% threshold) is isolated in two areas: Alberta, Canada, and western Alaska (Figure 4). Both areas of higher suitability are largely surrounded by >50% suitable climate possibly providing land that

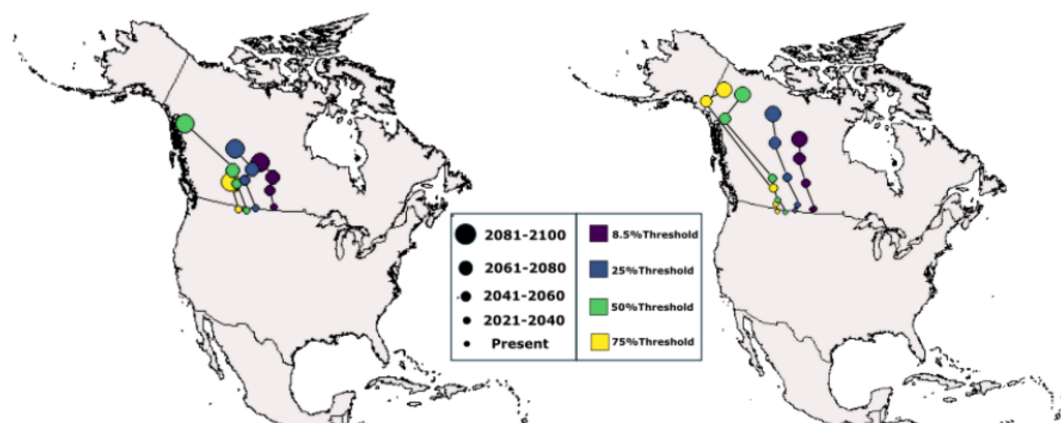


FIGURE 5

Map showing the geographic shift of the centroid for each subset of the climate suitability scores (8.5%, 25%, 50%, and 75%) for the RCP4.5 (left) and RCP8.5 (right) climate futures scenarios.

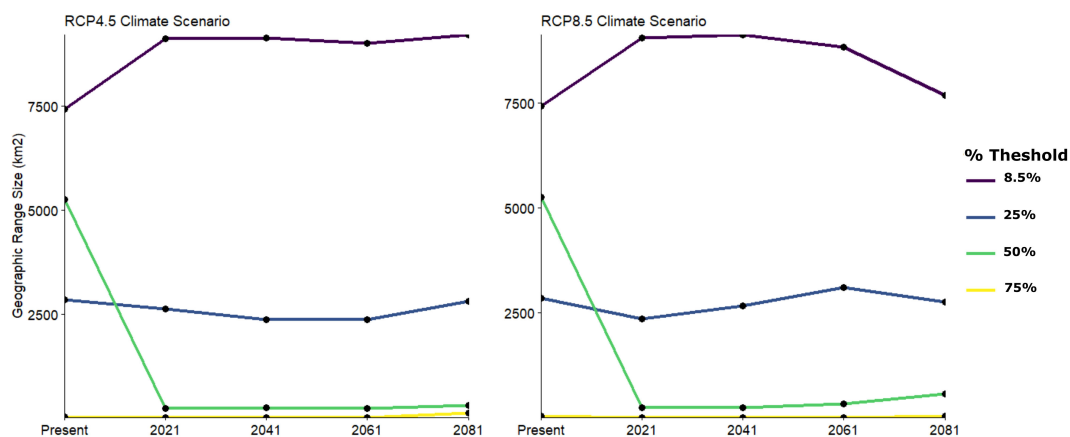


FIGURE 6

Range size within the $\geq 8.5\%$, $\geq 25\%$, $\geq 50\%$, and $\geq 75\%$ suitability thresholds for the RCP4.5 (left) and RCP8.5 (right) climate futures scenarios for the current climate and four future vicennials.

could be used for future corridors. Alaska and northern Canada are predicted to have significant increases in winter temperatures as well as summer and winter precipitation levels over the next 40 years (Deser et al., 2014). Increases in temperature and precipitation have the potential to increase net primary productivity by extending the growing season for vegetation providing greater food resources, although the extent of increased vegetation production will contend with seasonally determined photoperiod limitations for net primary productivity (Hobbie and Chapin III, 1998; Polley et al., 2013).

The trailing edge of suitable climate for bison also shifts north, leaving less suitable climate throughout the mid-latitude grasslands of the U.S., especially under RCP8.5 (Figure 4). Thus, most of the contiguous U.S. will experience a decline in climate suitability, and all of Mexico will fall below the 8.5% threshold by 2100 (Figure 3). Persistently low suitability that is predicted for the regions of the west coast, southwest, central U.S., and Mexico may result in health and sustainability challenges across all BMS sectors (Craine et al., 2015; Martin and Barboza, 2020a; Martin et al., 2021). In fact, the southwest is expected to experience severe drought with a $>2.5\%$ decrease in precipitation, leading to environmental consequences, such as decreased vegetation and reduced digestibility of the vegetation for grazers like bison (Polley et al., 2013).

