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Long-term research on avian conservation ecology in the age of global change and citizen science

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Long-term research on avian conservation ecology in the age of global change and citizen science

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Editorial: Long-term research on avian conservation ecology in the age of global change and citizen science

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Editorial on the Research Topic
Long-term research on avian conservation ecology in the age of global change and citizen science

Birds are among the most effective indicators of environmental change, and long-term avian research provides critical insights into biodiversity dynamics in the Anthropocene. Centuries of ornithological research combined with citizen science have produced some of the most comprehensive ecological trait datasets for any taxon, enabling detailed ecological and conservation assessments (Kittelberger et al., 2021a), including those of population trends and at-risk functional groups (Figure 1). Databases such as BIRDBASE (Şekercioğlu et al., 2025), combined with over two billion eBird records (Sullivan et al., 2009) now support global-scale analyses, including in historically understudied regions (Kittelberger et al., 2023).

Despite these advances, major data gaps persist in tropical regions where biodiversity is richest, yet monitoring is most limited. Integrated projects combining systematic monitoring, citizen science, education, and local engagement remain rare, even as global bird declines accelerate (Şekercioğlu et al., 2023). Many biodiversity hotspots also overlap with areas of frequent armed conflict (Hanson et al., 2009), creating additional barriers to sustaining research in some critical regions of high endemism (e.g. Kittelberger et al., 2021b).

This Research Topic synthesizes ten studies spanning tropical and temperate regions, urban and forested landscapes, and employing diverse methodologies from mist-netting and citizen science to molecular ecology. Collectively, these contributions underscore the importance of sustained avian monitoring and inclusive conservation strategies. We organize their findings under five overarching themes: trait-based vulnerability,

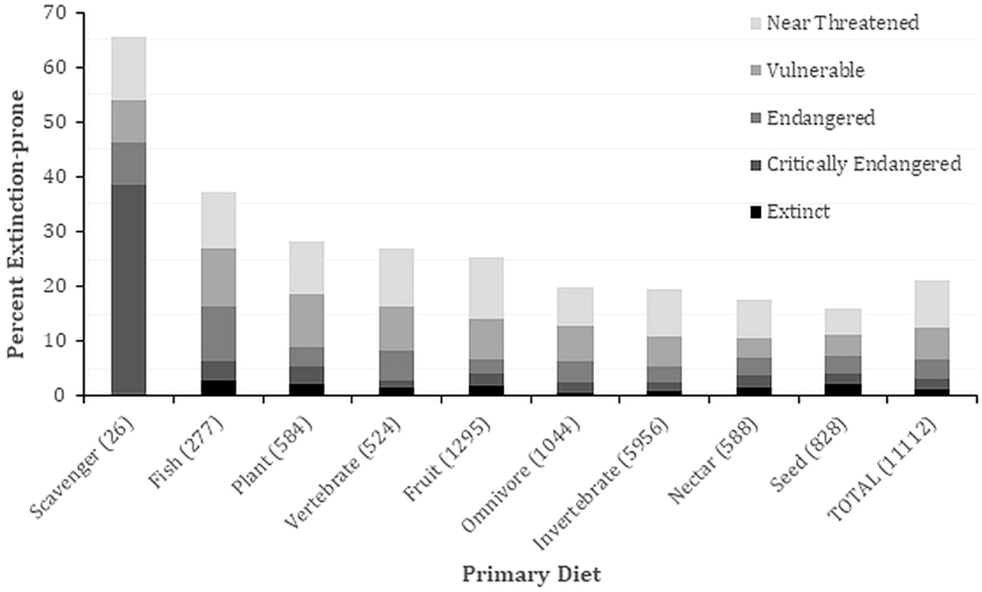

FIGURE 1
Percent of extinction-prone bird species based on primary diet preference (see Şekercioğlu et al. (2025) for diet descriptions). Conservation status is from BirdLife International (2025). The number of bird species which prefer that diet category most is in parentheses. Extinct includes species extinct in the wild.

demographic and physiological responses, climate impacts, landscape transformation, and integrative conservation approaches.

Trait-based vulnerability and community composition

Barrie et al. compared bird communities in primary versus logged forests in Equatorial Guinea, revealing a 47% reduction in individuals and the losses of ant-followers, mixed-species flock participants, and terrestrial insectivores in secondary forests. These guild-specific declines highlight the sensitivity of forest specialists to habitat degradation and reinforce the need for intact habitats, strengthening trait-based vulnerability frameworks widely applied under climate and land-use change (Cazalis et al., 2021; Jiguet et al., 2007). Nikolaou et al. extended this work by examining demographic and physiological traits of ant-following birds, uncovering demographic bottlenecks and variable body condition despite similar breeding status and stress hormone (fCORT) levels. These nuanced responses align with broader evidence that insectivores and forest specialists are particularly vulnerable to anthropogenic disturbance (Şekercioğlu, 2002; Powell et al., 2015).

Demographic stability and long-term monitoring

Long-term datasets provide critical insights into population dynamics and community stability. Wambugu et al. analyzed 13 years of mist-netting data of 18 understory bird species from Mt. Kasigau, Kenya, finding most understory species stable, though the endemic Taita White-eye declined—underscoring the need for continued monitoring. In a temperate context, Cooper (2025) examined nearly seven decades of Harvard Forest data, documenting turnover in one-third of species between years, with 18 colonizations and 16 declines since 1948. Colonizers were dominated by species near their northern range limits, rather than those expanding southward, while declines involved migratory and open-habitat birds. Forest interior species generally increased whereas declining species tend to favor open-country and shrubland habitats. Targeted management, such as clear-cuts and the removal of non-native conifer plantations, aided some declining species, illustrating the complex interplay of climate, habitat, and conservation actions.

Measuring and mitigating climate impacts

Mota et al. assessed climate change impacts on endemic and near-endemic birds in Colombia's Chocó hotspot. Using eBird data and climate projections, they modeled distributions for 27 species and found nearly universal losses of climate-suitable areas, driving upslope shifts and reductions in species richness. Scarlet-and-white Tanager and Chocó Warbler face the steepest losses—84% and 60%, respectively—threatening ecological services such as seed dispersal and insect control. These results emphasize the urgency of expanding protected areas, promoting reforestation, and enhancing habitat connectivity to match shifting climatic niches (Tingley et al., 2009). Integrating citizen science with ecological modeling offers a powerful framework for community-engaged conservation. Complementing these findings, Gale et al. demonstrated how precipitation patterns shape breeding phenology in Thailand's dry forests: extended droughts delayed egg-laying, while reduced rainfall postponed fledging, highlighting precipitation as a key driver of reproductive timing.

Landscape transformation and functional homogenization

Urbanization and land-use change are restructuring avian communities worldwide. Danmallam et al. analyzed African Bird Atlas data from Kenya and Nigeria, showing declines in taxonomic richness and functional diversity with increasing urbanization, alongside rising functional redundancy. Across gradients from pristine habitats to cities, ecological specialists were filtered out, reducing functional richness and ecosystem services. Although functional diversity increased slightly, patterns indicate a shift toward generalist-dominated assemblages, consistent with global biotic homogenization trends (McKinney, 2006). In Ecuador's Chocó region, a biodiversity hotspot also facing intense landscape transformation, Karubian et al. (2025) highlight the role of equity and inclusion in conservation success through two decades of community-engaged monitoring. By integrating Traditional Ecological Knowledge with scientific research, their approach produced tangible outcomes, including reserve establishment and youth programs, offering a replicable model for participatory conservation.

Integrative conservation and molecular approaches

Several studies underscore the value of linking ecological research with practical interventions. Briceño-Linares et al. documented population rebounds of Yellow-shouldered Amazons in Venezuela following habitat restoration, nest-site provisioning, and community education, with populations doubling and tripling on Bonaire and Margarita by increasing nesting success and, critically, by reducing poaching rates. Nikolaou et al. advanced conservation physiology by analyzing stress hormones (fCort), a sensitive indicator of sublethal disturbance, in birds exposed to selective logging. Finally, Esperanza et al. contributed a genomic perspective by examining transcriptomic responses of Common Murres to *Babesia* infection and oil contamination. RNA sequencing revealed hundreds of differentially expressed genes, with shared immune suppression and oil-induced lipid metabolism changes, illustrating mechanisms that heighten vulnerability to disease and environmental stressors. These findings demonstrate how molecular tools complement traditional monitoring and demographic indicators in measuring wildlife health (Acevedo-Whitehouse and Duffus, 2009) while supporting community-based conservation strategies essential for mitigating global change impacts on tropical and marine birds.

Synthesis and future directions

The ten papers in this Research Topic highlight key strategies for avian conservation: long-term monitoring to detect subtle ecological changes, trait-based approaches for identifying vulnerable species, tracking climate change impacts, leveraging citizen science and community engagement, and applying interdisciplinary methods from molecular ecology to spatial modeling. A common theme is the indispensability of long-term, locally grounded research for detecting ecological change and guiding conservation. Whether through mist-netting, citizen science, or molecular tools, these studies exemplify best practices. Birds remain vital indicators of ecosystem health; integrating ecological data, community knowledge, and interdisciplinary approaches is essential as global pressures intensify.

Author contributions

ÇŞ: Writing – original draft, Writing – review & editing, Conceptualization. MN-C: Writing – original draft, Writing – review & editing. NO-P: Writing – review & editing, Writing – original draft. JJ: Writing – review & editing. CP: Writing – review & editing. JT: Writing – review & editing.

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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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Comparative gene expression responses to *Babesia* infection and oil contamination in a seabird

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The common murre (*Uria aalge*) is a species of seabird particularly vulnerable to several environmental stressors, including parasitic infection and oil contamination. However, the molecular response to these stressors is severely understudied. This study investigated the common murre's transcriptomic responses to these stressors. Blood samples were collected from common murres undergoing rehabilitation at International Bird Rescue in Fairfield, CA. Total RNA was extracted from these samples, followed by library preparation and Illumina sequencing to generate whole transcriptome data. Differential gene expression analysis was conducted using DeSeq2 to identify genes significantly altered in response to oil contamination and parasitic infection. Differential gene expression analysis revealed 194 genes shared between oil-contaminated and infected birds, including key immune-related genes, such as *ANXA2*, *LY96*, and *LY86*. These genes play vital roles in mediating the production of pro-inflammatory cytokines. Gene Set Enrichment Analysis indicated significant alterations in stress, immune, and inflammatory responses, with additional lipid metabolism changes in contaminated birds. Our findings highlight the detrimental effects that these stressors have on wild birds. These findings suggest a generalized stress response and specific metabolic adaptations to oil exposure, providing insights for seabird conservation.

KEYWORDS

seabird, RNA sequencing, differential expression analysis, oil contamination, *Babesia*, gene expression, environmental stressors

1 Introduction

Seabirds are highly vulnerable to many major environmental stressors such as pollution, oil spills, habitat loss, and harmful algal blooms (Phillips et al., 2011; Orgeret et al., 2022). They are also increasingly susceptible to disease from parasitic infections, with host–parasite interactions expected to significantly shift as a direct result of climate change

(Khan et al., 2019). A seabird's chance of exposure to these conditions may be increased when compared to other taxa because they have long lifespans and can traverse various continents throughout a single annual cycle (Boulinier et al., 2016). Behaviors such as migration, foraging, and dispersal have been shown to be important factors in the spread of infectious diseases and parasite transmission (Boulinier et al., 2016). The common murre (*Uria aalge*) is a representative of the seabirds in their susceptibility to the effects of climate change and other stressors (Phillips et al., 2011; Piatt et al., 2020). At wildlife rehabilitation centers, common murres are regularly admitted exhibiting symptoms and injuries related to oil contamination, anemia, disease, and starvation (Hampton et al., 2003; Henkel et al., 2014; Duerr et al., 2016). These environmental stressors can have significant health consequences for seabirds, including increased susceptibility to diseases like babesiosis.

Babesia is a protozoan parasite that is transmitted by ticks of the genus *Ixodes*, and infects the erythrocytes of mammalian, reptile, and avian hosts, resulting in the disease babesiosis (Puri et al., 2021; Zaki et al., 2021). Infection can lead to malaria-like symptoms such as fever, anemia, jaundice, and death in severe cases (Ristic and Kreier, 1984; Peirce et al., 2003; Vannier et al., 2015). Historically, babesiosis has had devastating impacts on the cattle industry and domestic animals, and a majority of *Babesia* research has focused on humans, mice, cattle, and dogs (Igarashi et al., 1999; Brown et al., 2006; Miles et al., 2012; Iwasaki and Medzhitov, 2015; Torina et al., 2020; Kumar et al., 2023), leaving a large gap in knowledge on avian species' response to *Babesia* or apicomplexan parasites in general. The few investigations into the host's response to infections have presented evidence of the innate and adaptive immune pathways playing a major role, with differential expression of genes relating to IL-1β, TNF-α, and IFN-γ (Brown et al., 2006; Beletic et al., 2021; Smith et al., 2021). The species *Babesia uriae* was first identified in 2009 in common murres undergoing rehabilitation and has been identified by light microscopy of blood smears in approximately 30% of murres admitted to International Bird Rescue's California Wildlife hospital annually since 2016 (International Bird Rescue, unpublished; Yabsley et al., 2009). This parasite is closely related to *B. poelea* which infects brown boobies (*Sula leucogaster*) (Yabsley et al., 2009; Quillfeldt et al., 2011). Currently, there are 15 known species of avian *Babesia* which infect seabirds, and *B. uriae* is the first to be identified in a seabird in the Alcidae family (Peirce and Feare, 1978; Earle et al., 1993; Work and Rameyer, 1997; Merino, 1998; Peirce et al., 2003; Criado et al., 2006; Yabsley et al., 2006, 2009; Jefferies et al., 2008). Like other haemosporidian parasites in birds, acute infection is short and, if the individual survives this stage, results in chronic infection with lower parasitemia, regulated by the host's immune system (Valkiūnas, 2005). Understanding how common murres respond to *Babesia* infection is crucial, as this parasite is becoming increasingly prevalent in seabird populations. Existing research on avian babesiosis has primarily focused on other species, but studies like Videvall et al. (2015) on *Plasmodium* infection in siskins provide valuable insights into potential immune system responses.

Plasmodium species and *Babesia* are similar in their evolutionary history, infection dynamics, and disease outcomes (Clark and Jacobson, 1998; Djokic et al., 2021; Inoue et al., 2013), so a similar response to both parasites in birds would be expected. Videvall et al. (2015) investigated the avian transcriptome changes to *P. ashfordi* infection in Eurasian siskins (*Spinus spinus*) at different stages of parasitemia and found that differential gene expression correlated with infection time. Moreover, gene set enrichment analysis (GSEA) was performed and found that gene ontology (GO) terms such as "immune system process," "response to stress," and "cell death regulation" were significantly overrepresented during peak infection (Videvall et al., 2015). Studies on the immune response to *Babesia* in mice have found further evidence of the innate immune response to mediate disease pathogenesis (Hemmer et al., 2000). Coupled with additional stressors that can activate an immune response, disease and symptoms can be dramatically exacerbated (Clark and Jacobson, 1998; Ye et al., 2020). In a recent study on Hawaiian honeycreepers, Hawai'i 'Amakihi (*Chlorodrepanis virens*) were inoculated with *P. relictum*, the species of *Plasmodium* that led to the extinction of several species of honeycreepers (Paxton et al., 2023). This study focused on the host's immune response to avian malaria and found that differences in adaptive and innate immune responses led to differences in host outcome to infection (Paxton et al., 2023). Similar to *Babesia* infection, oil contamination also poses a significant health threat to common murres.

In addition to pathogens, common murres also face the effects of oil spills, either from anthropogenic sources or from natural seepages (Hampton et al., 2003; Henkel et al., 2014). Seabirds exposed to petroleum oil risk feather contamination and ingestion, leading to severe health problems with direct impacts to the animal's kidneys, liver, leukocyte populations, and blood cell physiology (Leighton et al., 1983; Fry and Lowenstine, 1985; Briggs et al., 1996). Feather contamination can cause a disruption of the bird's outer plumage, which is crucial to their survival in the cold marine environment and leaves the individual at risk of hypothermia and death (Jenssen, 1994). Previous clinical studies in common murres have shown that ingestion of oil led to consistent decreases in body weight despite normal food consumption, indicating metabolic and malabsorption issues (Khan and Ryan, 1991). Another study on the immunosuppressive effects of oil and duck plague herpesvirus found that mallard ducks dosed with cyclophosphamide (CY) exhibited an immune response like that of duck plague herpesvirus, and a combination of both CY ingestion and duck plague herpesvirus resulted in higher death tolls than those with either CY or herpesvirus (Goldberg et al., 1990). Investigations into the transcriptome changes in response to oil contamination have primarily been performed on marine microbial species, coral, mice, and plants (Rivers et al., 2013; Alvarez et al., 2018; Liu et al., 2020; DeLeo et al., 2021). However, one transcriptomic study on seaside sparrows (*Ammospiza maritima*) that were indirectly exposed to petroleum in the Deep-Water Horizon (DWH) oil spill found significant upregulation of genes relating to hepatocellular proliferation and liver regeneration, while genes relating to necrosis, liver steatosis, and apoptosis were inhibited (Bonisoli-Alquati et al., 2020).

These two stressors, oil contamination and disease, are anticipated to increase in prevalence and severity due to anthropogenic climate change. In the case of oil contamination, changing ocean temperatures can lead to the release of previously trapped oil reserves by way of melting permafrost. In the case of *Babesia*, rising temperatures can expand the geographic range and increase the abundance of the invertebrate vectors of protozoan parasites, including *Ixodes* ticks. Investigating how a marine organism responds to these stressors can provide valuable insight into the potential impacts of climate change on marine organisms and can lead to long-term studies that can help inform conservation efforts, as well as develop strategies to protect vulnerable populations. The goal of this study was to map the changes in gene expression in response to differing environmental conditions that common murres, as well as other marine organisms face in the wild. To accomplish this broader goal, we identified differentially expressed genes in common murres infected with *Babesia*, as well as those contaminated with petroleum oil. We then performed GSEA to explore which biological pathways were enriched by differentially expressed genes in each condition. We hypothesized that both *Babesia* infection and oil contamination would lead to distinct transcriptional responses in Common murres, with each condition inducing expression changes of genes associated with biological pathways relating to immune functions. This work represents the first step in understanding the commonalities, differences, and underlying biological processes that occur in response to parasitic infection and oil contamination in seabirds.

2 Materials and methods

2.1 Sample collection

Biological samples used in this study were selected from a larger set of 261 Common murre samples collected by the staff at International Bird Rescue (IBR) in Fairfield, CA between May 13, 2021, to August 30, 2022 (Supplementary Table S1). Because of the cost of RNA sequencing, the number of biological replicates chosen for each condition was limited to three, including three samples from Common murres either infected with *Babesia* or contaminated with oil, used as a control group. While more replicate numbers are recommended for this type of analysis (ideally 12 per condition), DeSeq2 has been shown to be suitable for 3 or fewer replicated when the fold-change threshold is set to 0.5, and limma when the fold-change threshold is set to 2.0 (Schurch et al., 2016).

While it is difficult to obtain samples of healthy adult seabirds, several factors were taken into consideration to ensure there was as much similarity between the samples as possible. Even though all samples were collected over the duration of roughly a year, samples chosen for our control group were collected during the summer months: June and July of 2021, and June of 2022. All birds that were sampled were found beached in Santa Cruz County, California, and did not exhibit any major visible bodily injuries. They were listed in the IBR database as emaciated and dehydrated. Further, although one sample was aged as a hatch-year and the other two were identified as after hatch-year, all three samples were roughly similar in weight (600–800 g). All samples had relatively similar packed cell volume (PCV) values (>30%), normal total protein (TP) values (>4.0 g/dL), and normal buffy coat (BC) values (0–1%) (Newman et al., 1997). All birds were hydrated with a 5% by body weight 0.9% NaCl solution by the IBR staff before blood samples were taken. Any medication, supplements, and anti-parasitic were administered after sampling had taken place. Birds chosen for the oil contamination group were visually diagnosed with petroleum oil feather contamination and were reported to the Oiled Wildlife Care Network (OWCN) by IBR staff. To limit the amount of variability of each sample, it was ensured that samples chosen were not also later diagnosed with other major ailments that would also affect gene expression (i.e. fractured bones, joint luxation, etc.). Each bird was sampled at the time of entry to the rehabilitation center before any treatment was given.

For each sample, whole blood was collected using a 25-gauge needle attached to a 1 mL syringe from the medial metatarsal vein. Approximately 0.1 mL of blood was drawn from each bird, enough to be stored in Queen's lysis buffer for DNA extraction (Longmire et al., 1997), in Invitrogen TRIzolTM LS ReagentTM (Thermo Fisher Scientific, Waltham, MA) for RNA preservation, as well as to make two blood smears for microscopy. The two blood smears were immediately set in methanol for fixation, and stained using JorVet Dip Quick Stain (Jorgenson Labs, Loveland, CO). Samples were frozen at −20°C until long-term storage was possible at −80°C at San Francisco State University prior to processing by the Avian Parasitology Laboratory.

2.2 DNA extraction and parasite detection

The Promega Wizard SV Genomic DNA Purification System was used to extract DNA from blood samples stored in Queen's Lysis buffer following manufacturer's instructions. Extracted DNA was stored at −20°C while unextracted DNA samples were kept at −80°C for long-term storage. 5' and 3' oligonucleotide primers [forward primer ITS15c (3'-CGATCGAGTGATCCGGTGAATTA-5') and reverse primer ITS13b (5'-GCTGCGTCCTTCATCG TTGTG-3')] were used, per Bostrom et al. (2008), and provided by Elim Biopharm Inc., Hayward, CA to amplify the ITS1 region of *Babesia* DNA. The thermocycler time and temperature profiles used are as follows: an initial activation step at 94.8°C for 1 min was followed by 35 cycles of amplification (94°C for 30 seconds, 62°C for 20 seconds, and 72°C for 30 seconds). The final extension was set at 72°C for 5 minutes, and then cooled to 4°C. Positive controls were identified using thin film microscopy and PCR, and PCR-grade water was used as a negative control. 91 common murre DNA extracts were tested for parasitic infection.

2.3 RNA extraction and sequencing

RNA was extracted from blood samples stored in TRIzol following the protocol in the Qiagen RNeasy Kit with the following modifications. A phenol-chloroform extraction was performed following the Qiagen RNeasy Lipid Tissue Mini Handbook to separate homogenate into aqueous and organic phases. Prior to extraction, samples were removed from −80°C and thawed to room temperature (approximately 15 minutes at room temperature). 200 mL of chloroform (ThermoScientific Chloroform 99% Extra Dry over Molecular Sieve, Stabilized AcroSeal) was added to the homogenate and shaken vigorously for 15 seconds and incubated on the benchtop at room temperature for 3 minutes. The samples were then centrifuged at 12,000 × g at 4°C for 15 minutes using an OWM Hermle Labnet Z 252 Mk Centrifuge. Standard extraction procedure was then applied until the column wash step. The Qiagen RNase-free DNase Set was added prior to the column wash procedure to ensure purity of the RNA. A final elution of 70 uL of RNase-free water was incubated on the column for 3 minutes and centrifuged at 12,000 g for 1 minute.

Total RNA was assessed for quality control using the Agilent Bioanalyzer Nano RNA chip (Agilent Technologies Inc. Santa Clara, USA) at San Francisco State University's Genomics/Transcriptomics Analysis Core (GTAC). Peaks were assessed by RNA Integrity Number (RIN) values, which ranged from 7.3 to 9.6. A baseline RIN value of 5.0 was set to ensure proper quality. Due to budget restrictions, 3 individuals with the highest RIN value were selected for sequencing as representatives of each condition as biological replicates: *Babesia*-infected, petroleum oil-contaminated, and a control group for a total of 9 samples. Library preparation and RNA sequencing was performed by Novogene Co., LTD (Sacramento, CA) using the NovaSeq PE150 sequencing platform and strategy. Paired-end reads were generated in fastq format and released onto a remote server at SFSU. The estimated average number of reads was 17.6 million reads.

2.4 Gene expression analysis

Files were released and downloaded from Novogene and uploaded on to servers at the California Academy of Sciences in San Francisco, CA, as well as to the galaxy bioinformatics platform (The Galaxy Community at usegalaxy.org). The common murre reference genome and gene annotation files (Accession Number: SAMN12253989) were also uploaded to the galaxy platform. Trimmomatic was used to trim adapter sequences using the default job resource parameters (Bolger et al., 2014) (Galaxy version 0.38.0). FastQC was used to check the quality of the reads using default parameters (Andrews, 2010) (Galaxy version 0.73 + galaxy0). HISAT2 was used to align the reads to the genome sequence using the default parameters, which resulted in binary versions of sequence alignment maps (BAM) (Kim et al., 2015) (Galaxy version 2.2.1 + galaxy1).

FeatureCounts was then used to quantify reads using the default parameters (Liao et al., 2014) (Galaxy version 2.0.1 + galaxy2). Differential gene expression was performed using Limma-voom using the Benjamini and Hochberg (1995) *p*-value adjustment method and the *p*-value adjusted threshold of 0.05 was used as a false-discovery rate control (Law et al., 2014; Liu et al., 2015) (Galaxy version 3.50.1 + galaxy0). The TMM normalization method and robust settings were used to protect against outliers. Results were validated by running the same tests on DeSeq2 using the default job parameters (Love et al., 2014) (Galaxy version 2.11.40.7 + galaxy2.

For this analysis, 9 (Table 1) were selected and divided into three representative groups comprised of 3 birds each: a control group, in which birds were not infected with *Babesia* or contaminated, a *Babesia*-infected group, and an oil-affected group. It was originally planned to include replicate samples from birds that were both infected with *Babesia* and contaminated, however, we did not obtain RNA samples that were of sufficient quality for sequencing and analysis (RIN<6.5).

Two separate analyses were performed using three groups of biological replicates. To test how parasitic infection affects the Common murre, the 3 control group samples were set against the 3 *Babesia* infected samples. The second analysis determined how oil-contamination affected gene expression. The 3 control group samples were tested against the 3 oil-contaminated samples. Expression table data was input into R and volcano plots with labeled genes of interest were created for each test using the ggplot2 and dplyr packages (R Core Team, 2023; Wickham, 2016) (Supplementary Tables S2, S3). R and Microsoft Excel were used to filter through the gene expression data to determine the amount of overlap between the two analyses.

2.5 Gene set enrichment analysis (GSEA)

Statistically significant differentially expressed genes from the limma-voom analysis, were input into the g:Profiler database to convert gene names to ENSEMBL ID's for GSEA (Raudvere et al.,

TABLE 1 Attributes of the 9 common murres selected for the analysis.

IBR ID	Admission Date	Age	Babesia Status	Contamination status
21–1386	7/23/2021	AHY	Negative	Non-Oiled
22–1159	6/20/2022	AHY	Negative	Non-Oiled
21–1233	7/9/2021	HY	Negative	Non-Oiled
21–1416	8/5/2021	AHY	Positive	Non-Oiled
21–1628	10/13/2021	HY	Positive	Non-Oiled
22–1342	7/7/2022	AHY	Positive	Non-Oiled
21–1515	8/20/2021	AHY	Negative	Oiled
22–0246	4/14/2022	AHY	Negative	Oiled
22–0341	4/27/2022	ASY	Negative	Oiled

2019). GSEA was performed in R using the ClusterProfiler package (Yu et al., 2012). Significantly expressed genes, in ENSEMBL format, and their associated fold change values were input into the package with the annotation file for *Gallus gallus* (org.Gg.eg.db) as a reference. While clusterProfiler offers curated gene sets for various organisms, avian annotations, excluding Gallus gallus, are currently unavailable. While using chicken gene sets might not perfectly capture common murre-specific biology, the enriched pathways still provided valuable insights into general stress response mechanisms potentially affected by the chosen stressors. The ontology parameter was set to test for biological function (BP) and set the *p*-value cutoff at 0.05. The Bonferroni-Hotchberg (BH) method for *p*-adjusted value to test for false positives (*q*-value). This method was performed for differentially expressed genes from each analysis. Pathways were identified and annotated using the Disease Ontology Semantic and Enrichment analysis (DOSE) (Yu et al., 2015).

3 Results

3.1 Transcriptome response

667 genes were differentially expressed ($p < 0.05$) in response to *Babesia* infection (Figures 1A, B). 380 (57%) genes were upregulated and 287 (43%) were downregulated (Table 2). Of these genes, 62 were unlabeled and had no known homologues. 39 of these unlabeled genes had a positive change in expression and 23 had a negative change in expression. The top significantly differentially expressed gene was Annexin A2 (*ANXA2*), which had a negative magnitude change in expression by the *Babesia*-infected group compared to the control group ($p < 0.05$).

Oil contamination elicited an even greater response, with 1454 total genes being differentially expressed (Figures 2A, B). Of those genes, 824 (57%) were upregulated and 631 (43%) were downregulated. 142 of these genes were unlabeled and had no known homologues. Of these uncharacterized genes, 72 were upregulated, and 70 were downregulated. The top significantly expressed gene was Interleukin-17 receptor protein E (*IL17RE*), which had a positive magnitude change in expression in the contaminated group. The proportion of significantly upregulated and downregulated genes (57% versus 43%, respectively) were the same in both analyses.

3.2 Similarities in gene expression and GSEA

We found that between the response to infection and the response to contamination, 194 of the same genes were differentially expressed by both groups (Supplementary Figure S1). This accounts for 32% of the genes that were expressed in response to infection and 17% that were expressed in response to contamination. This amount of overlap is much higher than what would be expected at random in response to different conditions ($p < 0.001$, Fisher's Exact Test). Out of the shared 194 genes, 188 were expressed in the same direction by both groups. This accounts for 97% of the shared genes, indicating most of the expression change to both conditions represent a generalized response to stress, also indicating that the stress response to *Babesia* and oil contamination are highly similar. The remaining 6 shared genes had opposite directional changes in expression (Table 3).

Genes differentially expressed in response to *Babesia* infection led to suppression of biological pathways related to immune response (Figure 3). The top two enriched Gene Ontology terms related to biological processes were 'defense response' and 'immune response.' Similarly, terms associated with the immune system were suppressed in response to contamination (Figure 4). "Immune response" and "inflammatory response" were highly significantly suppressed. In each of these instances, there are only two genes significantly driving these patterns. In the infection analysis, "defense response" suppression is driven by Lymphocyte antigen 96 (*LY96*) and Parkinsonism associated deglycase (*PARK7*). *LY96*, as well as Lyphocyte antigen 86 (*LY96*), are also driving the GO "Positive regulation of response to stimuli," and "immune response" is driven down by Pannexin 1 (*PANX1*) and MutL homolog 1 (*MLH1*). In the oil contamination analysis, both GO terms "immune response", and "inflammatory response" are driven by *LY96* and C-C Chemokine receptor type 5 (*CCR5*). Both analyses saw differential expressions of cytokines IL-17 and IL-18, as well as *TNFAIP3*. Contamination saw more DEG involved in cytokine pathways including *SKIL, IL5RA*, and *TNFAIP8*.

Also in the contamination group, ATPase phospholipid transporting 10A (*ATP10A*) and DENN Domain Containing 5B (*DENND5B*) drove "lipid transport." "Lipid localization was also driven by *ATP10A*, as well as Fatty acid binding protein 7 (*FABP7*). "Glycoprotein metabolic process" was suppressed by Sulfatase 1 (*SULF1*) and 2-Phospoxylose Phospatase 1 (*PXYLP1*). Some other DEGs relating to lipid metabolism were *PLA2G2E, ECHDC3, FADS1, FABP4, ACADL, LPIN2, CD36*, and *GATA2*. *PLA2GE* secretes inflammatory lipid mediators (Gubern et al., 2008; Silverstein and Febbraio, 2009; Qin et al., 2018), *ECHDC3* is involved in the biosynthesis of fatty acids (Sharma et al., 2019), *FADS1* encodes a fatty acid desaturase (He et al., 2018), *FABP4* is a gene related to the transport of fatty acids (Furuhashi et al., 2015), *ACADL* aids in fatty acid oxidation (Zhao et al., 2020), *LPIN2* is involved in lipid synthesis (Dwyer et al., 2012).

4 Discussion

In this comparative analysis of gene expression, we investigated the molecular impacts of both oil contamination and infection from an apicomplexan parasite, *Babesia*, in common murres, using three biological replicates for each condition. Despite the small number of biological replicates, the results generated from this analysis are consistent with previous studies exploring similar questions (Videvall et al., 2015; Bonisoli-Alquati et al., 2020). The programs employed in this analysis, DeSeq2 and Limma-voom, while not specifically designed for small sample sizes, utilize various techniques that are designed to handle data with various levels of

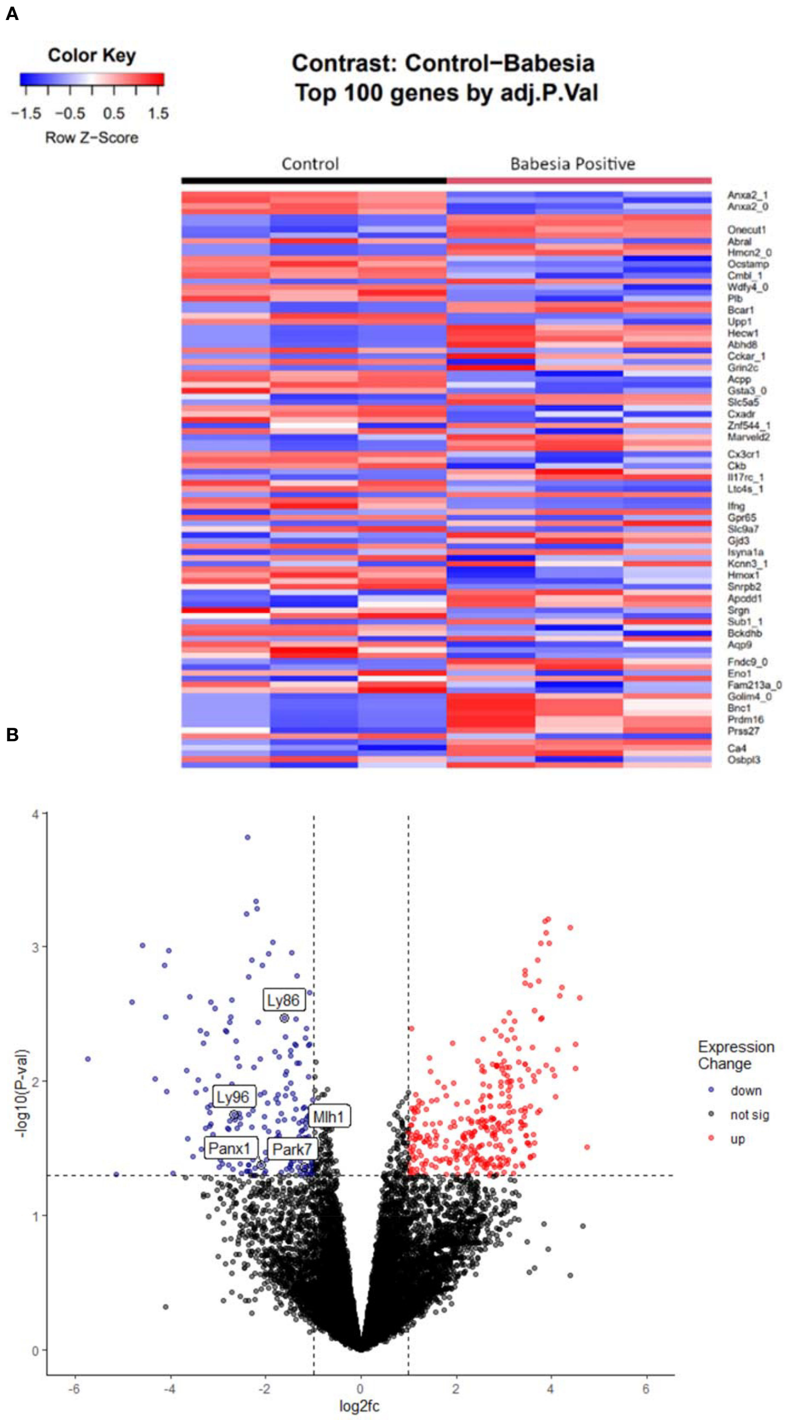

FIGURE 1

Heatmap **(A)** displaying the top 100 differentially expressed genes by adjusted *p*-value (*q*-value). Each column represents a sample, the left being the control group, and the right being the infected group. Each row represents a gene, with the magnitude of change in expression represented by a change in color (red being more upregulated, and blue being more downregulated). The volcano plot **(B)** displays the differentially expressed genes when analyzing the control group versus the *Babesia*-infected group. The log2(fold change) in gene expression is plotted on the x-axis, while the −log10 of the adjusted *p*-value is plotted on the y-axis. Genes that are significantly upregulated ($p < 0.05$ and log2foldchange ≥ 1) are shown in red, while genes that are significantly downregulated ($p < 0.05$ and log2foldchange ≤ -1) are shown in blue. Genes that are not significantly differentially expressed are shown in gray. Labeled genes, *LY96 LY96, MLH1, PANX1,* and *PARK7*, drive down GO terms related to immune response, defense response, and positive regulation of response to stimuli.

TABLE 2 Number of differentially expressed genes in response to *Babesia* infection and oil contamination in common murres.

DGE Analysis	Differentially Expressed Genes ($p<0.05$)	Positive change in gene expression (n)	Negative change in gene expression (n)
Control vs. *Babesia*-infected	667	380 (57%)	287 (43%)
Control vs. Oil-contaminated	1454	824 (57%)	630 (43%)

Columns indicate conditions, total number of significantly differentially expressed genes, and the number and ratio of genes that exhibited a change in expression ($p < 0.05$; $-1 \leq$ Log2foldchange ≥ 1).

biological variability (Love et al., 2014). Both programs use shrinkage estimators, such as the Wald statistic or the moderated t-statistic. This reduces the variance of the estimated log2 fold changes, especially for genes with low counts, which in turn helps to differentiate true biological signals from random noise that is more prevalent in datasets with fewer replicates (Love et al., 2014). Both tools also employ normalization procedures that account for technical variability between samples, ensuring that differences in gene expression are more likely due to the biological conditions that are being compared, rather than technical artifacts (Costa-Silva et al., 2017). While there is, of course, room (and a need) for an improved study involving more biological replicates, we believe our results are significant and represent a major first step in uncovering the effects of environmental stress on a severely understudied species.

4.1 Avian host response to *Babesia*

GSEA analysis determined that biological functions relating to the immune response were the top two enriched pathways from this analysis. Further, these two processes were driven to suppression by two genes each; Defense response was driven by *LY96* and *PARK7*, and inflammatory response was driven by *LY96* and *LY96*. While these processes are suppressed, it is likely that the host is not suppressing the entire immune system but dampening certain aspects of the immune response. Lymphocyte antigen 96 (*LY96*) is a transmembrane protein that has been known to play a role in inflammation, immune suppression, and T cell activation, however, the role of this gene in the context of *Babesia* infection and its impact on the immune system is not fully understood (Li et al., 2023). The role of *PARK7* in parasitic infection is also not well understood. The role of this gene is in antioxidative response and maintaining mitochondrial quality control (Wang et al., 2016). It is possible that *LY96* acts as a negative regulator of T cell activation, potentially contributing to the dampened inflammatory and defense responses observed in this analysis. This process is regulatory that eukaryotes possess to suppress overly aggressive immune responses to prevent tissue damage. For example, a study on the role of *LY96* in cancer progression found that suppression, or downregulation of *LY96* can inhibit cancer development (Nie et al., 2022). *PARK7* has been linked to inflammatory processes and may be a part of this suppression process.

While there is currently no information on the avian transcriptome response to *Babesia*, Videvall et al. (2015) analyzed the avian transcriptome response to *Plasmodium ashfordi* (2015), as well as the transcriptome of *P. ashfordi* while infecting an avian host (2017). Although *Plasmodium* and *Babesia* may elicit different overall transcriptome responses, we expect some level of overlap in the host response because both parasites undergo a life cycle stage where they infect, and destroy the red blood cells, leading to an inflammatory response (Clark and Jacobson, 1998; Hunt and Grau, 2003). Videvall et al. (2015) found differential expression of several genes that have also been found to be expressed by mice and humans in response to malaria infection. In the present study, two of these genes, Annexin A2 (*ANXA2*) and Lymphocyte antigen-86 (*LY96*), were downregulated in our *Babesia*-infected group. Both of these genes have also been widely found to be implicated in participating in the inflammatory response, however their role in *Babesia* infection is massively understudied.

ANXA2 has both anti- and pro-inflammatory roles in the innate immune response. *ANXA2* aids in macro autophagy by interacting with Atg16, a protein that is related to autophagy (Dallacasagrande and Hajjar, 2020). In the context of pathogen-caused infection, *ANXA2* plays crucial roles in the mediation of pro-inflammatory cytokines and promotion of anti-inflammatory signals (Dallacasagrande and Hajjar, 2020; Ma et al., 2021). There is also evidence that *ANXA2* may be used to facilitate infection by bacteria such as *Pseudomonas aeruginosa* and *Escheria coli* (Dallacasagrande and Hajjar, 2020). *LY96* is a protein-coding gene, that codes for the protein MD1, and has been shown to be produced by macrophages in the inflammatory response (Su et al., 2014; Thomas et al., 2016). The downregulation of these genes in *Babesia*-infected murres suggests potential mechanisms employed by the parasite to evade the host immune response. For instance, *ANXA2* deficiency might hinder the ability of immune cells to infiltrate *Babesia*-infected tissues, allowing the parasite to establish itself. Similarly, downregulation of *LY96* could suppress T-lymphocyte activation, thereby dampening the adaptive immune response. While these are speculative scenarios, they warrant further investigation to understand *Babesia*'s immunomodulatory strategies in common murres.

The presence of shared genes responding to multiple stresses points toward the possibility of a highly conserved host immune response to both babesiosis and malaria across species. Further research is required to interpret the precise mechanisms and implications of these shared genes in stress and immune responses.

Videvall et al. (2015) also analyzed the transcriptome of *P. ashfordi* after experimentally inoculating Eurasian siskins (*Carduelis spinus*). We compared the results of our *Babesia*-infected analysis to determine if any overlap in gene expression existed that may suggest expression from the *Babesia* parasite itself, rather than from the host. We found only one homologous gene that matched from this study, Subtilisin proteases 1 (*SUB1*; log fold

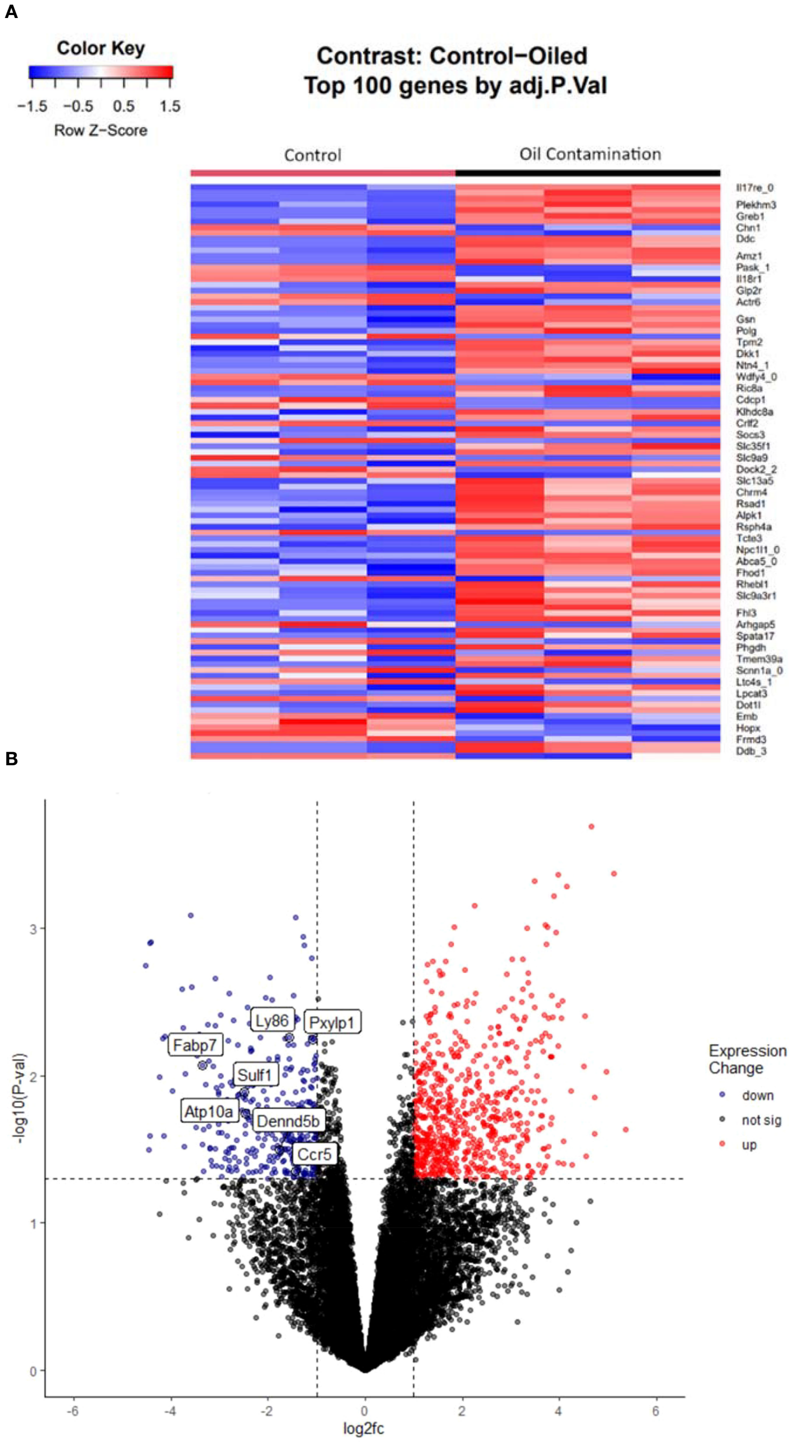

FIGURE 2
Heatmap **(A)** and volcano plot **(B)** displaying the top differentially expressed genes in response to oil contamination. Both figures show a much larger magnitude of differentially expressed genes, as described in Figure 1.

change = 2.9088, *p*-value = 0.00618). This gene encodes proteins with essential roles in the maturation and proteolytic processing of merozoite antigens (Beeson et al., 2016). Although only one gene was found to be similarly differentially expressed, this is not surprising because, despite both *Plasmodium* and *Babesia* being apicomplexan type parasites, it is likely that they have developed distinct needs within erythrocytes, which can lead to differences in gene expression. Many of the genes, however, were found within our dataset, but fell well beneath our significance cutoff. This is most likely because, while comparing data from *Plasmodium* and *Babesia* may provide useful context, it is important to consider the limitations of comparing two different species. While both species

TABLE 3 Summary of the 6 genes that were differentially expressed in both the *Babesia*-infected group and the oil-contaminated group that were expressed in opposite directions.