The greatest loss of suitable climate for bison will occur across Minnesota, the Dakotas, and southern Canada, inclusive of the prairie pothole region (PPR) (Figure 4). The prairie pothole region is a complex system of wetlands created from remnants of late Pleistocene glacial activity and pluvial Lake Agassiz spanning Alberta, Saskatchewan, and Manitoba of Canada, as well as Montana, Minnesota, Iowa, North Dakota, South Dakota of the contiguous U.S. (Muhammad et al., 2020). This region is important because of the biologically diverse ecosystems (Muhammad et al., 2020), but it is predicted that the wetland productivity will be severely impacted by both climate change and human-modified land-use changes to the area, impacting the ability of the region to support wildlife (Rashford et al., 2016). The PPR is predicted to rise in temperature by 4–6.5°C

over the next 60 years, likely causing significant changes to the hydrologic system (Muhammad et al., 2020).

The increase in range size of suitable climate above the optimal threshold (8.5%) into Alaska and Canada may provide ample opportunity for BMS expansion across all sectors (Figures 3, 6; Table 2). Although there is a northward shift of the leading and trailing edge for bison climate suitability by the end of the century, and much of the lower 48 states and Mexico fall below the optimal threshold of 8.5%, many herds are currently being maintained in areas deemed ‘unsuitable’ by our model. This suggests that herds falling under the suitable threshold of 8.5% have the potential for success but will likely need to adopt management strategies already being used by other herds in ‘unsuitable’ regions. The drastic drop in the range size of higher thresholds, such as the 50% threshold, is important to anticipate, but herds retaining suitability scores above the optimal threshold will likely require fewer intensive changes to management practices (Box 1).

Challenges to future bison sustainability

With changing temperature and precipitation negatively impacting the climate suitability of bison across the contiguous United States, southern Canada, and northern Mexico, the development and application of adaptive management strategies will be required to sustainably conserve bison within their physiological limits. Climate has the potential to impact environmental components that bison and the members of the BMS rely on, as well as the potential to impact bison health directly. These at-risk components include, but are not limited to, decreases in landscape surface water availability and rangeland forage quality and quantity, and increases in disease risk and water intake requirements (Gogan et al., 2005; Martin et al., 2018, 2021). With predicted environmental changes, the duration of gestation and timing of bison parturition—currently geographically variable—has

TABLE 2 Area of suitable climate for $\geq 8.5\%$, $\geq 25\%$, $\geq 50\%$, and $\geq 75\%$, under the RCP4.5 and RCP8.5 climate futures scenarios, total percent change from 2021 to 2100, and the amount of area overlap retained.

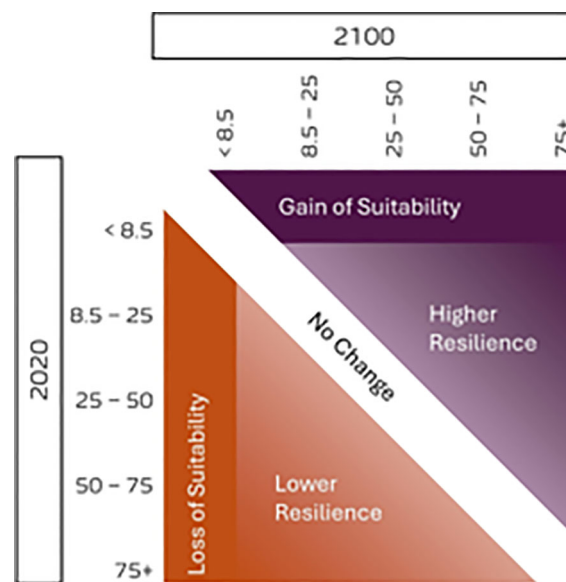
Climate future scenario	Suitability threshold	Area size (km ²) by time period					Change in area (%)	Retained overlap of area (%)
		Present	2021-2040	2041-2060	2061-2080	2081-2100		
RCP4.5	≥8.5%	7,436,126	9,116,599	9,144,573	9,018,063	9,203,190	+23.8	46.3
	≥25%	2,844,564	2,628,798	2,377,976	2,380,421	2,805,938	-1.4	88.3
	≥50%	5,260,723	249,236	253,004	239,833	313,378	-94.0	99.6
	≥75%	34,919	17,637	14,515	17,570	137,006	+292	0
RCP8.5	≥8.5%	7,436,126	9,058,573	9,115,612	8,825,945	7,686,914	+3.4	53.7
	≥25%	2,844,564	2,356,668	2,672,510	3,098,890	2,755,967	-3.1	11.7
	≥50%	5,260,723	246,890	240,453	330,108	570,047	-89.2	0.4
	≥75%	34,919	13,801	13,042	1,362	40,354	+15.6	0