Gene ID	ENSEMBL	Gene Description	Expression (Babesia)	Expression (Contamination)
CTSL	N/A	N/A	Down	Up
MAPK12	ENSGALG00010001611	Mitogen-activated protein kinase 12	Up	Down
PI4KB	ENSGALG00010028605	Phosphatidylinositol 4-kinase beta	Up	Down
LRRC34	ENSGALG00010016840	Leucine rich repeat containing 34	Up	Down
ABCG2	ENSGALG00010020622	ATP binding cassette subfamily G member 2	Down	Up
ARL4A	ENSGALG00010004029	ADP ribosylation factor-like GTPase 4A	Down	Up

are Apicomplexan type parasites, they belong to two distinctly different Apicomplexan orders that have diverged significantly, *Plasmodium* belongs to the order Haemosporidia, and *Babesia* belongs to Piroplasmida (Martinez-Ocampo, 2018). Furthermore, these two species have established unique life cycles and host-parasite interactions, the most distinct difference being that *Plasmodium* has a replication stage within the host's liver, and *Babesia* does not (Hakimi et al., 2022). Further exploration comparing the similarities and differences between these two genera would be greatly beneficial in the optimization of these types of wildlife genomic studies.

4.2 Avian host response to oil contamination

Functions relating to lipid transport and localization were affected in response to petroleum oil contamination (Figure 4). Lipid transport and localization involves the coordination of various pathways to move insoluble lipolytic products throughout the body (Feingold et al., 2020). This process is essential to organisms because lipids play major roles as the building blocks of cellular membranes, aid in energy storage, act as signaling molecules between and within cells, and are required for proper

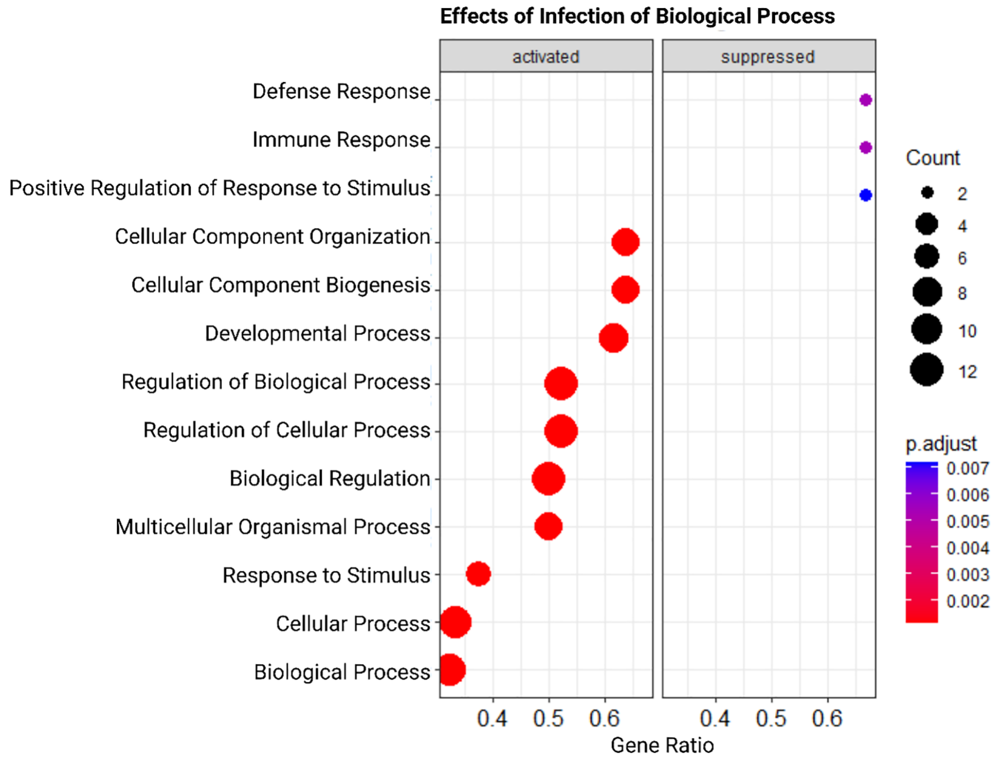

FIGURE 3
Dot-plot representation of Gene Set Enrichment Analysis (GSEA) results highlighting activated and suppressed biological functions in response to *Babesia* infection. Each dot represents a distinct biological function, positioned along the x-axis according to its enrichment score. Activated functions are shown on the left side of the plot, while suppressed functions are displayed on the right side. The color of each dot corresponds to the significance level of the enrichment score, with red dots indicating higher significance. The size of each dot represents the number of genes associated with a biological function. The x-axis represents the gene ratio, or the proportion of genes from the gene set that are present in the analyzed dataset. We can see that terms relating to immune response, inflammatory response, and response to stimulus are all suppressed.

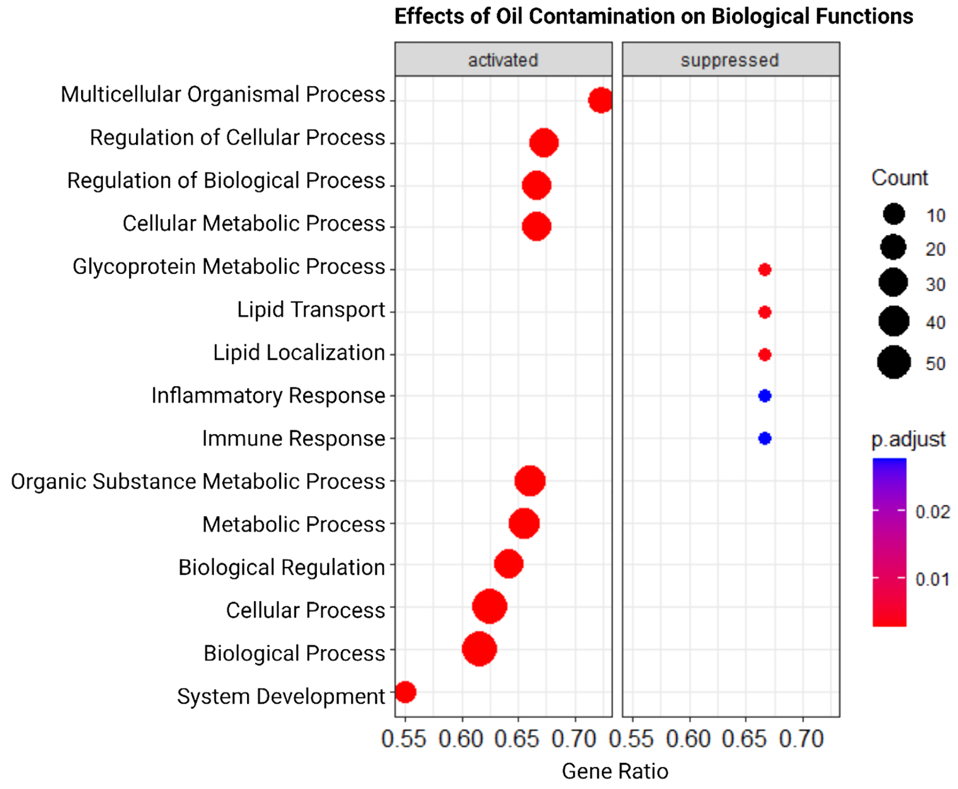

FIGURE 4
Dot-plot representation of Gene Set Enrichment Analysis (GSEA) results highlighting activated and suppressed biological functions in response to exposure to oil contamination, as described in Figure 3.

protein functions. Lipid processes related to metabolism are centralized in the liver, and damage to the liver can affect the lipid amounts circulating throughout the body (Arvind et al., 2000). Further, damage to the kidneys has also been associated with disturbing lipid metabolism (Trevisan et al., 2006). Studies of the effects of petroleum oil on seabirds have reported problems with the kidneys and liver, with damage to these organs being the leading cause of mortality among patients (Briggs et al., 1996). Common murres and Cassin's auklets (*Ptychoramphus aleuticus*) exposed to petroleum oil in a controlled study exhibited liver problems such as hepatocellular dissociation (Fry and Lowenstine, 1985).

Petroleum oil may also disrupt lipid processes by directly damaging the lipid bilayer of cellular membranes, interfere with proteins that are responsible for transporting lipids throughout the body, and altering lipid environments locally by bioaccumulating in tissues. Studies on Polycyclic Aromatic Hydrocarbons (PAHs) bioaccumulation in marine life are limited, however, a study on the effects of PAHs in gelatinous zooplankton found that bioaccumulation occurred either dermally or through ingestion, and that the lipophilic nature of PAHs are the main cause of accumulation in an organism's lipid content (Almeda et al., 2013). It is highly likely that the Common murres used for this study had significant levels of PAHs bioaccumulation because attempting to preen oiled feathers can likely lead to direct ingestion of PAHs. Dermal absorption of PAHs is also highly likely because contamination disrupts the barrier created by seabirds to protect them from the cold marine environment, leaving their skin exposed and vulnerable to further contamination.

Bonisoli-Alquati et al. (2020) studied the transcriptomes of Seaside sparrows (*A. maritima*) that were exposed, but not physically contaminated, to the Deepwater Horizon oil spill that occurred in the Gulf of Mexico in 2010. This was the only other published transcriptomic analysis of seabirds exposed to petroleum oil to our knowledge, and it was expected that our results would have many similarities, although the birds in that analysis were not physically contaminated by oil. Their results found significant upregulation of *cyp1a2*, a known marker of PAHs in birds and cytochrome p450 subunit member, as well as activation of the PAH-responsive aryl hydrocarbon receptor (AhR) pathway. While our results did not show upregulation of the *cyp1a2* gene, we found significant downregulation of other p450 subunit members: *cyp4b1_1* (log fold change = −2.536, *p*-value = 0.018), *cyp4b1_0* (log fold change = −3.3510, *p*-value = 0.029), and *cyp2r1* (log fold change = −1.0408, *p*-value = 0.0316).

The p450 family of enzymes (CYP), in humans, are membrane-bound proteins involved in drug detoxification and cellular metabolism (Zhao et al., 2021). In humans, the CYP 1 family is involved in drug metabolism, the CYP 2 family is primarily involved in drug and steroid metabolism, and CYP 4 is involved in fatty acid metabolism (Zhao et al., 2021). In the context of oil exposure, several studies have found expression of *cyp1a* in response to the deepwater horizon oil spill, mediated by AhR (Varanasi, 1989; Whitehead et al., 2012; Brewton et al., 2013; Dubansky et al., 2013; Crowe et al., 2014; Brown-Peterson et al., 2015; Xu et al., 2016, 2017). In a study of double-crested cormorants (*Phalacrocorax auratus*) experimentally dosed with synthetic (DWH Mississippi Canyon 252 oil), *cyp1a* was also found to have elevated expression levels in the liver (Alexander et al., 2017).

In the current study, *cyp1a2* is not expressed, however, AhR is. This gene has been shown to be a regulator of *cyp1a2* (Bonisoli-Alquati et al., 2020). This gene was significantly downregulated in our data, which may have led to the downregulation of *cyp1a2*, as well as other CYP enzymes such as *cyp4b1* and *cyp2r1*. A possible explanation for the downregulation of AhR, as opposed to the activation of this gene, is related to resource allocation by the birds. It is highly likely that the oiled common murres admitted to IBR that were selected for this analysis were in such poor condition, that AhR and CYP enzymes were turned off as a survival mechanism. This method of allocating resources would prioritize essential functions such as maintaining body core temperature and organ function. Further research is needed to understand how the p450 CYP enzymes behave once the birds have had enough supportive care to return to a state of homeostasis.

Bonisoli-Alquati et al. (2020) also detected upregulation of the insulin-like growth factor binding protein (*IGFBP1*) gene, which was assisted by expression of the serine/threonine-protein kinase Pim3 (*PIM3*). Our results show a similar upregulation of the *IGFBP1* gene in the oil contamination group (log fold change = 2.9766, *p*-value = 0.0128). This gene plays a major role in liver regeneration, giving further evidence that birds from our sample group experienced significant liver damage from PAH bioaccumulation. While *PIM3* was not significantly upregulated, *PIM1* was (log fold change = 1.4614, *p*-value = 0.0327), which is highly homologous to *PIM3* (Julson et al., 2022). An investigation of *PIM1* in knockout mice found expression of this gene to be associated with pancreatic, prostate, gastric, and colorectal cancers.

Finally, the Seaside sparrow study found *ELOVL5* and *ELOVL2*, two elongases involved in polyunsaturated fatty acid synthesis, significantly downregulated. These elongases have downstream control in the adipose tissue, and downregulation of these genes may function in preventing lipid peroxidation from oxidative insults. These two elongases were also found in Great tits (*Parus major*) in a study on the effects of urban environments (Watson et al., 2017). While *ELOVL5* and *ELOVL2* were not significantly downregulated, *ELOVL4* was (*elovl4_0* log fold change = −2.9362, *p*-value = 0.020002). The elongase family consists of enzymes involved in the elongation of very-long-chain fatty acids and may have overlapping functions (Wang et al., 2023). It is possible that in Common murres, *ELOV4* is the primary elongase for very-long-chain fatty acid synthesis, and in both Seaside sparrows and Great tits, *ELOVL5* and *ELOVL2* are the primary elongases.

4.3 Similarities in gene expression

As expected, *Babesia* and oil contamination saw DEGs relating to the innate immune system. NF-kB is a transcription factor that regulates expression pro-inflammatory cytokines, chemokines, innate immune cells, and T-cells (Liu et al., 2017). *TNFAIP8*, found to be induced by NF-kB (Niture et al., 2019), and *FABP7*, a promoter of NF-kB-driven inflammatory response (Killoy et al., 2020), were expressed by both groups. Birds that were contaminated with oil saw differential expression of genes associated with the regulation of Interleukin-1 beta (IL-1β), including *CASP4*, which regulates IL-1β synthesis in macrophages (Cheung et al., 2018), and *CASP8*, a gene that plays a role in modulating IL-1β and inflammation (Gurung and Kanneganti, 2015). IL-1β is a pro-inflammatory cytokine that is essential for the host's ability to defend against infection (Lopez-Castejon and Brough, 2011).

Both analyses saw differential expressions of cytokines IL-17 and IL-18, as well as *TNFAIP3*. Contamination saw more DEG involved in cytokine pathways including *SKIL*, *IL5RA*, and *TNFAIP8*. *SKIL* has been shown to play a role in immune escape by upregulating autophagy (Ma et al., 2020). *IL5RA* is an Interleukin 5-receptor subunit that has been implicated in the regulation of white blood cells (Cheong et al., 2005). *TNFAIP3* is a Tumor Necrosis Factor α-Induced Protein that mitigates the response to inflammation (Das et al., 2018). *TNFAIP8* is another Tumor Necrosis Factor α-Induced Protein that helps maintain homeostasis during an immune response (Niture et al., 2019).

4.4 Cellular processes

Both infection and contamination lead to the activation of various cellular processes in common murres (Figures 3, 4). Notably, terms such as "regulation of cellular process," "cellular metabolic process," and "cellular component organization" were found to be among the activated processes in both groups. The activation of cellular response pathways may be a direct consequence of cell invasion by parasites, as shown in previous studies (Sumbria et al., 2021). Additionally, cell stress caused by the presence of these stressors might also contribute to the regulation of cellular processes. Iron plays a crucial role in numerous cellular activities (Rockfield et al., 2018), and its deficiency is a leading cause of anemia (Warner and Kamran, 2023). Specifically, hemolytic anemia, a type of anemia where red blood cells are destroyed, can result from the destruction of red blood cells (Hill and Hill, 2018). *Babesia* directly invades and replicates in the host's red blood cells, ultimately leading to their destruction (Fry and Lowenstine, 1985; Niu et al., 2015; Wu et al., 2017). Similarly, ingestion of petroleum oil has been shown to cause hemolytic anemia in seabirds and other organisms (Leighton et al., 1983; Ostlere et al., 1988). The activation of cellular metabolic process and regulation of cellular process may be associated with the host's defense mechanism. Both parasitic infection and oil contamination can impose significant metabolic burdens on the host, and upregulation of genes associated with this process may reflect enhanced energy production needs by the increase of immune cell recruitment and tissue repair. It may also be involved in maintaining cellular stability, or homeostasis in response to disruptions or damage caused by inflammation (Chovatiya and Medzhitov, 2014). Therefore, the activation of cellular processes observed in this study might serve as a protective mechanism by the host to mitigate excessive destruction of red blood cells caused by these stressors.

Conversely, there exists the potential for the activation of cellular processes to possess negative consequences in the context of the inflammatory response. The initial increase of metabolic activity in response to cellular invasion is beneficial, however, prolonged increase of metabolic activity can become detrimental (Blanco and Kaplan, 2023). Dysregulation of immune response can lead to tissue damage, inflammation, and autoimmunity (Blanco and Kaplan, 2023). In the context of the current study, while unlikely, it is possible that the activation of cellular processes may be attributed to dysregulation of immune cells and metabolism. Further experimental research is required to elucidate the function of cellular processes in the context of these conditions.

5 Conclusion

The findings of this study highlight the detrimental effects of these environmental stressors on the immune system of common murres. Both apicomplexan infection and oil contamination appear to suppress immune response mechanisms, potentially leaving the birds more susceptible to infections and compromising their overall health. Moreover, this analysis reveals specific impacts of oil contamination on the lipid metabolism of common murres. Genes associated with lipid transport and lipid localization were significantly overrepresented in response to oil contamination. This suggests a disruption in the birds' ability to regulate lipid levels and perform essential functions related to lipid metabolism and glycometabolism. These results also highlight a need for more research in this field, ideally with more biological replicates to increase evidence of the genes observed in this study.

It is important to acknowledge that this study did not include technical replicates. This decision was made due to the author's opinion that the high cost does not justify the added value, given that most DE studies do not include technical replicates. The authors are confident that the results reported are robust despite the lack of technical replicates. It also is important to emphasize that the results generated in this study should be taken with caution, as the sequencing and analysis of the transcriptomes of wildlife is notoriously difficult. One major concern in the present study that should be considered is the method implemented in choosing a control group. The samples collected are all from seabirds admitted into a wildlife hospital after being found beached for an unknown duration of time. Regardless of if the individual displays physical injuries upon admission, there may be underlying physiological or internal ailments that display themselves after intensive supportive care and the bird is returned to homeostasis. However, given the trends found in this study when compared to other studies, the results yielded are significant. Because of the concerns with forming a control group, it should be stated that these results should be regarded as baseline data, emphasizing the need for further experiments. However, this study highlights the potential benefit of using wildlife admitted to rehabilitation centers to study how anthropogenic changes affect their genomic profiles. Longitudinal studies can be implemented to collect blood samples at different time intervals, as opposed to at one single point. This would allow the researcher to track changes in expression before and after oil contamination has been washed off, parasite burden before and after treatment, and overall health over time. Such research could also investigate the effects of oil contamination across different vulnerable species, such as Western grebes (*Aechmophorus occidentalis*), with the purpose of comparing the results. Experimental validation of the results generated from this study would also be useful in informing future projects implementing similar methods.

Overall, this research sheds light on the intricate molecular responses of common murres to two distinct stressors—apicomplexan infection and oil contamination. Understanding the shared and unique pathways affected by these stressors is crucial for developing effective conservation strategies and mitigating the detrimental impacts on the health and survival of these iconic seabirds. Further investigations into the underlying mechanisms and long-term consequences of these gene expression changes will be valuable in enhancing our knowledge of the impacts of environmental stressors on avian populations, and ecosystems.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary Material.

Ethics statement

The animal study was approved by Oiled Wildlife Care Network/International Bird Rescue IACUC. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

CE: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. RQ: Data curation, Writing – review & editing. RD:

Resources, Supervision, Validation, Writing – review & editing. SR: Formal analysis, Methodology, Software, Supervision, Validation, Writing – review & editing. RS: Funding acquisition, Resources, Supervision, Validation, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2024.1425484/full#supplementary-material

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Research, management, and conservation of the yellow-shouldered Amazon (*Amazona barbadensis*) across its range in the southern Caribbean and mainland Venezuela: 1980s to the present

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The yellow-shouldered Amazon (*Amazona barbadensis*) has been the object of a decentralized research and conservation program throughout its range, spanning mainland Venezuela, the Venezuelan islands of La Blanquilla and Margarita, and Aruba, Curaçao and Bonaire in the southern Caribbean. Multiple interventions have been implemented since the 1980s, primarily on the islands of Bonaire and Margarita, including nest protection, the provision of artificial nests, predator control, health monitoring, ecosystem restoration, community education and awareness. As a result, fledgling recruitment in these two locations has increased and populations have grown substantially. In this article, we summarize the interventions and their impact on population abundance and poaching of nestlings. The status of populations in the Venezuelan mainland continues to be uncertain – yellow-shouldered Amazons were observed recently in their historical distribution, but poaching is still widespread. A 2024 reintroduction in Aruba was the first step toward reestablishment of parrots in the island after being extirpated around 1950. Building on four decades of experience and work, a multi-stakeholder range-wide action plan produced with the vision that by 2031 *Amazona barbadensis* has functional, viable wild populations throughout its historical range. Steps taken to date suggest that this is within reach if past successes can be sustained and replicated elsewhere, particularly in mainland Venezuela.

KEYWORDS

Aruba, Bonaire, community education, conservation interventions, Curaçao, distribution, poaching, sustainability

1 Introduction

Since the 1980s, various organizations, mostly in Bonaire and Margarita Island (Venezuela), have implemented a wide portfolio of research initiatives and conservation interventions focused on the yellow-shouldered Amazon (*Amazona barbadensis*). The species was first categorized on the IUCN Red List of Threatened Species in 1988 as Threatened, assessed as Vulnerable between 1994 and 2017, and re-assessed as Near Threatened in 2021 due to changes in the method for estimating the Extent of Occurrence (BirdLife International, 2021). It is one of the smaller Amazon species with a weight range of 250-500 g. The beak is horn colored, the head is yellow with a hint of white around the nostrils and pastel-blue under the beak; this blue color is also visible in the fanned tail. The shoulders have a yellow patch. Juveniles have grey eyes that change to orange-yellow as they mature beyond 12 months of age (Figure 1). It is a monotypic species, with no sub-species recognized. The yellow-shouldered Amazon is endemic to our study region (Rodríguez-Ferraro, 2024).

Despite population increases in Bonaire and Margarita, poaching pressures continue throughout Venezuela. No major research or conservation efforts have taken place in mainland Venezuela, where two populations are known to exist (Rojas-Suárez and Rodríguez, 2015), or on La Blanquilla Island, where a small population (estimated at ~100 birds) is found (Rodríguez-Ferraro and Sanz, 2007). At the national level in Venezuela, *Amazona barbadensis* are listed as endangered (Rojas-Suárez and Rodríguez, 2015). For decades, they were considered regionally extinct in Aruba, after being recorded for the last time in 1955 (Voous, 1957). In 2024, they were reintroduced to the island. Although historical records suggest their presence in Curaçao (e.g., Hartert, 1893; Voous, 1983), no firm reports are available of an established, breeding wild population.

Throughout their geographical distribution (Figure 2), yellow-shouldered Amazons enjoy legal protection. In Bonaire, collection of wild parrots has been prohibited since 1952, though the law was not enforced until a pet parrot registration campaign took place in 2002 (Montanus, 2003). The campaign resulted in the registration of over 600 pet parrots. At the time this was more than the estimated entire wild population on Bonaire. Since 2002, no additional pet parrots have been registered and the number of

FIGURE 1
Pair of yellow-shoudered Amazons on verawood (*Bulnesia arborea*) in Macanao, Margarita Island, Venezuela. Photo: Vivek Menon.

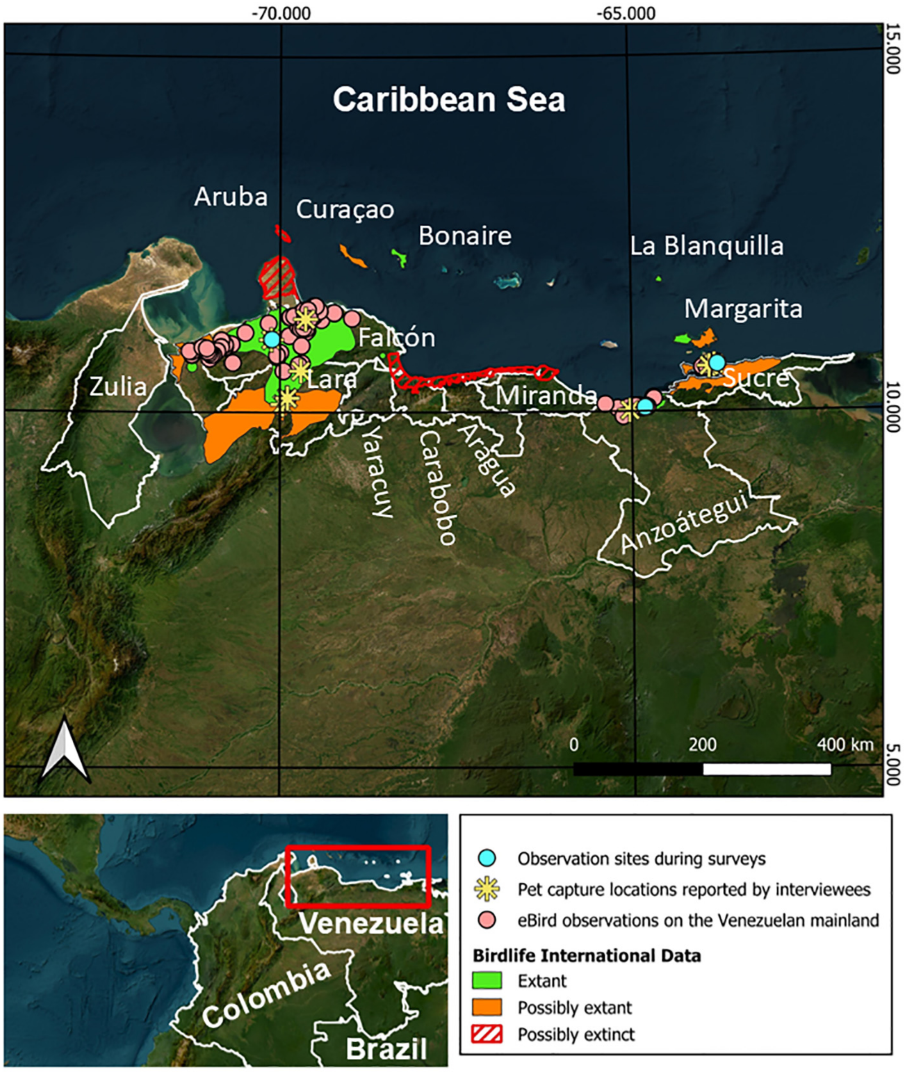

FIGURE 2
Geographical distribution of the Yellow-shouldered Amazon, according to BirdLife International and Handbook of the Birds of the World (2022), showing the location of field survey observation sites on mainland Venezuela, pet capture locations during interviews, and the location of eBird (2024) reports.

parrots kept as pets on Bonaire is thought to now be much lower (J. Haines, pers. obs.), although no census has taken place. In 2010 the yellow-shouldered Amazons were locally protected by island decree. In Venezuela, it has been illegal to capture and trade *Amazona barbadensis* since 1970, which was reinforced by an official decree in 1996 (Venezuela, 1970, 1996). In 2021, the Macanao Wildlife Reserve was established, protecting 12,000 ha of prime parrot habitat in Margarita (Minec, 2023). However, illegal trade and poaching are still common, as is the practice of keeping parrots as pets (Sánchez-Mercado et al., 2020a; b).

The primary threats to *Amazona barbadensis* are poaching, habitat loss, persecution arising from conflicts with farmers, and invasive species. The magnitude and importance of these threats varies across their geographic range. Interaction between threats amplifies their impacts, as was illustrated by the extinction of the yellow-shouldered Amazon in Aruba. Historically thriving, parrots faced a significant population reduction due to habitat degradation from urbanization, agricultural expansion, and deforestation. Simultaneously, they were subject to persistent persecution driven by cultural practice of shooting and poisoning as a crop pest. The last wild birds were reported by 1947 (Voous, 1983).

In Bonaire, illegal taking of chicks from nests occurs in several areas of the island. While historically this poaching is thought to have largely supplied local demand (i.e., pet owners on Bonaire), links with trade with Curaçao and international markets further afield have been recorded. In 2009, a chick ringed in the nest by researchers on Bonaire was found being kept as a pet in Curaçao. As Bonaire has few large trees, widespread deforestation led to the loss of dry forest habitat and the landscape became dominated in many areas by cactus scrub and introduced acacias. Donkeys and goats limited the regeneration of large trees. During the dry season parrots have been observed in roost sites within urban areas, presumably to take advantage of greater availability of food (Williams, 2009). In some areas of Bonaire, parrots are killed in large numbers as they are considered to be a pest on crops including sorghum and mangoes. Multiple incidents of shooting of parrots have been recorded, most recently in 2023 a parrot was rescued with a single puncture wound through the wing and body, indicative of being shot with an air-rifle or.22. Invasive animals have also played a relevant role as drivers of decline: predation of nests and adults by feral cats has been recorded, while nest cavities have been taken over by Africanized honey bees, a hybrid of the western honey bee (*Apis mellifera*), and the East African lowland honey bee (*A. m. scutellata*) (Williams, 2009).

Throughout Venezuela, the primary threat to yellow-shouldered Amazons is poaching, followed by habitat degradation, and to a much lesser degree human-wildlife conflict (Rojas-Suárez and Rodríguez, 2015). Keeping parrots as pets is widespread in the country (Sánchez-Mercado et al., 2020a; b; c), while anecdotal data suggest that in Margarita Island there are more parrots in people's homes than in the wild (J. M. Briceño-Linares, pers. obs.). The largest driver of habitat degradation in Margarita is open-sky sand mining for the construction industry (Briceño-Linares et al., 2011). As large trees grow in seasonal river beds, their removal to mine sand results in the elimination of parrots' nests, which are found in tree holes. Historical degradation of the vegetation of Margarita, which may have had lasting impact to the present, was caused by cattle grazing since colonial times (1500s onward) and goat grazing since the early 1900s (González, 2007). Killing of parrots that raid crops has been reported, but they are not frequent nor widespread (Rojas-Suárez and Rodríguez, 2015).

In 2021, stakeholders in the conservation of yellow-shouldered Amazons from throughout their range in the southern Caribbean and mainland Venezuela came together in a virtual workshop, facilitated by the IUCN Species Survival Commission (SSC) Conservation Planning Specialist Group (CPSG, 2020), to establish an agreed vision for the conservation of the species and outline a strategic plan for how this will be achieved. Here, we summarize the conservation interventions that have taken place over the last four decades focused on *Amazona barbadensis* and compile data on reproductive success and population estimates. Given that methods and interventions varied over time and between locations, we divided most methods and results by study site and then integrated our findings in the discussion. We consider how conservation interventions have impacted populations and ways forward for delivering the 2031 vision set out in the range wide action plan.

2 Methods

2.1 Study sites

Aruba is a 180 km^2 oceanic island located approximately 30 kilometers off the northern coast of Venezuela (Figure 2). Within the Kingdom the Netherlands, Aruba holds a distinctive status as a constituent country, transitioning from its previous affiliation with the Netherlands Antilles post their dissolution in 2010.

Bonaire, is an oceanic island (288 km^2) in the southern Caribbean, about 80 km from the coast of Venezuela (Figure 2). Bonaire was part of the Netherlands Antilles until the country's dissolution in 2010, when the island became a special municipality (officially, a "Caribbean public entity") within the country of the Netherlands.

Curaçao, is an oceanic island (444 km^2) of the Netherlands Antilles in the Southern Caribbean, about 70 km from the coast of Venezuela (Figure 2). Curaçao was part of the Netherlands Antilles until the country's dissolution in 2010, when the island became an independent country within the Kingdom of the Netherlands.

These islands have an average annual temperature of 28°C and receive low, irregular and localized rainfall. Average precipitation differs strongly between them (likely explained by difference in elevation). Curaçao has 600 mm/year currently (long term published average is 550 mm). Bonaire 463mm (1971-2000), Aruba 451 mm (1991-2020), over half of which falls between October and December. Near constant trade winds arrive from the east north-east with an average speed of 12.8 knots. Unlike the windward Caribbean islands, Aruba, Bonaire and Curaçao seldom experience hurricane force winds. These conditions favor a mixture of open cactus, thorn scrub and dry forest communities (De Freitas et al., 2005). Nests of yellow-shouldered Amazons in Bonaire are found across the island, north of the town of Kralendijk, in tree and rock cavities. A large proportion of known nest sites are in cavities found either in large boulders or on cliff faces (up to 20 m high), in either heterogeneous volcanic or limestone formations (De Freitas et al., 2005). On Bonaire, yellow-shouldered Amazons typically initiate breeding from late April/early May with chicks fledging approximately 90 days later (Martin, 2009; Williams, 2009). No nests have been reported in Aruba or Curaçao.

In Venezuela, yellow-shouldered Amazons live on the islands of La Blanquilla and Margarita, off the northeastern coast, and in two disjunct mainland regions to the northwest and north east of the country (Figure 2, Rojas-Suárez and Rodríguez, 2015). La Blanquilla (64.5 km^2) is an emerged island in the southern Caribbean Sea, 90 km northeast of Margarita Island, and 170 km northeast of Venezuela's mainland, with a maximum elevation of 30 m. Most of the island is covered by xerophytic vegetation, including dense cacti formations (Rodríguez-Ferraro and Sanz, 2007). In Margarita, yellow-shouldered Amazons occupy the western portion of the island, known as the Macanao peninsula. Spanning 330 km^2, Macanao's pronounced topography ranges from sea level to 745 m at the center of the peninsula. Mean annual temperature is 27°C, and mean total annual rainfall is 500 mm, with a marked dry season from January to May. Plant communities are dominated by open cactus/chaparral scrub with columnar cacti and legume trees. Seasonal riverbeds support permanent deciduous forests (Hoyos, 1985; González, 2007), where parrots nest. Mainland populations are found in dry forest similar to those of Macanao, in northeastern and northwestern Venezuela, but they have not been systematically studied, though some indirect analyses have been performed (Ferrer-Paris et al., 2014). The breeding season of *Amazona barbadensis* in Venezuela begins roughly when the dry season ends, with egg-laying typically beginning in late March. Eggs are laid in tree holes, incubated for approximately 26 days, and nestlings are fledged in 50–60 days (Rojas-Suárez, 1994a). The last nestling typically fledges in August (Sanz and Rodríguez-Ferraro, 2006).

2.2 Research and conservation activities

2.2.1 Aruba

2.2.1.1 Reintroduction

Yellow-shouldered Amazons were reintroduced to Aruba in 2024. This reintroduction followed the confiscation by Aruban authorities of 32 parrot chicks just under fledging age, allegedly smuggled from Venezuela in a fishing boat. Birds were hand raised, weaned and socialized as a cohesive group in captivity. Pre-release training involved training to recognize local flora known to form the diet of parrots on Bonaire, through exposure to the food type using a process of incrementally reducing the processing to serve as found in the wild on the branch.

From January 2024, 25 parrots were released in three cohorts (of 8, 8 and 9 respectively), staggered a week apart. Daily monitoring and the provision of supplemental feeding were carried out at feeding stations immediately adjacent to the release aviaries twice daily, once at dawn and again at dusk. At the 8-month mark, the most recent time for which data are available, 17 of 25 regularly returned to feeding stations, forming a cohesive flock showing strong site fidelity.

Challenges included predator encounters, particularly from peregrines (*Falco peregrinus*) and crested caracaras (*Caracara plancus*) which were seen to chase parrots. The parrot flock showed typical predator avoidance behavior and no predation events have been recorded. Notably, no evidence of predation from boas (*Boa constrictor*) has emerged yet, despite initial public concerns.

A long-term project in collaboration with European zoos is currently in the planning stage, aiming for regular translocations to reinforce the population. Strong government support has facilitated project development, with community engagement around the release informing the public. An extensive education program is planned for the future.

2.2.2 Bonaire

Conservation efforts for the Yellow-shouldered Amazon on Bonaire have experienced periods of varying intensity, initially spearheaded by governmental initiatives and later supported by non-governmental organizations (NGO). In 2006 field research into the ecology, behavior and threats was initiated, which formed the foundation for a range of conservation initiatives and the development of a locally-based NGO, Echo, focused on the conservation of yellow-shouldered Amazons. Partnerships between government, local and international NGOs and other civil society groups have sustained a combination of research, public awareness campaigns, law enforcement, and habitat restoration initiatives.

Sequence of conservation interventions carried out since 1980:

- 1980. Initiation of annual roost counts during the non-breeding season.
- 1998. STINAPA, the NGO mandated to manage Bonaire's national parks, launched an environmental education initiative together with the organization *Rare* using the Yellow-shouldered Amazon as its flagship species as part of a "pride campaign" (Scholtens and Butler, 1999).
- 2002. Launch of a pet amnesty program, resulting in the ringing and registration of 615 illegally kept pet parrots (Montanus, 2003).
- 2003. Annual public awareness campaigns initiated by local organization Salba Nos Lora timed to coincide with breeding season when risk of poaching at highest level (Salazar et al., 2019).
- 2006. Field research and nest monitoring initiated by University of Sheffield and World Parrot Trust (nest monitoring and poaching vigilance, description of methods below). Documentation of nesting areas with intensive monitoring of breeding productivity and causes of failure for approximately 25-30 nests annually from 2006 to 2010.
- 2007. Repair of 10 nests damaged by poachers and installation of a further 10 new nest boxes (Roberts et al., 2014).
- 2009. Echo launched to focus on conservation of yellow-shouldered parrots on Bonaire and Netherland Antilles. Echo maintained annual public awareness campaigns initiated by Salba nos Lora.
- 2009. Increase in law enforcement with house inspections by DROB (Dienst Ruimte en Ontwikkeling Bonaire, or Bonaire Spatial Planning and Development) leading to the confiscation of illegally held parrots.
- 2010. Implementation of the Nature Management Island Decree under the Nature Ordinance, protecting local species including the Yellow-shouldered Amazon.
- 2010. Introduction of a parrot club in schools and initiation of eco-tourism with parrot tours.
- 2010. Establishment of the Dos Pos Conservation Centre for the rehabilitation and care of seized illegally held parrots. Releases included 26 parrots between 2006-2013, 8 in 2016, 3 in 2017, and 6 in 2021.
- 2011. Confiscation of 14 yellow-shouldered Amazons destined for export to international markets.
- 2013. Native plant nursery created to grow trees for habitat restoration.
- 2015. Eleven herbivore exclusion zones, covering 33ha, created and replanted with trees. Campaign to encourage land owners to plant native food trees for parrots initiated.
- 2013-2023. Implementation of nest protection using hidden cameras. Surveillance was widely advertised in the media as a deterrent. Between 2015 and 2018, highly vulnerable nests actively monitored.
- 2018 Introduction of Wildlife Guardian group for secondary schools.
- 2019-2023. Intensive monitoring of 30-40 nests to measure nest productivity and poaching rates.

2.2.2.1 Roost counts

Counts at overnight communal roost sites have been conducted since 1980, but did not occur every year and varied in seasonal timing. Since 2005, these counts have been conducted annually on the last Saturday of January, during the non-breeding season. Counts are conducted by a team of citizen scientist volunteers who visit the different locations simultaneously to count numbers leaving roosts. In years when there were insufficient volunteers to visit all sites, priority was given to counting at those roosts that typically had the highest numbers of parrots in previous years. A methodological refinement was introduced in 2014, involving checks on roosts in the days prior to the annual roost count to determine the current activity levels at roost sites. Based on this information, priority was then given to counting at roosts that were most active. This approach was adopted to reduce the impact of the variability in survey effort (number of volunteers available) and patterns of roost use by parrots, on overall coverage. The selection of roost sites for counting each year was determined by the availability of volunteers and the priority assigned based on historic roost size and the results of the pre-count checks. Consequently, the specific sites counted varied each year with increasing effort over the years such that between 1999 and 2012, a mean of 20.27 ± SE 1.41 (11 - 27) and between 2013 and 2023 mean was 25.91 ± SE 1.38 (17-32). Prior to 2001 the total number of roost sites counted was rarely reported.

Counts of parrots leaving roost sites took place simultaneously across all locations selected. Counts were carried out by local volunteers with a range of experience from completely inexperienced with no training, through to the involvement of professional field biologists. Vantage points for counting parrots leaving each roost were pre-determined and all volunteers arrived at the designated point prior to dawn. The end of the counting period was determined either by 20 minutes passing since the last parrot sighting or two hours since the start of the count, whichever occurred sooner.

2.2.2.2 Nest monitoring

Nest inspections were carried out between mid-May and mid-September between 2006-2010 and 2021 and 2023, using a standardized approach. The locations of active nests were determined based on the behavior of breeding pairs (repeated entering of the cavity, copulation, allofeeding) observed during targeted observations in areas known to be used by nesting parrots. Yellow-shouldered Amazons on Bonaire consistently use the same nest areas and often the same cavities each year (Martin, 2009). Once determined as likely active, nest cavities were inspected at least once per week until nests were no longer active (chicks fledged successfully or nest failed). Where necessary abseiling and single rope technique where used to access nests in cliffside cavities. Inspections of nest contents were conducted as quickly as possible and nests were only approached while the parents were not in the nest to minimize disturbance. Nest contents were observed directly or with inspection mirrors, cameras and endoscopes for deeper cavities. A small number of nests were inaccessible and also monitored through observation of adult behavior. Such nests, where status could not be directly confirmed, are not included in our analysis. Causes of chick mortality and nest failure were identified where possible; for example, the presence of wire hooks used to pull chicks out of nests, or makeshift ladders suggested chicks had been poached from nests, injuries on dead chicks suggested attempted predation of infanticide. The timing of nestling mortality or nest failure was recorded, and nesting failure was considered to be "late" if it happened after 6 weeks. After this period natural causes of nest failure are rare and chicks are particularly vulnerable to poaching (Martin, 2009; Williams, 2009). Nest failure during this period is therefore considered to be suggestive of poaching, although the cause of failure could not always be determined.

2.2.2.3 Poaching vigilance

In response to escalating poaching concerns, particularly during the period 2021-2023, we implemented additional surveillance measures. Movement-sensitive camera traps were strategically deployed to provide surveillance at nests considered to be most vulnerable, including those with a history of poaching or those perceived to be easily accessible. Evidence of poaching incidents includes circumstantial indicators such as the presence of poaching tools (e.g., ladders, forked sticks, and wire for extracting chicks) and signs of nest cavity destruction (e.g., chainsaw damage to tree cavities). More direct circumstantial evidence includes sightings of people in the vicinity coinciding with the disappearance of chicks.

2.2.3 Curaçao

In 1999, the government of the Dutch Antilles issued an amnesty period where people could register their CITES-listed pets, including *Amazona barbadensis*. As they are included in the Specially Protected Areas and Wildlife (SPAW) annex 2, they also receive protection following the SPAW protocol being included in local legislation.

In 2001, the first Yellow-shouldered Amazon was registered, eventually reaching over 1,000 registered birds after a public campaign that involved local bird club volunteers and veterinarians. During the two years after the campaign, smuggled birds declined as recorded in patient logs at veterinary clinics. Despite campaign and legislation, however, parrot smuggling increased again. Occasionally, *Amazona barbadensis* are observed flying, which are likely escaped cage birds. Most birds are illegally brought in through fishing boats from Venezuela (May-July) and during the Bonaire regatta period in October. Due to a lack of proper quarantine facilities, confiscated birds are euthanized.

Fundashon dier en Onderwijs Cariben and Vetdoest have carried out an education project in Curaçao since 2002. Elementary and secondary school children are taught parrot conservation, why they should not keep a wild-caught parrot, and proper care should they own a pet parrot.

2.2.4 Venezuela

Research, management, and conservation activities began in the late 1980s, spearheaded by Silvius (1997) in Macanao and Rojas-Suárez (1994a; 1994b) in Macanao and La Blanquilla. Between 1990 and 1999, efforts focused primarily on understanding the reproductive biology of the yellow-shouldered Amazon, and increasing fledgling recruitment, with a focus on the largest known breeding area in Macanao. During this span, the number of yellow-shouldered Amazons fledged each year ranged between 23 and 81, with an annual mean of 53 (Provita, unpublished annual reports). Nestling losses averaged 49% annually, primarily due to poaching (Sanz and Rodríguez-Ferraro, 2006). Between 2000 and 2003, due to funding limitations and project restructuring, field activities were paused and re-designed, leading to a new phase of the project that continues to the present, with some variations over time that we describe below. Conservation interventions were summarized Briceño-Linares et al. (2011). Here, we update that list to the present in chronological order (Briceño-Linares and Rodríguez, 2022), we present the methods of previously unpublished annual censuses, and describe recent surveys designed to inform a current distribution map of *Amazona barbadensis* in mainland Venezuela.

Sequence of conservation interventions carried out since 2004 (all in Macanao):

- 2004. Environmental education at schools, creation of a team of EcoGuardians (originally called biomonitors), who are young men and women dedicated to carry out field work, nest repairs and 24-h surveillance.
- 2005. In addition to 2004's interventions, implemented foster nests and performed the pilot of an assisted breeding program.
- 2006. In addition to existing interventions, increased assisted breeding to all monitored nests.
- 2007. In addition to existing interventions, used artificial nests.
- 2008. In addition to existing interventions, brought in a veterinary doctor to monitor the health of nestlings and adults in nests, and had support from the municipal police to reinforce security in the field.
- 2009-2010. In addition to existing interventions, engaged with the National Guard, who accompanied the field team especially during the night.
- 2011 onwards. We settled on a stable protocol of three interventions: 24-hour surveillance by EcoGuardians, foster nests, and improved artificial nests. Environmental education at schools continued, but with a wider focus on all of the biodiversity of the island.