the potential to rapidly change by 2100 and should be regularly monitored (Gogan et al., 2005). Bison distributions are determined by humans, therefore, anticipating management strategy modifications as a result of a changing climate is essential due to the inability of bison to naturally disperse to track preferred climate.

Bison body size is phenotypically plastic, adapting physiologically to increases in temperature by decreasing at a relative rate of 41 ± 10 kg per °C, globally (Martin et al., 2018). This rate of body size change was demonstrated on a spatiotemporal scale using a continental spatial extent of data spanning the last 40,000 years. Regionally, modern bison today have a latitudinal gradient in body mass, declining by as much as 30% from north to south (Craine et al., 2015; Martin and Barboza, 2020a, 2020b; Craine, 2021). The temporal rate of body mass decline suggests that they could be nearly 50% smaller in some regions of North America by 2100 based on predicted end-of-century temperatures, specifically on a latitudinal gradient with lower body sizes at lower latitudes (Martin et al., 2018). Follow-up studies have found that body mass declines can be further compounded by chronic drought severity, which further reduce bison body size (Martin and Barboza, 2020a, 2020b). Reduction in body size will have critical effects on life history traits of bison by reducing growth rate, time to reach sexual maturity, decreasing longevity, and the size and number of offspring per individual (Martin et al., 2018; Martin and Barboza, 2020a, 2020b).

Potential cultural challenges with loss of bison suitability

Understanding and mitigating the impacts of climate change on bison populations is not just an ecological imperative but a social and cultural necessity for many communities across North America. The impending decline in climatic suitability for bison across the contiguous United States and Mexico will pose a substantial threat to ongoing reintroduction efforts on both tribal and public lands. These initiatives are not merely ecological endeavors but are deeply interwoven with social, cultural, and economic well-being semi-free-ranging public herds of bison serve to foster a profound connection between individuals and the natural landscape, thereby bolstering their commitment to the preservation and conservation of wild environments (Wilkins et al., 2019). For many Indigenous peoples, bison symbolize the systemic flourishing and abundance of life; bison are not merely animals but integral components of cultural identity, spiritual beliefs, and traditional ways of life, including roles in traditional ceremonies, language, and intergenerational knowledge transfer (Crosschild et al., 2021). This connection can inspire a deeper sense of stewardship and manifest as increased public engagement with conservation initiatives, support for protected areas, and a renewed appreciation for North American ecological heritage (Wilkins et al., 2019; Pejchar et al., 2021). Furthermore, bison reintroduction supports food sovereignty initiatives by providing a culturally relevant and sustainable food source, which can alleviate food insecurity and promote healthier diets within tribal nations (Janssen et al., 2021; Shamon et al., 2022; van Vliet et al., 2023;



BOX 1 Anticipated resilience outcomes of climate suitability anomalies from 2020 to 2100 (Figure 3). Localities with climate suitability that does not change will likely not require drastic management adaptations (white). All localities where climate suitability increases from 2020 thresholds to 2100 thresholds (purple) may have higher resilience for bison and, therefore, may experience fewer management challenges. Although, localities that were below the optimal threshold (8.5%) that then gain bison climate suitability may face challenges of habitat mismatch (boreal forests, tundra, etc.). Localities where climate suitability decreases from 2020 thresholds to 2100 thresholds (orange) may experience lower resilience for bison and, therefore, may face risks and hazards, such as heat waves, droughts, extreme humidity, and disease outbreaks. However, localities that show complete loss of climate suitability by the end of the century may encounter habitat mismatch in addition to heat waves, droughts, extreme humidity, lack of seasonality, and disease outbreaks. All of the above scenarios require management decisions and adaptive capacity.

Maxwell and Duff, 2024; Newton et al., 2024; Simpson et al., 2024). The re-establishment of bison herds often underpins sustainable economic practices, creating opportunities for land management, tourism, and the sale of bison products, thereby strengthening tribal economies (Feir et al., 2024).