2.2.4.1 24-hour surveillance by EcoGuardians

EcoGuardians are young women and men from Margarita Island, some of them identify as being previous poachers. Currently, there are 18, and they are paid a salary during the parrot breeding season, approximately between May and August. A camp is established at quebrada La Chica, the largest parrot roost in Macanao (Briceño-Linares et al., 2011), and they rotate to maintain 24-h surveillance of an area that included 98 nests (69 active in the 2024 breeding season): 47 in natural tree holes (38 active in 2024), 30 artificial PVC nests (14 active in 2024), and 21 improved artificial nests (17 active) (see nest descriptions below). Their role is to patrol the area, especially at night, but not to engage directly with any potential poacher that they encounter. Typically, the presence of EcoGuardians is sufficient to deter poachers.

2.2.4.2 Foster nests

Beyond the area patrolled by EcoGuardians there are additional nests that are too far away to monitor. Most of those nests, except a few located on very tall trees, are regularly poached. Fledglings from these high-risk nests are thus extracted and placed into foster nests at quebrada La Chica, where clutches are uniformly increased to 5 eggs. This technique was tested, standardized and implemented early in the project's history (Sanz and Rojas-Suárez, 1997), and continues to be used since.

2.2.4.3 Improved artificial nests

Three types of artificial nests have been tested: wood-boxes, painted PVC tubes covered at both ends and with mesh on the inside, and natural nests that were originally damaged by poachers, we cut off from the tree (always verawood, *Bulnesia arborea*), repaired, and hung from a branch of a tree with no natural nest (Briceño-Linares, 2010; Sanz et al., 2003). Wood-boxes were unsuccessful and no longer implemented, but the other two designs continue to be used.

2.2.4.4 Annual censuses

Censuses were carried out at six permanent roosts located throughout Macanao: Quebrada La Chica, San Francisco, Guainamal, Chacaracual, La Vieja and Caño de Maíz (Rojas-Suárez, 1994a, 2015). All roosts were censused simultaneously for three consecutive days from 4:30 pm to 7:00 pm. A week before the census, a pre-census was carried out throughout the peninsula to locate the best roost observation points, as they may shift. Over the years, counts have been carried out at different times of the year (before, during and after the breeding season), but here we only include post reproductive counts, which typically are carried out between August and December. Each day, the team of observers, which include at least one experienced team member, but also include volunteers and team members in training, count the birds as they come in to roost for the night. Here, we report the largest number recorded each day to minimize underestimating population size (Rodríguez-Ferraro and Sanz, 1996). Censuses were not performed all years, or by a consistent team of observers. We therefore reported only years where a formal census was carried out, and also provide notes on the reliability and confidence of each year's estimate according to our knowledge and experience. For example, years where surveys were led by a team member with several years of experience, and all participants had been involved at least one year prior, ranked highest.

2.2.4.5 Mainland surveys

In 2023, we carried out two exploratory surveys in the Venezuelan mainland, to document the presence of *Amazona barbadensis* within the two mainland regions identified in the past (BirdLife International, 2021; Rojas-Suárez and Rodríguez,

TABLE 1 Abundance estimates for the yellow-shouldered Amazon in Bonaire.

Period	Methodological approach	Mean roost count ± s.e.
Pre-2005	Timing of counts inconsistent	531 ± 135.1
2005-2009	Timing standardized from 2005 onwards	513.6 ± 80.2
2010-2014		754.2 ± 65.1
2015-2019	Pre-roost count checks introduced	934.2± 95.7
2020-2023		1151.6 ± 172.8

2015). Surveys were conducted in the states of Sucre and Anzoátegui in northeastern Venezuela between 3 to 14 September 2023, the states of Lara, Falcón and the eastern coast of Zulia in the northwest between 6 to 14 November 2023.

Opportunistic sampling was employed whereby we traveled by car though the region, stopping at towns along the way to identify and interview people who owned captive parrots, particularly *Amazona barbadensis*. The interview protocol comprised a series of semi-structured questions aimed at gathering information on the wild and captive populations of *Amazona barbadensis* in the locations visited, including the timing of breeding, the locations of nesting trees and overnight roost, feeding habits in the wild and captivity, poaching methods, and the market price of chicks in the illegal trade. Interviewees were informed that the interviews were part of a study on the yellow-shouldered Amazon, aimed at understanding its conservation status across different parts of its distribution. In each location, a local guide accompanied the team to facilitate trust and rapport with the interviewees.

3 Results

3.1 Bonaire

3.1.1 Abundance

Counts in the 1980s and 90s, which involved highly variable survey efforts, typically totaled around 300 parrots. Since 2005 when the timing of counts was standardized, reported numbers of parrots have gradually increased. The mean annual count for the most recent period (2018-2023) was 1 130.17 ± 130.31 s.d. (755-1 779); approximately double the number counted between 2005-2010 of 513.6 ± 80.2 s.d. (277-669)(Table 1). Variation in survey efforts over this period may account for some of the apparent increase and unpublished analyses controlling for survey effort suggest a more modest, but nevertheless statistically significant increase in numbers.

Abundance estimates made using distance method point counts between 2009-2017 estimated the population on Bonaire to be 2 924 ± 340 parrots across a survey region covering 17 000 ha (Rivera-Milán et al., 2018). However, uncertainty over the suitability of these survey methods for this species and situation mean that abundance estimates based on roost counts are typically used by civil society and government organizations on Bonaire.

3.1.2 Nest productivity and poaching

Between 2006 and 2010, a mean of 24.6 (15-38) active yellow-shouldered Amazon nest attempts (i.e. displaying eggs or chicks) were monitored annually (Table 2). Of these, a mean of 52% (12.8) successfully fledged at least one chick. Recorded nest success was higher between 2021 and 2023, during which 76.2% (a mean of 15.0 of 19.7 breeding attempts) were successful. Productivity per successful nest did not differ considerably between the two periods, with a mean of 1.92 (1-4) chicks fledged per nest between 2006 and 2010 and 2.08 ± 0.13(1-4) chicks between 2021 and 2023.

TABLE 2 Nest productivity for the yellow-shouldered Amazon in Bonaire.

Year	Active nests monitored	Nests successfully fledged (% of nests monitored)	Number of chicks fledged per successful nest (mean +-se)	Nests poached (% of nests that would have otherwise fledged)
2006	13	10 (76.9%)	2.17 ± 0.32 (1-4)	0 (0.0%)
2007	29	9 (31.0%)	1.91 ± 0.28 (1-3)	3 (25.0%)
2008	28	9 (32.1%)	1.50 ± 0.20 (1-3)	4 (30.7%)
2009	28	12 (42.9%)	2.33	4 (25.0%)
2010	25	15 (60.0%)	1.67 (1-3)	2 (11.7%)
Mean	24.6	12.8 (52.0%)	1.92 (1-4)	2.6 (20.3%)
2021	22	19 (86.4%)	2.26 ± 0.25 (1-4)	2 (10.5%)
2022	20	12 (60.0%)	1.88 ± 0.12 (1-2)	0 (0.0%)
2023	17	14 (82.4%)	1.92 ± 0.14 (1-3)	0 (0.0%)
Mean	19.7	15.0 (76.2%)	2.08 ± 0.13(1-4)	0.67 (4.5%)

Between 2006 and 2010, 13 poaching incidents were detected, accounting for 20.3% of active breeding attempts that would have otherwise fledged chicks (Table 2). Poaching was monitored using camera traps between 2021 and 2023, where no definitive poaching events were recorded. However, two incidents were suspected based on the absence of chicks in the nest during the late nesting stage and observable changes to the nest environment, such as opened cavities and signs of disturbance. These accounted for only 4.5% of active breeding attempts that would have otherwise fledged chicks during this period.

3.2 Venezuela

3.2.1 Abundance

The first censuses were carried out in 1989, and continued with interruptions and variations in reliability until the present (Table 3). Estimates with higher confidence are concentrated during the first and last few years of the time series. In the 1990s, we recorded a fairly rapid growth in population size from about 700 in 1989 to around 1,800 in 1996. Between 2001 and 2017, numbers oscillated between 800 and 1,600 birds, probably more due to methodological inconsistencies than to true changing population sizes, though there is some evidence that this was a time of rapid degradation due to increased mining intensity of at least two of the roost sites, which could have affected parrot populations (Rojas-Suárez, 2015). During the last few years, 2020-2023, our confidence on the estimates is high and the population seems to have settled around 2,000 birds.

TABLE 3 Annual census counts for the yellow-shouldered Amazon in the Macanao Peninsula of Margarita Island.

Year	Number of birds	Confidence
1989	700	M
1990	750	H
1991	800	H
1992	914	H
1993	1,514	H
1994	1,580	H
1995	1,768	H
1996	1,842	H
2001	1,689	L
2002	1,800	L
2003	1,271	M
2009	816	M
2010	935	M
2011	1,480	H
2012	776	M
2013	1,055	M
2015	1,600	M
2016	1492	M
2017	1,500	M
2018	1,282	H
2019	1,544	H
2020	2,109	H
2021	1,951	H
2022	1,962	H
2023	2,155	H

Confidence is a subjective assessment of the reliability of the estimate, based on the experience of the field team (H, high; M, medium; L, low).

3.2.2 Nest productivity and poaching

Between 2004 and 2023, we recorded 1,756 birds fledging from monitored nests, and 144 lost to poachers, which represent 8% of the total (Table 4). Two main trends are revealed by the data: increase of the number of birds fledged over time and decrease of proportion poached. During the first five years (2004-2008) the mean number of birds fledged was 45.8, rising to 178.4 during 2019-2023. The first time that more than 100 parrots fledged was 2018, while this number has been larger than 200 between 2021 and 2023. Likewise, the mean proportion of birds poached during 2004-2008

TABLE 4 Nest productivity and poaching for the yellow-shouldered Amazon in the Macanao peninsula of Margarita Island.

Year	Birds fledged	Birds poached (%)
2004	25	32 (56)
2005	56	12 (18)
2006	72	0 (0)
2007	23	34 (60)
2008	53	10 (16)
2009	66	1 (1)
2010	40	8 (17)
2011	50	16 (24)
2012	27	0 (0)
2013	77	4 (5)
2014	61	0 (0)
2015	97	10 (9)
2016	47	5 (10)
2017	44	2 (4)
2018	126	4 (3)
2019	140	0 (0)
2020	140	3 (2)
2021	202	3 (1)
2022	202	0 (0)
2023	208	0 (0)
Total	1,756	144 (8)

was 30%, dropping to a mean of 1% during 2019-2023. Poaching rates have remained consistently low during more than a decade.

3.2.3 Mainland surveys

Keeping parrots as pets was found to be widespread among residents in the towns visited. Of 39 people interviewed during both routes combined, 38 kept parrots, and of these 32 were *Amazona barbadensis*. Most obtained their parrots as presents from friends or family, and reported to have had the parrot from four months ago to up to 27 years ago. The mean age was 6.7 years. All were reported to have been taken from a nest or obtained by placing a net on a tree and trapping them.

Wild populations of parrots were observed during the survey. Direct counts were performed at communal overnight roosts in three locations (Figure 1). During 4-7 September 2024, 74 parrots were observed in Guayacán, Sucre state, during 9-12 September 2024, 184 parrots were counted al Laguna El Juncal, next to the José Antonio Anzoátegui Petrochemical Complex, Anzoátegui State, while on 13 November, >1,120 parrots were recorded roosting at El Pedregal in Falcón state. The field guides of our surveys in Falcón, Julio Loyo, Luis Loyo and Endri Chirinos, visited the border between Falcón and Zulia state on 11-12 February 2024, and observed yellow-shouldered Amazons around the towns Quisiro, Papayo and La Cuadra (eBird, 2024), confirming their presence where they were considered possibly extant (Figure 1).

4 Discussion

Monitoring of wild populations of yellow-shouldered Amazons on two southern Caribbean islands, where multi-faceted and varied conservation interventions have been implemented since the late 20th century, indicates that populations have increased over the last two decades. While it is not possible to attribute these increases to any specific conservation intervention with certainty, improvements in breeding success associated with reductions in nest poaching suggest that interventions aimed at reducing poaching likely played a significant role in population recovery in both situations, as has been demonstrated for other Neotropical parrots (Wright et al., 2001). In contrast, recent surveys in mainland Venezuela suggest high rates of poaching persist and reinforce concerns over the long-term viability of these populations in the absence of focused conservation efforts.

In both Margarita Island and Bonaire, conservation efforts have been sustained over extended periods of time, apparently leading to the recovery of populations. The opportunity to explore multiple interventions and the ability to secure long-term funding have probably been key to success (Sodhi et al., 2011; Parks et al., 2022). In both instances, these interventions have varied over the years, adapting to changing circumstances, due to variation in the availability of funding, the involvement of governmental and various non-governmental organizations, changing personnel, political environments and emerging threats. These situations and challenges have varied considerably between the two islands. However, both situations can be characterized by sustained multi-decadal efforts involving and variously led by diverse stakeholders. In Bonaire the pro-active involvement of the island government, working closely with locally-based non-governmental organizations has likely been an important ingredient of success. The long-term commitment and support of an international organization, the World Parrot Trust, which has supported and worked closely with all stakeholders to provide financial, operational and technical support for conservation efforts on Bonaire for close to two decades, has also been critical. Similarly, in Margarita, the Venezuela-based organization Provita has been working in Macanao for the past two decades, with repeated support from organizations such as the Whitley Fund for Nature, Loro Parque Fundación, World Land Trust and Arenera La Chica – Hato San Francisco, in addition to municipal and state government agencies. The sporadic and variable conservation efforts in the face of diverse circumstances are likely representative of many conservation challenges in the region and around the world. The consistent positive outcomes of the two sites, however, demonstrate the power of partnerships, long-term commitment and persistence, and should be cause for optimism.

While it is ideal for research teams to implement systematic, carefully designed protocols leading to statistically robust analyses, the primary goal of conservation efforts is to mitigate threats and achieve population increases in threatened species. Achieving these outcomes can be complex and non-linear. Despite differing protocols over the years, field teams in Bonaire and Margarita have quantitatively demonstrated improvements in the status of yellow-shouldered Amazons. This further highlights the importance of adaptive management and sustained, multi-year financial support for achieving long-term conservation success (Briceño-Linares et al., 2011; Parks et al., 2022).

Preliminary observations on the Venezuelan mainland, combined with citizen science reports, allowed us to verify the persistence of populations of yellow-shouldered Amazons in the northeast and northwest of the country (Figure 2). Though our surveys were not aimed at formally estimating population size or measuring the intensity of poaching, we found that two topics deserve future analyses. First, poaching for pets continues to be widespread. Caged yellow-shouldered Amazons were found at all of our interview locations. Second, yellow-shouldered Amazons continue to inhabit mainland sites reported in the past, but appears to be absent in the central-northern part of the country (Figure 2). The fact that more than 1,000 parrots were counted one day at a single overnight roost site in El Pedregal, Falcón state, plus a number of recent eBird records between Falcón and Zulia, are encouraging. However, the long-term viability of this population in the face of significant poaching to supply local demand for pets and likely markets further afield is far from certain. Seizures of yellow-shouldered Amazons in Bonaire in 2011 and Aruba in 2022, indicate an international dimension to poaching and trafficking.

The current IUCN Red List assessment for the species assumes an overall declining population that approaches but does not exceed the threshold of 10% over three generations (25.5 years) (criterion C1) and that a population reduction projected, inferred or suspected in the future approaches 30% over the same length period (criterion A3cd) (BirdLife International, 2021). Inferring from apparent levels of exploitation for local and international trade within the species distribution in mainland Venezuela, we consider that it is plausible and likely that these thresholds are met or exceeded (particularly regarding C1) and that this information should be taken into account in assessments of population trends informing future Red List reassessments.

A range-wide action plan is in the final stages of publication (Briceño-Linares et al., 2024). Stakeholders from Aruba, Bonaire, Curaçao and Venezuela, plus collaborators from other parts of the world were actively involved in workshops and as reviewers. Based on the information and experience accumulated over the last four decades, the group converged on achieving the vision that by 2031 the yellow-shouldered Amazon has functional, viable wild populations throughout its historical range. That by 2031, three wild populations are under evidence-based management programs and at least one population is reintroduced at a location where it went extinct. The plan foresees commitment and engagement of local communities that apply sustainable use principles, a reduction of the drivers of historical population decline, and the establishment of an international network of collaborators that supports these efforts. The first steps have been taken with the reintroduction of yellow-shouldered parrots into Aruba. Evidence-based management is also taking place in Bonaire and Macanao. Expanding evidence-based management to Aruba, assuring that the work in Bonaire and Macanao continues, exploring options in Curaçao, and initiating research or conservation activities in mainland Venezuela are the next steps in assuring that the decline of the yellow-shouldered Amazon is halted and reversed.

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

The animal study was approved by Instituto Venezolano de Investigaciones Científicas. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

JB-L: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – review & editing. JA-A: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – review & editing. JC: Funding acquisition, Investigation, Project administration, Writing – review & editing. AD: Project administration, Supervision, Writing – review & editing. OD: Investigation, Writing – review & editing. JH: Conceptualization, Investigation, Methodology, Writing – review & editing. EH: Investigation, Methodology, Writing – review & editing. RM: Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing, Conceptualization. PM: Conceptualization, Investigation, Methodology, Supervision, Writing – review & editing. GN: Investigation, Methodology, Writing – review & editing. LS: Funding acquisition, Investigation, Methodology, Writing – review & editing. BS: Writing – review & editing, Conceptualization, Funding acquisition, Methodology, Project administration. FS: Conceptualization, Formal analysis, Methodology, Writing – review & editing. JR: Conceptualization, Data curation, Funding acquisition, Investigation, Supervision, Writing – original draft, Writing – review & editing.

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Conflict of interest

OD is the owner of VetDoest.

The remaining authors declare that the research 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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Climate-driven distributional shifts in Chocó endemic birds of southwest Colombia

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Introduction: Climate change poses a significant threat to bird communities, especially forest-dwelling and narrowly distributed species, which are expected to experience severe range contractions and higher extinction risks compared to widely distributed and open-area species. The Chocó region in southwestern Colombia, known for its rich bird endemism, is particularly vulnerable.

Methods: We analyzed potential distribution shifts for 27 endemic and near-endemic bird species in the Chocó region using eBird occurrence records and climate projections. We modeled species distributions under low and high greenhouse gas emission scenarios for 2050 and 2070, comparing these projected distributions to current forested and protected areas to evaluate future conservation needs.

Results: Our findings indicate that nearly all species are projected to lose climate-suitable areas under at least one future scenario, resulting in a regional decline in species richness. Changes in species richness are most pronounced near the Colombia-Ecuador border, suggesting a shift to higher elevations. Notably, the Scarlet-and-white Tanager (*Chrysothlypis salmoni*) is predicted to suffer the greatest losses in climate-suitable area, both within protected and forested regions.

Discussion: These results highlight the urgency of expanding the protected area network and conserving key forested regions to help species adapt to climate change. By providing projected distribution maps and potential range shifts, our study underscores the importance of modeling future distributions to support conservation strategies for at-risk species and the ecological services they provide in tropical montane regions.

KEYWORDS

global warming, population decline, forest cover, neotropics, tropical ornithology, KBA Río Ñambí, conservation biology

1 Introduction

Climate change is expected to cause population-level modifications to bird communities, leading to contractions, expansions, or shifts in their distributions due to global warming (Şekercioğlu et al., 2008; Wormworth and Şekercioğlu, 2011; Mota et al., 2022). The response to climate change may vary among species, with those inhabiting tropical forests and having restricted distributions expected to experience more drastic reductions in their ranges (Şekercioğlu et al., 2012; de Moraes et al., 2020), as these species are unlikely to keep pace with rapid changes in precipitation and temperature patterns (Román-Palacios and Wiens, 2020). Conversely, generalist species, such as those found in degraded environments or across wide elevational or latitudinal gradients, may experience expansions in their ranges due to the capacity to exploit a broad variety of resources (Sales et al., 2020). As a result, the expected change in species richness in future climate scenarios poses a challenge for conservation planning (Vale et al., 2018), as currently protected areas could become unsuitable for species that play essential ecological roles (Şekercioğlu, 2006; Littlefield et al., 2019), thereby threatening natural systems.

Tropical forests, recognized for being the world's most biodiverse regions (Raven et al., 2020), have lost most of their original cover to agricultural and pasturelands (Taubert et al., 2018), with the majority of the remaining forest still unprotected (Stan et al., 2024). Climate change may intensify this scenario, as many regions are anticipated to experience increased warmth and aridity (Sales et al., 2020), posing a dire risk to species already threatened by habitat degradation. Additionally, there is uncertainty about whether protected areas can still match new climate suitable areas for species in the future (Littlefield et al., 2019), especially in the understudied tropics (Harris et al., 2011). For example, endemic monkey species in the eastern Amazonian rainforest are projected to vanish from most of their current distribution in the future when considering both forest loss and climate (da Silva et al., 2022). In particular, the Chocó ecoregion in northwestern South America emerges as a crucial conservation priority, as it still retains a substantial amount of forest cover (Anaya et al., 2020). The Chocó Endemic Bird Area (EBA) is located across much of the Pacific slope of the Andes in western Colombia and northwestern Ecuador, and is also part of the larger Tumbes-Chocó-Magdalena biodiversity hotspot that extends from the Darién lowlands of eastern Panama to northwestern Peru (Devenish et al., 2009; Sánchez-Nivicela and Montenegro-Pazmiño, 2022). Recent discoveries of undescribed species and new distributional records of other species in the area emphasize the significance of this region as a hotspot (Guevara Andino and Fernandez-Fernandez, 2020; Amaya-Vallejo et al., 2021; Velandia Perilla et al., 2021). The Chocó is the ninth most biodiverse vegetation hotspot globally, with close to 3,000 endemic species and around 11,000 total plant species in an area covering around 0.2% of the planet's surface (Pérez-Escobar et al., 2019); among birds, the Chocó has the highest number of endemic bird species of any EBA on the continent, with over 60 species recognized as endemic to the Chocó region (Devenish et al., 2009; Sánchez-Nivicela and Montenegro-Pazmiño, 2022; BirdLife International, 2024b). However, the Chocó has been negatively affected by major habitat loss through deforestation as well as other anthropogenic pressures such as hunting and poaching, making this region a critical conservation priority (Sánchez-Nivicela and Montenegro-Pazmiño, 2022; BirdLife International, 2024a). Furthermore, projections already indicate the risk of local extinctions of bird species in this region in the coming decades (Velásquez-Tibatá et al., 2013), underscoring the urgency of addressing this understudied issue in the region to support future conservation efforts.

Birds, known for their sensitivity to environmental changes, play a crucial role in revealing patterns essential for future biodiversity conservation (Triviño et al., 2018). These avian species contribute to ecosystem functioning by providing a range of ecological services (Şekercioğlu et al., 2016). They facilitate natural forest regeneration by moving seeds between fragments, promote genetic variability through pollination, regulate populations of other species like insects, and prevent disease outbreaks by scavenging on carcasses (Şekercioğlu, 2006; Mäntylä et al., 2011; Ogada et al., 2012; Martínez and García, 2017; Wessinger, 2021). However, recent projections indicate that many bird species may struggle to find suitable climate conditions in the future, leading to a depletion in richness and alterations in community composition (Miranda et al., 2019; Mota et al., 2022), which could compromise these essential ecological services. Additionally, the loss of frugivorous birds may severely limit plants' capacity to track climate change due to reduced long-distance seed dispersal (Fricke et al., 2022). For Western Hemisphere landbirds, intermediate extinction estimates by Şekercioğlu et al. (2008), based on climate-induced changes in distributions, range from 1.3% (1.1°C warming) to 30.0% (6.4°C warming). Birds confined to the Chocó ecoregion could experience even more drastic reductions in their current distributions compared to species found elsewhere, as their restricted geographic ranges make them particularly vulnerable to losing suitable climate conditions (Velásquez-Tibatá et al., 2013). For example, the loss of climate-suitable areas could result in an approximately 75% reduction in the distribution of the Choco Vireo (*Vireo masteri*), a species exclusively found in the region, while the loss is expected to be smaller for the Wattled Guan (*Aburria aburri*; ca. 28%), a species whose distribution also extends into Peru (Velásquez-Tibatá et al., 2013). Furthermore, information on changes in the distribution of Chocó endemic birds is relatively scarce, limiting the implementation of appropriate conservation strategies to ensure their long-term persistence.

In this study, we used ecological niche models to predict the distribution of 27 endemic or near-endemic birds within the Chocó region, with a focus on species occurring in southwest Colombia, under different climate scenarios. We focus on the ranges of these species not only within this targeted Colombian region but also across the Chocó and the entirety of a species' current distribution. Specifically, we aimed to assess distributional changes and conservation needs of these species, considering current forested and protected areas. We anticipated a reduction in species distributions, with variation across species that may be more sensitive and specialized, and a lower proportion of suitable areas within forested and protected areas in future scenarios. We predict that some Chocó endemics will likely disappear from southwestern Colombia, and we expect to observe heightened population fragmentation across species' ranges.

2 Methods

2.1 Study area

We assess species distributions, both present and future, across two spatial scales. In our first, broad spatial scale, we examine distributions across the entirety of the Chocó region and, to some extent, part of the Tumbes-Chocó-Magdalena hotspot that occurs in western Colombia and Ecuador (this is due to the fact that some of the species noted as Chocó endemics (BirdLife International, 2024b) have eBird records that fall outside of the established Endemic Bird Area (EBA)). There are various interpretations in the literature of what specifically constitutes the Chocó region (i.e., Pérez-Escobar et al., 2019), so we have chosen to interpret the Chocó area specifically as that which encompasses the designated EBA (Devenish et al., 2009; Sánchez-Nivicela and Montenegro-Pazmiño, 2022). For our second spatial scale, we focused on the region centered around the Nariño department in southwestern Colombia, where there are several mid-elevation reserves in the Chocó that are focused on avian conservation and protection, including Nature Reserve La Nutria-Pimán, La Planada Nature Reserve, OECM (other effective area-based conservation measure) Bangsias BirdLodge, OECM San Antonio, and KBA (Key Biodiversity Area) Río Ñambí.

2.2 Species selection

When determining which species to include in this analysis, we selected 27 species (Table 1) that we have been actively capturing and therefore studying during bird banding operations in the Colombian Chocó, from 2021 to 2024, at the Río Ñambí and Bangsias reserves located near Altaquer in the Barbacoas Municipality. Our selected species therefore largely consisted of the more abundant and less threatened birds within the Chocó (at least via bird banding), though our list does include some range-restricted and threatened species as well (i.e., Hoary Puffleg [*Haplophaedia lugens*] and Cloud-forest Pygmy-Owl [*Glaucidium nubicola*], respectively). This approach allows us to use these largely widespread and banding-sampled species as best-case indicators for predicting potential changes that may also affect less frequently encountered and more cryptic species (i.e., Choco Vireo). Our list also includes species that feed on a variety of items, including fruits, invertebrates, vertebrates, and nectar, meaning these species play important roles in different ecological functions (Table 1).

All 27 species are either endemic or near-endemic to the Chocó Endemic Bird Area (EBA). Endemic species were identified using the BirdLife International (2024b) definition, which classifies a species as endemic if its range is entirely confined to the EBA. For species not currently listed as endemic by BirdLife International, we performed an additional review by cross-referencing the species' projected ranges with the boundaries of the Chocó EBA to determine if they could be considered endemic based on geographical restriction. Near-endemic species, on the other hand, are those that are not exclusively confined to the Chocó EBA but have a significant portion of their range within this region. Specifically, the three near-endemic species included in this study are restricted to the greater Tumbes-Chocó-Magdalena biodiversity hotspot and have distributions that largely overlap with the Chocó EBA.

2.3 Avian data preparation

We downloaded the complete eBird world dataset (www.ebird.org) until the end of 2022 (ebd_prv_relDec-2022) and filtered the records for 27 Chocó bird species using the R package *auk* (Strimas-Mackey et al., 2023). We considered only complete checklists with all species reported and approved. Then, we eliminated inconsistencies such as duplicates, records at sea, and those matching centroids of municipalities using the R package *CoordinateCleaner* (Zizka et al., 2019). Finally, we filtered the records of each species to obtain the maximum number of occurrences that were at least 5 km apart, to avoid geographical bias, using the R package *spThin* (Aiello-Lammens et al., 2015). The final number of records for each species in the study are listed in Table 1.

While the eBird taxonomy follows that of the Clements checklist, we followed the avian taxonomic classifications of BirdLife International and the global bird checklist of the BirdLife Taxonomic Working Group (BirdLife International, 2024a) since it is used by the IUCN Red List for designating global threat assessments of species (IUCN, 2024). The only main discrepancy between these two taxonomies is for Chestnut-throated Solitaire (*Cichlopsis chubbi*), which is currently recognized, along with two other highly disjunct populations in South America that are treated by BirdLife as separate species, by Clements/eBird as a subspecies of Rufous-brown Solitaire (*C. leucogenys*). This taxonomic discrepancy was accounted for during the eBird data filtering process, since the *chubbi* population is the only one among the Rufous-brown complex that occurs in the Chocó region.

2.4 Climate data and ecological niche modeling

We obtained 19 bioclimatic variables (Table 2) for the baseline and future scenarios (2050 and 2070) with a spatial resolution of 2.5 arcminutes from the WorldClim platform (Fick and Hijmans, 2017). These variables are derived from precipitation and temperature measurements and largely used in ecological studies (Prieto-Torres et al., 2020; Oliveira-Silva et al., 2022). We considered three Global Climate Models (GCMs): IPSL-CM6A-LR, MIROC6, and MPI-ESM1-2-HR, and two Shared Socio-economic Pathways (SSPs): 245 and 585. The selection of these GCMs was based on their better performance with respect to

TABLE 1 Bird species included in the study.

IOC 14.2	English Name	Scientific Name	Primary diet	Endemic (E/NE)	IUCN	Records
2749	White-whiskered Hermit	*Phaethornis yaruqui*	Nectar	NE	LC	190
2944	Violet-tailed Sylph	*Aglaiocercus coelestis*	Nectar	E	LC	140
3055	Hoary Puffleg	*Haplophaedia lugens*	Nectar	E	NT	23
3101	Brown Inca	*Coeligena wilsoni*	Nectar	E	LC	101
3165	Velvet-purple Coronet	*Boissonneaua jardini*	Nectar	E	LC	62
3177	Rufous-gaped Hillstar	*Urochroa bougueri*	Nectar	E	LC	75
3181	Purple-bibbed Whitetip	*Urosticte benjamini*	Nectar	E	LC	54
3204	Empress Brilliant	*Heliodoxa imperatrix*	Nectar	E	LC	65
4931	Purple Quail-Dove	*Geotrygon purpurata*	Seed	E	EN	21
9221	Cloud-forest Pygmy-Owl	*Glaucidium nubicola*	Vertebrate	E	VU	40
11149	Toucan Barbet	*Semnornis ramphastinus*	Fruit	E	NT	93
15170	Uniform Treehunter	*Thripadectes ignobilis*	Invertebrate	E	LC	77
16797	Choco Tapaculo	*Scytalopus chocoensis*	Invertebrate	E	LC	50
17488	Pacific Flatbill	*Rhynchocyclus pacificus*	Invertebrate	NE	LC	59
18212	Orange-breasted Fruiteater	*Pipreola jucunda*	Fruit	E	LC	54
18429	Club-winged Manakin	*Machaeropterus deliciosus*	Fruit	E	LC	78
30148	Chestnut-throated Solitaire[a]	*Cichlopsis chubbi*	Fruit	E	NT	9[b]
30153	Black Solitaire	*Entomodestes coracinus*	Fruit	E	LC	62
34715	Yellow-collared Chlorophonia	*Chlorophonia flavirostris*	Fruit	E	LC	64
36291	Choco Warbler	*Myiothlypis chlorophrys*	Invertebrate	E	LC	78
36515	Ochre-breasted Tanager	*Habia stolzmanni*	Fruit	NE	LC	93
36707	Scarlet-and-white Tanager	*Chrysothlypis salmoni*	Fruit	E	LC	58
37478	Indigo Flowerpiercer	*Diglossa indigotica*	Nectar	E	LC	61
37533	Purplish-mantled Tanager	*Iridosornis porphyrocephalus*	Fruit	E	NT	97
37623	Glistening-green Tanager	*Chlorochrysa phoenicotis*	Invertebrate	E	LC	97
37636	Moss-backed Tanager	*Bangsia edwardsi*	Fruit	E	LC	36
37677	Rufous-throated Tanager	*Tangara rufigula*	Fruit	E	LC	93

[a] Note that this species is considered by other taxonomic authorities as a subspecies of Rufous-brown Solitaire (*C. leucogenys*).

[b] Note that these records correspond to Rufous-brown Solitaire records within the Chocó region only.

English and scientific name taxonomy follows that of BirdLife International (2024b). IOC: ranking of birds in the IOC 14.2 World Bird List; Endemic: species that are either endemic (E) or near-endemic (NE) to the Chocó Endemic Bird Area (NE species are endemic to the Tumbes-Chocó-Magdalena Hotspot); IUCN: IUCN Red List 2023 threat rankings. Records represent the number of occurrences left after the procedure to minimize geographical bias (spatial thinning of occurrences).

frequency and persistence errors in the South America region (Cannon, 2020). The SSPs represent optimistic and pessimistic greenhouse gas emission scenarios, with the optimistic scenario corresponding to a global temperature increase of up to 3°C on average, and the pessimistic scenario corresponding to an increase of up to 5°C on average compared to the preindustrial period (O'Neill et al., 2014). For each species, we used the R package *ENMwizard* (Heming et al., 2019) to perform a Pearson correlation analysis considering all bioclimatic variables and selected those below the cutoff value of 0.7 to minimize multicollinearity (Dormann et al., 2013).

We modeled the ecological niche of Chocó bird species using the MaxEnt algorithm (Phillips et al., 2006). This algorithm is widely used in the literature (Velásquez-Tibatá et al., 2013; Corrêa et al., 2019; Zhu et al., 2021), and its superior performance over other algorithms has already been demonstrated (Mota et al., 2022).

TABLE 2 Bioclimatic variables derived from temperature and precipitation data obtained from WorldClim – Global climate and weather data (www.worldclim.org).

Variables	Description
Bio1	Annual mean temperature
Bio2	Mean diurnal range (mean of monthly max temp–min temp)
Bio3	Isothermality (Bio2/Bio7) (×100)
Bio4	Temperature seasonality (standard deviation ×100)
Bio5	Max temperature of warmest month
Bio6	Min temperature of coldest month
Bio7	Temperature annual range (Bio5-Bio6)
Bio8	Mean temperature of wettest quarter
Bio9	Mean temperature of driest quarter
Bio10	Mean temperature of warmest quarter
Bio11	Mean temperature of coldest quarter
Bio12	Annual precipitation
Bio13	Precipitation of wettest month
Bio14	Precipitation of driest month
Bio15	Precipitation seasonality (coefficient of variation)
Bio16	Precipitation of wettest quarter
Bio17	Precipitation of driest quarter
Bio18	Precipitation of warmest quarter
Bio19	Precipitation of coldest quarter

We optimized two important parameters of MaxEnt: regularization multiplier and feature classes, thus generating 70 models per species. We employed the "block" and "jackknife" methods for cross-validation (Shcheglovitova and Anderson, 2013; Roberts et al., 2017). Subsequently, we ranked the best models based on the lowest omission rate (OR) and the highest area under the curve (AUC) (Boria et al., 2017). Next, we projected the models onto future climate scenarios (GCMs and SSPs) and generated consensus models by averaging the best models for each species and scenario (see details in Mota et al., 2022). We used the Maximum Training Sensitivity plus Specificity threshold to convert the final models into binary maps of 2.5 spatial arcminutes resolution representing "suitable" or "unsuitable" climate areas. This threshold is indicated for presence data only (Liu et al., 2013) and is more restrictive than other thresholds, which aligns with the projections for our species. Subsequently, we created a buffer around occurrence records for each species with a radius of 100 km and cropped the binary maps to reduce overprediction (Mendes et al., 2020). The buffer size was selected based on the distance between the western Andean slope and the coast, which we assumed to be accessible areas for the studied species. We used these cropped binary maps to calculate species richness by climate scenario using the R package *divraster* (Mota et al., 2023). The chosen variables by species and their percentages of contribution are listed in Supplementary Table S1.

2.5 Total, forested, and protected areas

We used the binary maps to calculate the total climate suitable area for each species and climate scenario. We acquired Land Cover Type 1 for the year 2022 from the MCD12Q1 product Version 6.1, available in the U.S. Geological Survey Earth Explorer platform (www.earthexplorer.usgs.gov). We extracted the forest cover class and converted it to a spatial resolution of 2.5 arcminutes. We overlaid the binary maps with the forested areas to calculate the climate suitable area within the current forested area.

Additionally, we acquired the maps of protected areas from the World Database on Protected Areas platform (www.protectedplanet.net) and converted them from a vector to a raster file with a spatial resolution of 2.5 arcminutes. We overlaid the binary maps with the protected areas to calculate the climate suitable area within the current protected areas.

We used the R package *terra* (Hijmans et al., 2023) to transform the data and to measure the area in square kilometers. All calculations and graphing were conducted in R (version 4.4.1; R Core Team, 2024) and QGIS (version 3.34; QGIS, 2024).

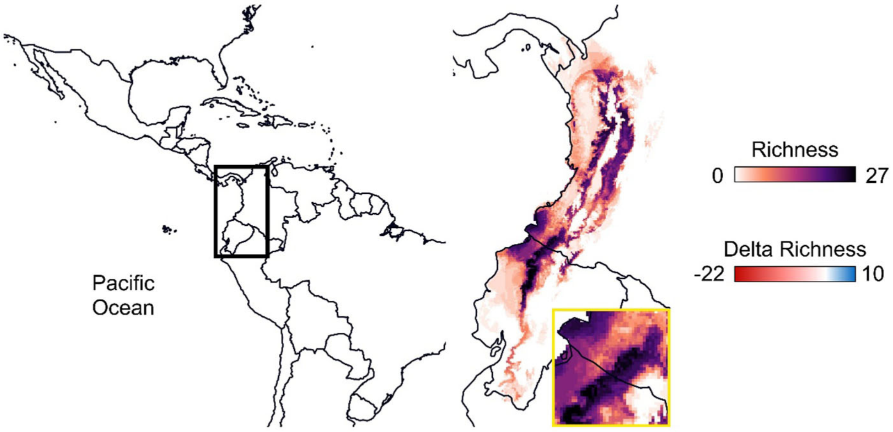
3 Results

Among the 27 Choco bird species of southwestern Colombia in our study, species fed mostly on fruits (n = 11), followed by nectar (n = 9), invertebrates (n = 5), seeds (n = 1), and vertebrates (n = 1). Their ecological niche models showed a good fit, with the Area Under the Curve (AUC) higher than 0.7 for all but one species (Pacific Flatbill, *Rhynchocyclus pacificus*), which showed an intermediate fit with an AUC of 0.68. The average AUC value was 0.78, while the Omission Rate (OR) value was 0.17, ranging from 0.06 to 0.36 (Supplementary Table S2).

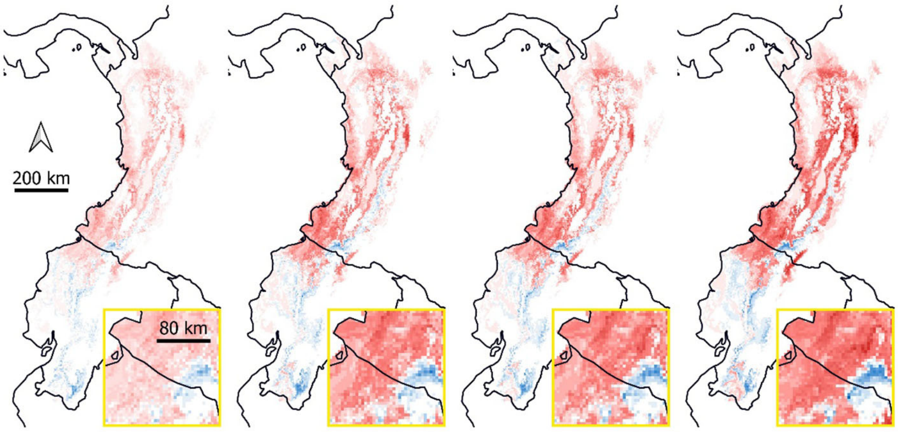
Our projections indicate that the highest concentration of species in the baseline scenario is located in the southern Chocó region and on the west and east sides of the Andes Mountains in southwestern Colombia and northwestern Ecuador (Figure 1A). Nearly all species are forecast to lose suitable climate areas in at least one future scenario in these same areas, leading to an overall reduction in species richness (Figures 1B–E). A small increase in the number of species is projected in some currently less diverse regions, including highland areas near the Colombia-Ecuador border and the east side of the Andes Mountains in southern Ecuador (Figures 1B–E). These delta richness patterns are consistent across all future scenarios but become more evident in the 2070 pessimistic scenario, with up to 22 species losses and 10 species gains (Figures 1B–E).

The average of the total climate suitable areas is 2.7–2.8 times larger than the suitable area within forested areas, 3.6–3.9 times larger than the suitable area within protected areas, and 7.3–7.7 times larger than the suitable area within both forested and protected areas for all climate scenarios evaluated. Additionally, the average suitable area decreases from the baseline to future scenarios for all classes. This reduction is higher from the baseline to the 2070 pessimistic scenario, whereas the reduction is lower but similar from the baseline to the optimistic scenarios and to the 2050 pessimistic scenario (Figure 2) (Table 3).

Choco Warbler (*Myiothlypis chlorophrys*) is projected to lose the largest total climate-suitable area in the optimistic scenarios



a) Baseline



b) Optimistic 2050 c) Optimistic 2070 d) Pessimistic 2050 e) Pessimistic 2070

FIGURE 1
Species richness in the baseline scenario **(A)** and the difference between the richness in the baseline and future scenarios [delta richness; **(B–E)**] for 27 endemic or near-endemic bird species across the Chocó in Colombia and Ecuador, with a subset region depicted that focuses on southwestern Colombia. In the baseline richness map **(A)**, darker colors represent areas with suitable climate conditions for a higher number of species. In the delta richness maps **(B–E)**, red indicates areas where species are projected to contract their distributions, while blue indicates areas where species are projected to expand. The future scenarios represent optimistic (SSP245) and pessimistic (SSP585) greenhouse gas emission pathways for 2050 and 2070.

(2050: 53%; 2070: 55%) and the pessimistic 2050 scenario (60%). In the pessimistic 2070 scenario, however, greater losses are expected for Scarlet-and-white Tanager (*Chrysothlypis salmoni*) (84%). Both species are also projected to lose a significant portion of their suitable areas within forests. The Yellow-collared Chlorophonia (*Chlorophonia flavirostris*) is expected to lose the highest amount of suitable area within protected areas in the optimistic scenarios (2050: 41%; 2070: 42%), whereas greater losses in the pessimistic scenarios are anticipated for Scarlet-and-white Tanager (2050: 54%; 2070: 84%). When considering forested and protected areas together, the largest contractions in suitable area are projected for the Moss-backed Tanager (*Bangsia edwardsi*) in the optimistic scenarios (2050: 55%; 2070: 57%) and the pessimistic 2050 scenario (55%). In contrast, the Purple Quail-Dove (*Geotrygon purpurata*) is projected to be the least affected by climate change, proportionally, with a small gain in suitable area ranging from 4% (341 km^2) within forested areas in the pessimistic 2050 scenario to 25% (534 km^2) within forested and protected areas combined in the pessimistic 2070 scenario. The Ochre-breasted Tanager (*Habia stolzmanni*) is also expected to be less affected in terms of total suitable area under the pessimistic scenarios, with a modest gain of 3-5% (3218-6985 km^2).

4 Discussion

Our results indicate that climate change is projected to induce significant changes in the species richness of birds that are endemic or near-endemic to the Chocó, especially in southwestern Colombia, with three-quarters of these bird species [in our study]

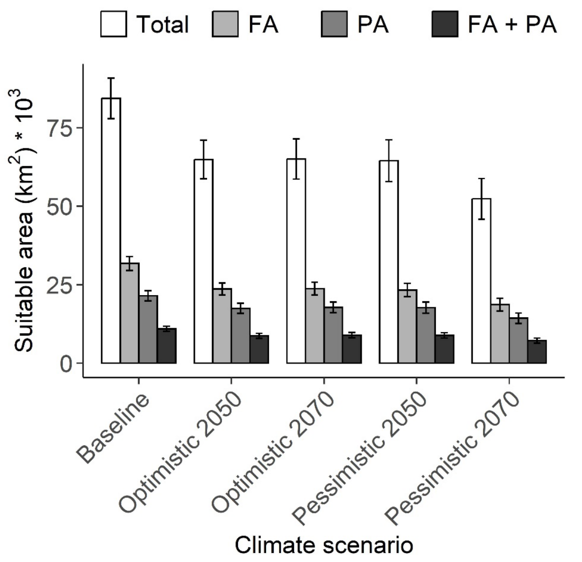


FIGURE 2
The average climate suitable area in squared kilometers for 27 endemic or near-endemic bird species across the Chocó in Colombia and Ecuador by climate scenario. Total: whole suitable area, FA: suitable area within forested areas, PA: suitable area within protected areas, and FA + PA: suitable area within forested and protected areas simultaneously. Vertical bars indicate the standard error of the mean. The future scenarios represent optimistic (SSP245) and pessimistic (SSP585) greenhouse gas emission pathways for 2050 and 2070.

at risk of extinction. Almost all species are expected to experience a reduction in their global distributions in at least one future climate scenario, resulting in a decline in the average suitable area. In addition, the suitable area within forested and protected areas is much smaller compared to the total suitable area, highlighting the urgent need to expand the protected area network in the region.

The change in total species distribution across all future climate scenarios ranged from -84% to +6%, with an average loss of 28%, resulting in a reduction of 81% in species richness (Figure 1, Supplementary Table S3). The potential loss of species was expected, given the already restricted distributions of Chocó birds, and our findings align with other studies that reported drastic losses for endemic birds (Hoffmann et al., 2020), as well as a positive relationship between range size and suitable area loss (Mota et al., 2022). Furthermore, the regions projected to experience high species losses and high species gains are predominantly at intermediate and high elevations, suggesting potential upslope shifts of birds in the future. This pattern mirrors trends observed in other parts of the world (Freeman and Class Freeman, 2014; Freeman et al., 2018, 2021; Neate-Clegg et al., 2020, 2021; Neate-Clegg and Tingley, 2023). These results emphasize the value of modelling future distributions of montane species to forecast potential elevational range shifts and climate-driven extirpations (Freeman et al., 2018; Nowak et al., 2019; Hoffmann et al., 2020). Additionally, the protected area Cotacachi Cayapas (WDPA, 2024), which represents the highest species richness in the baseline scenario, is located near a region projected to remain stable in the future (Figure 1). Expanding this protected area southwards could be an effective conservation strategy to address climate change impacts.

Supporting our prediction, the proportion of suitable area within forested and protected areas is considerably smaller compared to the total suitable area, regardless of the climate scenario, and it is also expected to decrease in the future (Figure 2; Supplementary Table S3). This suggests that, despite the availability of sites presenting favorable climate conditions, without vegetation, forest birds will not persist. This is supported by the higher vulnerability of forest species to climate change, as predicted in other studies (Miranda et al., 2019; Sales et al., 2020). Increasing forest cover in southwestern Colombia may help mitigate these impacts, not only because of the benefits of microclimatic conditions provided by natural vegetation but also to promote connections between potential refuge areas (Flórez-Paí, 2016; Frey et al., 2016; Guevara et al., 2016). Furthermore, the proportion of suitable areas within protected areas is even lower, representing only one-fourth of the total on average (Supplementary Table S3). This underrepresentation of species distribution within protected areas has been reported previously, highlighting the need to expand the coverage of these areas (Vale et al., 2018; Ivanova and Cook, 2020; Critchlow et al., 2022). Moreover, as a consequence of suitable area loss induced by climate change, Chocó birds are expected to show more fragmented distributions (Figure 3), a pattern already observed for other Colombian species (Velásquez-Tibatá et al., 2013). The expansion of the protected area network may prevent the isolation of bird populations and their risk of extinction by serving as corridors between suitable areas (Littlefield et al., 2017) that increase the connectivity of critical habitat at local and landscape scales (Şekercioğlu, 2009; Palacio et al., 2020).

As we expected, changes in birds' suitable areas vary among species (Supplementary Table S3). The species expected to suffer larger contractions on average in their distributions feed primarily on invertebrates (Choco Warbler; -61%) and fruits (Yellow-collared Chlorophonia; -59%). Similarly, forest frugivore birds from the Atlantic and Amazon forest are also expected to lose a significant portion of their current distributions (Miranda et al., 2019; Mota et al., 2022). Moreover, species such as White-flanked Antwren (*Myrmotherula axillaris*) and Choco Poorwill (*Nyctiphrynus rosenbergi;* this species has been observed but not yet captured at the Río Ñambí and Bangsias reserves by the authors), are also expected to lose climate suitable area greater than 80% in the future corroborating the high risk of forest insectivore birds as well (Velásquez-Tibatá et al., 2013; Miranda et al., 2019). The loss of

TABLE 3 The average climate suitable area in square kilometers for 27 endemic or near-endemic bird species across the Chocó in Colombia and Ecuador is presented by climate scenario.

Scenario	Area	Mean	SD	SE	CI Lower	CI Upper
Baseline	Total	84360	33441	6436	71746	96974
Optimistic 2050	Total	64868	31860	6132	52851	76886
Optimistic 2070	Total	65015	33233	6396	52479	77550
Pessimistic 2050	Total	64496	34584	6656	51451	77541
Pessimistic 2070	Total	52350	33716	6489	39632	65068
Baseline	FA	31740	11487	2211	27407	36074
Optimistic 2050	FA	23632	10037	1932	19846	27417
Optimistic 2070	FA	23738	10651	2050	19720	27756
Pessimistic 2050	FA	23313	10994	2116	19166	27460
Pessimistic 2070	FA	18662	10604	2041	14662	22661
Baseline	PA	21462	8610	1657	18214	24709
Optimistic 2050	PA	17467	8375	1612	14308	20626
Optimistic 2070	PA	17766	8663	1667	14498	21033
Pessimistic 2050	PA	17691	9079	1747	14266	21115
Pessimistic 2070	PA	14316	8648	1664	11054	17579
Baseline	FA + PA	10939	4331	833	9305	12573
Optimistic 2050	FA + PA	8736	4020	774	7219	10252
Optimistic 2070	FA + PA	8936	4186	806	7358	10515
Pessimistic 2050	FA + PA	8838	4361	839	7194	10483
Pessimistic 2070	FA + PA	7181	4104	790	5633	8729

Total: whole suitable area, FA: suitable area within forested areas, PA: suitable area within protected areas, and FA + PA: suitable area within both forested and protected areas simultaneously. SD: standard deviation, SE: standard error, and CI: 95% confidence interval. The future scenarios represent optimistic (SSP245) and pessimistic (SSP585) greenhouse gas emission pathways for 2050 and 2070.

these species could affect the provision of essential ecological functions, particularly seed dispersal and insect control, by reducing the natural regeneration of forests and increasing leaf damage in plants (Şekercioğlu, 2006; Mäntylä et al., 2011; Wenny et al., 2016; Martínez and García, 2017). Furthermore, Purple Quail-Dove seems to be favored by future climatic conditions in the Chocó region, though this gain is still small in absolute terms, representing a 25% increase within forested and protected areas, totaling only 534 km² (Supplementary Table S3). In this case, protected areas such as Serranía de Los Paraguas and Cotacachi Cayapas are particularly important for the species' conservation, especially since the Purple Quail-Dove is already considered endangered due to habitat loss (del Hoyo et al., 2020). Indeed, birds in the Colombian Andes have declined across a century due primarily to reductions in forest cover resulting from land-use change, deforestation, and habitat fragmentation (Palacio et al., 2020), indicating that suitable climatic conditions alone cannot ensure the species' persistence.

5 Conclusion

Our study represents the first assessment of future climate change impacts on endemic and near-endemic Chocó birds in southwestern Colombia, offering valuable insights for conservation planning. While a higher number of records could increase the predictive power of our models, and taking into account other factors such as dispersal scenarios and species-specific traits could provide deeper insight into species' responses to climate change, our findings nevertheless essentially contribute to the limited information on climate change impacts in this biodiverse region. Importantly, we provide projected distribution maps and potential elevational range shifts, for 27 Neotropical bird species under different climate scenarios (Figure 3, Appendix B) – these projections will be useful for conservation efforts and better understanding trends in resident bird populations. The potential loss of these species could jeopardize essential ecological services such as seed dispersal, pollination, and insect control, leading to

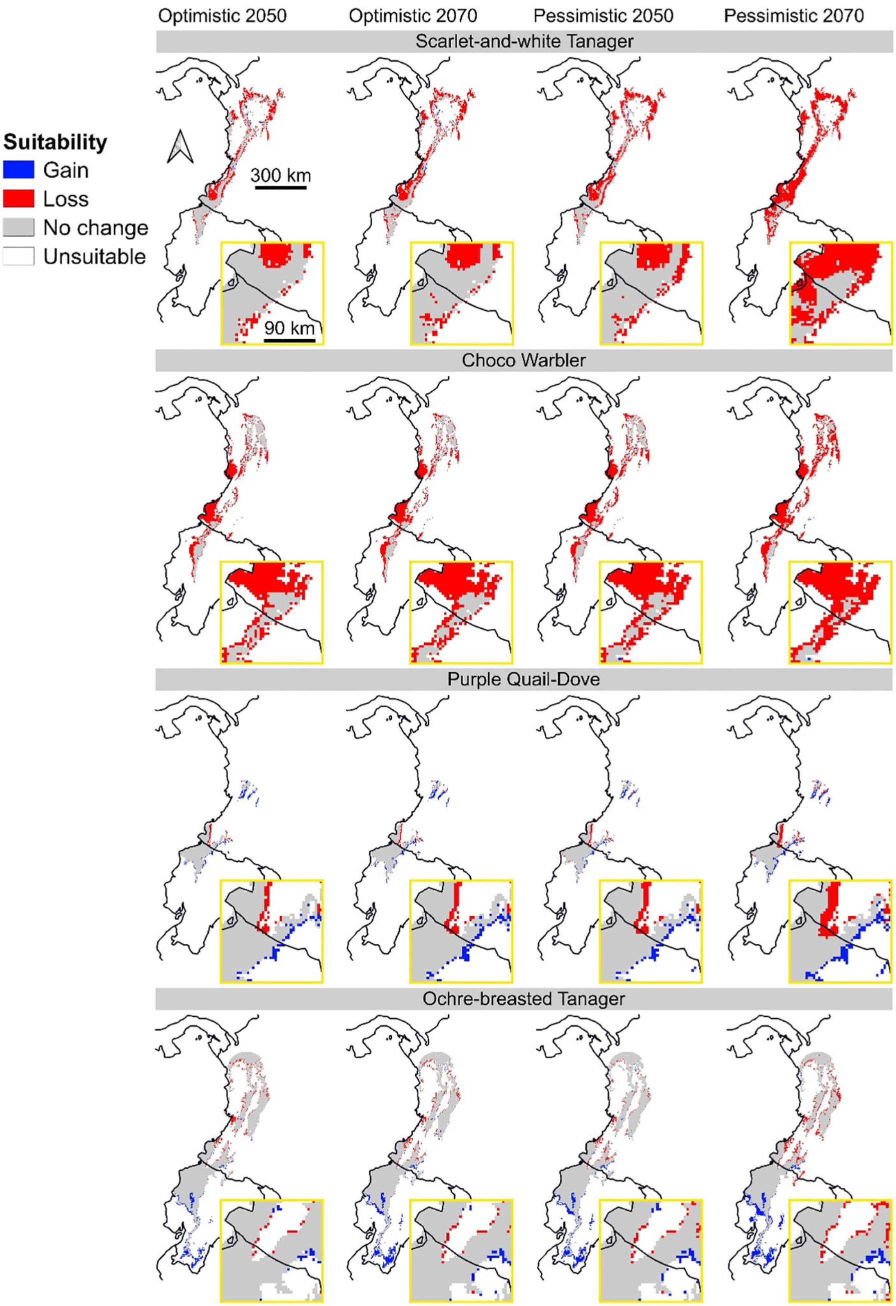


FIGURE 3
Changes in climate suitable areas for the Scarlet-and-white Tanager (Chrysothlypis salmoni), Choco Warbler (Myiothlypis chlorophrys), Purple Quail-Dove (Geotrygon purpurata), and Ochre-breasted Tanager (Habia stolzmanni) across the Chocó region in Colombia and Ecuador. Colors indicate changes in climate suitable area between baseline and future scenarios, with red indicating contraction, blue expansion, gray stability, and white no suitable climate conditions. The future scenarios represent optimistic (SSP245) and pessimistic (SSP585) greenhouse gas emission pathways for 2050 and 2070. The suitability change for all species is available in Appendix A.

cascading effects on other species affecting the entire community and reducing its resilience to disturbances. Moreover, eBird, one of the most well-known and widely used citizen and community science initiatives around the world (Kittelberger et al., 2023), serves as an important source of bird occurrence data globally and is an important tool for forecasting species distributions in the future (Delfino, 2023; Liu et al., 2023). To mitigate the potential losses of suitable habitats and facilitate species' range shifts, reforestation and habitat restoration should be prioritized alongside the expansion of protected areas throughout the biome. These strategies are vital for enhancing habitat connectivity and creating corridors that allow species to move between fragmented areas, thereby maintaining biodiversity and the ecosystem services they provide. Such combined efforts will be crucial in sustaining bird populations and their ecological roles in the Chocó region under future climate scenarios.

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

FM: Writing – original draft, Writing – review & editing, Conceptualization, Data curation, Formal analysis, Methodology, Visualization. KK: Writing – original draft, Writing – review & editing, Conceptualization, Visualization. CF-P: Writing – review & editing. ÇŞ: Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2024.1412440/full#supplementary-material

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Changes in breeding activity of Southeast Asian songbirds in response to the severity of the dry season

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Droughts are expected to become more frequent and severe as the climate changes. Tropical songbirds likely reduce reproductive output during extreme droughts such as El Niño events in Southeast Asia as a tradeoff for reducing mortality risks. However, the timing of these rainfall responses and the extent of these reproductive costs are largely unknown in this region. Here we quantified how the amount and frequency of rainfall impacted nest initiation (first egg dates), and how the amount of rainfall may impact the duration of nesting in a given season (last expected fledging date). We tested these hypotheses on seven species of understory passerines in a secondary dry evergreen forest in northeastern Thailand. Using ten years of data (2014–2023) we examined the relationship between rainfall examining both total amounts occurring at key parts of the year (such as just prior to the breeding season) as well the number of "no-rain" days (rainfall gap) on (1) first egg dates and the (2) last expected fledging date of a given season. More severe dry seasons (longer time gaps in rainfall) caused longer delays in the start of egg laying and gap days tended to have a stronger effect than total rainfall. Lower breeding season rainfall resulted in later fledge dates for four species; lower rainfall amounts during the dry season resulted in later fledge dates for three species. There was no relationship between first egg dates and last expected fledging dates for any target species. Overall, it appears that droughts are likely shortening the breeding seasons of many tropical forest birds, but the reproductive costs are still difficult to estimate precisely. Further investigation is also recommended as to how rainfall is affecting nesting success particularly whether greater rainfall is regularly associated with earlier end of season fledging dates.

KEYWORDS

climatic variability, drought, expected fledging dates, first egg dates, long-term study, tropical birds

Introduction

Droughts are expected to become more severe and frequent as the climate changes (Trenberth et al., 2014; Fu, 2015). For many tropical species, variation in precipitation is used to time breeding (Skagen et al., 2018; Hidalgo Aranzamendi et al., 2019; Halali et al., 2021) and overall is a critically important parameter driving natural selection (Siepielski et al., 2017). It is therefore likely that changes in rainfall could have substantial impacts on seasonal fecundity. Although tropical songbirds likely reduce reproduction during extreme droughts (Brawn et al., 2017; Martin and Mouten, 2020), the few long-term studies available suggest that this behavioral flexibility is critical because it allows songbirds to buffer some of the mortality risks associated with breeding during extreme droughts (Martin and Mouten, 2020), such as El Niño events in Southeast Asia. Furthermore, even without El Niño events, Southeast Asian rainfall patterns are normally highly variable (Chang et al., 2005), and especially so in some seasonal evergreen forests of the region (Bunyavejchewin, 1999). In these forests, El Niño events represent one point on a continuum of rainfall, whereby reproductive effort in response to rainfall also likely lies on a continuum (Cruz-McDonnell and Wolf, 2016), suggesting that understanding rainfall effects or thresholds will be important for modeling climate change impacts on tropical forest songbirds of this region. For example, if rainfall fails to reach some minimum volume and/or frequency, this may cause a majority of individuals of some species to forgo breeding in a given season (Martin and Mouten, 2020; Boersma et al., 2022), while for other species individuals may only pause breeding for a few weeks or even a few months (Grant et al., 2000).

Precipitation can serve as a reliable predictive cue of food availability, especially in insectivorous birds (Poulin et al., 1992; McKinnon et al., 2015; Hidalgo Aranzamendi et al., 2019). Thus, the demographic impacts of the timing, frequency and amount of rainfall may be dramatically different depending on the details, such as the microhabitat use of the bird species of interest and the forest type (Martin and Mouten, 2020). This may also imply that bird populations in forests which typically receive less rainfall may have less prey available and be particularly vulnerable if there are long-term reductions in rainfall compared to similar forests that typically receive more rainfall (Poulin et al., 1992). Furthermore, the impacts of El Niño events will also likely vary depending on when a species typically breeds, such that early to middle dry season nesters may face more disruption (have to pause reproduction longer) than those species normally nesting later in the dry season. It is also possible that if rains arrive later, that birds will complete the breeding season later, which may mitigate some of the impacts on seasonal female fecundity. The objective of this paper was to quantify how the amount and frequency of rainfall impacts nest initiation (first egg dates), how much first egg dates are delayed by drought and whether rainfall can predict breeding season end dates.

Here we present a long-term nesting study to examine these questions. Most long-term studies in the tropics do not have detailed data on nest initiation dates and the length of breeding seasons because nest finding is typically labor intensive and involves a steep learning curve (Martin and Mouten, 2020); but here we provide an analysis based on 10 years of nesting data initially used to study nest predation and nest-site selection (e.g., Khamcha et al., 2018; Somsiri et al., 2019; Khamcha and Gale, 2020; Phringphroh et al., 2024). We predicted that decreases in rainfall would be associated with delays in first egg dates at the start of the season and that increases in rainfall during the breeding season would promote more nesting, indicating later expected fledging dates at the end of a given season.

Methods

Study area

The study was conducted in the Sakaerat Environmental Research Station (hereafter, Sakaerat), Nakhon Ratchasima Province, northeastern Thailand (14.4928°N, 101.9150°E). Sakaerat is a 78 km^2 UNESCO biosphere reserve connected to the Phuluang Non-hunting forest reserve of 92 km^2. Sakaerat's elevation ranges from 280 to 762 m above sea level. A five-lane highway (Route 304), rural communities, and agricultural lands surround Sakaerat. Sakaerat has two major forest types: dry evergreen forest and dry dipterocarp forest, plus patches of tree plantations, as well as small patches of grassland and bamboo. The investigation was carried out in secondary (~40 years post logging) dry evergreen forest in a long-term research plot (Figure 1), which was established in 2012 as a 36-ha plot and expanded to 56-ha in 2020. Between 2013 to 2023, the average annual rainfall and temperature were 1,214 mm (range 798–1,530 mm) and 28°C (range 9–40°C), respectively. The rainfall was highly variable, but typically less than half of the amount reported from the previous forest bird long-term study site in the region (Kinabalu Malaysia) (Martin and Mouten, 2020). The dry season in Sakaerat occurs roughly from November to April (Thompson and Landsberg, 1975). The plot has a relatively high density of regenerating woody stems and small trees ~1,064 stems/ha (Somsiri et al., 2019). The research plot was set up using a 50 × 50 m grid marked with ~60 cm tall PVC pipes. We also collected data on the nest predator community in our study area during this time period, which included both arboreal and terrestrial mammals, snakes and birds, the most dominant being northern pig-tailed macaque *Macaca leonina*, accipiters *Accipiter* spp., cat snakes *Boiga* spp. and Blanford's bridle snake *Lycodon* cf. *davisonii* (Khamcha et al., 2018; Somsiri et al., 2019; Khamcha and Gale, 2020; Phringphroh et al., 2024).

Nest finding and monitoring

Nest searching was conducted throughout the breeding seasons (January to August) of 2013 to 2023 on the plot following the methods described in Pierce et al. (2019) and Khamcha and Gale (2020). The dry and rainy seasons overlap with the breeding season of our focal species (the dry season typically runs from November to

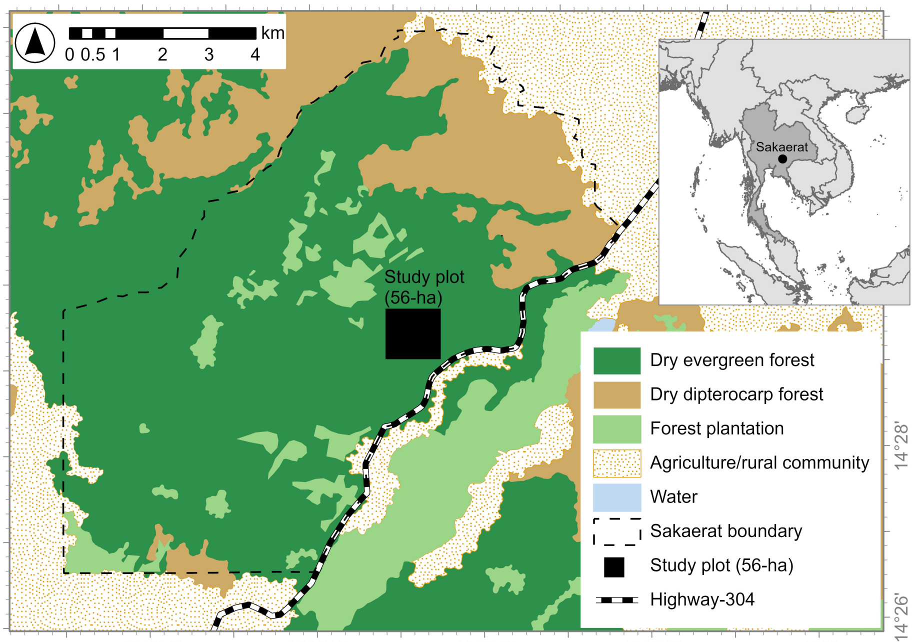

FIGURE 1
Study area map with the location of the 56-ha study plot in the Sakaerat Environmental Research Station, Nakhon Ratchasima Province, northeastern Thailand.

April, and the wet season May to October) (Khamcha et al., 2018). We systematically searched for nests using behavioral cues of adult birds as well as direct visual searches. We prioritized eight relatively common resident species for which larger numbers of nests could be located per season. We focused primarily on eight species of understory-nesting birds, with first egg dates typically ranging from early January to late March, with two species in average rainfall years initiating nesting in January, three species in February, and three species in March (Supplementary Table S1, Supplementary Figure S1). Nests included three types: dome on the ground (Puff-throated Babbler *Pellorneum ruficeps*), open cavity (shallow cavities in rotten stumps or branches in which an incubating or brooding adult bird is at least partly visible) (White-rumped Shama *Copsychus malabaricus*, and Indochinese Blue Flycatcher *Cyornis sumatrensis*), and open cup nests (Black-naped Monarch *Hypothymis azurea*, Stripe-throated Bulbul *Pycnonotus finlaysoni*, Puff-throated Bulbul *Alophoixus pallidus*, Abbott's Babbler *Malacocincla abbotti*, and Scaly-crowned Babbler *Malacopteron cinereum*). Once nests were found, we recorded the species, type of nest, date found, first active date (first laying date), stage of each nest (egg versus nestling), and nest height (measured using measuring tape). We checked all active nests every two to three days until failure or success was determined. Ground nests or low nests (< ~1.5 m) were directly examined, whereas higher nests (>1.5 m height) were checked using a mirror or mobile phone on a pole or observed indirectly through parental activity at the nest (e.g., adults carrying food or nest material). There was very little variation in clutch sizes within a species (Supplementary Table S1). Due to manpower limitations, we had relatively few females of our target species color-marked, although we did have a small number of Puff-throated Babbler, Scaly-crowned Babbler, and White-rumped Shama marked. Thus, we were usually unable to confirm the number of clutches produced by a given female in a given season. We also did not have data on female body condition. We did have access to data from color-marked individuals of Abbott's Babbler, Puff-throated Bulbul, and Black-naped Monarch from a previous study in Khao Yai National Park ~60 km to the southwest of our Sakaerat plot. Khao Yai receives nearly twice as much annual rainfall than Sakaerat. Nevertheless, based on these data from Sakaerat and Khao Yai most of our target species were confirmed to be capable of producing multiple clutches in a given season (Supplementary Table S1). In addition, waterproof infrared surveillance video cameras (placed ≥1.5 m away from nests) were used to keep track of active nests (defined as having at least one egg). Cameras operated continuously, capturing 24-hour video footage. The recordings were used to determine nest fates, adult behavior, and identify potential predators. Cameras remained in place until nest fates (success or failure) were confirmed.

Rainfall data

The rainfall data were obtained from five permanent weather stations located within a 2-km radius of the study plot. Rainfall was measured hourly using research-grade Delta-T Devices WS-GP1 compact weather stations (Delta-T Devices Ltd., Cambridge, UK). The hourly rainfall data from each station were summed to obtain daily totals, which were then averaged across the five stations.

Statistical analysis

We assessed effects of two rainfall parameters as indexes of the severity of the dry season on nest initiation (first egg dates): (a) the early season rainfall (cumulative rainfall from just before the start of the dry season (1 October) up until one week prior to the first egg date of a given species for that year) and (b) the rainfall gap (the largest number of consecutive "no-rain" days from 1 October to 31 March) which typically occurred towards the end of the dry season. For assessing the effects of rainfall on the timing of the end of breeding season (latest fledging date of the season), (c) we used the total amount of rainfall from 1 October up until 31 March to represent overall dry season rainfall, and (d) the total amount of rainfall from October 1 up until 31 July (typically the end of the breeding season for most species) to represent total rainfall during the breeding season (Figure 2). As we never found an active nest prior to December 1st in any of the study years, we labeled day 1 of each season as 1 December for counting egg days (Julian dates). We also tested the potential impact of any delays in first egg days on the end of breeding season using the last expected fledging date of the latest nest found in a given season. Due to limited manpower, we were unable to ring most adult females of the target species, making it difficult to determine clutch order. We were limited to assessing the likely first and last clutches of each species within a given season. Therefore, the first nest found during the season was used as the indicator of the start date for that species for that year and the last predicted fledging date was used to estimate the end of a given season. Although using mean (or median) first egg dates for this analysis would have been more robust, our dataset presented challenges. The extremely high predation rates and rapid renesting rates we observed made it possible for a female to lay an egg, have it depredated, rebuild a nest, and re-lay within a few days (~less than one week). Because most females were not uniquely marked, therefore to ensure that only first nests of a season were included in this assessment, we limited our analysis to the first active nest found in a given season for a given species, although we did check these dates for the presence of outliers.

Prior to running the statistical analysis, we calculated the nesting period of each focal species using data from the nests for which the exact first egg date, and/or hatching and fledging dates are indicated (Supplementary Table S1). The first egg dates for nests without this data were extrapolated from hatching or fledging dates, or, when not possible, by using mid-points of the earliest and latest possible first egg dates, based on average incubation and fledging periods. The last expected fledging dates were also calculated using the same approach.

Following Martin and Mouten, 2020, we removed the data from the year 2013 to account for the learning curve for nest finding. After we removed 2013 all models improved. To assess the influence of rainfall parameters, early season rainfall (cumulative rainfall from 1 October to one week prior to the first egg date), rainfall gap (the largest number of consecutive "no-rain" days from 1 October to 31 March), dry season rainfall (cumulative rainfall from 1 October to 31 March), and breeding season rainfall (cumulative rainfall from 1 October up until 31 July) on nest initiation (first egg date) and last expected fledging date of each focal species, we constructed Generalized Linear Models (GLMs) with appropriate error structures (Poisson/negative binomial) using the package glmmTMB (Brooks et al., 2023). The decision for selecting a given model distribution depended on the assumption of equal mean and variance for the Poisson distribution. If the variance exceeded the mean (indicating overdispersion), the negative binomial distribution was considered more suitable as it accounts for this overdispersion. To assess the overall effects of rainfall parameters on nest initiation and the last expected fledging date for all species combined, we used Generalized Linear Mixed Models (GLMMs), with species assigned as a random effect. To evaluate the influence of rainfall parameters on first egg dates, each set of models for each species included a single-variable model of either rainfall gap or early season rainfall and a constant model. Similarly, to assess the influence of rainfall parameters on last expected fledging date of each focal species, each set of models included a single-variable model of either dry season rainfall or breeding season rainfall and a constant model. We used Akaike's Information Criterion adjusted for small sample size (AICc) for ranking models (Akaike, 1973; Burnham and Anderson, 2004). We considered the strength of evidence for the two rainfall parameters influencing the delays in first egg days and last fledging days using beta coefficients and the 85% confidence intervals following Arnold (2010). We evaluated the data for outliers, overdispersion using the DHARMa package (Hartig, 2022) and all models passed all assumptions. Abbott's Babbler is scarce in the study plot and was the only species that had insufficient data for analysis, probably due to our inability to consistently find nests of this species each year. For each target species in a given season, to assess the correlation between the first egg date of the first nest found and the expected fledging date of the last nest found, we used the Kendall rank

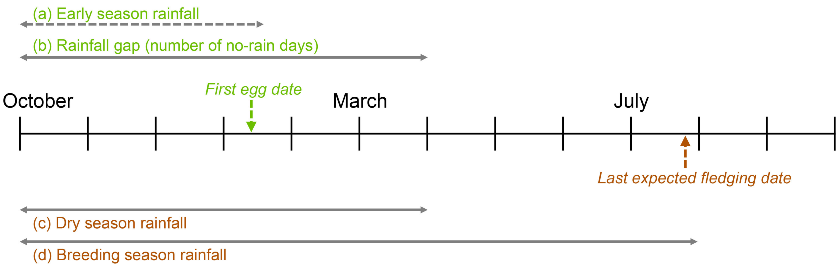

FIGURE 2
A graphical depiction of the variables being assessed on an annual timeline. The dashed line indicates that the data will vary for different species.

correlation coefficient. We tested the relationship between rainfall gap and total dry season rainfall on expected fledging date also using the Kendall rank correlation coefficient. Additionally, we examined the relationship between total dry season rainfall and total number of active nests for each focal species for a given season; however, our results indicated that there was no significant correlation between rainfall and the number of active nests observed per species (P> 0. 07). All statistical analyses were performed in program R version 4.3.1 (R Core Team, 2023).

In this paper, we did not include an analysis of the impact of rainfall on nest success and failure; however, these aspects have been thoroughly addressed in Phringphroh et al. (2024). Following Phringphroh et al. (2024), lower nest success was associated with periods of higher rainfall for Indochinese Blue Flycatcher, Scaly-crowned Babbler, and Puff-throated Babbler. Additionally, Phringphroh et al. (2024) found that increased rainfall correlated with a higher rate of nest predation by the top four nest predators.

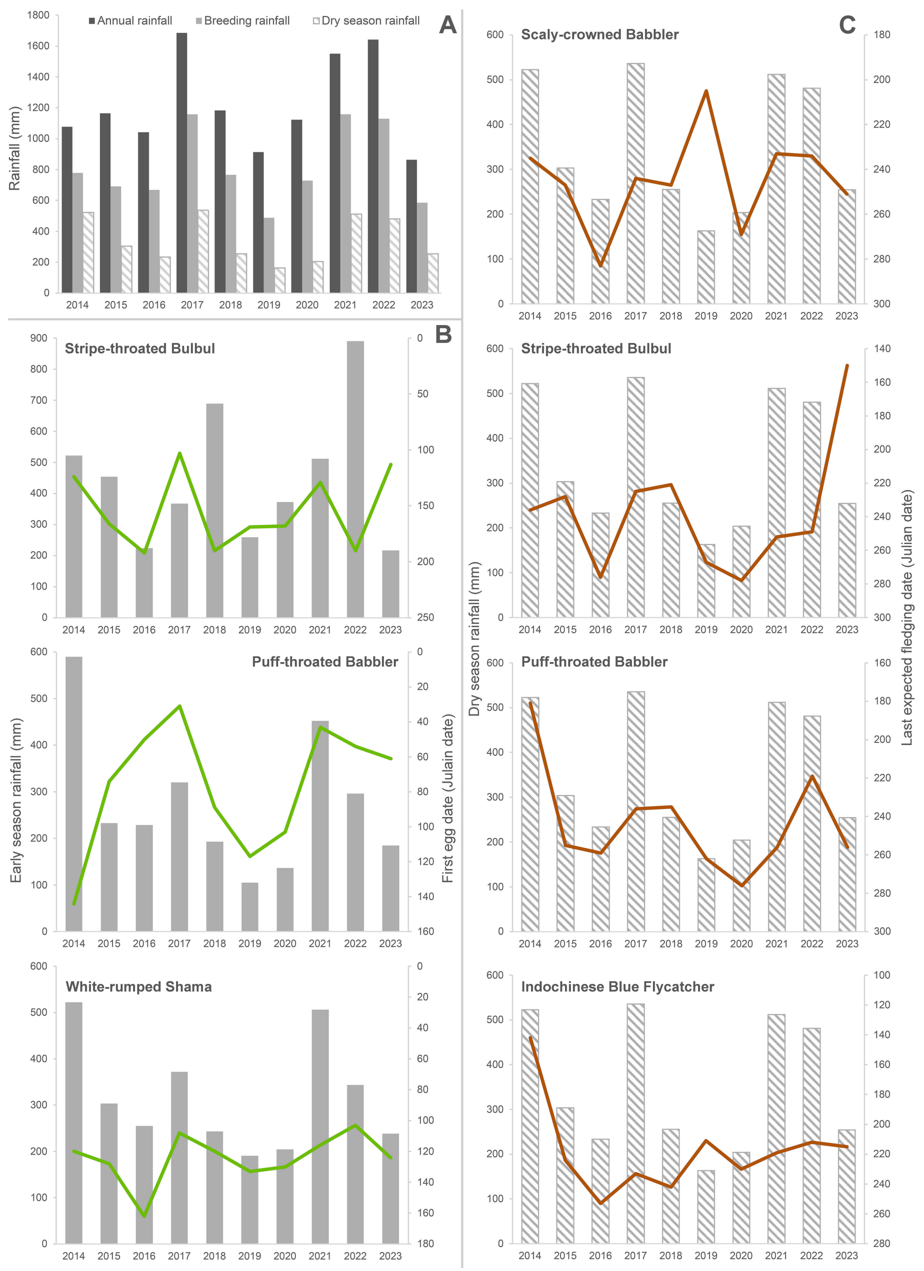

FIGURE 3
(A) Total annual rainfall (1 October–30 September), cumulative dry season rainfall (1 October–31 March), and breeding season rainfall (1 October–31 July) for years 2014–2023 at Sakaerat Environmental Research Station, Nakhon Ratchasima, Thailand. **(B)** Cumulative early season rainfall significantly influenced first egg dates of three species: Stripe-throated Bulbul, Puff-throated Babbler, and White-rumped Shama. **(C)** Cumulative dry season rainfall significantly influenced last expected fledging dates of four species: Scaly-crowned Babbler, Stripe-throated Bulbul, Puff-throated Babbler, and Indochinese Blue Flycatcher. Lines indicate the Julian dates for the first egg dates and the last expected fledging dates for each species for each year.

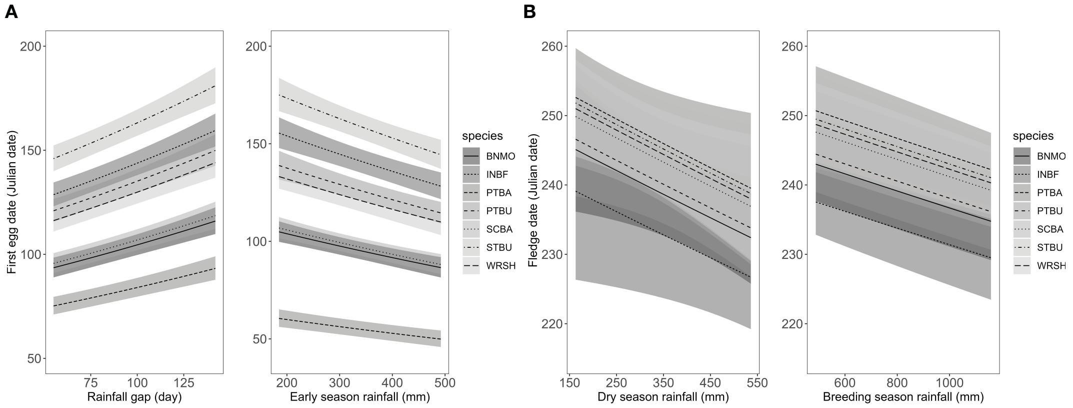

FIGURE 4
(A) Predicted first egg dates for the community of seven focal songbird species (all seven focal species combined) in relation to rainfall gap (the largest number of consecutive "no-rain" days from 1 October to 31 March) and early season rainfall (cumulative rainfall from 1 October until one week before the first egg date). Mean predicted estimates for each species are shown as distinct black lines, with their 85% confidence intervals in gray. **(B)** Predicted last expected fledging dates for the community of seven focal songbird species (all seven focal species combined) in relation to dry season rainfall (cumulative rainfall from 1 October to 31 March) and breeding season rainfall (cumulative rainfall from 1 October to 31 July). Mean predicted estimates for each species are shown as distinct black lines, with their 85% confidence intervals in gray. BNMO, Black-naped Monarch *Hypothymis azurea*, INBF, Indochinese Blue Flycatcher *Cyornis sumatrensis*, PTBA, Puff-throated Babbler *Pellorneum ruficeps*, PTBU, Puff-throated Bulbul *Alophoixus pallidus*, SCBA, Scaly-crowned Babbler *Malacopteron cinereum*, STBU, Stripe-throated Bulbul *Pycnonotus finlaysoni*, WRSH, White-rumped Shama *Copsychus malabaricus*.

TABLE 1 Coefficient estimates of rainfall parameters with standard errors (SE) and 85% lower (85%LCI) and upper (85% UCI) confidence intervals influencing the first egg dates and the last expected fledging dates of focal species during the breeding seasons of 2014–2023 at Sakaerat Environmental Research Station, Nakhon Ratchasima, Thailand.

Parameters	Coefficients (β)	SE	85% LCI	85% UCI
Black-naped Monarch				
First egg date				
Rainfall gap	0.00284	0.00234	-0.00053	0.00621
Early season rainfall	-0.00088	0.00076	-0.00197	0.00020
Last expected fledging date				
Dry season rainfall[a]	-0.00015	0.00014	-0.00035	0.00006
Breeding season rainfall[a]	-0.00004	0.00008	-0.00015	0.00007
Puff-throated Bulbul				
First egg date				
Rainfall gap*	0.00794	0.00196	0.00512	0.01076
Early season rainfall	-0.00009	-0.00134	-0.00202	0.00183
Last expected fledging date				
Dry season rainfall[a]	0.00008	0.00014	-0.00012	0.00028
Breeding season rainfall[a]	0.00007	0.00008	-0.00004	0.00017
Stripe-throated Bulbul				
First egg date				
Rainfall gap*	0.00267	0.00182	0.00005	0.00530
Early season rainfall*	-0.00096	0.00055	-0.00175	-0.00017

(Continued)

TABLE 1 Continued

Parameters	Coefficients (β)	SE	85% LCI	85% UCI
Last expected fledging date				
Dry season rainfall[a]*	-0.00029	0.00014	-0.00049	-0.00008
Breeding season rainfall	-0.00012	0.00011	-0.00029	0.00004
Scaly-crowned Babbler				
First egg date				
Rainfall gap	0.00326	0.00298	-0.00103	0.00754
Early season rainfall	-0.00078	0.00104	-0.00227	0.00071
Last expected fledging date				
Dry season rainfall*	-0.00037	0.00015	-0.00059	-0.00015
Breeding season rainfall[a]*	-0.00018	0.00008	-0.00030	-0.00005
Puff-throated Babbler				
First egg date				
Rainfall gap*	0.00622	0.00409	0.00033	0.01212
Early season rainfall*	-0.00342	0.00077	-0.00453	-0.00232
Last expected fledging date				
Dry season rainfall[a]*	-0.00051	0.00014	-0.00071	-0.00031
Breeding season rainfall[a]*	-0.00016	0.00007	-0.00027	-0.00005
White-rumped Shama				
First egg date				
Rainfall gap[a]*	0.00244	0.00081	0.00128	0.00360
Early season rainfall[a]*	-0.00048	0.00025	-0.00084	-0.00012
Last expected fledging date				
Dry season rainfall[a]	-0.00017	0.00014	-0.00037	0.00003
Breeding season rainfall[a]	-0.00006	0.00007	-0.00017	0.00004
Indochinese Blue Flycatcher				
First egg date				
Rainfall gap	0.00140	0.00134	-0.00052	0.00332
Early season rainfall	-0.00037	0.00044	-0.00099	0.00026
Last expected fledging date				
Dry season rainfall*	-0.00055	0.00032	-0.00101	-0.00009
Breeding season rainfall	-0.00001	0.00024	-0.00035	0.00033

[a] modeled with Poisson, the rest were modeled with negative binomial.

* indicates significant influence on the first egg date or the last expected fledging date.

The rainfall parameters included the largest number of consecutive "no-rain" days (rainfall gap), the cumulative rainfall from 1 October until one week before the first egg date (early season rainfall) of a given target species, the cumulative rainfall in the dry season from 1 October to 31 March (dry season rainfall), and the cumulative rainfall from 1 October to 31 July (breeding season rainfall).

Results

Over the 11 breeding seasons from 2013 to 2023, we used > 10,000 hours for nest searching; we located 1,314 active nests from 32 species including 1,159 nests of our focal species (Supplementary Tables S1, S2). The study period overlapped one "very strong" (2015–16) and one "strong" (2023–24) El Niño event and two "moderate" La Niña events in 2020–21 and 2021–22 as well as weak El Niño and La Niña events in five other years (https://ggweather.com/enso/oni.htm); overall, there was notable variation in annual rainfall in Sakaerat (Figure 3A).

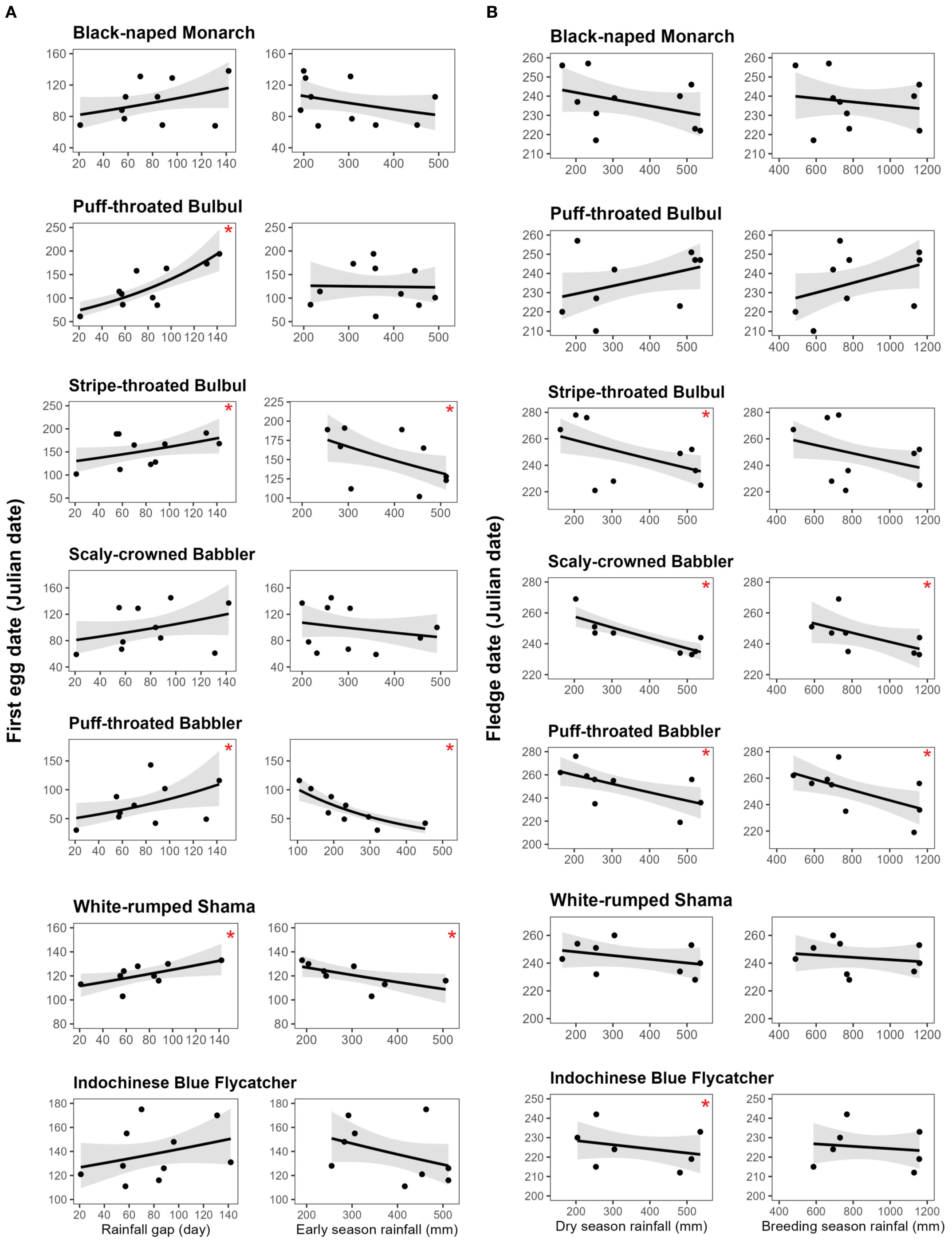

FIGURE 5
(A) Predicted first egg dates of seven focal songbird species relative to rainfall gap (the largest number of consecutive "no-rain" days from 1 October to 31 March) and early season rainfall (cumulative rainfall from 1 October until one week before the first egg date). Mean predicted estimates are shown as black lines, with their 85% confidence intervals in light gray. * indicates significant influence on the first egg date. **(B)** Predicted last expected fledging dates of seven focal songbird species relative to dry season rainfall (cumulative rainfall from 1 October to 31 March) and breeding season rainfall (cumulative rainfall from 1 October to 31 July). Mean predicted estimates are shown as black lines with their 85% confidence intervals in light gray. * indicates significant influence on the last expected fledging date. .

First egg date

Overall, we found significant effects of rainfall gap (β = 0.00247, SE = 0.00037, 85% CIs = 0.00193 – 0.00301) and early season rainfall (β = -0.00062, SE = 0.00013, 85% CIs = -0.00082 – -0.00043) on the timing of nest initiation across all species combined (Figure 4A). All seven focal species (excluding Abbott's Babbler) had the same trends in which lower early season rainfall was associated with delays in first egg dates (Table 1). Likewise, longer gaps in dry season rainfall were associated with increases (delays) in

TABLE 2 The correlation between first egg dates and the last expected fledging dates of the latest nests found in a given season for 10 breeding seasons from 2014–2023 at Sakaerat Environmental Research Station, Nakhon Ratchasima, Thailand.

	Correlation coefficients (tau)	p-value
Black-naped Monarch		
First egg date x Last expected fledging date	-0.06820	0.78680
Puff-throated Bulbul		
First egg date x Last expected fledging date	0.08989	0.71940
Stripe-throated Bulbul		
First egg date x Last expected fledging date	0.04495	0.85750
Scaly-crowned Babbler		
First egg date x Last expected fledging date	-0.04495	0.85756
Puff-throated Babbler		
First egg date x Last expected fledging date	0.25355	0.34540
White-rumped Shama		
First egg date x Last expected fledging date	0.44947	0.07249
Indochinese Blue Flycatcher		
First egg date x Last expected fledging date	0.28889	0.29120

first egg dates (Table 1; Figure 5A). Rainfall gap reached statistical significance for four species (Puff-throated Babbler, Puff-throated Bulbul, Stripe-throated Bulbul, and White-rumped Shama), whereas only three of these species (Puff-throated Bulbul was the exception) showed significant trends with early season rainfall (Figures 3B, 5A). Altogether, rainfall gap was a consistently better predictor of first egg date than early season rainfall.

Last expected fledging date

Rainfall during the dry and breeding seasons appeared to have significant, yet moderate, effects on the last expected fledging dates for all species combined (β = -0.00017, SE = 0.00001, 85% CIs = -0.00026 – -0.00001 for dry season rainfall and β = -0.00001, SE = 0.00037, 85% CIs = -0.00001 – -0.000003 for breeding season rainfall; Figure 4B). For six of our seven focal species with sufficient data, dry season and breeding season rainfall were negatively associated with last expected fledging date (more rainfall was associated with earlier expected end of season fledging dates), with four species showing significant trends for dry season rainfall (Figure 3C) and two of the same four showing significant trends for breeding season rainfall (Table 1; Figure 5B).