Benefits and applications of methods

The approach presented here provides a comprehensive, quantitative definition of climate suitability through a deep-time perspective and subsampling method that prioritizes climate and impacts over the long term (Figure 2). Our method for predicting future shifts in suitable climate for bison is widely applicable across regions and species with pre-modern records and will help provide greater insight into the climate and habitat niches of species. Furthermore, it will better identify potential geographic ranges for potential restoration or dispersal of species (Figure 4) as well as necessary management adaptations (Box 1). By including paleontological, archeological and historical data, we aim to capture changes at the margins, which are expected to be where suitability shifts originate as extreme weather events, such as heat waves, blizzards, and floods, occur more frequently and intensely, with longer durations, and in previously unaffected areas (Redford et al., 2016; Plumb and McMullen, 2018). While the IUCN Red List

and other similar datasets of species ranges are important and informative for understanding more recent reductions or expansions of species ranges, modern distributions can be unreliable in demonstrating a species' true ecological, environmental, and climatic niche. Surprisingly, present-day suitable climate calculated using our model has little overlap with the current IUCN Red List bison distribution (Figure 1).

Our approach also accounts for bison's over-represented historic record being ecologically anomalous because of historically unique economic markets (e.g., robe trade (Feir et al., 2024)) and social impacts (e.g. European diseases (Stoneberg Holt, 2018)) that would preferentially inflate occurrences of the species in some areas. To include such a large dataset, this approach considers deflated geological preservation by focusing on true occurrences and not assuming true absences in the pre-modern record; absences may be areas of suitability without any specimens recorded (i.e., extent of occurrence used by IUCN (IUCN SSC Red List Technical Working Group, 2021; Mancini et al., 2024). Yet, even with the subsampling approach, more recent climate was likely still over-represented in the final climate envelope model due to the extent of the sampling bias in recent time bins compared to the earliest time bins. We suggest that this minimal over-representation of more recent climate may be beneficial because bison have experienced adaptive changes, such as an overall reduction in body size over the last 40,000 years and nuanced body size reductions over the last five

decades (Martin et al., 2018; Martin and Barboza, 2020a), alongside changing climate, resulting in modern bison that are likely more well-adapted to recent conditions (Martin and Barboza, 2020a, 2020b).

Study limitations

We were limited to evaluating climate suitability instead of habitat suitability because of a lack of environmental and vegetation data at a similar temporal resolution. The examination of vegetative variables may restrict or expand potential suitable areas for bison identified in our study and may enable assessment of local impacts across specific locations for bison herds seeking distinct management guidance. Additionally, although bioclim can produce more accurate results than GLM envelope models and that align with results generated by Maxent (maximum entropy) approaches (Lawing and Polly, 2011), a limitation of this method is that the two tail ends of the distribution are treated equally, even if they are unequal. Ecologically, we know that the upper and lower end of a variable have a different magnitude of impact on a species. For instance, when evaluating a range of temperature, a species' greater sensitivity to either colder or warmer temperatures is not recognized in the model.

Conclusion

With this approach, our study can provide insight into geographic areas that will likely experience changes in suitable climate for bison, potentially causing new challenges or intensifying current challenges, which only become more prevalent when considering the restricted dispersal of bison. Bison continues to be a species of ecological, cultural, and societal importance, which is reflected in their multifaceted classification as free-ranging wildlife, as wild with limitations, and as livestock, depending on jurisdiction and tenure. By utilizing 21,000 years of pre-modern bison occurrences, we demonstrated a likely northwest shift in suitable climate for bison by 2100 with an expansion in geographic range as temperatures continue to increase. There will be a decline in suitability across the contiguous United States and Mexico that coincides with an increase in suitability in Canada and Alaska. By anticipating future consequences of climate change, the sectors of the BMS can increase their resiliency by considering development of inter-sector management strategies that take advantage of suitable climate and leverage adaptive management.

Data availability statement

The datasets presented in this study can be found in online repositories. All climate datasets and R code can be found at: https://figshare.com/projects/Significant_Northwest_Shift_in_Suitable_

[Climate_Expected_for_North_American_Bison_by_the_Year_2100/262132](#).

Author contributions

AS: Conceptualization, Formal Analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. JM: Conceptualization, Data curation, Funding acquisition, Investigation, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – review & editing, Methodology. BB: Writing – original draft. EO-C: Conceptualization, Data curation, Validation, Writing – review & editing, Investigation. MH: Data curation, Validation, Writing – review & editing, Conceptualization, Investigation. CW: Data curation, Validation, Writing – review & editing, Conceptualization, Investigation. JR: Validation, Writing – review & editing, Funding acquisition, Resources. RS: Funding acquisition, Validation, Writing – review & editing, Conceptualization, Data curation, Investigation, Project administration, Resources, Software, Supervision, Visualization, Methodology.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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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.2025.1695457/full#supplementary-material>

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