First egg date vs. last expected fledging date

For all seven focal species there was no correlation between first egg date and last expected fledging date (Table 2) indicating that the relative timing of the end of the season typically could not be predicted from the date the nesting season started.

Discussion

Our ten years of data suggest longer gaps in rainfall led to longer delays in nest initiation dates for our community of seven species overall. The same pattern was observed at the individual species level for at least four of the target species. Lower dry season rainfall and breeding season rainfall were both correlated with last expected fledging dates for the community overall. Individually, lower dry season rainfall affected four species and lower breeding season rainfall affected three species in predicting later last expected fledging dates. There was no relationship between first egg dates and last expected fledging dates for any of the seven target species. Interestingly, for predicting first egg dates, rainfall gap performed slightly better than total rainfall as a predictor for the community as well as for individual species, suggesting that the duration and likely the timing of rainfall is at least as important or likely more important than the overall amount of rainfall. There were no clear patterns as to which of the seven focal species showed statistically significant effects from rainfall in the timing of first egg dates. However, the coefficient for the effect of rainfall gap was positive in all seven focal species and likewise the total rainfall coefficient was negative for all species, this suggested that all of our target species were likely affected similarly but that a combination of issues related to uncertainties in estimating first egg dates and small sample sizes of both nests and years limited the statistical power of our tests for some species. Interestingly, the trends were likewise consistent but in the opposite direction for the last fledging dates, whereby more rainfall during the dry season (including months prior to normal breeding) or more rainfall later in the breeding season was associated with negative coefficients (earlier last fledging dates for six of our seven species). Dry season rainfall was an overall somewhat better predictor of last fledging date compared to breeding season rainfall.

Currently we do not have arthropod or fruit availability data to assess quantitatively and in detail how rainfall is impacting the likely food resources of our target species, but numerous studies have documented that rainfall and length of dry periods have a large effect on local arthropod (e.g., Newell et al., 2023) and fruit abundance (e.g., Wright et al., 1999). Nevertheless, four of our seven species with sufficient data did show significant associations with rainfall, although there was no clear pattern as to why these four showed significant effects and the other three did not, but as we noted above, our samples were limited by a number of factors. One of the main uncertainties was related to our limited ability to reliably find the first nests of the season of a given species; i.e., there was some possibility that first egg dates may have been influenced by the nest-finding experience of the field crew of the particular year. Nest finding, and especially in tropical forests, has a steep learning curve (Martin and Mouton, 2020) and a few species (e.g., Indochinese Blue Flycatcher) were particularly challenging to find. Anecdotally, we noted clear differences in nest-finding abilities among observers and that some observers were uniquely adept at finding a small subset (two to three) of the focal species, but typically found few of the other species in a given season.

We detected a negative relationship between rainfall and the last expected fledging date, with higher rainfall in the dry season (and to some extent breeding season rainfall) correlated with an earlier expected fledging date. One hypothesis is that higher rainfall years may be associated with higher reproductive success across a season, which in turn may allow for adults to finish the season earlier (i.e., rainfall may reduce the number of nesting attempts required to fledge young). In contrast, it is also possible that increased rainfall may actually be having the opposite effect in which recently published work from our plot suggests that increased rainfall was associated with increased activity of the top four predators in the study area (Phringphroh et al., 2024) and that perhaps adults may quit re-nesting after several failed re-nesting attempts. However, our data from nearly the exact same set of species from a nearby study site (Khao Yai) suggests that individual females of at least one of our target species (Puff-throated Bulbul) can attempt up to seven clutches in a single season (Pierce et al., 2019) also suggesting that many individuals may persist with nesting regardless of the predation pressure. Nevertheless, this nearby site was notably wetter than Sakaerat, so it is possible that fecundity rates are lower at Sakaerat compared to Khao Yai.

We found a complex relationship between rainfall and nest productivity that will require further study to untangle. In general, rainfall quantity and timing affected the fecundity of our focal species. Overall, decreased rainfall appears to be reducing the length of breeding seasons in particularly dry years, but that during wetter years breeding also seems to finish earlier. To quantify the demographic effects we will need to accurately measure individual female fecundity. Furthermore, rainfall undoubtedly is having similar effects elsewhere in the tropics, particularly in drier forests such as Sakaerat. We also suspect that forests (such as Khao Yai) with a similar community of birds but which receive significantly more rainfall may be more "buffered" from ENSO events for example (Poulin et al., 1992) and would therefore also be useful for additional comparative studies.

Data availability statement

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

Ethics statement

The animal study was approved by King Mongkut's University of Technology Thonburi Institutional Animal Care and Use Committee and the Department of National Park, Wildlife and Plant Conservation, Thailand. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

GG: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing. RA: Data curation, Investigation, Methodology, Resources, Validation, Visualization, Writing – review & editing. DK: Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Validation, Visualization, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2024.1457478/full#supplementary-material

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Ecological consequences of urbanization in Afrotropical bird communities: present and future prospects

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Introduction: Urbanization, characterized by the rapid expansion of human settlements and development, greatly impacts biodiversity, especially where developments and human settlements are not guided by proper environmental consideration.

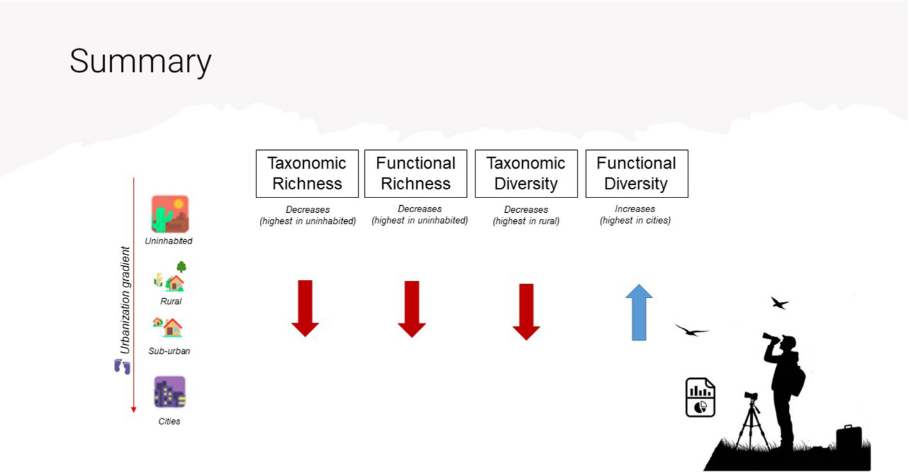
Methods: We used data collected through citizen science projects under the African Bird Atlas Project, based on standardized protocols to gather bird occurrence data. Species' ecological traits, related to foraging behavior, habitat speciality, and body mass, were analyzed to assess functional richness and functional diversity (FD) represented by Rao's quadratic entropy. Geospatial data, including the Global Human Settlement Layer and Human Modification Index (HMI), along with the probability of urban expansion up to 2030, were integrated to examine the impact of urbanization using Bayesian models.

Results: Our findings reveal a marked decline in taxonomic richness, diversity, and functional richness associated with increasing urbanization and human modification, with a similar pattern observed along the gradient from mostly uninhabited areas to cities. However, FD increased with urbanization from uninhabited areas to cities. The relationship between FD and HMI was nonlinear, showing an initial negative trend that became positive as HMI increased. This suggests a transition in bird communities, where generalist species thrive in urban environments, potentially replacing specialized species and leading to functional redundancy.

Discussion: Despite the complex relationships observed, urbanization has a predominantly negative impact on the richness and diversity of Afrotropical bird communities. The decline in avian diversity and functional richness has important implications for ecosystem functions and services, crucial for biodiversity and human well-being. Our research provides valuable insights into the ecological impacts of urban expansion and emphasizes the importance of preserving natural habitats amidst growing urban landscapes.

KEYWORDS

Afrotropical bird communities, citizen science, conservation strategies, functional diversity, urbanization



GRAPHICAL ABSTRACT

Summary of taxonomic and functional richness and diversity trends along the urbanization gradient. Taxonomic Richness, Functional Richness, and Taxonomic Diversity decrease with increasing urbanization, as indicated by the downward red arrows (highest in uninhabited and rural areas). Functional Diversity, as measured by Rao's Quadratic Entropy, increases in more urbanized environments, as shown by the upward blue arrow (highest in cities).

Introduction

Urbanization, characterized by the rapid expansion of human settlements and infrastructure, has become a global phenomenon, transforming natural environments with significant implications for biodiversity (Grimm et al., 2008; Mckinney, 2008). By 2010, over 50% of the world's population resided in urban areas, and projections indicate that by 2050, this figure will rise to 70% (UN, 2012). For Africa, the projected tripling of urban land cover by 2030, is particularly concerning as it will lead to substantial habitat loss across the continent (Seto et al., 2012). This ongoing urban development will result in increased predator presence (Baker et al., 2008; Fischer et al., 2012), elevated noise levels (Proppe et al., 2013), and forest fragmentation (Zipperer et al., 2012), with substantial influence on community composition (Marzluff, 2001), and ecosystem functioning (e.g. Blair, 1996; Ferenc et al., 2014; Lim and Sodhi, 2004; Marzluff, 2001; Pautasso et al., 2011).

The composition of bird communities in urban areas is a function of species tolerance and adaptive capacity. Species sensitive to habitat disturbances are classified as "urban avoiders" (McKinney, 2002) or "urban-sensitive" (Garden et al., 2007), while those thriving in urban environments are called "urban exploiters" (McKinney, 2002) or "synanthropes" (Marzluff et al., 2001; Cresswell et al., 2020). Both categories are impacted differently by urbanization (DeGraaf and Wentworth, 1986; Isaksson, 2018), with specialized species (because of their life-history and ecological traits) being impacted the most (Evans et al., 2011; Sol et al., 2014). The negative effects of urbanization on bird communities have been extensively documented globally and in Africa (see Chamberlain et al., 2017; Oliviera et al., 2017; Ibáñez-Álamo et al., 2017; Lee et al., 2021; Sol et al., 2020). Considering the growing human population and the subsequent increased urbanization globally (United Nations Department of Economic and Social Affairs, 2019), understanding species' responses to anthropogenic pressures are paramount for guiding conservation measures (Newbold et al., 2018).

Because birds are well known, and are good indicators of environmental health (Fraixedas et al., 2020), they are invaluable when studying the impacts of urbanization on habitat structure and composition (Chace and Walsh, 2006; MacGregor-Fors et al., 2009; Reis et al., 2012; Bregman et al., 2014; Marzluff, 2016). Numerous studies have documented varying trends in how urbanization affects bird abundance and diversity (Palacio et al., 2018; Carvajal-Castro et al., 2019; Korányi et al., 2021). While some studies report minimal influence of urbanization on bird diversity (Korányi et al., 2021), others link increased urbanization to reduced diversity (Sol et al., 2017, 2020). Conversely, a few studies report increased bird diversity with rising urbanization (Batáry et al., 2018; Filloy et al., 2019). Beyond bird abundance and diversity, it is essential to consider birds for the ecological roles they play in seed dispersal, pollination, pest control, nutrient cycling, and scavenging (Lundberg and Moberg, 2003; Pigot et al., 2016; Şekercioğlu et al., 2016; Sekercioglu, 2006). These roles not only sustain ecosystems but also ensure human wellbeing (Cardinale et al., 2012); for example, loss of scavengers, has been shown to lead to an increase in diseases (García-Jiménez et al., 2021, 2022).

The functional traits that support bird's roles in environments have been extensively documented in recent studies (Pigot et al., 2020; Tobias and Pigot, 2019), allowing for detailed characterization of bird communities with unmatched precision. To better understand impacts of urbanization on vital ecosystem functions and services (Sol et al., 2020), an effective method is to examine functional diversity. Functional diversity encompasses the identity, variety, and relative abundance of phenotypic traits in organisms that affect key ecosystem processes (Díaz et al., 2007; Petchey and Gaston, 2006; Tilman, 2001). Studies are particularly needed in the tropical regions including Africa, where rapid population growth has led to accelerated urbanization (Seto et al., 2011, 2012). However, only a few studies have investigated how urbanization affects bird ecological roles in Africa (Chamberlain et al., 2017; Lee et al., 2021; Njoroge et al., 2014; van Rensburg et al., 2009; Awoyemi et al., 2024). Awoyemi et al. (2024) examined the impact of urbanization on biodiversity metrics within cities in a single country, utilizing a paired sampling approach to compare urban and non-urban areas. To gain a more detailed insights, future studies could explore the effects of urbanization on bird community and ecosystem functions across a finer urbanization gradient and at a broader scale.

Here, we investigate the impacts of urbanization and human modification on taxonomic and functional metrics both in Nigeria and Kenya. Nigeria and Kenya average population densities are estimated at 226 humans/km^2 and 97 humans/km^2, respectively (United Nations, 2019). Both countries fall within the Afrotropical region with rich but declining biodiversity (Cazzolla Gatti et al., 2015). Nigeria is situated on the East Atlantic Flyway, while Kenya sits on the East Asia-East Africa Flyway, making both countries crucial for the conservation of migratory birds. Yet, the impact of urbanization on biodiversity in these landscapes is relatively understudied (Ibáñez-Álamo et al., 2017; Magle et al., 2012), mainly due to limited local capacity and funds (Awoyemi and Ibáñez-Álamo, 2023).

Building on Oliviera et al. (2017), Newbold et al. (2015), and Sol et al. (2017), we compare bird diversity across four levels of urbanization (settlement types): cities, suburban areas (moderately urbanized environments), dispersed rural areas (slightly human-modified), and mostly uninhabited areas (MUAs) in Kenya and Nigeria. We hypothesize that urbanization negatively impacts taxonomic and functional richness and diversity of African bird communities. Specifically, as urbanization intensifies, we expect to observe a decline in both the number of species (taxonomic richness) and the unique ecological function of the species (functional richness). Additionally, we anticipate that urban expansion will reduce the overall diversity of bird communities, leading to more homogenized assemblages with fewer distinct species and functional roles. We also anticipate that uninhabited and rural areas will have higher taxonomic and functional richness and diversity than suburban areas and cities, reflecting the negative impact of urbanization on bird communities.

Materials and methods

Data collection and study extent

We used data collected through the African Bird Atlas Project (ABAP), specifically originating from the country-level citizen science projects: the Nigerian Bird Atlas Project (hereafter, NiBAP) established in 2015, and the Kenya Bird Map (hereafter, KBM) founded in 2013. NiBAP and KBM rely on citizens to collect and submit bird data through data collection cards, each representing a full observation record for a specific time and location (pentad), also known as checklists. These projects adhere to protocols established by the Southern African Bird Atlas Project (hereafter, SABAP; Underhill, 2016), ensuring standardized data collection and reporting procedures. Citizens participating in these projects survey and record birds within a 5-minute x 5-minute grid (approximately 9 km x 9 km square) referred to as a pentad. Survey lists of birds are reported as either full protocol cards or *ad hoc* cards. Full protocol cards are records from a minimum of two hours of focused survey over a maximum five days within each pentad, covering different vegetation types. Where citizen scientist spends less than 2 hours including reports of incidental bird observation, those submission are considered *ad hoc* cards (Tende et al., 2024). Both full protocol and *ad hoc* cards are essential for reporting species distribution, and provide presence data on species in a pentad (Figure 1).

Full protocol card submission allows for calculation of species reporting rate as an index of abundance. The index tell how frequently a species is recorded in all full protocol cards submitted within a pentad, and ranges from 0 (never recorded) to 1 (recorded in all full protocol cards) (see Lee et al., 2017, 2021; Figure 1).

Data pre-processing and cleaning

We extracted raw bird distribution records from NiBAP (932 species in 228,019 records) and KBM (1373 species in 266,708 records). To ensure data integrity, we used only vetted species lists available at Birdmap Africa - Nigeria and Birdmap Africa - Kenya, filtering the records to include only species present in these lists. After cleaning the data, we retained 914 unique species with 227,420 records for Nigeria and 1,069 species with 265,276 records for

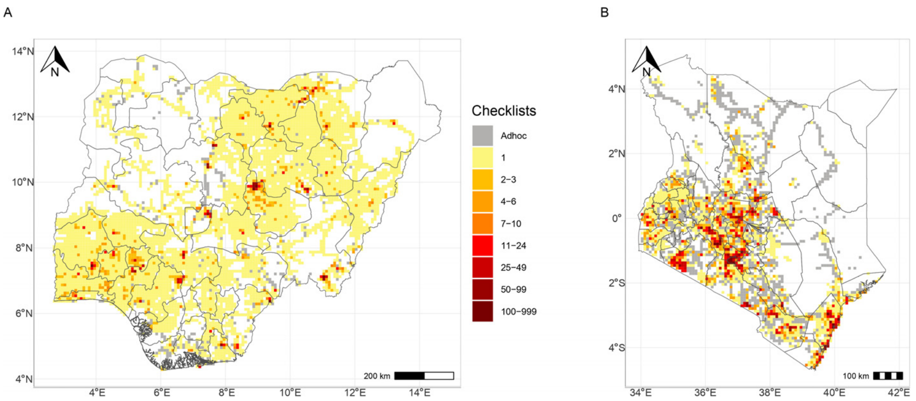


FIGURE 1
Coverage maps of Nigeria **(A)** and Kenya **(B)**, indicating the number of checklists submitted with Group 4+ checklists used for this analysis, shown in darker shades.

Kenya. We also filtered coverage grids in both countries to include only those pentads where at least four full protocol cards had been submitted over the years across the study period, following the methodology of previous studies (Lee et al., 2017). This step ensured that we focused on reliable data subsets. Finally, we integrated the functional traits dataset (see Supplementary Table S1) with the reporting rates dataset to enrich the ecological context.

Analysis of functional guilds

To describe the functional traits of our bird species, we compiled published data describing the foraging behavior, habitat specialization and masses for all the bird species. Each species was categorized based on 13 functional traits primarily related to diet, body mass, and habitat specialization (Appendix I). Dietary classifications followed the framework provided in (Child et al., 2009), which associates dietary categories with ecological roles. We did this because the functional role of a species in an ecosystem may be more directly inferred by how the species uses resources (Petchey and Gaston, 2006; Oliviera et al., 2017). For instance, scavengers contribute to carcass and waste disposal and help in disease control, while carnivores help manage rodent populations. Species that primarily rely on fruits (frugivores) aid in seed dispersal, whereas insectivores (insect eating birds) help control invertebrates (Whelan et al., 2015; Chan et al., 2016; Lee et al., 2021). Additional categories include piscivores, ecological engineers (such as woodpeckers and barbets), habitat specialists (including biome-restricted species and primary forest specialists), and species foraging in aquatic environments. Each classification was binary and non-exclusive, allowing species to belong to multiple dietary classes, particularly omnivores. A comprehensive list of species and their assigned functional traits is available in the Supplementary Data Sheet S1. The mass values were primarily sourced from “The Handbook of the Birds of the World”. We supplemented any missing mass data by referencing online resources such as the Global Biodiversity Information Facility (GBIF-www.gbif.org) or national museum ringing records. Functional richness is vital because it is a measure of the functional traits present in a community, thus presenting only presence/absence of species functional traits. However, previous studies have revealed abundance-based metrics to be more influential on ecosystem functions (Petchey and Gaston, 2006; Newbold et al., 2012). Rao’s quadratic entropy presents a perfect opportunity to bridge this bias. It accounts for species richness, while also capturing trait identity, abundance and variety (Ricotta et al., 2016).

Geospatial data acquisition

We extracted the Global Human Settlement Layer (GHSL (Melchiorri, 2022), available for download from the Copernicus Emergency Management Service (https://human-settlement.emergency.copernicus.eu/download.php?ds=smod). This dataset identifies settlement typologies using two-digit codes: City (30), Dense Town (23), Semi-Dense Town (22), Suburban (21), Village (13), Dispersed Rural (12), Mostly Uninhabited Area (11), and Water Grid (10). These typologies are represented at a 1 km resolution.

To determine the dominant settlement type within each pentad (9 km x 9 km, encompassing 81 GHSL cells), we used the ‘geobgu::raster_extract’ function in R. By applying the base R modal function, we identified the most prevalent settlement type, resulting in five classes: City, Suburban, Dispersed Rural Area, and Mostly Uninhabited Area. Additionally, we obtained the Global Human Modification of Terrestrial Systems dataset, referred to as the Human Modification Index (HMI), from the Socioeconomic Data and Applications Center (SEDAC). This dataset quantifies human impact on terrestrial lands through 13 stressors, with values ranging from 0 (minimal impact) to 1 (intense modification) (Kennedy et al., 2019, 2020).

We also obtained a dataset offering a 2.5 arc-minute resolution probability of urban expansion from the year 2000 to 2030. This dataset utilizes a Monte Carlo model to forecast the likelihood of urbanization for non-urban grid cells by 2030, providing valuable insights into global urban land cover changes. Unlike the categorical GHSL layer, the HMI and urbanization layers provide numerical values, enabling a fine-scale gradient analysis. We resampled/upscaled these layers to a 5-minute × 5-minute resolution (approximately one-twelfth degree) to maintain spatial congruity with our avian data and ensure consistent analysis across all datasets.

Conceptual framework: directed acyclic graph

The Directed Acyclic Graph (DAG) (Figure 2) illustrates the intricate causal relationships between human modification, human settlement, urban expansion, and their effects on avian taxonomic and functional diversity. The bidirectional connections indicate that urbanization and settlement patterns mutually influence each other. Additionally, the probability of urban expansion (P(Urban Expansion)) reflects the likelihood of further encroachment driven by existing modifications and settlements, which may adversely affect bird taxonomic and functional richness due to habitat fragmentation and resource reduction. Overall, this DAG underscores the feedback loops between human activities and ecological outcomes.

Data analysis

All our analyses were conducted using R version 4.2.3 (R Core Team, 2023). We calculated standard measures of functional diversity, including functional richness (FRic) and Rao's Q, using the 'fundiversity' package (Grenié and Gruson, 2023). Reporting rate in pentads was used as a proxy for abundance measures (Underhill, 2016). Functional diversity, represented by Rao's Q, describes the variability in ecological functions across species within a community, while functional richness (FRic) reflects the range of ecological traits, unweighted by abundance (see Table 1 for further metrics definitions). Additionally, we calculated taxonomic richness as the count of distinct species in each pentad and used the Shannon-Weiner diversity index to measure taxonomic diversity, utilizing the 'vegan' package (Oksanen et al., 2018). For each metric of taxonomic and functional richness and diversity, we employed Bayesian hierarchical (mixed) models fitted in STAN (Carpenter et al., 2017) using the 'brms' package (Bürkner, 2021) to compare across settlement types. These models included random effects at the pentad level to account for spatial variability. The 'modelr' and 'tidybayes' packages were used to create a grid of predictor values, add posterior predictive draws, and compute and visualize contrasts between settlement levels using 'ggplot2'. We then conducted pairwise contrast analyses of the predicted posterior distributions across the settlement types (City, Semi-Urban, Rural Area, and Uninhabited Area). We further investigated the relationship between each metric of taxonomic and functional richness and diversity and human modification of the environment, as well as the potential impact of urban expansion on avian communities. The sampling process involved four chains with 2000 iterations each, with the first 1000 iterations used for warm-up. Convergence and model fit were assessed through posterior predictive checks, effective sample size, and Rhat values close to 1.

Results

A total of 914 species across 89 bird families were recorded in Nigeria, while 1069 species across 94 families were recorded in Kenya. In both countries, the majority of species (>90%) are classified as Least Concern, with 27 Threatened species recorded in Nigeria (3 Critically Endangered, 11 Endangered, and 13 Vulnerable) and 44 in Kenya (5 Critically Endangered, 20 Endangered, and 19 Vulnerable) according to the IUCN Red List (BirdLife International, 2024). Kenya supports 225 habitat specialists, compared to 179 in Nigeria. Additionally, both countries host urban-adaptive species, with 40 in Nigeria and 50 in Kenya. A detailed list of species is provided in Supplementary Data Sheet S2.

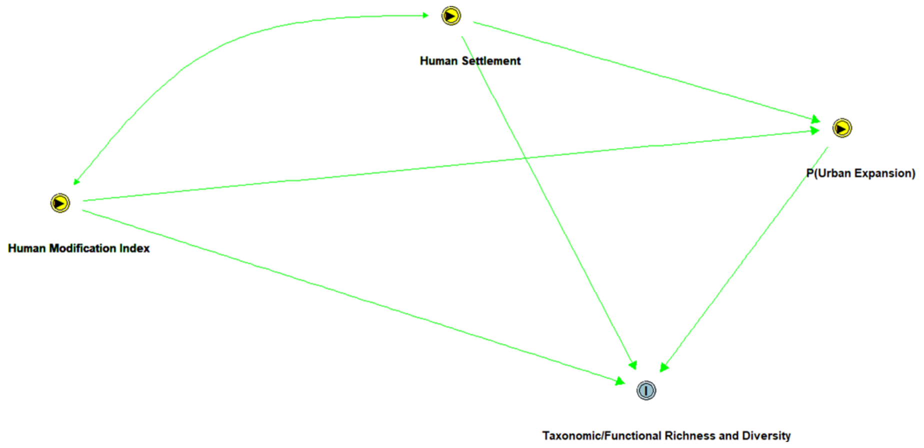


FIGURE 2
Directed Acyclic Graph (DAG) illustrating the interplay of human modification, settlements, and probability of urban expansion on taxonomic/functional richness and diversity.

TABLE 1 Taxonomic and functional richness and diversity metrics and their definitions.

Metric	Mathematical Definition	Explanation	Function Used	Source
Species Richness (SR) or Taxonomic Richness	SR = Number of unique species (S)	The total number of distinct species observed in a community.	dplyr:: n_distinct()	R Core Team (2023)
Functional Richness (FRic)	The volume occupied by species in trait space, calculated by constructing a convex hull around the trait values of all species within a community.	Represents the range of functional traits in a community. Higher FRic implies greater trait diversity.	fundiversity::fd_fric()	Villéger et al. (2008)
Taxonomic Diversity or Shannon Index	$H' = -\sum_{i=1}^{s} p_i ln(p_i)$	Measures species diversity, accounting for both richness and evenness, where p_i is the proportion of individuals of species i; higher values indicate greater diversity.	vegan:: diversity()	Shannon and Weaver (1949)
Functional Diversity (Rao's Quadratic Entropy, RaoQ)	$FD = \sum_{i=1}^{s}\sum_{j=1}^{s} d_{ij} p_i p_j$	Measures functional diversity as the abundance-weighted sum of pairwise trait distances d_{ij}between species. In this formula, p_i and p_j represent the relative abundances of species i and j in a community. Rao's Q captures how diverse is the community considering both traits and species relative abundance, with greater values indicating higher diversity.	fundiversity:: fd_raoq()	Rao (1982)

Effects of urbanization levels (settlement types)

Taxonomic richness (Figure 3A) and functional richness (Figure 3B) decreased across the gradient from rural to suburban to city areas, indicating fewer species and traits in more urbanized environments. However, taxonomic diversity (Figure 3C) was highest in rural areas, followed by suburban, uninhabited, and city areas. Conversely, functional diversity (Figure 3D) was highest in city areas and lowest in uninhabited areas, with intermediate functional diversity values in rural and suburban areas.

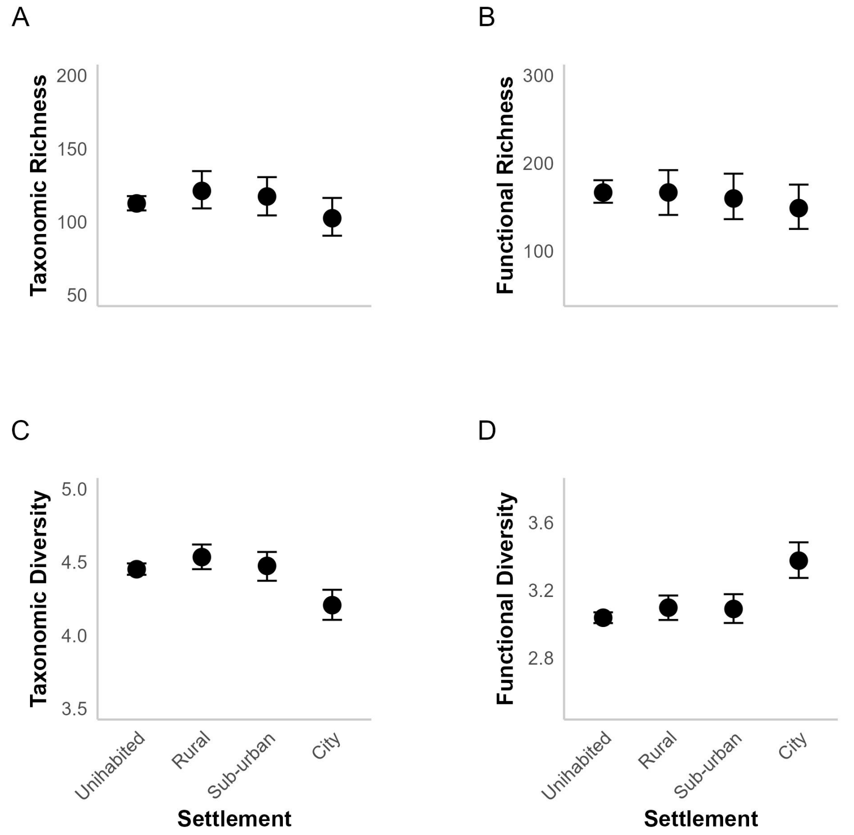


FIGURE 3
Conditional effects plot of the differences in taxonomic richness **(A)**, functional richness **(B)**, taxonomic diversity **(C)**, and functional diversity **(D)** across different levels of urbanization. Each plot shows the 95% credible intervals for the respective metric.

Our analysis revealed strong evidence that taxonomic richness decreased with increasing urbanization such that rural areas had higher taxonomic richness (i.e., a greater variety of species) than cities (median difference ± SD: Rural – City: 14.885 ± 15.520 [95% CI: -2.493, 57.996]; Posterior Probability (PP) = 0.951, Evidence Ratio (ER01) = 19.202, Table 2A). Additionally, both suburban areas and uninhabited areas had higher richness than cities (Suburban – City: 13.659 ± 14.702 [95% CI: -4.347, 53.868]; PP = 0.926, ER01 = 12.605, and Uninhabited – City: 9.233 ± 10.593 [95% CI: -4.262, 37.579], PP = 0.910, ER01 = 10.173, respectively, Table 2A). However, we did not find substantial differences between Suburban – Rural, Uninhabited – Rural, and Uninhabited – Suburban contrasts (Table 2A), as their

TABLE 2 Results of contrast analyses on taxonomic and functional richness and diversity between different settlements, including the median, standard deviation (SD), and 95% credible intervals (CI) of contrasts from posterior estimates.

A. Taxonomic Richness

Contrast	Median	SD	95% CI	PP	ER01	ER10	
Rural - City	14.885	15.520	[-2.493, 57.996]	0.951	19.202	0.052	**
Sub-urban - City	13.659	14.702	[-4.347, 53.868]	0.926	12.605	0.079	*
Sub-urban - Rural	-1.429	12.076	[-27.587, 22.583]	0.435	0.770	1.299	
Unihabited - City	9.233	10.593	[-4.262, 37.579]	0.910	10.173	0.098	*
Unihabited - Rural	-5.564	9.446	[-30.397, 7.903]	0.191	0.236	4.236	
Unihabited - Sub-urban	-4.012	9.688	[-28.946, 10.731]	0.274	0.376	2.656	

B. Functional Richness

Contrast	Median	SD	95% CI	PP	ER01	ER10	
Rural – City	10.704	31.502	[-28.052, 102.481]	0.753	3.049	0.328	
Sub-urban – City	13.717	35.808	[-27.542, 122.161]	0.800	4.000	0.250	
Sub-urban – Rural	2.756	28.194	[-49.083, 70.430]	0.585	1.410	0.709	
Unihabited – City	17.819	31.512	[-7.582, 118.312]	0.924	12.158	0.082	*
Unihabited – Rural	6.752	23.053	[-29.706, 68.699]	0.728	2.670	0.375	
Unihabited - Sub-urban	4.379	24.584	[-45.008, 62.039]	0.626	1.674	0.597	

C. Taxonomic Diversity

Contrast	Median	SD	95% CI	PP	ER01	ER10	
Rural – City	0.325	0.066	[0.198, 0.459]	1.000	Inf	0.000	**
Sub-urban – City	0.269	0.068	[0.132, 0.397]	1.000	Inf	0.000	**
Sub-urban – Rural	-0.058	0.062	[-0.181, 0.068]	0.170	0.205	4.882	
Unihabited – City	0.245	0.052	[0.140, 0.345]	1.000	Inf	0.000	**
Unihabited – Rural	-0.083	0.047	[-0.174, 0.010]	0.038	0.040	24.974	
Unihabited - Sub-urban	-0.025	0.049	[-0.122, 0.072]	0.302	0.432	2.317	

D. Functional Diversity

Contrast	Median	SD	95% CI	PP	ER01	ER10	
Rural – City	**-0.277**	**0.067**	**[-0.417, -0.147]**	**0.000**	**0.000**	**Inf**	
Sub-urban – City	**-0.282**	**0.067**	**[-0.421, -0.156]**	**0.000**	**0.000**	**Inf**	
Sub-urban – Rural	-0.005	0.058	[-0.124, 0.107]	0.464	0.864	1.157	
Unihabited – City	**-0.337**	**0.055**	**[-0.448, -0.233]**	**0.000**	**0.000**	**Inf**	
Unihabited – Rural	-0.059	0.048	[-0.166, 0.031]	0.094	0.104	9.638	
Unihabited - Sub-urban	-0.055	0.046	[-0.141, 0.036]	0.122	0.139	7.197	

Posterior probability (PP) and evidence ratio (ER) are shown: ER01 supports the directional hypothesis (PP > 0) and ER10 supports the alternative hypothesis (PP< 0). PP > 0.85 is shown with a single asterisk, and those that exceed 0.95 are shown with double asterisks. The relationship with functional diversity substantially supported the alternative hypothesis and is highlighted in bold.

distributions, including the 95% credible intervals, closely intersected the zero-effect line (Figure 4A).

Generally, uninhabited, rural, and suburban areas showed higher functional richness than cities. The difference was most discernible between Uninhabited and City areas (median difference ± SD: 17.819 ± 31.512 [95% CI: -7.582, 118.312], PP = 0.924, ER01 = 10.158, Table 2A); all pairs except 'Uninhabited – City' have their 95% credible interval intersecting the zero mark (Figure 4B).

On diversity, our results indicated that rural, uninhabited, and suburban areas clearly had higher taxonomic diversity (highlighted in light blue in Figure 4C) compared to cities (Rural – City: 0.325 ± 0.066 [95% CI: 0.198, 0.459]; Suburban – City: 0.269 ± 0.068 [95% CI: 0.132, 0.397]; Uninhabited – City: 0.245 ± 0.052 [95% CI: 0.140, 0.345]; PP = 1, ER01 = Inf; Table 2C). We found no substantial differences between Uninhabited – Rural, Uninhabited–Suburban and Suburban - Rural, as the evidence was weak (PP< 0.85, ER< 5, Table 2C), with the distribution intersecting with zero effect mark. Conversely, there was strong evidence for greater functional diversity in cities compared to rural, suburban, and uninhabited areas (Rural – City: -0.277 ± 0.067 [95% CI: -0.417, -0.147]; Suburban – City: -0.282 ± 0.067 [95% CI: -0.421, -0.156]; Uninhabited – City: -0.337 ± 0.055 [95% CI: -0.448, -0.233]; PP =1, ER01 = Inf; Table 2D) as highlighted in light blue in Figure 4D. Comparisons between Suburban – Rural, Uninhabited – Rural, and Uninhabited – Suburban displayed negligible differences, with distributions closely intersecting the zero-effect line, indicating limited evidence for variation in functional diversity outside cities.

Effect of human modification and urban expansion on taxonomic and functional richness and diversity

The following section presents the patterns in the relationship; a more detailed model summary can be found in the Supplementary Tables S1 and S2. Generally, the models demonstrated a good fit, as indicated by Rhat values close to 1, High Effective Sample Size (ESS), and proper mixing of the Markov chains.

Figure 5 illustrates the relationships between HMI and taxonomic and functional richness and diversity. Overall we found a predominantly negative relationship in taxonomic richness and diversity and functional richness across different levels of human modification. Areas with higher HMI tended to support fewer species and a reduced variety of functions that species perform (Figures 5A–C). However, the relationship between functional diversity and the HMI was complex and nonlinear (Figure 5D). Initially, functional diversity decreased, but reversed to increasing trend at higher levels of HMI. Despite this variability,

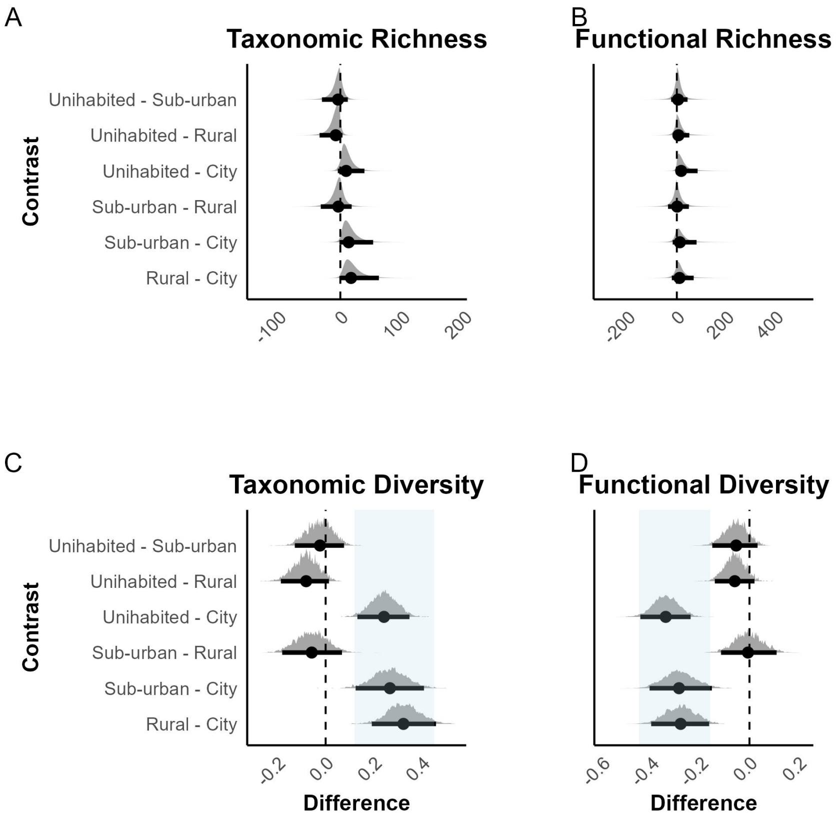


FIGURE 4
Predicted posterior contrasts in taxonomic and functional richness and diversity. **(A)** Taxonomic richness, **(B)** Functional richness, **(C)** Taxonomic diversity, and **(D)** Functional diversity. Each dot represents the median parameter estimate, and the thick horizontal bars represent the 95% credible intervals. Distributions intersecting zero indicate uncertainty or negligible differences, while shifts to the right of zero (dotted line) suggest higher values for the parameter on the left-hand side, and shifts to the left indicate lower values for the parameter on the right.

the overall findings suggest that human activities exerted varying effects on functional diversity.

Finally, we investigated the impact of urban expansion on the taxonomic and functional richness and diversity (detailed model estimates are provided in the Supplementary Table S2). Taxonomic richness (Figure 6A), functional richness (Figure 6B), and taxonomic diversity (Figure 6C) as a function of urban expansion showed similar patterns: an initial decline, followed by a slight rise as the probability of urban expansion increases, with a pronounced decrease observed at higher probabilities (around 75% and above, Figures 6A–C) up to 100% probability of urban expansion. In contrast, there was a slight and steady increase in functional diversity with increasing urban expansion (Figure 6D), indicating that some functional traits may persist or even become more prevalent in urbanized environments. Overall, our findings indicate that urbanization has a complex but predominantly negative impact on the richness and diversity of African bird communities.

Discussion

Urbanization, as a form of global change, has been shown to significantly alter the physical environment (Kaye et al., 2006), creating new environments and opportunities for species. Consequently, urbanization often leads to variations in bird community metrics across different gradients (Sol et al., 2020; Petersen et al., 2022). Our results indicate that taxonomic richness and diversity were notably higher in Mostly Uninhabited Areas (MUAs) compared to cities. MUAs, characterized by more natural or “pristine” vegetation, offer a variety of habitats conducive to diverse bird communities. The availability of suitable habitats is critical for species distribution and with urbanization natural or near-natural environments are transformed for housing, industrial, or commercial purposes, leading to habitat loss for bird communities (Donnelly and Marzluff, 2006; Sandström et al., 2006; Croci et al., 2008). This change shape communities by filtering out some species while allowing others to replace them. In some cases, certain bird species may remain if fragments of near-natural habitats persist (Haire et al., 2000).

Over time, urbanization results in the replacement of specialist species by generalists (Oliviera et al., 2017; MacLean et al., 2018), as specialists are more susceptible to environmental changes. As the specialists are filtered out of the urban areas (Evans et al., 2011; Sol et al., 2014; Fischer et al., 2015), the unique functional traits they contribute to ecosystem functioning are lost, potentially leading to lower functional richness in the urban centers with crucial conservation implications (Fischer et al., 2015; Sol et al., 2014). This corroborates findings from other studies indicating that urbanization drives species decline (McKinney, 2006; Ibáñez-

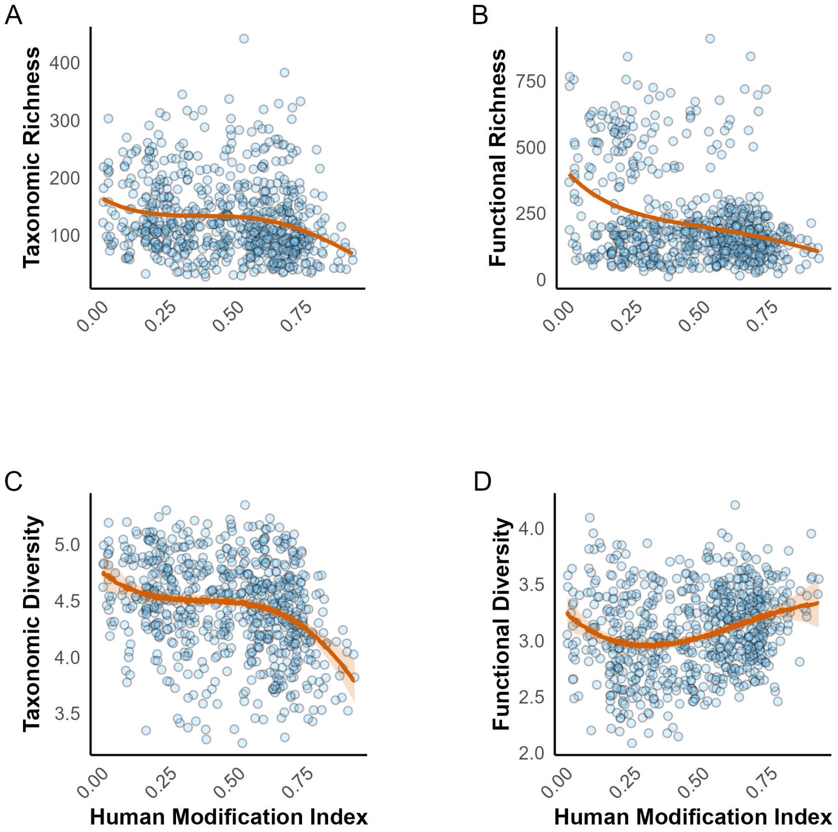


FIGURE 5
Effect of human modification on taxonomic and functional richness and diversity. **(A)** Taxonomic richness, **(B)** Functional richness, **(C)** Taxonomic diversity, and **(D)** Functional diversity. Each plot shows the 95% credible intervals for the respective metric.

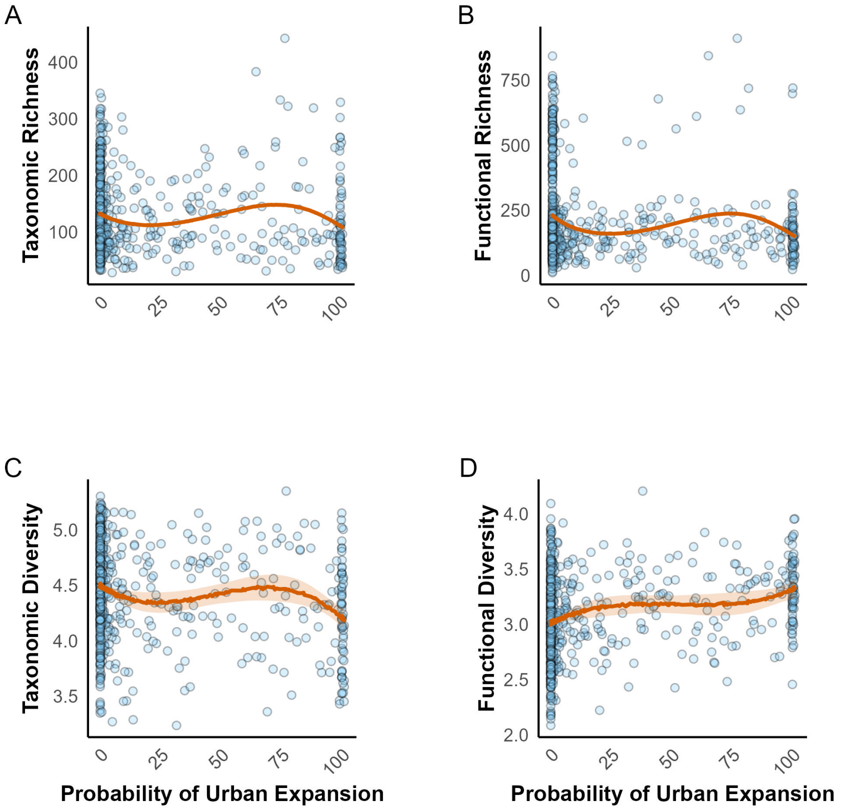


FIGURE 6
Effect of urban expansion on taxonomic and functional richness and diversity. **(A)** Taxonomic richness, **(B)** Functional richness, **(C)** Taxonomic diversity, and **(D)** Functional diversity. Each plot shows the 95% credible intervals for the respective metric.

Álamo et al., 2017). On the other hand, functional diversity increased with the urbanization gradient, with cities exhibiting a higher functional diversity than MUAs. However, a continuous increase in HMI revealed a possible decline, indicating that while cities may initially support a diverse range of functional traits, excessive human modification eventually reduces this diversity after reaching a tipping point. This pattern suggests a transitional phase in bird communities, particularly in newer cities, where species are still adapting. Over time, as seen in established cities like Nairobi, only a few adaptable species may persist, leading to shifts in community composition, such as the disappearance of Hooded Vultures (*Necrosyrtes monachus*), which were once common in Kenya (Odino et al., 2014), and the proliferation of Marabou Storks (*Leptoptilos crumeniferus*). This "undulating" relationship might reflect the dynamic nature of species adaptation in response to urbanization. Additionally, while functional diversity is expected to decline at some point with urbanization (Fischer et al., 2015; Sol et al., 2020), our findings agree with Lee et al. (2021), who reported slightly higher functional diversity in urbanized areas as compared to non-urbanized areas. One explanation for this could be because functional diversity is an abundance-weighted metric that is easily influenced by the proliferation of generalist and disturbance tolerant species. Urbanization could also result in humans providing other sources of food through human modification of habitats. For example, the gardens, refuse dumps and ornamental plants could provide additional sources of food in urban areas (Pauw and Louw, 2012).

Our findings reveal variability in the relationship between the urbanization measures and bird community metrics, thus highlighting the importance of employing various metrics in evaluating the effects of urbanization on bird communities (Matuoka et al., 2020; Sol et al., 2020; Lee et al., 2021; Petersen et al., 2022; Suárez-Castro et al., 2022). These findings are critical for managing landscapes especially in the face of growing urbanization. HMI negatively influenced taxonomic diversity, taxonomic richness and functional richness but had an unstable relationship with functional diversity. Functional diversity initially declined with the human modification index, then followed by a subsequent increase in the functional diversity as the human modification increased. Our result suggests that though species richness declines, there may be no clear change in abundance along the urbanization gradient and in some cases certain species may inflate the total abundance of individuals (Chamberlain et al., 2017). One possible reason for this is that the total abundance may limit species richness such that where there are more individuals, the resources available may not be able to support more species, thus some species will have small populations, leading to their extirpation in such environments (Gaston, 2000). For this reason, species richness could be lower in cities (with higher human modification index), while functional diversity is either maintained (Lee et al., 2021; Callaghan et al., 2023) or higher as we have found. As more habitats are modified with increasing urbanization, there will be fewer habitats available to meet the niche requirement of bird communities (Grimm et al., 2008; Pautasso et al., 2011; Oliviera et al., 2017). For example, there is a decline in food availability along an urbanization gradient (Shochat et al., 2006), which thus limits the species found within the cities. However, cities may provide more feeding opportunities for raptors as well as reduced predation on them (Chace and Walsh, 2006). Thus, settlement-types with some natural habitats will provide more habitats to meet the natural requirements of more bird species, thus leading to an increase in taxonomic and functional richness.

Both the Human Modification Index (HMI) and the likelihood of urban expansion negatively influenced taxonomic diversity, taxonomic richness, and functional richness but positively influenced functional diversity. Our results suggest that although species richness declines, the overall abundance of individuals may not change clearly along the urbanization gradient. In some cases, certain species may disproportionately contribute to the total abundance (Chamberlain et al., 2017). One possible reason for this is that total abundance may limit species richness such that in environments with more individuals, available resources may not support additional species, leading to smaller populations and eventual extinction of some species (Gaston, 2000). Consequently, species richness could be lower in cities (with higher Human Modification Index), while functional diversity is either maintained (Lee et al., 2021; Callaghan et al., 2023) or higher, as we have found. As more habitats are modified with increasing urbanization, there will be fewer habitats available to meet the niche requirements of bird communities. For example, food availability declines along an urbanization gradient (Shochat et al., 2006), limiting the species found within cities.

Habitats are lost due to urbanization and specialists are replaced by generalists (De Coster et al., 2015), resulting in high species turnover rates. This could result in some niches not being utilized, thus providing opportunities for invasive species to explore (Jonason et al., 2017). Such opportunities could also lead to high populations of specific species, which could increase functional diversity in cities. For example, some studies have shown urbanized areas to have more individuals of fewer species (Chace and Walsh, 2006; Chamberlain et al., 2017). This is a probable reason why species richness declined while functional diversity increased with the urbanization gradient.

Furthermore, functional richness is determined by the presence or absence of specific traits in the niche space, while species-abundance-based diversity and differences among species influence functional diversity (RaoQ index) (Botta Dukát, 2005). This further highlights the effect that the number of individuals has on functional diversity. As a result, functional diversity may decrease if species richness increases. As species with unique traits are filtered out, it increases the average dissimilarity among species. On the other hand, both intermediary levels of urbanization and the MUAs had higher species richness due to the availability of suitable habitat, which allows the occurrence of both specialists and generalists. Additionally, if species occupying the same functional space replace each other, it does not influence functional trait diversity, thus masking species loss and changes in species composition when only functional diversity is considered (De Coster et al., 2015). For example, habitat loss had little or no influence on functional diversity but resulted in species loss and changes in species composition in forest bird communities (Coetzee and Chown, 2016; Matuoka et al., 2020). This highlights the need to incorporate more metrics in understanding the influence of urbanization on bird communities since functional diversity alone may not provide a comprehensive understanding of changes in bird communities.

Conclusion

The continuous growth in population will cause more people to live in cities by 2050. This highlights the need for a functioning ecosystem as it is critical for human well-being (Cardinale et al., 2012). While our results add to the already existing body of knowledge on the effects of urbanization on bird communities, it also gives insight into the future. Our results provide evidence that urbanized areas will allow functional diversity to increase while functional richness, taxonomic richness and diversity decline. A hundred percent probability of urban expansion leads to decrease in taxonomic richness, functional richness and taxonomic diversity but at the same time results in a corresponding increase in functional diversity. This result is critical for landscape management and urban planning. We should be cautious to draw conclusions that functional diversity increasing with urbanization is positive as this may not necessarily benefit bird conservation, ecosystem functioning and human wellbeing. As generalists replace specialists, they are able to provide a wide range of functional traits within urban centers. With more generalists, there is high niche overlap which eventually causes functional redundancy. While increased functional diversity in urban environments may mitigate the impact of species loss on ecosystem function to some extent, the loss of specific species within the ecosystem results in the disappearance of their unique traits. This can create gaps within the ecosystem, particularly, in communities with lower functional redundancy (Winfree et al., 2015). The replacement of specialists by generalists can also lead to functional redundancy as some niches are left unoccupied. For instance, if insectivorous birds that control insect population (Whelan et al., 2015) are filtered out of the cities, it could lead to pest outbreaks. Also, an increase in green areas will result in a corresponding increase in habitat diversity within cities, thus creating more niches that meet the ecological needs of bird communities (Oliviera et al., 2017). We therefore suggest that urban planners should incorporate natural vegetation within urban centers to maintain other community and functional indices within urban centers.

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 authors.

Author contributions

BD: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. PN: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. II: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. AK: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing. TT: Conceptualization, Data curation, Funding acquisition, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing. SN: Data curation, Funding acquisition, Project administration, Resources, Validation, Writing – original draft, Writing – review & editing. PN: Data curation, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing. CJ: Conceptualization, Supervision, Writing – original draft, Writing – review & editing. BO: Project administration, Resources, Writing – original draft, Writing – review & editing. UO: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing. AC: Resources, Supervision, Writing – original draft, Writing – review & editing. RT: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing, Methodology.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2024.1503408/full#supplementary-material

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Community-engaged research enhances the scientific quality and societal impact of a long-term avian monitoring program in northwest Ecuador

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Introduction: There has been a growing realization that a more inclusive approach to research can provide both ethical and practical benefits. Long-term avian monitoring programs, and indeed the academic and research community as a whole, are still learning how best to implement these methodologies effectively.

Methods: This paper provides information on a twenty-plus-year effort to conduct community-engaged avian monitoring in northwest Ecuador, with a focus on how this approach has impacted the quality and scope of the project's science and broader societal impacts. We focus on three case studies that have been proceeding for varying lengths of time to highlight various stages of project development and maturity.

Results: A community-engaged approach has improved the quality of our scientific research by adding traditional ecological knowledge (TEK), technical capacity, and intellectual contributions to our monitoring efforts. Community-engaged research has also enhanced the breadth and quality of societal impacts, in terms of education, capacity building, and conservation, particularly in the formation of an ecological reserve that protects threatened species and habitat. We also discuss systemic and local challenges, and potential strategies to overcome these challenges

Discussion: We conclude that community-engaged research can improve the intellectual merit and broader societal impacts of long-term avian monitoring, and we advocate for continued investment, efforts, and careful reflection on best practices in this space.

KEYWORDS

avian monitoring, broader impacts, Chocó biogeographic zone, community-engaged scholarship, conservation, traditional ecological knowledge TEK, research methods

1 Introduction

Long-term monitoring of bird populations is a core element of the ornithologist's toolbox that underlies many key advances in the field. These studies provide unique insights into the demography, movement, and response of avian communities to changing environmental conditions. This information is crucial to our understanding of basic ecological, behavioral, and evolutionary processes and theories. It is also of fundamental importance for conservation, as it enables scientists and managers to monitor the trajectories of populations, species, and communities. In today's rapidly changing world, long-term monitoring provides important insight into how climate change, habitat transformation, disease, and other factors may be affecting bird populations (Pollock et al., 2022). Without this information, our collective ability to detect trends, manage populations, and influence policy would be significantly diminished.

Meaningful inclusion of local residents in avian monitoring projects can benefit both the quality of the science and the translation of research into conservation policy and action (Figure 1). Participation of locals in research, decision-making, and action that influences their surrounding environment leads to the development of grassroots leadership (Baptista et al., 2024). Several names have been given to this basic methodological approach, including community-engaged research (Hale, 2008), participatory-action research (Fals-Borda, 1991), and activist research (James and Gordon, 2008), but all share a similar goal: involving community members as active collaborators in the research process via co-design, co-implementation, and co-dissemination of results. Much of the conceptual framework and

FIGURE 1
Key principles of FCAT's approach to long-term, community-engaged research. **(A)** FCAT researcher (white shirt) draws upon traditional ecological knowledge (TEK) to teach a visiting researcher about a key ecological process, in this case seed dispersal of the palm *Oenocarpus bataua* by the long-wattled umbrellabird; **(B)** FCAT researcher and visiting researcher collaborating on research they co-designed on seed dispersal in this system; the research benefits from a series of technical advances developed by the FCAT researcher including pulley systems to place mist nets and motion-activated cameras high in the canopy; **(C)** FCAT researcher shares uses the research as a catalyst for broader dialog about ecology and conservation with local audiences, in this case members of the *Nueva Generación* Environmental Youth Club; **(D)** an alumnus of the *Nueva Generación* Environmental Youth Club goes on to become an FCAT researcher; she is shown here observing a long-wattled umbrellabird dispersing seeds from intact forest to a 'tree island' planted by FCAT in an abandoned pasture, hastening the recovery of the pasture back to intact forest indicated in panel **(A)**. The arrows are meant to indicate that each four stages of this community-engaged research model feeds into the next.

application of community-engaged research has taken place within the social sciences, with relatively little representation from STEM (i.e., Science, Technology, Engineering and Mathematics). However, local residents and the traditional ecological knowledge (TEK) they hold can add value to the identification of salient research questions and hypotheses, project design, use of appropriate methods, data collection, and interpretation of results (Ramos and Culver, 2024) (Figures 1A, B). Moreover, the attitudes and actions of local residents often play a large role in shaping the degree to which research translates into real-world conservation actions (Baptista et al., 2024) (Figures 1C, D). For these reasons, effective community-engaged research is increasingly recognized as a priority among researchers and funding agencies in STEM.

Community-engaged research is particularly important in the tropics and Global South for four reasons. First, baseline ecological knowledge is sparse relative to northern temperate areas, so data generated by these studies is of exceptional importance, and inclusion of local residents in the research process can have substantial benefits for the breadth and quality of data collected (Adams et al., 2014; Haelewaters et al., 2021; Singeo and Ferguson, 2023). Second, these areas are of the highest importance for avian conservation, because they contain high biodiversity and endemism, in addition to high (and sometimes extreme) levels of threat from habitat loss and other anthropogenic impacts (Myers et al., 2000). Third, because enforcement of environmental regulations is sometimes limited, local resident actions often take on an outsized role in determining conservation outcomes in these regions. Fourth, research often takes place within or adjacent to traditionally marginalized communities with a long history of colonial, parachute-style research from Western institutions (Stefanoudis et al., 2021), and effective community-engaged research represents one concrete way to address this issue and break the cycle (Tuhiwai Smith, 2022). Yet, community-engaged research efforts in the tropics and Global South (and beyond) are still relatively rare, and those that do exist vary widely in terms of their goals, design, implementation, and efficacy (Görg et al., 2014; de la Torre and Morelos-Juárez, 2022; Ortega-Álvarez and Casas, 2022). Openly sharing the details of ongoing and past efforts can help scientific and conservation researchers to develop a more refined understanding of what approaches are likely to be most impactful and successful in the context where they work.

Here, we describe key elements of a community-engaged avian monitoring project in the Chocó biogeographic zone of northwest Ecuador. The project is a collaboration between local resident researchers associated with FCAT (Fundación para la Conservación de los Andes Tropicales), an Ecuadorian non-profit that manages a private reserve, and international or Ecuadorian researchers and students based at universities or other research-focused organizations. We focus on two key questions. First, in what ways has community engagement influenced the quality and trajectory of our scientific research? Second, to what degree and in what ways has community-engaged research had societal impacts beyond the generation of scientific knowledge of avian populations? To highlight how community-engaged research may evolve over time, we address these questions in the context of three monitoring programs of differing lengths: long-wattled umbrellabird behavioral ecology, now entering its third decade; white-bearded manakin evolutionary ecology and behavior, begun four years ago; and point count surveys of avian diversity in a restoration context, currently in its second year. In doing so, our goal is to provide a more detailed and nuanced understanding of how community-engaged research can be adopted or expanded in long-term avian monitoring efforts, and beyond.

1.1 Project context & overview

Latin America is justifiably revered for its biological diversity, but even against this impressive backdrop, the Chocó Biogeographical Region of western Colombia and northwestern Ecuador stands out. For example, the Chocó presents exceptional levels of floristic diversity (> 11,000 species) and the highest number of range-restricted endemic bird species (62) in the western hemisphere (Salaman, 1994; Birdlife International, 2024). However, the Chocó is also notable for extreme threat levels driven by extensive deforestation, habitat conversion, and unsustainable removal of plants and animals from the ecosystem. It was identified as one of the original 25 ‘biodiversity hotspots’ and continues to be considered among the global priorities for conservation of biodiversity (Myers et al., 2000).

Our project is based in and around the 121,376 ha Reserva Ecologica Mache Chindul (REMACH) in Esmeraldas Province, Ecuador (Figure 2). The area has a long history of human occupation and use that dates back at least to the Jama period (1,500 years BCE) and likely involved substantial land clearing for agriculture (M.P. Ordoñez, personal comment). According to the 2010 national population census (latest available), 6,466 people live within the boundaries of REMACH (Marcillo et al., 2016). Inhabitants of the REMACH are primarily from three distinct ethnic groups: Indigenous Chachi (17% of the reserve population), Afroecuadorians (10–15% of the reserve population), and *colonos* or mestizo settlers (65% of the reserve population) (Ministerio del Ambiente del Ecuador, 2005). Chachi and Afro-Ecuadorian presence in the area pre-dates the arrival of mestizo colonists by several generations.

Perlin and Leguizamón (2024) provide a useful overview of the socio-historical context of the region, with particular reference to mestizo residents. Between 1964 and 1994, incentivized by land reform policies enacted by the Ecuadorian Institute for Agrarian Reform and Colonization (*Instituto Ecuatoriano de Reforma Agraria y Colonización*, known as IERAC), families migrated to the region, primarily from Manabí, the province neighboring Esmeraldas province to the South. Today the area is divided into small- to mid-sized farms (of about 10 ha on average) where the primary agricultural activities are cacao cultivation (92% of their study population) or pasture for cattle ranching (50% of their study population). Most households rely primarily on a market economy to meet their needs; the profits generated by selling agricultural products fund the purchase of food, medicine, and other household costs. Notably, since acquiring their farmland, families reported that they cleared an average of 92.5% of their total hectarage to make room for agriculture and provide financially for their families. Local residents express a desire to provide security (in the form of land

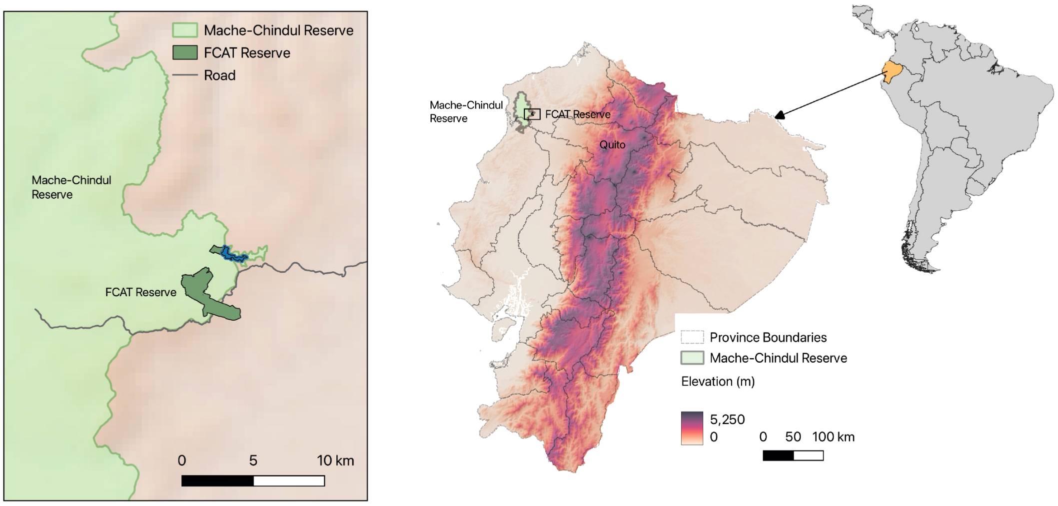

FIGURE 2
Map of the FCAT Reserve in the context of Ecuador and South America. The box to the left shows the location of the FCAT Reserve (dark green), the primary study area, in relation to the larger Reserva Ecologica Mache Chindul (REMACH, light green) and the Laguna de Cube (blue) in northwestern Ecuador. In the center image, the location of the FCAT Reserve and REMACH within Ecuador are shown. To the right, Ecuador is highlighted in orange in the context of wider South America.

tenure, access to education and medical care, and a healthy and clean environment) to future generations, but their own precarity drives them to act against these longer-term interests in the form of agriculture-driven deforestation (Perlin and Leguizamón, 2024).

Mirroring the broader trend of deforestation across the Ecuadorian Chocó, recent studies demonstrate a total loss of 10.1% of forested area from 2000–2008 in REMACH, making it the ecological reserve with the highest deforestation rate within the Ecuador Protected Areas System (SNAP) (Van Der Hoek, 2017; Kleemann et al., 2022). Deforestation rates within the boundaries of REMACH are slightly lower than outside the reserve. There are clearly major disconnects between the law establishing the reserve which outlined accepted activities within the boundaries (*i.e.*, prohibiting extractive enterprises within the reserve) and the reality of the lived experience of local people residing within the boundaries of REMACH. This, along with an ambiguous land tenure system stemming from the aforementioned land reform policies enacted by IERAC and a lack of informed consent by all residents during reserve establishment in the 1990s, has led to tension between residents and representatives of the Ministry of Environment who are tasked with managing activities within the reserve (Perlin and Leguizamón, 2024). Foreign and locally-funded NGOs have actively supported ecological conservation in the area, yet they have mixed track records in terms of the sustainability and longevity of projects and providing alternative sources of income for locals (Perlin and Leguizamón, 2024).

Fundación para la Conservación de los Andes Tropicales (FCAT) is an Ecuadorian NGO that owns and operates the FCAT Station and Reserve (Figure 2), most of which is situated inside the borders of REMACH. A core component of the mission of FCAT is to enable, enhance, and support research that serves to (i) advance basic knowledge, (ii) train Ecuadorian, US, and international students, (iii) build local capacity, and (iv) achieve real-world conservation gains. FCAT members began working together in 2003 in the nearby, privately owned Bilsa Biological Reserve, which is owned by another Ecuadorian NGO, the Jatun Sacha Foundation. Bilsa is the largest continuous forest area in the REMACH area (3,500 ha) and was the main focus of FCAT's research efforts for nearly a decade. FCAT members went on to form a legally recognized Ecuadorian non-profit organization in 2011 and expanded from Bilsa to include research on privately owned farms and patches of forest throughout REMACH (e.g, Walter et al., 2017). FCAT established the FCAT Reserve in late 2018 via an initial purchase of 164 ha. In 2019, FCAT constructed a field station with housing for 60 people and basic laboratory facilities that serves as a base for ongoing research and conservation programs. At present, the reserve is 656 ha in size.

FCAT's research program is anchored in a community-engaged approach (Figure 1). In principle, this means that local residents collaborate on a non-hierarchical, horizontal playing field with formally trained scientists. The idea is that team members from very different backgrounds each bring a distinctive, valuable suite of talents, skills, knowledge, experience, perspectives, and capacities to a shared research effort. The degree to which this is realized has varied considerably across projects, years and teams over the past 20 years, but this philosophy has been central to FCAT's research program from its inception to the present. At present, FCAT employs more than 20 local resident researchers and supports a portfolio of research projects; some are led and implemented exclusively by FCAT (*e.g.*, climatic conditions; plant phenology), some are close collaborative efforts with external scientists (*e.g.*, habitat restoration); and some are conducted by external scientists with minimal logistical and administrative support from FCAT. Complementing these research projects are a suite of social programs that include a youth environmental club, a women's art collective, and a regenerative agriculture project.

2 Case studies

This article examines some of the ways in which FCAT's model of community-engaged research has influenced the trajectory of our scientific research and the nature and breadth of any societal impacts arising from that research. Community-engaged research is built on relationships, both interpersonal as well as between individuals, the natural system, and the research process. Both types of relationships develop over time, and as a consequence, the nature of community-engaged research projects are also likely to change. As such, we present case studies from lines of research that are at early, mid, and mature stages, in reverse chronological order. The information presented below is largely qualitative in nature; in future work we plan to assess scientific, social, and conservation impacts using both qualitative and more quantitative approaches.

2.1 Long-wattled Umbrellabird

2.1.1 Project overview

Cephalopterus penduliger, the long-wattled umbrellabird, is endemic to the Chocó forests along the western slope of the Andean cordillera in Colombia and Ecuador (Snow, 1982; Del Hoyo et al., 1992). The species is considered Vulnerable to extinction by the IUCN due to habitat loss and fragmentation, with an estimated total population size of less than 15,000 individuals across its range (IUCN, 2022). The long-wattled umbrellabird is known for its striking appearance and lek mating system (Snow, 1982; Jahn et al., 1999; Kirwan et al., 2011), but many gaps in our knowledge of basic biology and conservation status persist.

Our work with the long-wattled umbrellabird began in 2003 and represents our team's longest continuing avian monitoring project. The principal investigators on this research have been two local residents Jorge Olivo and Domingo Cabrera and two international researchers Luke Browne and Jordan Karubian. JO, DC and JK began working together on umbrellabird research at the Bilsa Biological Station in early 2003. This initial connection was enabled and strengthened by Carlos Aulestia, the manager of the Bilsa Reserve at the time, and Luis Carrasco, an Ecuadorian ornithologist working at Bilsa. These relationships and individuals served as the nucleus for future growth of FCAT. Renata Durães Ribeiro, a tropical ornithologist, joined the project in 2006 and LB joined in 2011 as a PhD student. The seven of us continue to work together at FCAT, over twenty years later.

Monitoring of the umbrellabird has evolved over time, and has involved many local, Ecuadorian, and international researchers and students. Initially, the project had two main goals, one related to sexual selection and mating dynamics, and a second related to characterizing habitat use, foraging ecology and reproductive biology to inform conservation planning. Moreover, characterizing natural history and basic biology have always been a focus, in part because the species was so poorly known at the inception of this project. In the early years of the project, we surveyed large areas of forest within and adjacent to Bilsa, searching for active lek sites. Upon discovery, we began to monitor active leks on a continuous basis to characterize patterns of activity and male courtship displays (Olivo et al., in review). We also characterized female behavior, nesting biology, and nestling development, as well as foraging ecology and social behaviors away from the lek (Olivo et al., in review). This baseline of natural history information, which we continue to gather, provides a foundation for additional research on umbrellabird behavioral ecology. It also serves as a vehicle for similar, descriptive studies of endemic, threatened and poorly known Chocó avifauna such as banded ground-cuckoo *Neomorphus radiolosus* (Karubian et al., 2007) and brown wood-rail *Aramides wolfi* (Karubian et al., 2011).

Observations of umbrellabirds foraging at large-seeded tree species and subsequently regurgitating or defecating those seeds at lek sites raised questions about how frugivory by umbrellabirds impacts progeny survival and subsequent distributional patterns of the plant species they feed on. One of the key food sources for umbrellabirds in REMACH is *Oenocarpus bataua*, a canopy palm that produces a large-seeded fruit that relatively few resident bird species besides umbrellabirds and toucans are able to ingest and disperse (Mahoney et al., 2018). After showing that umbrellabirds disperse a large proportion of seeds they ingest into the lek (Karubian et al., 2012), we explored the ecological consequences of umbrellabird directed dispersal into the lek by comparing *Oenocarpus* seedling survival and growth in lek sites to control areas outside the lek (Karubian et al., 2016). We also characterized recruitment by *Oenocarpus* and other palm species across a range of habitat types in REMACH (Lueder et al., 2022). In another study, we evaluated how *Oenocarpus* phenology may intersect with observed patterns of behavior (Ramirez-Parada et al., 2020). We also used molecular analyses of dispersed seeds to explore the degree to which umbrellabirds from different lek sites overlap in foraging range (Ottewell et al., 2018). And, given the high incidence of forest loss in our project area, we assessed habitat fragmentation and habitat loss may disrupt the processes we observed in natural settings (Walter et al., 2017). Taken together, this body of work has improved our collective understanding of the basic biology and behavioral ecology of umbrellabirds, and their indirect effects on plant genetic and ecological diversity.

2.1.2 Impacts of community engagement on scientific research

2.1.2.1 Traditional ecological knowledge

Local researchers JO and DC entered the project with a high degree of baseline traditional ecological knowledge (TEK), gained by growing up in and interacting with rainforest habitat and flora and fauna throughout their lives. Their lived experience also provides an ability to navigate through the forest that far exceeds that of most visiting researchers. These attributes have enabled exceptional contributions to our research program, such as discovery of new leks. Umbrellabird leks are sparse on the landscape (the pairwise distance between neighboring leks is 1.8 km; Ottewell et al., 2018), and this work requires surveying large areas of the forest and navigating to lek sites by following the sounds of male calls, audible up to one mile away. This TEK also contributed to finding nests of umbrellabirds and other poorly known, threatened species (Karubian et al., 2007, Karubian et al., 2011, Olivo et al. in review), observations of close mutualisms with certain tree species (Figure 1A) and other novel information about diet (*e.g.*, umbrellabirds killing and eating snakes), and predation attempts (*e.g.*, a large hawk attacking an umbrellabird); and documenting previously unappreciated associations between umbrellabirds and other species (*e.g.*, oropendolas, toucans, and fruitcrows); and finding individuals of particular tree species in a given phenological state (*e.g.*, ripe fruits or flowering) to enable research on frugivory (Mahoney et al., 2018) or pollen flow (Diaz-Martin et al., 2023).

2.1.2.2 Technical contributions

JO and DC contribute a degree of technical capacity and capability that enables our team to collect types of data that otherwise would not have been tractable (Figure 1B). For example, JO and DC developed and refined a method to place mist nets up to 25 m above the forest floor to capture umbrellabirds in the canopy. To do so, they built and used catapults to shoot nylon fishing cords attached to weights above major tree limbs, then created a pulley system to raise and lower the mist nets. This technique had been used previously in other contexts, but they were unaware of these antecedents when they developed it. JO and DC also developed a novel system to raise motion-activated camera traps high into the canopy to record instances of fruit removal at fruiting palms and other trees while anchoring each camera in place to avoid spurious or blurry photos due to wind movement. To do so, they designed a pulley system with a series of guy lines from the cameras to nearby trees to hold it in place. JO was fundamental in developing a sampling methodology involving playback and audio/visual surveys for estimating the occupancy of umbrellabirds and secretive ground-dwelling birds such as the banded ground-cuckoo and brown wood rail in forest fragments (Walter et al., 2017). These and other technical contributions underlie fundamental information for our research project, including the ability to measure, ring and attach tracking units to birds and to characterize frugivory patterns and foraging ecology.

2.1.2.3 Intellectual and natural history contributions

There is a long history in ecology and evolutionary biology of natural history observations leading to the development of new hypotheses, conceptual frameworks, and theoretical insights, and the observational ability and natural history talents of local residents have spurred a number of such advances in the context of the umbrellabird project (Figure 1A). One example is the observation that umbrellabirds may be effectively "eco-engineering" their habitat by creating "gardens" of their preferred food sources in lek sites via seed dispersal. This led to the development of tests about whether this results in a survival advantage for these seeds (Karubian et al., 2012) and predictions about the degree to which males from different leks may overlap in foraging range (Ottewell et al., 2018). Observations of males moving in a coordinated manner away from lek sites generated predictions and preliminary tests about the ecological and evolutionary underpinnings of this unexpected behavior (Anderson et al., 2023). One topic that has raised considerable interest and speculation among our team, but not yet resulted in a formal study, is 'floating males' that do not appear to hold steady territories on a single lek. JO and DC have each co-authored at least ten peer-reviewed publications, each of which involves a meaningful intellectual contribution.

2.1.3 Societal impacts of community engagement

2.1.3.1 Education

As longtime community residents and leaders in our project area, JO and DC are well positioned to share the rationale, methods, results and implications of our team's research on umbrellabirds (and other topics) locally (Figure 1C). Educational activities directed toward local adults and children include informal talks, powerpoint presentations, and experiential learning in the field. Prior to electricity being available in the mid-2010's, JO and DC would carry generators and fuel long distances to arrive at communities and make powerpoint presentations (today, logistics are much easier). JO and DC have also moved into a role as educators and mentors to visiting students and scientists at the FCAT Reserve. As co-instructors on multi-day field courses, they give formal and informal presentations about their research and professional trajectories and help to co-lead short-term student projects on a wide range of topics. They also train and mentor undergraduate and graduate students and PhD-level scientists conducting longer-term independent research projects at FCAT. For example, they provided LB with training in how to identify focal species of plant and bird at various life stages and how to identify frugivore seed deposition sites, and HLA in radio tracking. JO and DC also educate constituents at regional and international scales. They have participated in multiple conferences in Ecuador and internationally (Colombia, Peru) and presented oral and poster presentations, each receiving formal recognition for the quality of their presentations and impact. Serving as lead or co-authors of scientific publications has also helped disseminate their work on an international scale.

2.1.3.2 Capacity building & professional development

JO and DC build local capacity by training fellow local residents and FCAT staff in research methodologies, study design, and interpretation of results, including radio tracking, phenology, plant identification, and camera trap placement and management. They have also helped to identify the need for and to arrange workshops by professionals in themes relevant to local communities, including crop management and water security. They also played a significant role in inspiring younger locals to join FCAT, and then training them in a range of methods (Figure 1D). It is also worth noting that JO and DC built significant capacity during their two decades of work on the project. They learned GPS, computation, compass, radio telemetry, mist netting and handling birds, scientific research design, repeatability, hypothesis formulation and testing. This professional development also extends to public speaking, preparing presentations, and running workshops as well as participation in professional development events such as regional workshops and conferences. While working on the project, DC returned to his studies and graduated from high school, and JO received the Local Conservation Hero Award from the Disney Conservation Fund.

2.1.3.3 Conservation

JO and DC have gathered and published data that have informed IUCN classifications of endangered species such as the banded ground-cuckoo and long-wattled umbrellabird. By gathering reliable data on these and other at-risk populations, they provide necessary justification to convince funders to invest in land purchase and reserve establishment. For example, they identified key tracts of forest to prioritize for conservation, due to the number and density of threatened species residing within them, helped to negotiate their purchase and management with local landowners, and have directly contributed to restoration of degraded habitats on that land. On a social level, their ability to interact with local residents as peers may enable more effective communication with locals about challenges, opportunities, and strategies associated with conservation relative to official representatives of an NGO or the government.

2.2 Project Manacus

2.2.1 Project overview

Among the most common and charismatic birds in our study area is the white-bearded manakin *Manacus manacus*, one of four manakin species found on the FCAT Reserve. This species is notable for its unusual courtship behavior: males create display courts on the forest floor where they leap between saplings and smash their wings together behind their backs to produce explosive 'snapping' sounds (Bodony et al., 2016), and females visit male courts to join in coordinated 'dances', assess male quality, and mate. Male display courts are clustered together in areas called leks, and one or a few males obtain the vast majority of copulations. Perhaps unsurprisingly, considering their abundance in Neotropical secondary forests, remarkable display behavior, and high degree of male reproductive skew, manakins in the genus *Manacus* have served as important systems for studies of sexual selection (*e.g.*, McDonald et al., 2001; Shorey, 2002; Stein and Uy 2006; Barske et al., 2011; Schlinger et al., 2013; Bennett et al., 2021).

We have studied white-bearded manakins at the FCAT Reserve since late 2020 in the context of H. Luke Anderson's dissertation project. A primary aim of Project Manacus is to better integrate sexual selection theory with ecology—two fields that have been traditionally largely separate, potentially due to the historical split between natural selection (concerned with survival, fecundity, and an organism's fit with the environment) and sexual selection (concerned with mating and fertilization success, as well as individual preferences and traits that often seem to defy expectations of natural selection; Darwin 1871). Manakins offer an exciting opportunity to bridge this gap due to their unusual natural history, foraging ecology, and mating system. Because the white-bearded manakin is a generalist frugivore, a major environmental variable we are tracking through time is the abundance of ripe fruit in proximity relative to male display areas. Males spend up to 90% of their time on courts during breeding periods (Snow, 1962), and thus resources at small spatial scales (*e.g.*, in the area immediately surrounding courts) may be important drivers of male allocation to display behavior. The project aims to track sexual selection dynamics in our population longitudinally, given that intra-annual variation in resource availability, precipitation, and other variables may impact the form, strength, and direction of sexual selection (Cornwallis and Uller 2010; Miller and Svensson 2014). To achieve this, we are using motion-activated camera traps at male display courts to constantly monitor patterns of male display, female visitation, and mating among color-banded individuals while concurrently tracking the availability of fruit resources around male display courts via twice-monthly visual surveys.

Thus far, we have uncovered a number of interesting connections between frugivory, resource ecology, and sexual selection processes in the manakin system. First, we have extended findings in Amazonia that manakins situate leks on resource "hotspots" (Ryder et al., 2006), demonstrating that the number of fruiting plants, total fruit biomass, the number of melastomes, and fruiting plant diversity is significantly higher at manakin leks and display courts compared to surrounding forest (Casement et al., in prep). We have also experimentally demonstrated that manakin gut passage accelerates the germination of *Miconia rubescens*, a common melastome shrub, suggesting that manakins may be effective dispersers of key pioneer species in regenerating secondary forest habitats (Rompf et al., 2024). Finally, we have observed previously unappreciated connections between fine-scale fruit availability and male sexual trait expression, with average fruit biomass within 10 m of male display courts positively predicting male display rates, which in turn predict rates of female visitation (Anderson et al., 2024). Radio telemetry has revealed that male movements are centered around lek areas, yet space use is largely distinct even among individuals belonging to the same lek. With continued monitoring, Project Manacus aims to further resolve the ways that ecological fluctuations over space and time interact with individual genotypes to shape sexual selection processes in natural contexts, potentially providing insight into the mechanisms maintaining genetic variation under strong sexual selection (*i.e.*, the so-called 'paradox of the lek'; Kotiaho et al., 2008).

2.2.2 Impacts of community engagement on scientific research

2.2.2.1 Traditional ecological knowledge

Project Manacus has benefited tangibly from community members' TEK and familiarity with the local area. When manakins were identified as a group of interest in 2020, local researchers JO, DC, and Nelson González, along with Luis Carrasco, conducted an initial survey of Reserva FCAT and Bilsa Biological Station to locate display grounds of all lekking manakin species in the area (*i.e.*, redcapped manakin, *Ceratopipra mentalis;* velvety manakin, *Lepidothrix velutina;* golden-winged manakin, *Masius chrysopterus;* and white-bearded manakin, *Manacus manacus*). These surveys involved exploring large swathes of unmapped forest habitat, which was facilitated by the local knowledge and navigational skill of community members. Ultimately, this survey generated data for a publication about lek habitat selection by manakins (Sheehy et al., in review) and helped inform HLA's decision to focus on the white-bearded manakin due to the species' relative abundance and proximity of leks to research facilities.

Local resident Jairo Cabo became involved in Project Manacus in 2021, bringing considerable local and traditional ecological knowledge that advanced the science. A major longitudinal component of Project Manacus involves visually surveying ripe fruits around male display courts. In part due to his experience in agriculture and crop cultivation, as well as his familiarity with the local flora, JC was able to quickly and accurately define and identify various stages along the continuum of fruit ripeness for multiple plant species, dramatically reducing the time required to conduct surveys. JC is able to survey all display courts in the population in 2–3 days, which would have previously required ~3 surveyors to accomplish. With JC leading data collection, we have been able to consistently conduct twice-monthly surveys at all male display courts, and nearly 3 years of this data has been collected to date.

Local residents often rapidly develop competence in mist net extraction with little training or guidance, which may be due in part to their experience with traditional gill-netting techniques. JC explains his process: weighted nets are tossed into rivers at night to capture fish sleeping on the riverbed; when nets are tossed, they sink to the bottom and cause fish to startle and swim upward, trapping their gills and spines in the net. Extracting fish from these nets requires similar technique and fine motor control as extracting birds from mist nets: the direction of entry and points of entanglement are identified, and careful yet confident movements disentangle the animal. The aptitude of local residents in mist netting procedures has been essential for the success of Project Manacus and other avian monitoring projects in the FCAT Reserve.

Importantly, the TEK of local residents also keeps visiting researchers safe while conducting fieldwork. For example, tracking manakins with radio telemetry requires following birds away from established trails, often in regenerating areas with dense undergrowth or fallen debris. These conditions can be dangerous, as terrestrial venomous snakes like Chocoan bushmasters (*Lachesis achrochorda*) and fer-de-lance (*Bothrops asper*) are common at the site. These dangers are also present during visual fruit surveys: observers must sometimes reach into dense shrubs to expose and count fruits, and highly camouflaged eyelash palm-pitvipers (*Bothriechis schlegelii*) may be coiled among the foliage. JC, JO, and others provide constant reminders to step only in locations where the ground is fully visible, using long sticks or other implements to probe occluded areas on the ground or in bushes before proceeding. Residents also regularly share valuable local knowledge about snake behavior (*e.g.*, bushmasters are particularly likely to emerge after rainstorms to warm themselves) and a variety of other potential hazards (*e.g.*, bullet ants, poisonous plants), helping to ensure the safety of students and volunteers involved with Project Manacus.

2.2.2.2 Technical contributions

Following the initial survey of leks, local resident Nelson González was instrumental in early mist netting efforts to begin banding and monitoring manakin study populations, building on previous mist netting experience with umbrellabirds and other species in the area, which was essential given that HLA had limited experience in these techniques at the time. Later in the project, JO leveraged his extensive experience tracking long-wattled umbrellabirds to train HLA in radio telemetry methods. Telemetry can be challenging in rugged forested landscapes, as radio waves emitted from transmitters may reverberate in ravines and valleys (making it difficult to determine the origin of the signal) or be disrupted by trees and ridgelines (preventing signal detection altogether). JO and HLA spent several weeks tracking together, with JO transferring essential knowledge of the nuances and challenges of tracking in difficult tropical environments and enabling HLA to eventually undertake tracking efforts independently. The long-term involvement of local residents in avian research has meant that, in addition to providing crucial TEK, local residents are also able to train visiting researchers in scientific research methods like mist netting and radio telemetry.

JC's involvement in the project coincided with the initiation of larger-scale camera trapping operations at male display courts at our site, and he immediately made important methodological contributions to camera trap placement and court discovery. Prior to his involvement, camera traps were mostly affixed to tree trunks or other existing vegetation near male display courts, which greatly constrained camera placement. However, like many local resident farmers, JC is highly skilled with a machete and immediately suggested cutting smaller branches and dead wood to be used as camera posts. The facility with which JC could accomplish this greatly improved the speed and flexibility of camera placement. Given that as many as 35 cameras may be placed in the field at a given time, and cameras need to be regularly moved as courts become active or inactive, this was an essential time-saving innovation. In addition, JC is a keen observer, which has translated to being highly skilled at discovering manakin display courts in the field. Unlike other species and subspecies in the genus *Manacus*, which may clear fairly large areas of the forest floor for their courts, the cleared area created by males in our population is relatively small (~30 cm) and can easily be overlooked. False positives are also common: sites that upon first glance appear to be display courts may actually be game trails or mammal resting sites, as agoutis and pacas create similar cleared areas among secondary forest saplings, leading to wasted camera hours. JC has noted several criteria that, when met, reliably identifies a court: (1) vertical saplings surrounding the cleared area will be cleaned of all moss; (2) plants in the area immediately around the court have a 'chewed up' appearance, as the court-holding male gradually rips small pieces of leaves to dismantle a plant that is too large to directly move; and (3) claw marks are sometimes visible on the sticks most heavily used by the male. Confirming the presence of these three criteria prior to placing a camera improved the success rate of display court identification and, in turn, the efficiency of data collection.

A major ambition of Project Manacus has been achieving continuous data on display and mating behavior across variable ecological conditions for multiple annual cycles. Such data may yield important insights into sexual selection processes, as tropical birds often breed opportunistically throughout the year (Stouffer et al., 2013), and monitoring behavior during a set 'breeding season' may yield only a portion of the information about mating success and reproductive skew in a given population. Crucially, the involvement of JC in the project has enabled continuous data collection in the system even when HLA and other foreign researchers are not present at the site.

2.2.2.3 Intellectual and natural history contributions

Through Project Manacus, JC has spent hundreds of hours in lek sites, and his observations have yielded important natural history information and raised interesting questions about this understudied subspecies (*M. manacus leucochlamys)*, many of which may eventually lead to formal investigations. For example, he has frequently observed males displaying in mobile groups on the border of lek areas and away from established courts: as many as 11 individuals (including both adult and green-plumaged males) display in close proximity, often leaping between branches in the mid-story or sub-canopy in a circular fashion. Because these groups appear to contain a mixture of adult and juvenile males, JC speculates that the adult males in the group may be directing the flock or teaching the younger males how to produce the display. Given that little is known about the learning and development of complex motor displays (Spezie et al., 2022), this may represent a valuable avenue of future research in manakins. In addition to field-based observations, JC also conducts preliminary reviews of videos while transferring SD card data to hard drives and reports interesting natural history observations. For instance, he directed HLA to a peculiar video gathered in April 2024 that captured an adult male mounting a juvenile male, which has been reported in a population of *M. m. gutterosus* in the Brazilian Atlantic forest (Cestari, 2017) but had not been documented in our population. Natural history information such as this generates a slew of questions for further research, with JC noting that whenever he thinks he understands *Manacus*, he observes something that defies his expectations and motivates him to learn more.

To date, resource monitoring around male display courts has uncovered connections between fine-scale fruit availability and sexual selection processes: males with high densities of fruit immediately surrounding their courts display at higher rates, and females preferentially visit males with high display rates (Anderson et al., 2024). However, JC has anecdotally observed that, over longer timescales, phenological disconnects may occur between fruit availability and display behavior. He has noted that periods of high population-level display rate often seem to occur in times of low landscape-level availability, potentially suggesting that birds accumulate important energy reserves during periods of high resource availability that influence display and mating outcomes later in the annual cycle. JC has also expressed interest in monitoring the display and foraging behavior of males at leks occurring in cacao plantations, which harbor few fruit resources for males. Whether sexual selection dynamics at these sites differ from resource-rich leks in secondary forest habitat remains an area of interest for further study.

2.2.3 Societal impacts of community engagement

2.2.3.1 Education

JC has used Project Manacus as a platform for sharing his knowledge with community members and international visitors to the FCAT station. On six occasions, he has led visitors on tours of lek sites, explaining the ecology of the system and sharing personal observations from the field. He has also developed and given two lectures about the project to visiting field courses and friend-and-ally groups (including foundation donors).

2.2.3.2 Capacity building and professional development

Thus far, JC has built considerable capacity via his involvement with Project Manacus, developing proficiency with computers, data entry, use of GPS and other instruments, radio telemetry, mist netting, camera trapping, behavioral observation, experimental methods, and public speaking. On a professional level, he has given poster presentations of research results at Ecuador's national ornithological conference (Reunión Ecuatoriana de Ornitología) and plans to continue doing so in the future. On a personal level, JC appreciates how the project enables him to learn new skills, gain new knowledge, and participate in the investigation of nature. Like formally trained researchers, community members are motivated to participate in science by the inherent joy that comes from curiosity, investigation, and discovery.

JC has also engaged his family members in various phases of the research process. His wife and children enjoy reviewing camera trap footage, and numerous extended family members have joined JC and HLA in mist netting excursions in the field. In addition, several other local residents have been trained to accomplish the tasks associated with Project Manacus (*e.g.*, maintaining camera traps, monitoring lek sites, surveying fruit resources) so that data collection can continue if JC is unable to work or more hands are required for experimental manipulations.

2.2.3.3 Conservation

To date, the conservation impacts of Project Manacus have primarily been through raising awareness of local conservation issues. The camera trapping component of Project Manacus generates considerable 'bycatch', including videos of charismatic local mammals and birds. JC curates interesting videos from the camera trap footage and shares them with his family and friends via social media, which increases awareness and appreciation of the local fauna among community members. Some videos are also featured in FCAT social media posts, which helps raise attention about the reserve and its biodiversity to a broader audience. In addition, JC's engagement with research at FCAT is a common topic of conversation with community members unaffiliated with the organization, helping to raise awareness and interest about the methods, motivations, and findings of research within the reserve. The white-bearded manakin has also become a minor symbol among local resident researchers, who sport an image of the bird on the sleeves of their local soccer team, providing a conversation-starter about conservation issues and biodiversity in the area. Youth members of the environmental club also reported particularly enjoying learning about manakins during visits to the reserve, suggesting that the charismatic nature of this species offers a promising avenue for sparking the interest of community members in biodiversity and conservation themes more broadly.

2.3 Monitoring birds in regeneration plots using point counts

2.3.1 Project overview

Bird species respond in different ways to changes in habitat structure, stature and plant composition (Menger et al., 2017). Understanding these changes at both individual species and avian community levels is a useful surrogate to comprehend the effects of habitat recovery on biodiversity either after natural or assisted regeneration processes (Bregman et al., 2014). A higher bird species richness is expected in landscapes that combine secondary forests at different growth stages with primary forest and borders as compared to large fragments of continuous mature forest (Blake and Loiselle, 2001; Martínez-Núñez et al., 2023). However, community composition differs as species more tolerant to open, human-modified habitats dominate in young secondary growth while forest-based species prevail in more mature forests (Barlow et al., 2007; Sekercioglu, 2012).

In order to assess changes in community composition and bird species abundances in experimental regeneration plots in the FCAT Reserve, we are currently undertaking a bird monitoring project using point counts. This bird monitoring is part of the "Choconexión" restoration project carried out by FCAT since 2021 in collaboration with Dr. Leighton Reid and Dr. Rakan Zahawi. This landscape-scale experiment, which currently covers 42 ha, examines how different combinations of reforestation methodologies impact biodiversity, carbon, and economic trajectories. A key element of the experiment is to understand how the diversity and community composition of important bioindicators, such as birds, recover over time in these experimental plots relative to reference forested areas. Another key goal is to assess the degree to which restoration plots in which FCAT plants tree species that produce bird-friendly fruits (*e.g.*, figs) are associated with more abundance or species richness of frugivorous birds, which might indicate increased seed dispersal into these sites. As such, avian monitoring represents a crucial means of assessing the efficacy and outcomes of the competing restoration methods being compared in the Choconexión experiment.

In November 2022, we set up six point count stations in each of two experimental regeneration parcels (12 total stations). Each point count station is surveyed six times in the morning and three times in the afternoon in every field visit, alternating the surveying sequence in order to start each observation day at a different point count. Bird counts have been carried out by Juan Freile and two local residents, Gregory Paladines and Gloria Loor, since the very first day of monitoring. In each point count we undertake 10-minute counts of all birds observed, estimate distance to the nearest 5 m within a 50-m radius and estimate height above the ground. As of August 2024, we have carried out four complete 12-day surveys in the rainy season (January–June) and two complete 12-day surveys in the dry season (July–December). The remaining surveys will be carried out until four surveys have been conducted in each season. In the future, we plan to expand sampling to include reference mature forest plots and use of passive audio recorders, and we are beginning relevant pilot work.

To date, 160 species have been recorded. Regeneration plots are dominated by species tolerant to degraded areas that includes omnivorous tanagers, sallying flycatchers, and granivorous seedeaters. Point counts situated in areas with taller secondary growth, more vegetation strata or those closer to forest borders have more forest-based species like bark-searching and understory insectivores and forest-dependent frugivores. Interestingly—and despite the short timespan covered by our study—in some point counts that have experienced a marked growth of secondary trees and bushes during our surveying period, forest-dependent species have already been observed. This apparent turnover in species from pasture-tolerant to more forest-based includes observations of species endemic to Chocoan lowland rainforests like orange-fronted barbet *Capito squamatus* and scarlet-browed tanager *Heterospingus xanthopygius*.

The three researchers started working in the field in November 2022, with JF training GP and GL, who had no previous training in point count sampling and bird identification. Training in species identification is being performed both in the field and in intensive office sessions using updated field guides to the birds of Ecuador (Ridgely and Greenfield, 2001; Freile and Restall, 2018) and online resources. Karlson and Rosselet (2015) recommend progressive accumulation of observation experience and skills for beginning birders, prior to focusing on the intricacies of morphological, structural and behavioral diagnostic characters. However, we were compelled to work simultaneously on both of these approaches to species identification and field surveying when initiating point count sampling. To reduce mistakes, species identification in the field by GP and GL is most of the time corroborated by JF, the professional ornithologist. Ultimately, we aim to continue monitoring in the long-term with GP and GL fully in charge of field work and data compilation, and this current stage of training is a critical step toward this goal.

2.3.2 Impacts of community engagement on scientific research

2.3.2.1 Traditional ecological knowledge

Local researchers GP and GL have demonstrated a rapid learning ability in species identification and in the point count protocol, but particularly in species identification. This is partially explained by the fact that they already knew some of the species by their local names or knew some bird species vocalizations. To date, both researchers identify with confidence the 60 most abundant species and are rapidly learning to identify less abundant taxa. Further, their previous general knowledge of local nature has helped them notice that some bird species rely on open habitats (*e.g.*, cultivated land and cattle pasture) and others are more forest-dependent, even though they did not have a name for many of those 'small brownish or yellowish birds'. For several species, they knew basic natural history information that resulted either in easier identification learning or in understanding their relative abundance in the sampling plots. For example, GP and GL were already aware that crested guan *Penelope purpurascens* and rufous-headed chachalaca *Ortalis erythroptera* differed in their tolerance to forest disturbance, that there are two look-alike toucan species that occupy fragmented landscapes but rely on forest patches for long-term survival, and that caciques and oropendolas perform seasonal movements. These phenomena have been witnessed during our sampling; the chachalaca is more often found in the regenerating plots than the guan, the two toucans are readily identified by voice, and the chestnut-headed oropendola *Psarocolius wagleri* has only been recorded in the drier months when *Erythrina* trees are blooming.

2.3.2.2 Technical contributions

As a consequence of being raised in the rural area neighboring the FCAT Reserve and their sharp vision, GP and GL began the project with strong pre-existing skills in detecting birds and calculating distance to the birds in the different vegetation strata sampled. These abilities complemented the poorer vision capacity of JF and resulted in more visual detections in most point counts than expected if point counts were performed by a single observer. In fact, in some sampling sessions JF only took notes of birds counted and verified species identifications if needed. Further, GP knew the sampling plots prior to establishing point counts, and his knowledge was decisive for determining the most appropriate places to survey, as were GL and GP's skills navigating in this rough, mountainous terrain. Lastly, their developing identification skills—both visual and auditory—have led to increasing confidence by JF on the species they observe, resulting in increasing time to observe and detect more birds on his own. At least two species originally misidentified by JF on the basis of voices were later reidentified when heard, detected and described by GP and GL. Although we have already recorded c. 40% of the species known to occur in the area (Carrasco et al., 2013), new species are found in every new field session, many of them first spotted by either GL or GP.

2.3.2.3 Intellectual and natural history contributions

Since this project is only in its second year of development, it is premature to assess the impacts of community members' engagement in hypothesis development, tests, and scientific outcomes.

2.3.3 Societal impacts of community engagement

2.3.3.1 Education

GP and GL have been working in the point count project for less than two years, but they have been involved in other activities at the FCAT reserve for 2.5 and 3 years, respectively. GP is a former member of the FCAT's 'Nueva Generación' local youth environmental club and has played a leading role in the club, and he has also worked for other projects including palm sampling and tree phenology. Meanwhile, GL is one of the first women working for FCAT involved in fieldwork and research, rather than the more typical professional gender role of cooking and cleaning the station. As such, she is forging a critical role inspiring young women from neighboring communities that participation in scientific studies and conservation action is possible. Her impact in the community is only in the very beginning. Being a young mother raising her children alone and working part-time in catering services and part-time as a field researcher in FCAT, she also manages her cacao plantation alone and is planning on starting an online university career, demonstrating to other local women that empowerment and courage can make the difference in a society marked with gender inequity and disparities. The outcomes of their roles as young environmental leader and field researcher (GP) and young environmental leader, role model, and mother (GL) will be seen in the next few years and can be witnessed in the fact that the youth environmental club increased in participation from 15 in January 2023 to 30 in January 2024.

2.3.3.2 Capacity building and professional development

To date, GL and GP have participated in birdwatching meetings and ornithology training workshops despite their 'green' careers in bird-related topics. Both participated in the XII South American Bird Fair in Mindo, Ecuador, staffing the FCAT stand and providing visitors with information about the reserve and its ongoing projects and activities. GP participated as a speaker in a round table discussion about the vision of local birders and young researchers regarding nature conservation, observation, and study. At FCAT, they often participate as field assistants for visiting international students and in field courses, and were coauthors on a presentation at VIII Reunion Ecuatoriana de Ornitología. Yet, GP and GL believe they need further training in bird research protocols, including data systematization, georeferencing, basic data analysis, and use of research and identification devices and other resources, as well as in the theoretical background of bird biology, morphology, and evolution. At the beginning of the project, GL felt compelled to learn and start identifying birds and applying a field protocol, two activities she was largely unaware of beforehand.

2.3.3.3 Conservation

GP has participated in the youth environmental club since its conception and is, as such, perceived as a young local conservation leader. Yet, he sees little influence on adults, including members of his own family. Similarly, GL has experienced mostly negative attitudes from her adult relatives and friends when she tells stories about the birds she is studying or when she seeks to highlight the importance of forest conservation. Despite these adverse attitudes, both feel they can have a positive influence on children and youth, as they already experience with relatives, in GP's case with the youth club, and in GL's case with her own children. Getting involved in a bird research project has been a life-changing experience for GL, who currently feels a connection with birds made out of joy and tranquility. She could inspire other local women to see a future in conservation related issues, either with FCAT or not.

3 Challenges

We have encountered several challenges implementing and scaling our model of long-term community-engaged research, many of which are likely to be shared more widely (Table 1). We have struggled with integrating community-engaged research with the norms and expectations of the academic establishment in two important ways. First, the scientific publishing system has several explicit and implicit barriers in place that limit the equitable inclusion of local community members as authors. English being the *de facto* language of science represents a major barrier for both the consumption and production of science for local community members from non-English speaking areas (Amano et al., 2016), including this study. The increased availability of translated abstracts is a step towards increasing access to non-English speaking communities, though the vast majority of the scientific literature remains inaccessible, often behind expensive paywalls. Implicitly, negative bias in the review process for authors coming from non-English speaking countries may work against inclusion of local community members on publications, though a double-blind review process may address this bias (Fox et al., 2023).

Second, at many universities the processes for evaluation of professional accomplishments (*e.g.*, PhD thesis committee review, promotion and tenure system) has been slow to recognize and reward community-engaged scholarship, in part because the products generated by community-engaged research (*e.g.*, workshops, reports that do not pass through formal peer review) may not fall into long-established categories used as indices of professional achievement in academia (*e.g.*, publications, conference presentations) (Barnes et al., 2016). This creates tensions at all levels of academia in which there can be a perceived or real trade-off between investing in community-engaged research vs. increasing traditional metrics of scholarly success (Hale, 2008). In our own experience, we have found that investing in a community-engaged approach may take more time at the onset of a project, but that it pays substantial dividends over the longer term, as described in this article.

TABLE 1 Challenges our team encountered implementing community-engaged research program and strategies for overcoming them.

Challenges	Strategies for overcoming
Academic publishing system	• Recognizing local contributors with authorship on published works • Double-blinded peer review
Faculty evaluation/ promotion	• Recognizing and valuing broader societal research impacts beyond publishing
Technology access/training	• Holding workshops for local residents to learn to use word processing, data entry software • Funding for technology transfer
Communicating research to residents	• Hosting gatherings where local residents can visit the reserve, engage in cultural exchange with researchers, and learn about research aims and outcomes • Visiting local schools to present information about research and conservation initiatives • Publishing article abstracts or entire articles in multiple languages
Social and ethical considerations	• Regularly providing formal and informal venues for stakeholders and community members to give feedback on conservation initiatives

A third, generalizable challenge is related to technology access and capacity. Especially in the early years of this project, technological barriers have been a hindrance to community-engaged research: many local community members lacked access to internet and electricity and the technical training necessary to effectively use tools like email and word processing and data entry software. Also, when equipment fails it can take months to replace it. Overcoming these technological barriers requires significant and ongoing investments of time, resources, and support that may disincentivize both international researchers and local residents from engaging in collaborative research.

At the local scale, perceptions and relationships with communities outside the FCAT Reserve are mixed, and there are opportunities to strengthen communication, understanding, and ties. The FCAT station is run and staffed by local residents from one dozen communities surrounding the reserve, and strong relationships exist with many locals through family ties and friendships. JC notes that community members and friends unaffiliated with FCAT are often curious about the work occurring within the reserve, but many others are unaware of or misinformed, for example equating FCAT with the Ministry of Environment. Moreover, other members of the FCAT team note more complicated reactions from family and community members that can include jealousy and mockery. Expanding past and current efforts at outreach, demonstrative teaching, and communication with community members and schoolchildren outside FCAT about research motivations, methodologies, and results is likely to help demystify the goals and activities of the organization and local resident staff while providing important context and education (Holt-Giménez, 2006). Hands-on experiential learning can be particularly effective; for example, JC describes his own first experience holding a bird in the hand as “magical”, stating that such close proximity to such a delicate creature brought him a new appreciation of the biodiversity around him.

Scaling up, we also draw attention to the complex societal and ethical dynamics that arise when community-engaged research involves actors from dramatically different social, cultural and economic backgrounds and contexts (Wilson, 2020; Tuhiwai Smith, 2022). On the one hand, our community-engaged research model can be seen as an engine for societal change, via a ‘one hand feeds the other’ dynamic in which the community engagement improves the quality of the research while also providing economic and educational opportunities for participating local resident researchers. For example, community-engaged research has helped attract research funding by improving both the intellectual merit as well as broader impacts of our science, which in turn has resulted in job creation and resources for education and capacity building, as well as providing funding for the establishment of the FCAT Reserve and associated infrastructure. At the same time, it is critically important to acknowledge important ethical and practical considerations involved with leveraging international funding to influence dynamics in rural, developing landscapes like the area around FCAT (Lewis 2016; Incite, 2017). For example, locals face personal, familial, and logistical challenges when navigating working at FCAT and maintaining their own farms; there are issues with economic stability due to short term, project-based funding cycles; economic benefits tend to be restricted to locals employed by or working directly with FCAT; and, in some cases, local resident researchers have used income from FCAT to pay for the costs of extending their agricultural footprint.

These are complex issues that extend far beyond the scope of long-term avian monitoring *per se*. At the same time, they cannot be ignored or overlooked: they are unavoidable and of critical importance for the long-term success of this and other projects. Our perspective is that addressing these ongoing and very challenging issues requires change on multiple scales. This involves advocating for more equitable and transparent practices in the publishing process (Ruelas Inzunza et al., 2023) and for additional investment in technology and capacity building in the Global South. On the local scale, we believe that interdisciplinary, grassroots strategies can promote forest conservation on privately managed land while acknowledging and respecting local residents' reliance on agriculture to provide for their families. Iterative, long-term partnerships between researchers and local residents creates space for cooperative creativity, bringing us closer to better striking a balance between positive ecological and social outcomes.

4 Discussion

Over the past several decades, there has been a growing realization among scientists and funding sources that a more inclusive approach to research is needed, for both ethical and practical reasons. Accordingly, community-engaged research has received considerable attention and interest, but STEM practitioners (and indeed the academic community as a whole) are still learning how to implement these methodologies effectively. This paper seeks to advance these initiatives by providing information on a twenty-year effort to conduct community-engaged avian monitoring in northwest Ecuador (Figure 3).

A community-engaged approach has improved the quality of our scientific research via TEK, much-needed technical capacity, and valuable intellectual contributions. Moreover, a community-

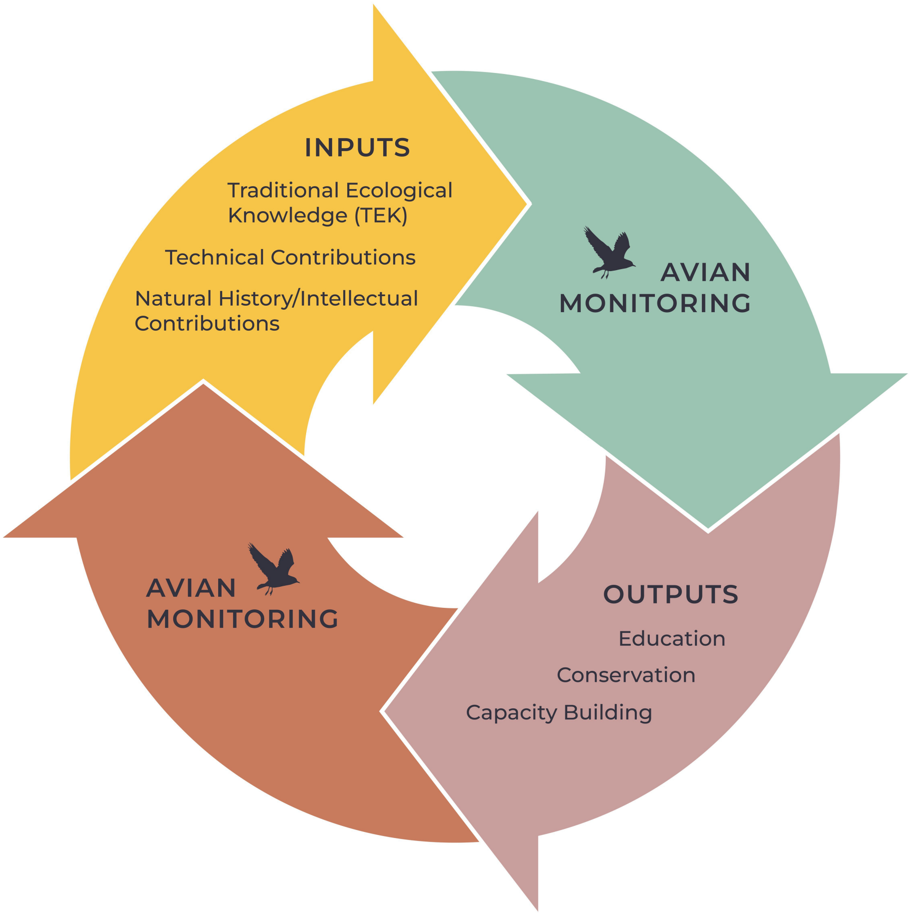

FIGURE 3
Schematic illustrating how FCAT's community-engaged approach to avian monitoring research improves both the quality of the science and its societal impact. As time goes on, a positive feedback loop can develop between the 'inputs' and 'outputs' of the avian monitoring research.

engaged approach has enabled year-round data collection, providing an opportunity for novel insights into ecological interactions, behaviors, and seasonal patterns that would not have been possible with the more restricted cadence of research typically followed by university-based researchers working at remote field sites. Community-engaged research has also enhanced the breadth and quality of societal impacts, in terms of education, capacity building, and conservation, particularly through the formation of an ecological reserve that protects threatened species and habitat. In our case, it has served as a vehicle for conservation and education activities that have helped establish the long-wattled umbrellabird as a flagship symbol for conservation. Based on these findings, we conclude that community-engaged research can improve the intellectual merit and broader societal impacts of long-term avian monitoring, and we advocate for continued investment and efforts in this space. In future work, we aim to present quantitative and systematic evaluations of the conservation project and its societal impacts (per Suich and Dawson, 2023); data collection toward this end is ongoing.

Collaborative identification and development of research questions and hypotheses, along with relevant methods to address them, is one sign of a healthy community-engaged research project because it requires meaningful interchange between residents and scientists (Figure 1A). In our experience, this process often plays out via an ongoing dialogue that spans many years and follows a predictable sequence, beginning with observations of unusual or unexpected behaviors or phenomena in the field. This then leads to speculation about the observed event or pattern, why or how it might be occurring, and what its significance might be. In some cases, these speculative explanations (*i.e.*, hypotheses) have been both directly relevant to established theoretical areas in ecology, behavior, or evolution and testable (Figure 1A). Through additional conversation, we fleshed out these predictions and worked together to generate and pilot a research plan to test them, followed by implementation. As we all continued to learn about the natural system and the existing bodies of relevant work, our collective ability to work as a team to identify, frame, and interrogate research questions improved.

We also noted a general, iterative cycle of development and refinement of research capacity in the context of a community-engaged approach. As farmers living and working in rural areas, local people have ample opportunities to design and implement solutions to practical fieldwork problems without outside assistance, and therefore enter research projects with a baseline level of technical, engineering, and problem-solving capacity far exceeding that of most university-trained researchers coming from other areas (Figure 1B). They apply this capacity to meet practical needs of various research projects (*e.g.*, capturing birds or recording frugivory events in the canopy), and they gain new insights into the natural history and ecology of the local system by viewing and interpreting the results of that data collection. This leads to at least two important advances: a refined understanding of how to engineer even more elegant technical solutions, and an increased ability to identify biological questions that could be addressed via these technical solutions. For visiting scientists, the progression is often characterized by a growing appreciation of how significant the gaps in knowledge and capacity are when one attempts to translate theory and ideas into on-the-ground research, and by extension how much value the TEK, technical capacity, and intellectual contributions of local resident counterparts can contribute.

The key attributes that make this aspect of community-engaged research possible are active curiosity about how the natural world works; inclination, and language to talk about it; and the resources and energy to do the work. Another crucial take-home point is that this process requires years (not weeks or months) to play out: in our experience, there is no substitute for time in the development of healthy and productive community-engaged working relationships. The case studies presented here, which fall along different points of this timeline, help to illustrate this point.

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

The animal study was approved by Tulane Institutional Animal Care and Use Committee and all research was conducted in accordance with appropriate permits and institutional requirements.

Author contributions

JK: Conceptualization, Investigation, Methodology, Writing – original draft, Writing – review & editing. JO: Conceptualization, Investigation, Methodology, Writing – review & editing. DC: Conceptualization, Investigation, Methodology, Writing – review & editing. JF: Conceptualization, Investigation, Methodology, Writing – original draft. LB: Conceptualization, Investigation, Methodology, Writing – original draft. HLA: Conceptualization, Investigation, Methodology, Writing – original draft, Writing – review & editing. JC: Conceptualization, Investigation, Methodology, Writing – review & editing. GP: Conceptualization, Investigation, Methodology, Writing – review & editing. GL: Conceptualization, Investigation, Methodology, Writing – review & editing. LP: Conceptualization, Investigation, Methodology, Writing – original draft.

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Conflict of interest

The authors declare that the research 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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Many winners, few losers: stable bird populations on an Afrotropical mountain amidst climate change

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Organisms in mountainous areas are frequently exposed to climatic extremes and are among the most vulnerable to climate change. Long-term studies on birds along elevational gradients, which are vital in understanding species dynamics, are rare in tropical mountains, which limits the ability to understand their population trends in the face of climate change. We modelled local abundances of understorey bird species (N=18) over a 13-year period (2011–2023) in Mt. Kasigau, Kenya, using mist netting data collected along an elevational gradient. Our models show relatively stable bird abundances in the study period. However, we found two distinct population crashes that affected most species in 2015 and 2022, suggesting that changes in local dynamics may lead to heavy declines of bird populations in mountainous regions. Most species had stable local abundances in the study period, but parametric bootstrapping revealed a declining trend for a few species, including an endemic, threatened species. We highlight the importance of mountainous regions in maintaining relatively stable populations in the face of global environmental transformation such as posed by climate change, and the dynamism of bird species populations across relatively small spatial-temporal variations. While mountain ecosystems are viewed as potential refugia for biodiversity in the face of a warming climate, further studies are needed to understand the drivers of short and long-term declines in bird populations at higher elevations, especially in tropical Africa.

KEYWORDS

elevational gradient, Afrotropical, understorey birds, climate change, Mount Kasigau, refugia

Introduction

Biodiversity declines in the Anthropocene continue to increase compared to the presumed prehuman background rate, with profound effects on ecosystem functioning and services (Loss et al., 2015; Rosenberg et al., 2019). Tropical ecosystems are important biodiversity reservoirs compared to other biomes, but their integrity continues to be threatened by existential anthropogenic threats such as habitat loss, climate change, unregulated harvest, and other forms of human-caused mortality (Barlow et al., 2018a; Ceballos et al., 2015; Gardner et al., 2009; Pollock et al., 2022; Rosenberg et al., 2019). Increasing temperatures coupled with changing rainfall patterns in the tropics are expected to impact species' distribution patterns and population dynamics (Freeman et al., 2018; Freeman and Class Freeman, 2014; Magurran et al., 2010; Toms et al., 2012), in addition to driving upslope range shifts of lowland tropical species across taxa (Freeman et al., 2018; Freeman and Class Freeman, 2014). There is strong theoretical and empirical evidence indicating that tropical biotas are more strongly affected by anthropogenic ecosystem changes than their temperate counterparts (Colwell et al., 2008; Sekercioglu et al., 2008). Due to the global importance of tropical forests as carbon sinks and biodiversity, mitigating anthropogenic impacts on ecosystems and conserving tropical biodiversity has become an increasingly urgent research priority (Barlow et al., 2018b; Pollock et al., 2022). Despite general consensus that loss of montane forest habitat can lead to a decline of these small and isolated populations that are already elevationally constrained (Guo et al., 2013; Lomolino, 2001; McCain, 2009), few studies exist along elevational gradients especially in tropical Africa (Kittelberger et al., 2021). Furthermore, few elevational studies in Africa have focused on species trends despite the continent having steep elevation gradients many of which are unprotected (Elsen et al., 2018; La Sorte et al., 2014; Sheldon, 2019).

Baseline data are urgently needed to document how tropical species along elevational gradients have responded and will respond to rising temperatures, deforestation, and other anthropogenic threats (Freeman and Beehler, 2018b). However, there is a scarcity of baseline data in the tropics on species' distributions (Collen et al., 2008; van der Hoek et al., 2020). There are few published elevational baselines of raw data that include the number of individuals of each species detected (Freeman et al., 2018a; Freeman and Beehler, 2018b; Pagaduan and Afuang, 2012). Here, we used a 13-year (2011 to 2023) population study of understory birds along an elevation gradient of a tropical montane forest – the longest study of its kind in the Eastern Arc Mountains – to evaluate long-term population trends from an isolated but intact forest reserve in southern Kenya. We used the number of unique individuals captured as an index of abundance (Pollock et al., 2022) and modelled the populations of 18 out of the 56 resident bird species, with the goal of determining how their abundances had changed over the 13-year sampling period.

Methods

Study area

We conducted our study along an elevational gradient of Mt. Kasigau (Figure 1), the northeastern most mountain of the Eastern Arc and coastal forests biodiversity hotspot (Myers et al., 2000). These ancient crystalline mountains are characterized by high species richness and the higher concentration of endemic species richness compared to other hotspot locations, but face among the highest

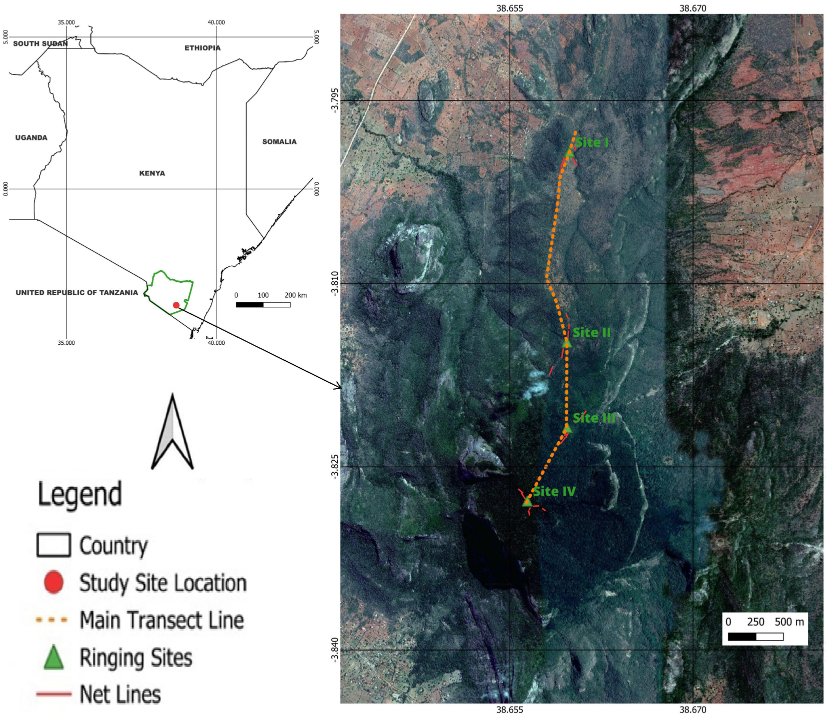

FIGURE 1
Location of Mt. Kasigau in Taita Taveta County, Southern Kenya. We conducted our study along a transect traversing the mountain's elevation gradient with four ringing stations. The mist net configuration is also shown.

degrees of habitat fragmentation and loss (Newmark, 1998). The climate in the surrounding lowlands is semiarid, with average annual rainfall in the 300–500 mm range that is largely irregular and prone to fail. However, the mountain itself receives relatively higher rainfall owing to its higher elevation and forest cover, which captures cloud precipitation brought in by southeast trade winds originating from the Indian Ocean (Aerts et al., 2011). There are typically two rainy seasons, in November and April, known as the grass rains and the long rains, respectively. The rainfall pattern is bimodal alternated with a long (June–September) and a short (January–March) dry period (Aerts et al., 2011). The mountain slopes are fairly steep, rising from 600 to 1641 m within 6km. Floristically, two distinct vegetation types characterize the mountain. The lower elevations are characterized by the Vachellia-Commiphora Dryland Savannah, which transitions into patches of grassland and open shrubs in mid-elevations. Dominant species include *Vachellia tortilis*, *V. nilotica*, *V. busseio*, *Commiphora africana*, *C. campestris*, and *C. confusa*. A few emergent hardwoods include *Terminalia spinosa*, *Melia volkensii*, and *Boscia coriacea*, with the occasional *V. zanzibarica*. The higher elevations are characterized by cloud montane forest, with characteristic trees including *Cola greenwayi, Newtonia buchananii, Sysygium* sp. and *Diospyros* sp. (Birdlife International, 2025).

Data collection

We established mist net lines at four sites, each approximately 230m in elevational difference, along a 3.5km long transect on Mt. Kasigau. We set the transect on the northern side of the mountain which is relatively uniform in gradient and is more accessible and practical for ringing owing to fewer cliffs and rock faces (Figure 1). We designated the sites numbers I–IV from the lowest to the highest, with the basic vegetation type, composition and net line characteristics as described below (Amakobe, 2020).

- Site I (858m asl) is characterized by bushland vegetation type, with numerous dryland species. Dominant trees include *Vachellia hockii*, *Euphorbia quinquecostata* and *Commiphora baluensis*, while dominant shrubs include *Grewia bicolor* and *Catunaregam nilotica*. There is evidence of human disturbance, albeit minimal, through firewood collection, livestock grazing and isolated incidences of logging on this site. There are three net lines on this site (96m, 84m and 120m).
- Site II (1104m asl) is characterized by woodland vegetation type, with tall trees up to 20m in height and an open canopy cover of above 20%. Bushes and shrubs dominate the ground layer. Dominant trees include *Dombeya kirkii*, *Olea africana* and *Manilkara sp* with *Croton pseudopuchellus*, *Combretum exalatum* and *Searsia natalensis*. There are five net lines on this site (48m, 48m, 60m, 36m and 108m).
- Site III (1321m asl) is characteristic of evergreen forest vegetation type, largely consisting of tall, broad-leaved trees, shrubs and climbers. Trees and shrubs in this site are largely evenly distributed. Typical trees include *Rawsonia lucida*, *Sorindeia madagascariensis*, *Tabernaemontana stapfiana*, *Dracaena steudneri*, *Garcinia volkensii* among others. There are two main shrub species at this site, *Piper capense* and *Diospyros natalensis*. There are three net lines on this site (96m, 72m and 132m).
- Site IV (1547m asl) consists of montane cloud forest of trees, shrubs and climbers with several species endemic to the area (including the larger Taita Hills Forests). Dominant trees are mainly *Myrica salicifolia* and *Psychotria lauracea*, with several other trees present in lower frequencies, including *Newtonia buchananii*, *Turraea holstii*, *Xymalos monospora*, *Sorindeia madagascariensis*, *Tabernaemontana stapfiana* among others. The main shrubs on this site are *Dracaena steudneri*, *Diospyros natalensis* and *Piper capense*. There are four net lines on this site (60m, 60m, 84m and 96m).

We ringed birds using standard mist netting procedures (Karr, 1981), using permanent mist net lines (positions) established at the four elevations (Figure 1). We undertook 1 to 4 sampling sessions a year, making as much effort as possible to sample birds in the one dry (January–February or July) and one wet (April–May or September–October) season annually. Sampling was suspended in 2016, 2017 and 2018 due to funding constraints, resuming again in 2019. During a sampling session, we undertook ringing at all 4 sites along the transect, each for two days, making a sampling session 8 days in total. Net lines were evenly spaced on each site, and a daily trapping effort of a total of 300 meters of mist nets per site operated for 6 hours (6:00 am to 12:00pm) maintained constant in all the 4 sites. We checked mist nets at 1-hour intervals to ensure prompt removal, processing, and release of captured birds. We restricted our assessment of species richness to understorey bird communities, i.e., 0–4m above the forest floor (Derlindati and Caziani, 2005) as these are the most reliably caught by mist nets (Karr, 1981). During periods of inclement weather, especially heavy rains, we temporarily closed the nets to pause sampling, resuming after weather conditions improved. We marked all individual birds with uniquely numbered aluminum rings and identified them to the species level using *Birds of Kenya and Northern Tanzania* (Zimmerman et al., 1999) field guide and expert knowledge.

Data analyses

We performed all analyses in R 4.4.0 (R Core Team, 2024) loaded into RStudio 2024.04.1 Build 748 for Windows. Our analysis aimed to determine the long-term trends of bird species abundance between 2011 and 2023. Despite evidence of idiosyncratic variations in bird abundances over long timescales in this population (see Amakobe, 2020; Wambugu et al., 2024), the focus of this study was to estimate long-term trends for individual bird species. We modelled the local abundance for all the species from which we captured at least 20 individuals (N=18 species). We used the number of unique individuals captured from the same species in each sampling session and site as a proxy for their local abundance (e.g. Blake and Loiselle, 2015a; Pollock et al., 2022). We chose this index because our sampling protocol is designed to minimize behavioral avoidance of mist nets by sampling at each site for only two days per session, and this index is expected to be reliable with this type of dataset (Remsen and Good, 1996). When we contrasted the number of captures obtained on the first and second day of each sampling session per site, the paired Wilcoxon signed-rank test indicated a statistically significant difference ($W = 1998$, $p = 9.74 \times 10^{-6}$) in the number of samples collected on the first sampling day of each session at each site (median = 14) compared to the second day (median = 10). Specifically, the number of samples collected on the second day was significantly lower than the first day (Supplementary Figure S1), which indicates a slight but consistent net avoidance within sessions. Nevertheless, we did not observe systematic declines in captures between sessions (Supplementary Figure S1) or consistent increases in captures after prolonged periods without sampling, suggesting that the number of unique individuals captured was a reliable index of abundance in the long-term.

We completed our local abundance dataset post-fieldwork by including absences whenever a given species was not recorded in a season-site combination in which it was detected at some point during the study period. We modelled local abundance as a function of the year and included site and season as covariates to account for their potential influence. We did not include net hours as an offset to account for differing sampling efforts, since they remained fairly stable across the study, with 6h per day and 2 sampling days per session at each site. There was a maximum of one session per season each year of study.

We first fitted a generalized linear model using Poisson distribution for all 18 species, using the function *glmmTMB* from the homonymous R package, v. 1.1.9 (Brooks et al., 2017). We verified the overdispersion of the models with the function *overdisp.test* included in the script *diagnostic_fcns.r* (Fischer et al., 2024). For those species whose models showed evidence of overdispersion (i.e., the variance is greater than the mean as indicated by the dispersion parameter being significantly greater than 1) (N=16), we fitted 3 additional models: Poisson distribution corrected for zero-inflation, negative binomial type 1 and negative binomial type 2. Negative binomial type 1, also known as quasi-Poisson, has a linear parameterization and is particularly useful when the variability of the data grows proportionally to the mean. Type 2 presents quadratic parameterization, and thus, it is more suitable when the variability increases exponentially (Ver Hoef and Boveng, 2007). We used Akaike's Information Criterion (AIC) to select the best-fitting model for each species. If the model with the lowest AIC presented overdispersion, then the model with the second lowest AIC was selected for the species. We verified the deviance and Pearson residuals of the selected, as well as the simulated residuals derived with the function *simulateResiduals* of the package DHARMa v.0.4.6 (Hartig and Lohse, 2022), to ensure the absence of systematic deviances of the assumptions.

Since the impact of losing a certain number of individuals depends on the initial population size, we aimed to account for this to ensure meaningful comparisons across species. Following Pollock et al. (2022), we computed two metrics derived from the slopes associated with the year (β_{year}), which is the rate of change in the predicted number of unique individuals captured each year (see Supplementary Table S1 in the Supplementary material for raw β_{year} estimates). The first metric was the annualized proportional change in abundance (APC) (i.e., $e^{\beta-1}$), which informs about the expected yearly change in the local abundance and, as such, conveys the speed of the change, with greater absolute values representing quicker changes in the abundance. The second metric was the total proportional change (TPC) (i.e. $e^{\beta t-1}$), which represents the total local abundance variation over the full study period of 13 years. For both metrics, we calculated 95% confidence intervals by substituting β_{year} with its corresponding confidence interval values. We categorized the local abundance trends as "increasing" if the 95% confidence interval only contained positive values, "decreasing" if the interval was negative and "stable" if the interval contained zero. We calculated an additional measurement of the total local abundance change by subtracting the predicted number of individuals at the end of the study (2023) according to the best-fitted model from those predicted at the beginning (2011) (Δn). In order to obtain a confidence interval of the predicted local abundance increment, we performed parametric bootstrapping. This consisted of repeating 100 times the process of simulating data for each species based on their best-fitting model, refitting the model with the new sample and using it to calculate the corresponding increment. This measure captures the number of individuals expected to have been gained or lost in the local abundance over the study period.

Results

The trends in the number of species captured at each site over time in Mt. Kasigau elevational transect are shown in Figure 2. We registered a total of 2149 bird captures constituting 1755 unique individuals from 61 species in 30 families over the 19 sampling sessions that took place in 9 years, i.e. 2011–2015, 2019 and 2021–2023 (Figure 2; Supplementary Table S1). The total sampling time amounted to approximately 912 net hours within the 13-year period. Out of the 61 species registered in the study period, 18 species had at least 20 individual captures and were used in our models (Figure 3).

Overall, the models indicated that 15 of the 18 species analyzed (83.33%) had stable local abundances between 2011 and 2023 (Figure 4; Supplementary Table S1). The exceptions were the Green twinspot (*Mandingoa nitidula*, APC= −0.16, $APC_{95\%CI}$ = [−0.23, −0.09]; TPC= −0.90, $TPC_{95\%CI}$= [−0.97, −0.69]), and the Taita White-eye (*Zosterops silvanus*, APC=−0.11, $APC_{95\%CI}$= [−0.18, −0.04]; TPC=−0.78, $TPC_{95\%CI}$= [−0.92,−0.40]), whose declines were statistically significant, and the Eastern Nicator (*Nicator gularis*, APC= 0.07, $APC_{95\%CI}$= [0.02, 0.14]; TPC=1.54, $TPC_{95\%CI}$=[0.23, 4.23]) whose increase was statistically significant.

When we compared the estimated increments in local abundance obtained through parametric bootstrapping (Δn) between 2011 and 2023 (Figure 5; Supplementary Table S2), our results differed slightly. In this case, besides the Green twinspot (Δn= −12.31; $\Delta n_{95\%CI}$= [−19.81, −7.65]) and the Taita White-eye (Δn=−2.89; $\Delta n_{95\%CI}$= [−7.53, 0.4]), the Red-throated Twinspot

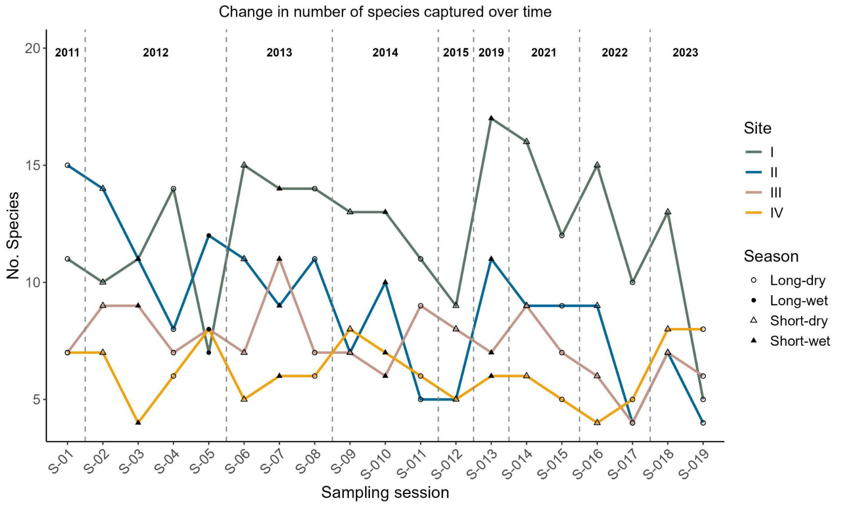

FIGURE 2
Variation in the number of species captured per site over time in Mt. Kasigau elevational transect and number of ringing sessions conducted.

(*Hypargos niveoguttatus*) also showed a decreasing trend in this analysis ($\Delta n = -9.61$; $\Delta n_{95\%CI} = [-2268.93, -1.74]$. According to theparametric bootstrap on the local abundance increment, four species showed a local abundance increase. As in the previous analysis, Eastern Nicator (*Nicator gularis*, $\Delta n = 4.77$; $\Delta n_{95\%CI} = [0.92. 8.1]$) was one of them. The other three were White-starred Robin (*Pogonocichla stellata*, $\Delta n = 3.26$; $\Delta n_{95\%CI} = [1.31, 5.04]$), Bleating Camaroptera (*Camaroptera brachyura*, $\Delta n = 3.26$; $\Delta n_{95\%CI} = [1.19, 5.13]$), and Bearded Scrub-robin (*Cercotrichas quadrivirgata*, $\Delta n = 2.54$; $\Delta n_{95\%CI} = [0.27, 4.79]$).

Discussion

Our results show a stable population trend for most studied bird species in Mt. Kasigau, despite inter-seasonal and inter-year fluctuations (Figure 5). These results are in line with those in Manu National Park (Peru), where bird populations and rainfall were found to remain reasonably stable in a 40-year period (Martínez et al., 2023). However, our models are in contrast with those of other recent studies on montane bird population trends in tropical and Paleartic region that report generalized declines over

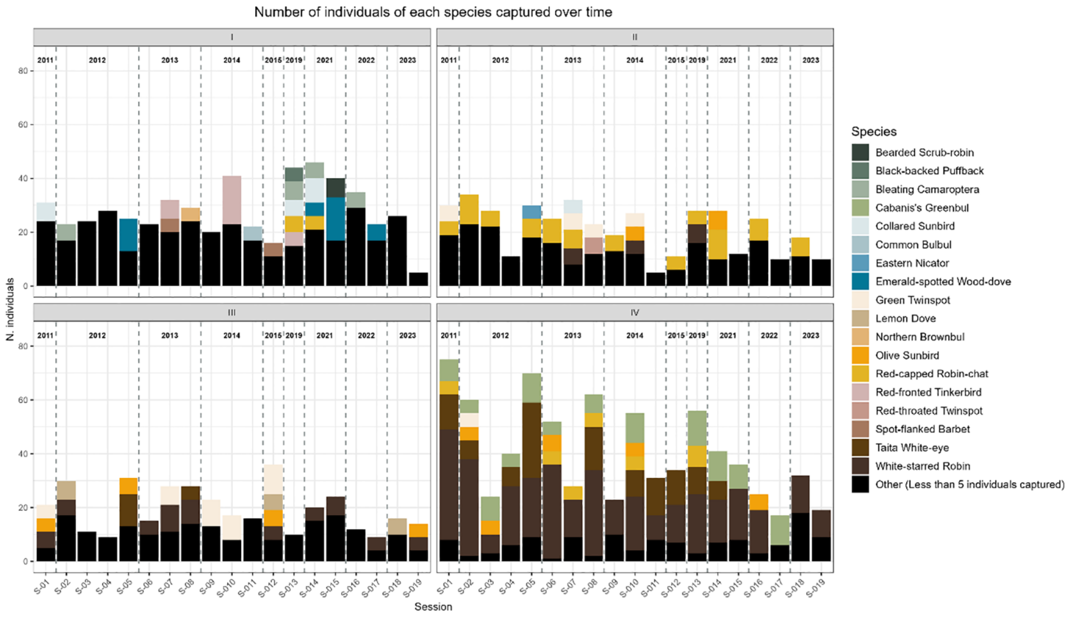

FIGURE 3
Number of individuals captured for each species yearly at each site, showing the 18 species modelled. All other species were reclassified in the graphs as "other" to simplify the graph.

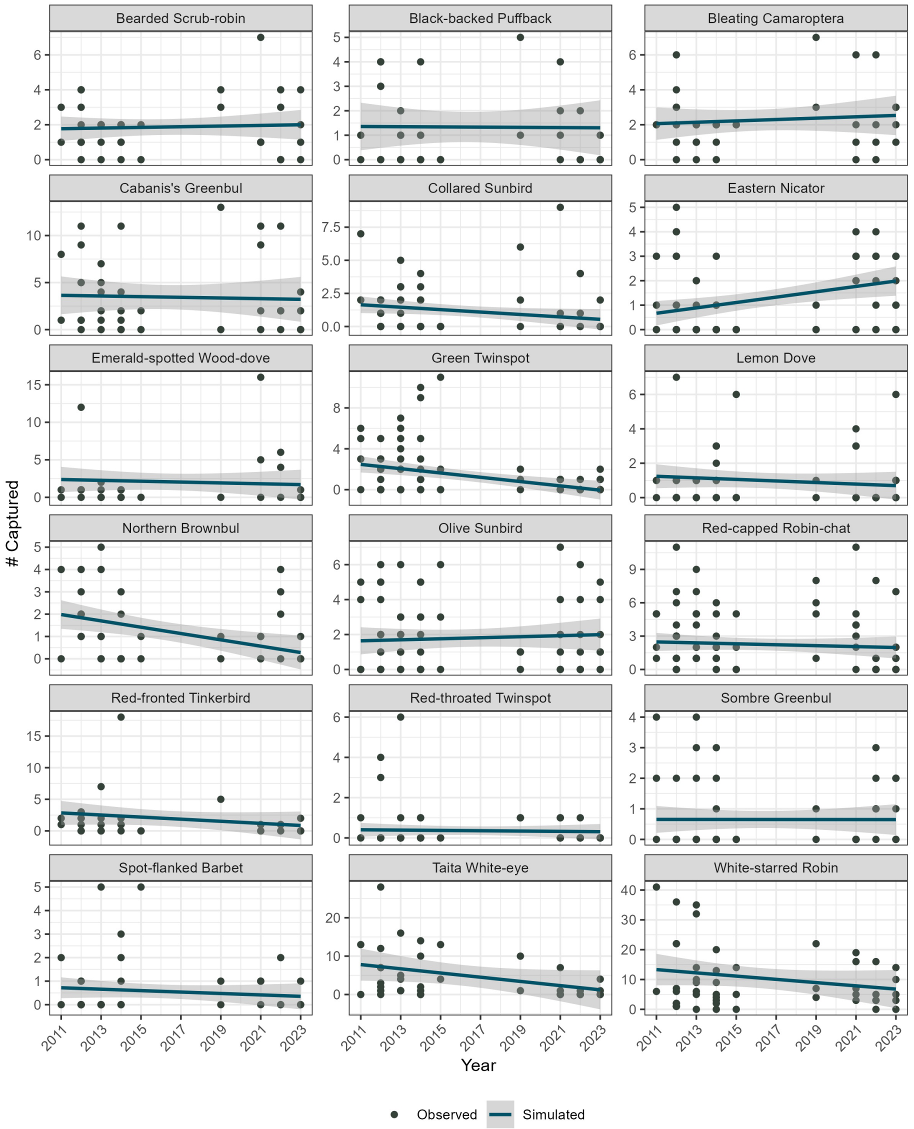

FIGURE 4
Observed and simulated trends in bird abundances in Mt. Kasigau, southern Kenya.

the last decades (Blake and Loiselle, 2024; Brown et al., 2019; Lehikoinen et al., 2014; Neate-Clegg et al., 2021; Pollock et al., 2022; Riegert et al., 2021; Zamora and Barea-Azcón, 2015). Many tropical mountains have experienced changes in their climatic conditions and vegetation structure, implying changes in species niches that are likely to be driving the population fluctuations (de la Fuente et al., 2023; Dulle et al., 2016; Riegert et al., 2021). In contrast, the vegetation cover in Mt. Kasigau has remained largely stable over the study period, as have the temperatures at the sampling sites and the rainfall at the county level (Nyambariga et al., 2023). This general intactness of the montane forest habitat in Mt. Kasigau, which is largely devoid of human activities besides small scale firewood collection in the lower altitudes, livestock grazing in dry conditions and ecotourism, may explain the largely stable bird populations. Further, tropical climates are assumed to have constant environmental conditions which lead to constancy of resources and, hence, more stable populations especially in areas unaffected by significant human activities (Blake and Loiselle, 2015a; Sigel et al., 2006).

Despite this apparent stability, the declining trend for a globally threatened endemic species Taita white-eye, *Zosterops silvanus*, alongside Green twinspot *Mandingoa nitidula* (Figures 4, 5) may be indicative of changing habitat parameters or species-specific life history factors that do not favour these species. These declines are not likely to be caused by habitat changes as there has been minimal human disturbance in our study area during the course of the study. Besides natural tree-falls and isolated cases of selective removal of high-quality timber trees, small scale firewood collection and ecotourism are unlikely to have caused these declines. An increase in ecotourism may lead to negative impacts on birds due to behavioural changes caused by noise (Canaday, 1996), but there has not been a substantial increase in this activity during the study to affect bird populations. This suggests that other factors besides habitat changes may be driving these declines and may include but

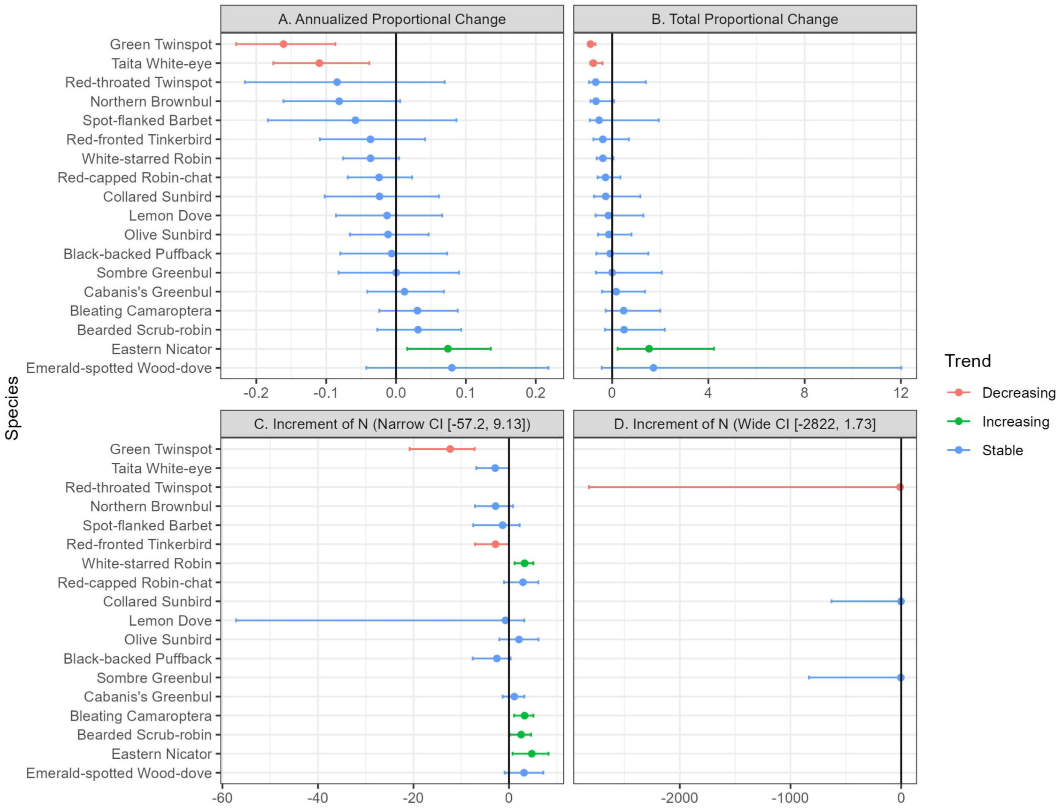

FIGURE 5
Local abundance change metrics between 2011 and 2023 for the 18 bird species modelled, from Mt. Kasigau, Kenya. **(A)** Annualized proportional change (i.e., $e^{\beta-1}$) represents the expected yearly change in the local abundance and, as such, conveys the speed of the change, with greater absolute values representing quicker changes in the abundance. **(B)** Total proportional change (i.e. $e^{\beta t-1}$) represents the total local abundance variation over the full study period of 13 years. In both cases, β represents the slope of the covariate year (β_{year}) in the model chosen for each species. **(C)** Increment of N represents the number of individuals expected to have been gained or lost in the local abundance over the study period, estimating confidence intervals by bootstrapping. Due to their large confidence intervals, three species were depicted on a separate graph (i.e., **D**), employing a larger scale than the graphs on the left **(C)**.

are not limited to disease and/or climate change. There have been earlier sentiments regarding the declining Taita White-eye when the species was suspected to have experienced a population crash in Mt. Kasigau (BirdLife International, 2022). The decrease in the Taita White-eye's abundance is particularly concerning since Mt. Kasigau was identified as the species' stronghold in the late 1990s, estimated to harbour 78% of the world's population of this threatened species (Mulwa et al., 2007). A potential cause contributing to the Taita White-eye's abundance declines could be inbreeding, which can cost lifetime fitness in birds (Harrisson et al., 2019). Supporting this hypothesis is that the gene flow between Mt. Kasigau and Taita Hills populations is scarce owing to isolation of the former, and the percentage of heterozygosity is relatively low (Habel et al., 2014). Inbreeding has been shown to have a lifetime fitness cost in birds (Harrisson et al., 2019). Restricted dispersal and frequent inbreeding within "sky island" systems, such as Mt. Kasigau for the Taita White-eye, can occur even in highly mobile bird species (Ceresa et al., 2024). In contrast, the Eastern Nicator showed remarkable increases in its abundance in the same period. Further studies are needed to understand the underlying causes of these population changes despite relatively stable rainfall and temperature conditions across the study period. Moreover, other species in the same diet guilds similar to these species have not experienced similar population changes.

Despite overall stability in bird populations, our analyses show short term dips and peaks in bird population trends. These dips may be attributable to the number of sampling sessions undertaken: there was only one sampling session undertaken in 2011, 2015 and 2019 while there were 2–4 sessions in all other years. However, periodic dips and peaks in bird abundances have been observed in other studies and have been hypothesised to be the effect of large-scale climatic cycles, such as El Niño-Southern Oscillation (ENSO) which can affect bird populations in different ways across geographical regions (Ballard et al., 2003; Blake and Loiselle, 2015a; LaManna et al., 2012). These ENSO events may not only influence the breeding success on birds both positively and negatively but could also affect their foraging behaviour and diet. In our study area, periodic changes in weather parameters were suggested as driving these periodic declines in an earlier study (see Wambugu et al., 2024). Data from the Kenya Meteorological Department (Kenya Meteorological Department, n.d) reveals that both 2011 and 2015 corresponded to La Niña and El Niño extreme weather periods, respectively, which may partly explain these dips in bird population trends in our study. It is however worth noting that many of the species in our study were only captured in one or two years at each site. Thus, our dataset only provides an indication of the general trend in bird community over time but it's unclear regarding the turnover between species.

Several species were consistently present in the first half of the study (2011–2015) but absent in the second half (notably Common bulbul and Lesser Honeyguide in Site I; Spotted Flycatcher in Site II; and African Pygmy Kingfisher and African Goshawk in Site III). Likewise, other species appeared in the second half such as the Red-throated Twinspot and the Variable Sunbird in Site I. Other studies have termed similar observations as winner–loser species replacements, which may be triggered by changes in habitat parameters (Lees and Peres, 2006; Tabarelli et al., 2012). Winner–loser patterns are clearer in human–modified landscapes due to widespread habitat changes (e.g. Filgueiras et al., 2021) but less so in more intact habitats. In our study, these changes appear to have occurred immediately after population collapse, thought to be due to changes in resource availability as a result of unconfirmed events (Figure 2).

Conclusion

Our study shows that most bird species populations in Mt. Kasigau remained stable despite reported declines in similar locations elsewhere in the tropics. This stability indicates the role of montane areas as refugia for birds in the face of a warming climate, along with other anthropogenic pressures. Our study further emphasizes that relatively small mountain regions can play an important role in maintaining stable bird populations as global environmental transformation continues to escalate. However, future studies should focus on species-specific life history aspects to better understand population trends of Afromontane birds, especially those that appear to be undergoing 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

The animal study was approved by National Commission for Science, Technology and Innovation (NACOSTI, Kenya) and the East African Bird Ringing Scheme. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

MW: Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. LM: Data curation, Formal analysis, Methodology, Resources, Software, Visualization, Validation, Writing – original draft, Writing – review & editing. BA: Data curation, Investigation, Project administration, Resources, Supervision, Writing – review & editing. MG: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that Generative AI was used in the creation of this manuscript. Technical support for R code writing was obtained from ChatGPT (GPT-4, OpenAI, https://openai.comb, October 2023), Gemini (Large language model, Google AI, https://gemini.google.com/, 2023) and Microsoft Copilot (GPT-4 Conversational AI Model. Microsoft, https://copilot.cloud.microsoft/, 2024).

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2025.1520857/full#supplementary-material

SUPPLEMENTARY TABLE 1
Number of unique individuals captured each year in each site for each species. Site I: 858m asl, Site II: 1104m asl, Site III: 1321m asl, Site IV: 1547m asl.

SUPPLEMENTARY TABLE 2
Summary of Results for Modelled species (n=18) along the Mt. Kasigau Elevational transect.

SUPPLEMENTARY FIGURE 1
Number of captures in days 1 and 2 of each sampling session and site

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Insights on avian life history and physiological traits in Central Africa: ant-following species have young-dominated age ratios in secondary forest

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The Congo Basin rainforest and adjacent Lower Guinea Forest constitute the second largest tract of lowland tropical rainforest in the world. As with the rest of the continent, human population is increasing rapidly and forest degradation is ubiquitous. Forest degradation through logging has pervasive negative effects on ecosystems, but selective logging is considered less impactful than clearcutting. Recent research in Afrotropical forest shows that certain avian species and guilds are more affected by selective logging than others (e.g., specialist insectivores such as followers of *Dorylus* driver ants); however, the mechanisms behind these patterns are poorly known. In an eight-year mist-netting effort in Equatorial Guinea, we caught 1193 birds in primary forest and high-grade selectively logged forest to determine the effect of disturbance on six demographic and physiological measures on birds. We compared five life history and population traits for ten insectivorous species: proportion of breeding and molting birds, molt-breeding overlap, bird age, and a body mass index. We also analyzed the concentrations of the stress hormone feather corticosterone (fCORT) in five species. All three strict ant-following species (*Alethe castanea*, *Chamaetylas poliocephala*, *Neocossyphus poensis*), and the Muscicapid robin *Sheppardia cyornithopsis* had a higher proportion of first year birds in secondary forest. Furthermore, two ant-followers, *A. castanea* and *C. poliocephala*, had a higher proportion of individuals molting in primary forest. Finally, only *Illadopsis cleaveri* had higher body condition in secondary forest. We found no differences in breeding status, molt-breeding overlap or fCORT between forest types. Using a long-term mist-netting effort, we use measures taken from birds in-the-hand to go beyond insights from point counts alone; we gain valuable insights into the demography and physiology of Afrotropical birds occupying variably degraded lowland tropical rainforest.

KEYWORDS

Afrotropics, disturbance, first year birds, ant-following birds, understory birds

1 Introduction

The Afrotropics account for approximately 30% of the world's tropical forest (Malhi et al., 2013); of those forests, 89% are found in Central Africa (Malhi et al., 2013; Mayaux et al., 2013). The Congo Basin accounts for 90% of the carbon stored in Africa's terrestrial systems (Saatchi et al., 2011; Baccini et al., 2012) and plays a major role in regulating the continent's climate (Maynard and Royer, 2004).

Deforestation in sub-Saharan Africa is driven primarily by small-scale clearing for rotational agriculture (Tyukavina et al., 2018) and non-mechanized selective logging (Laporte et al., 2007; Rudel, 2013; Curtis et al, 2018; Tyukavina et al., 2018). Clearing for large-scale industrial agriculture, which accounted for approximately 55% of global tropical deforestation between 2000-2005 (Hansen et al., 2008), accounted for under 1% of the deforestation in Central Africa between 2000-2014 (Tyukavina et al., 2018). However, while some estimates have suggested that 84-93% of the deforestation has taken place in Central Africa has occurred because of clearing for small-holder agriculture (Curtis et al., 2018; Tyukavina et al., 2018), others have suggested that logging may contribute as much as 30% of the region's deforestation after considering the indirect damage from logging operations (e.g., the creation of supporting infrastructure like skid trails and logging roads) (Laporte et al., 2007).

About 10% of all tropical forests are selectively logged on a regular basis (Blaser et al., 2006; Edwards et al., 2014). Some tropical forest nations, including several Central African countries (Puettmann et al., 2015), have introduced selective logging regulations to reduce deforestation through clearcutting while satisfying timber demand more sustainably (Drigo et al., 2009). As a result, large parts of the Afrotropical rainforest have been subject to high-grade selective logging, a practice which involves the harvest of only large, high-value trees such as Okoume (*Aucoumea klaineana*) (Akindele and Onyekwelu, 2011).

The ecological impact of selective logging on biodiversity differs among tropical regions. In Amazonia, for example, selective logging decreased avian species richness and abundance (Barlow et al., 2006) whereas in Southeast Asia, selective logging had no effect on avian species richness or abundance (Sodhi et al., 2010; Edwards et al., 2011).

Because selective logging is pervasive throughout the tropics and is increasing in extent within the Afrotropics, it is imperative that we understand how this form of forest degradation impacts birds. Birds act as integral components of tropical ecosystems (Sekercioglu et al., 2016; BirdLife International, 2018) and perform functions critical to the integrity of these systems, many of which benefit humans either directly or indirectly, including pest control, pollination, and seed dispersal (Sekercioglu, 2002; BirdLife International, 2018). Although selective logging is demonstrably less detrimental to biodiversity than more intensive forms of timber extraction, there is considerable evidence from across the tropics that suggest it can have negative effects on bird species richness and abundance (Sodhi et al., 2008, Sodhi et al., 2010; Edwards et al., 2011) as well as functional diversity (Bregman et al., 2016). Furthermore, it is now well-established that logging impacts community composition, with a shift in species composition most often resulting in forest interior specialists being replaced by functionally similar forest generalist or gap-/edge-preferring species (Dranzoa, 1998; Sodhi et al., 2008). The implications of changes in forest structure on species are not consistent and depends on various intrinsic characteristics, including diet, foraging mode, habitat and dietary specialization, morphology, and breeding biology (Sodhi et al., 2008; Hamer et al., 2015).

While our understanding of how selective logging impacts tropical avian communities is increasing, gaps still exist (Burivalova et al., 2015; Gray et al., 2007). This is particularly true for the Afrotropics (Cazzolla et al., 2015; Watson et al., 2017), where inconsistencies persist (Gray et al., 2007). Existing research from the Afrotropics suggests that selectively logged forests can support lower species richness and abundance in comparison to undisturbed primary forests (Arcilla et al., 2015; Beier et al., 2002; Dale et al., 2000; Newmark, 2006; Watson et al., 2004); maintain pre-logging levels of richness but prompt shifts in community composition and thus function (Kofron and Chapman, 1995; Dranzoa, 1998; Cordeiro et al., 2015; Arcilla et al., 2015); and/or decrease the relative abundance of forest-dependent species (Newmark, 2006; Dranzoa, 1998; Arcilla et al., 2015; Cordeiro et al., 2015). Avian biodiversity in tropical forests can be an effective indicator of ecosystem health reflecting the long-term impacts of selective logging (De Heer et al., 2005). However, most studies focus on broader patterns of diversity at the community level, whether taxonomic (e.g., Tchoumbou et al., 2020), functional (e.g., Bregman et al., 2016; Mestre et al., 2020), or phylogenetic (e.g., Mestre et al., 2020). While this line of questioning is important, we must also identify patterns within individual species that may be driving community-level patterns. For instance, by considering specific guilds of birds within forest fragments in Kenya, Peters and Okalo (2009) determined that only the most specialized ant-following insectivores had declined. This example reinforces the understanding that obligate or near-obligate ant-following species, i.e., species that depend on predatory driver ants for foraging, are more sensitive than generalist species across the tropics (Peters et al., 2008; Waltert et al., 2005; Barrie et al., in review). Furthermore, in a review of the effects of selective logging across tropical forests, Burivalova et al. (2015) showed that differences in the intra-guild body sizes of species were also influenced by selective logging. In some guilds, larger bodied species were positively impacted by selective logging, whereas in other guilds small-bodied species were negatively affected (Burivalova et al., 2015). Looking at the physiological state of individual birds in selectively logged forests can provide a more holistic understanding of how these species are affected by selective logging (Fefferman and Romero, 2013). There are many aspects that could affect birds' physiological state in secondary forests; for example, reduced resources, decreased canopy cover, and higher densities of predators (Sekercioglu, 2002; Cosset et al., 2021).

Life history traits can be used to highlight potential effects of selective logging on understory birds. For example, breeding and molting are energy and resource intensive stages in a birds' life (Salvantes and Williams, 2003; Romero, 2002). They are both dependent on food availability (Wikelski et al., 2000; Marini and Durães, 2001), which can be more limited in selectively logged tropical forests than primary forests (Ross et al., 2018). In a comparative study, Coddington et al. (2023) found a 61% reduction in the proportion of breeding birds following fragmentation, indicating human disturbance can influence the breeding behavior of understory birds. Unlike temperate birds that experience well-defined molting periods and breeding seasons, relative climatic stability in the tropics means that some tropical birds can experience overlap in their molting and breeding seasons (Webster and Handley, 1986). Some birds adjust to the cost of this overlap with slow feather growth rate or molting fewer feathers simultaneously (Echeverry-Galvis and Hau, 2013). A possible scenario is that birds in suboptimal habitat breed and molt at the same time during periods of resource abundance; birds in primary forest are then less likely to breed and molt simultaneously due to a more consistent resource pool (Freed and Cann, 2012).

Population traits such as age ratios can also be used to highlight potential effects of selective logging on understory birds. In territorial bird species, the social dominance hypothesis predicts that age ratios in poor-quality habitats will be young-dominated as older and stronger individuals already occupy and protect territories in better-quality habitats (Hannon and Martin, 2006). These predictions may be exaggerated in the tropics, where territoriality is often experienced year-round (Stutchbury and Morton, 2001) compared to temperate regions where territories are defended during defined breeding seasons. Additionally, tropical songbirds typically have a higher longevity than their temperate counterparts (Snow and Lill, 1974; Williams et al., 2010). However, their mortality rates in disturbed forest are often higher (Ruiz-Gutierrez et al., 2008), creating space for younger birds to move in. In addition to age ratios, body condition can provide insight into an individual bird's health and thereby the quality of the habitat it occupies (Jakob et al, 1996). Specifically, mass corrected for body size (hereafter 'body condition') is a simple condition index that can identify individuals under nutritional stress (Stevenson and Woods, 2006). For example, in Borneo, a study of 55 bird species showed that frugivorous and omnivorous birds that occupied selectively logged habitats had reduced body size compared to conspecifics occupying primary forest (Messina et al., 2021). Finally, poor-quality habitats can cause long-term increases in birds' stress hormones (e.g., feather corticosteroid (fCORT) Bortolotti et al., 2008), thus one might expect higher fCORT in disturbed secondary forest relative to primary forest.

Here, we tested the hypothesis that high-grade selectively logged (hereafter 'secondary forests') have demographic and physiological effects on understory bird species. We tested this hypothesis using life history (molt and breeding) and population traits (age ratios) as well as fCORT and body condition of ten understory insectivores. We selected understory insectivores based on evidence that this guild is particularly vulnerable to anthropogenic disturbance (Dale et al., 2000; Watson et al., 2004; Jarrett et al., 2021; Powell et al., 2015; Barrie et al., in review), especially Afrotropical ant-followers (Peters et al., 2008; Peters and Okalo, 2009, Jarrett et al., 2021; Barrie et al., in review). If secondary forest is indeed a suboptimal habitat relative to primary forests, we predict that birds in secondary forests will have (1) a lower breeding and molting prevalence and a higher prevalence of molt-breeding overlap, (2) a higher proportion of first-year birds and (3) lower mean body condition and higher fCORT concentrations.

2 Methods

2.1 Study area

Data were collected by Biodiversity Initiative at two locations in Equatorial Guinea: Cuidad de la Paz (hereafter 'La Paz') during the sunny dry season (December-January) from 2016 to 2023 and one cloudy dry season in 2022 (1128 captures) and about 65 km south at Altos de Nsork National Park (hereafter 'Nsork') in 2014 (65 captures) for a total of eight field seasons. In La Paz, mist nets in the primary forests were over 500 m from the nearest road and at least >1.5 km from the closest settlement; the canopy is closed. The secondary forest site is adjacent to the city; the north and west side are bounded by ~70-m wide paved roads, a ~50-m wide dirt road on the southern portion, and high-tension power lines on the east (30 m wide with vegetation 2-3 m high which is regularly trimmed) effectively isolated the eastern portion (Barrie et al., in review). The canopy of the secondary forest plot remains closed, but it has been commercially logged in the past decades and continues to be regularly selectively logged; it was most recently logged in about 2018. Both forests had similar canopy height (primary: 14.1 m ± 0.5 SE m; secondary 14.1 ± 0.4 SE m). Although primary forests had a higher canopy cover and visibility through the understory when compared to the secondary forests (canopy cover: primary: 88 ± 1.3 SE m; secondary 83 ± 2.2 SE m; visibility: primary: 9.5 ± 0.5 SE m; secondary 7.5 ± 0.4 SE m). At Nsork, primary forest sites were located approximately 800 m into the national park (i.e., north and west) from a road bordering the southern edge of the park. Secondary forest was located <500 m from a main road and had been selectively logged over at least the last three decades. Based on LANDSAT satellite imagery, primary forests at both locations in Nsork were selectively logged as late as the 1980's but have remained intact since.

2.2 Data collection

We captured birds using mist nets (12 m x 2.5 m); net lanes (Nsork n=6, La Paz n=20) were set up at two sites in each forest type and moved every two days. We opened the nets at about 6:30 AM and closed after six hours. We identified every individual captured to species level when possible, and we recorded standard morphometric measurements (mass [grams], natural wing chord [mm], and tail length [mm]), breeding condition (presence of a brood patch, degree of cloacal protuberance), sex (when possible), and molt status (symmetrical flight feather molt only). We collected a single rectrix (tail feather) from adult birds to be used in fCORT analysis.

We defined the bird's age following a molt-based aging system (Wolfe-Ryder-Pyle, hereafter 'WRP' [Wolfe et al., 2010, Wolfe et al., 2021]). All species captured exhibit a complex basic molt strategy where juveniles undergo a preformative molt into a unique formative (post-juvenile) plumage prior to adopting their adult basic plumage (Howell et al., 2003). Species exhibiting this molt strategy are further divided into two groups: those with a complete preformative molt (where individuals replace all of their juvenile feathers) or a partial-to-incomplete preformative molt (where individuals replace only some of their juvenile feathers). In species that undergo complete preformative molts, the formative and adult basic plumage are virtually indistinguishable. Therefore, we used different age groups for species that undergo complete or partial preformative molts. For species with complete preformative molts, juveniles were defined as individuals that had not undergone their preformative molt (i.e., birds in their juvenile plumage) and the rest were grouped as "adult" birds. For birds with partial preformative molts, we defined first year birds as juvenile birds (juvenile plumage) or adolescent birds (formative plumage) and the rest were defined as adults.

2.3 Focal species

We used data from ten understory insectivorous species, including a subset that are specialized ant-following species, as both groups are particularly vulnerable to anthropogenic disturbance at a Pantropical scale (Peters and Okalo, 2009; Powell et al., 2015). The three specialized ant-followers were *Alethe castanea, Chamaetylas poliocephala*, and *Neocossyphus poensis*. Of the African ant-following species, these three have been identified as the specialized ant-followers, depending most heavily on driver ant swarms to forage (Willis, 1986; Peters et al., 2008; Craig, 2022). Furthermore, at our site, these species attended swarms at disproportionally higher rates compare to other regular to occasional ant-following insectivores and displayed behavioral adaptations for tracking and locating ants similar to obligate ant-followers in the Neotropics (Rodrigues, 2024). Understory insectivores included *Illadopsis rufipennis*, *I. fulvescens*, *I. cleaveri*, *Hylia prasina*, *Sheppardia cyornithopsis*, *Bleda notatus*, and *B. syndactylus*. These species forage for insects and other invertebrates near the forest floor and are similarly vulnerable to anthropogenic disturbance. While these species sometimes also attend ant swarms, they do not specialize on driver ants. We pooled *I. rufipennis* and *I. fulvescens* captures as *Illadopsis* sp. due to their similar ecological niches and challenges in differentiating them in the field.

2.4 Feather corticosteroid quantification

We measured fCORT concentrations and performed extraction using the protocol described by Bortolotti et al (2008) and ELISA kits (Corticosterone ELISA kit; Neogen Corporation, Ayr, UK), as validated by Carbajal et al. (2014). For *A. castanea*, *B. notatus*, and *C. poliocephala*, we used 20 rectrices (ten from each forest type). For *B. syndactylus* we used 16 rectrices (six from primary and ten from logged forest forest), and for *Illadopsis* spp. We used 14 rectrices (eight from primary six in logged forest).

2.5 Statistical analysis

We used generalized linear mixed models (GLMMs) to determine how life history and population traits differed between forest types (R version 4.2.2 and the lme4 package (Bates et al., 2015; R Core Team, 2022). We fit seven models with breeding status (binary), molting stage (binary), breeding-molt overlap (binary), age ratio for species that undergo complete preformative molt (binary), age ratio for species that undergo partial preformative molt (binary), fCORT (numerical) and body condition (numerical) as response variables. The explanatory variables were the individual effects of forest type and species, and their interaction. We included year (i.e., field season) as a random effect. To avoid pseudoreplication, we only included the first capture of each individual per season (individuals are often captured repeatedly in a day or season) leaving us with 792 birds of our focal species in primary forest and 401 in secondary forest. Best-fit models were selected using likelihood ratio tests, starting with the most complex model, followed by subsequent reverse step-wise deletion of non-significant terms. We thought it important to model the age ratio separately depending on the molting strategy as the age groups were different depending on the molt strategy of the species. Models were used to predict (predictMerMod function in the lme4 package, v1.1-26; (Bates et al., 2015) life history and population traits for each species.

3 Results

3.1 Proportion of breeding and molting individuals

We found no effect of forest type on the probability that an individual was breeding (94/792 in primary and 38/401 in secondary) or undergoing molt-breeding overlap (10/325 in primary and 12/190 in secondary) for any of the focal species (LRT vs best-fit: $X^2 = 8.14$, P = 0.52, df = 1192; $X^2 = 0.44$, P = 0.52, df = 514) (Table 1). However, the best fit model showed that forest type had a significant effect on the probability that a bird was molting (337/792 in primary and 178/401 in secondary) (LRT vs best-fit: $X^2 = 25.69$, P < 0.01, df = 1192) (Table 1). Two ant-following species were significantly more likely to be molting in primary forests than in secondary forests: *A. castanea* and *C. poliocephala* (Figure 1).

3.2 Age ratio

For birds that undergo a complete preformative molt, we found no effect of forest type on the probability that a bird was a juvenile bird (22/290 in primary and 17/170 in secondary) (LRT vs best-fit: $X^2 = 6.26$, P = 0.39, df = 459) (Table 1). In contrast, the best fit model for species that undergo a partial preformative molt showed that forest type had a significant effect on the probability of a bird being on its first year (91/369 in primary and 60/139 in secondary) (LRT vs best-fit: $X^2 = 20.82$, P < 0.0001, df = 514) (Table 1). *A. castanea*, *C. poliocephala*, *N. poensis* and *S. cyornithopsis* had higher probability of a bird being on its first year in secondary forests compared to primary forests (Figure 2).

3.3 Body condition and feather corticoid

The best fit model for body condition showed that forest type had a significant effect (LRT vs best-fit: $X^2 = 19.84$, P < 0.05, df = 1192) (Table 1). The only species that showed a significant difference in body condition was *I. cleaveri*, which weighed on average 7 g/mm more (6.67%) in secondary forest (Figure 3). We detected no effect of forest type on the amount of fCORT for any species (LRT vs best-fit: $X^2 = 0.88$, P = 0.97, df = 89) (Table 1).

4 Discussion

Our study delved into avian responses to selective logging in an Afrotropical lowland rainforest, revealing insights into breeding and molting prevalence, population age ratios, body condition, and stress. Many avian studies rely on point counts or transects to determine some index of abundance or density among habitats, but density can be a misleading index of habitat quality (Van Horne, 1983). By capturing birds and determining their age, mass, molting status, etc., we were able to obtain additional insights on measures that have demographic consequences for bird populations. This work contributes to the broader literature on avian responses to forest disturbance and presents unique findings that enhance our understanding of how birds are affected by anthropogenic disturbance. Noteworthy patterns emerged in age ratio and molting behavior (Table 2).

4.1 Breeding, molting and age ratio

Breeding and molting are both costly life history traits (Romero, 2002). We expected to find a higher proportion of birds breeding, molting in primary forests as they have access to more food resources, more cover, and lower densities of predators (Sekercioglu, 2002; Cosset et al., 2021). We also expected a higher proportion of birds undergoing molt-breeding overlap in secondary forest. However, we did not identify any differences in the proportion of breeding birds or molt-breeding overlap between the two forest types. This might suggest that forest disturbance does not affect the breeding status of our focal species; in other words, the ability to physiologically mobilize the body into breeding condition *per se* does not appear to be limiting population growth/ maintenance at our study system. This was also the case in tropical rainforests in Malaysia where understory birds in primary and selectively logged forests showed no difference in their breeding status (Yap et al., 2007).

TABLE 1 The best fit models for each life history or population trait at the species.

Life history or population traits	Fixed effects included in the best fit model	Random effect	Chi-squared value	P-value	Sample size
Breeding Status	Null Model: No fixed effects	Year	8.14	0.520	1193
Molting Birds	Forest Type + Species + Forest Type * Species	Year	25.69	0.002*	1193
Molt-Breeding overlap	Null Model: No fixed effects	Year	0.44	0.505	515
Age - partial incomplete	Forest Type + Forest Type * Species	Year	20.82	>0.001***	515
Age - complete	Null Model: No Fixed Effects	Year	6.26	0.391	460
MBS	Forest Type + Species + Forest Type * Species	Year,Age	19.84	0.019 *	1193
fCORT	Null Model: No Fixed Effects	Year	0.88	0.972	90

The fixed and random effects for each model are shown, if the best-fit model included any. Model selection was carried out by starting with the most complex model and carrying.
* refers to a p-value smaller than 0.05 and *** to a p-value lower than 0.01.

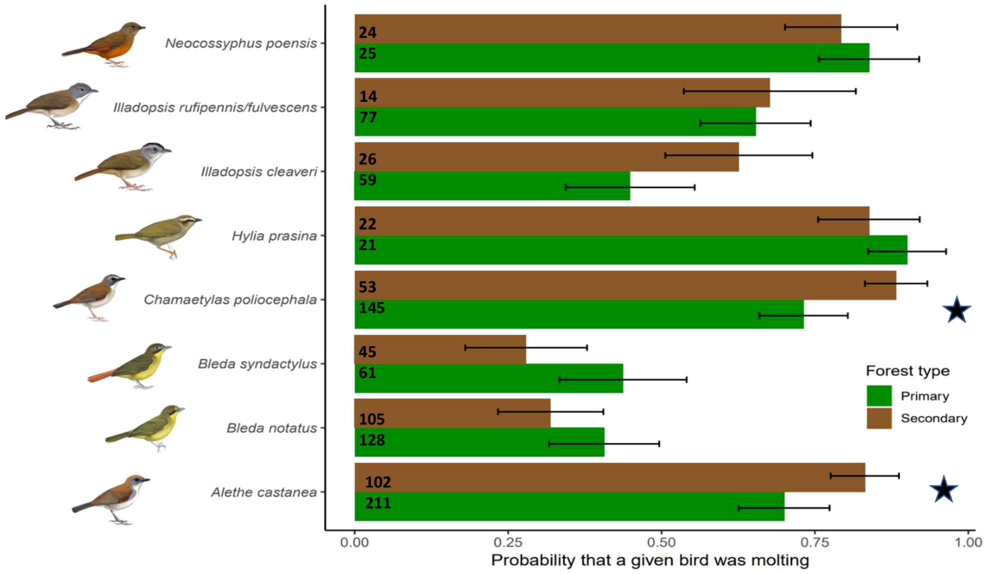

FIGURE 1
Probability that a given bird was molting in primary (green) and secondary (brown) forest as predicted from the best fit model. Numbers represent the sample size of individual bird captures. Error bars represent 95% confidence intervals. Stars indicate statistical significance at alpha = 0.05. Species illustrations by Faansie Peacock.

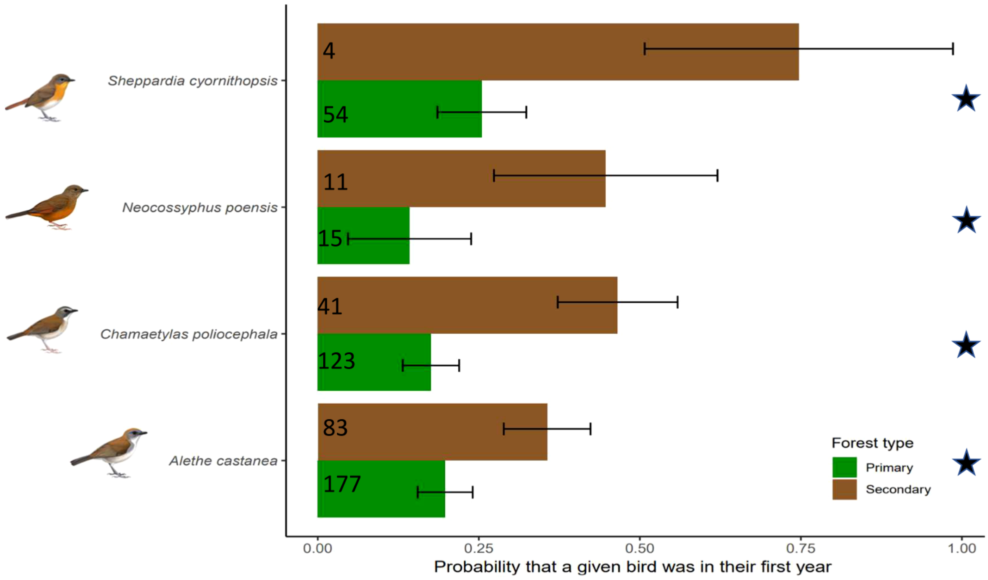

FIGURE 2
Probability that a given bird was in their first year in primary (green) and secondary (brown) forest as predicted from the best fit model. Numbers represent the sample size of individual bird captures. Error bars represent 95% confidence intervals. Stars indicate statistical significance at alpha = 0.05. Six species are excluded because they have complete pre-formative molts and are thus indistinguishable from adults just weeks after leaving the nest and a different model examined the age ratio. Species illustrations by Faansie Peacock.

With that said, relatively little is known about the annual cycle of Central African birds. Regional variation may be possible, particularly in species that occupy the entire Congo Basin as well as forests of East Africa and/or West Africa (in the case of the latter species); regional influences on annual life cycles could be present for other more geographically restricted species as climatic influences on seasonality across the Congo Basin and into the Lower Guinea Forest. Though differences may vary subtly, they may appreciably impact the timing and duration of breeding and molting periods. It is possible that our study did not capture the optimum breeding period for these species due to the temporally limited nature of our study. Incorporating data from the cloudy dry season and shoulder seasons where feasible may

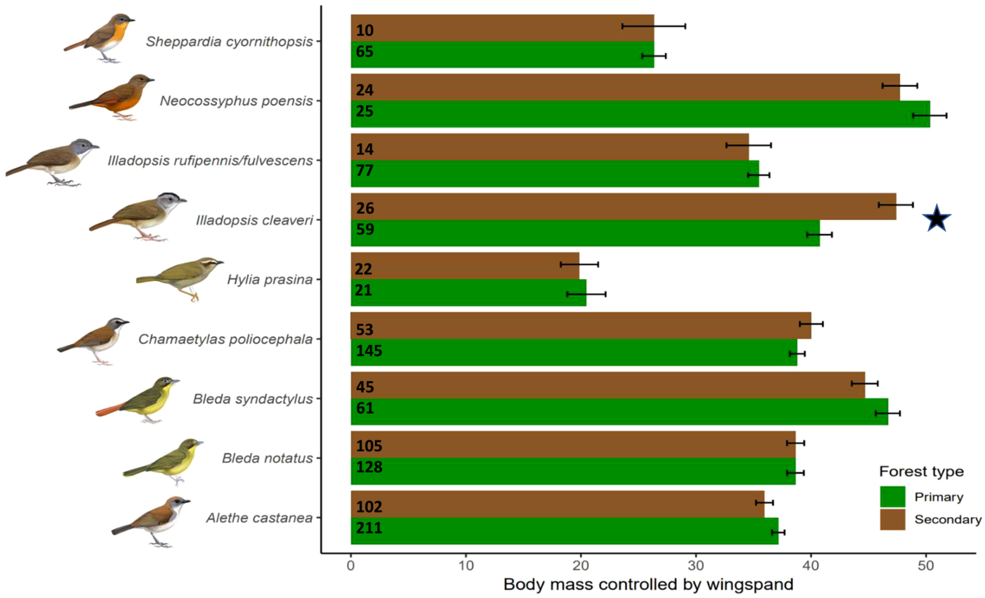

FIGURE 3
Body condition (body mass corrected by wing length) of birds captured in primary (green) and secondary (brown) forest as predicted from the best fit model. Numbers represent the sample size of individual bird captures. Error bars represent 95% confidence intervals. Stars indicate statistical significance at alpha = 0.05. Species illustrations by Faansie Peacock.

TABLE 2 Summary of statistically significant differences in life history and population traits between the primary and secondary forest for each bird species.

Species	Molt strategy	Capture rate (from Barrie et al., in review)	Proportion of birds breeding	Proportion of birds in molt	Molt-breeding overlap	Age	MBS	fCORT
Alethe castanea	Partial preformative	Higher in Primary	NS	Higher in Primary	NS	More first year birds in Secondary	NS	NS
Bleda notatus	Complete preformative	NS	NS	NS	NS	NS	NS	NS
Bleda syndactylus	Complete preformative	NS	NS	NS	NS	NS	NS	NS
Chamaetylas poliocephala	Partial preformative	Higher in Primary	NS	Higher in Primary	NS	More first year birds in Secondary	NS	NS
Illadopsis cleaveri	Complete preformative	Higher in Primary	NS	NS	NS	NS	Higher in Secondary	NS
Illadopsis rufipennis/ fulvescens.	Complete preformative	Higher in Primary	NS	NS	NS	NS	NS	NS
Hylia prasina	Complete preformative	NS	NS	NS	NS	NS	NS	
Neocossyphus poensis	Partial preformative	NS	NS	NS	NS	More first year birds in Secondary	NS	
Sheppardia cyornithopsis	Partial preformative	Higher in Primary	NS	NS	NS	More first year birds in Secondary	NS	

NS indicates no significant difference.

provide further insights into how the annual life cycle may be influenced by habitat degradation.

Additionally, our study did not address other demographic markers such as hatching or fledging success. With higher densities of predators and fewer resources, it is likely that primary forest specialists relegated to selectively logged forests will have more failed breeding attempts (Thiollay, 1999; Cosset et al., 2021).

In contrast, we found that the proportion of molting birds in two ant-following bird species was higher in primary forests. In Malaysia, species sensitive to forest degradation molted in higher proportions in primary forest compared to secondary forests (Yap et al., 2007). We expected this to be the case, since prior research indicated that species could alter their annual molt in habitats according to food availability (Marini and Durães, 2001). Foster (1975) suggested that suspension of molt could be an environmental adaptation to ensure successful breeding attempts. If secondary forests are indeed more challenging environments for these birds (e.g., fewer *Dorylus* ants to follow), this may increase the likelihood that a bird would alter their molt cycle to ensure a successful breeding attempt and avoid the consequences of molt-breeding overlap. All of the above could be caused due to reduce raid activity of *Dorylus* ant activity during the dry season is in secondary forests reducing the foraging opportunities for ant-following birds (Kumar and O'Donnell, 2009). This is likely because secondary forests have a more open canopy and a more unstable microclimate making the birds more vulnerable during the dry season (Cao and Sánchez-Azofeifa, 2017). As a result, these birds would delay their molt cycle to a later season with a higher resource availability, although we are unable to test for that as our data was collected during the dry season. The two ant-following species that had the higher molting probability in primary forests (*A. castanea* and *C. poliocephala*) are also captured about twice as often in primary forest at our study site, suggesting that they are sensitive to forest disturbance (Barrie et al., in review).

Among the study species we could age more precisely (due to partial preformative molts creating distinct molt limits), we found a higher proportion of first-year birds in second growth forest. Variation in age ratios across different forest types can be attributed to several mechanisms. First, obligate ant-following birds in the Neotropics hold large, non-exclusive home ranges and although they exhibit low territoriality, they are, however, aggressive and compete for the most profitable regions at swarm fronts (Willson, 2004). Although little is known about their behavior, low territoriality and high competition at swarm fronts have similarly been observed in African ant-followers (Brosset and Erard, 1986). This competition for space at the swarm front intensifies in denser populations (Willson, 2004). Therefore, it is likely that some species may adhere to an ideal despotic distribution where young and potentially dispersing individuals select habitats with fewer antagonistic individuals (Fretwell and Calver, 1969) resulting in young and dispersing birds occurring in second growth forest, habitats characterized by lower densities of ant-following birds (Barrie et al., in review). Regardless of the mechanism, a population with a higher proportion of first year birds is less productive, as first year birds have a lower survival rate and are first-time breeders, which results in lower population growth rate (Pyle et al., 2020).

4.2 Body condition and fCORT

We did not detect any differences in body condition for all but one species; contrary to our predictions, *Illadopsis cleaveri* had a higher body condition in secondary forests (Figure 3). We speculate that changes in vegetation structure in the secondary forest may have benefitted *I. cleaveri*—the smallest-bodied and smallest-billed *Illadopisis* at our site—perhaps releasing it from competition from the other, larger *Illadopsis* species that also spend much time on the forest floor looking for arthropods. Indeed, *I. fulvescens/rufipennis* is nearly absent from the secondary forest; *I cleaveri* is also quite rare there (Barrie et al., in review) but perhaps is better adapted to the secondary forests' more cluttered understory. Jones et al. (2022) describe similar results in a study looking at changes in the body condition of 20 understory birds across a gradient of deforestation in tropical forests in Western Andes of Colombia. They found that some species benefited from the changes in the vegetation structure allowing them to increase their body condition, which then had a positive effect on their breeding condition.

We investigated the fCORT levels of six species as an integrated measure of physiological stress aggregated over the period of feather growth (Messina et al., 2020). However, we did not identify any differences in fCORT levels between the forest types for our focal species. Previous work (Bortolotti et al, 2008) has indicated fCORT levels are most closely associated with the frequency or magnitude of a CORT stress response (i.e., acute stress). Therefore, the lack of a difference suggests there is no difference between habitats in physiological stressors, specifically during the period of feather molt. It is possible that differences do exist between habitats at other points in the annual cycle, or in baseline CORT levels, where elevated levels would indicate chronic stress, such as that caused by prolonged food shortage (e.g., Marra and Holberton, 1998). Future work could consider blood CORT levels at multiple timepoints and challenge experiments to both quantify baseline levels and the magnitude of the stress response between habitats, although this approach presents methodological challenges in the field (e.g., Wingfield et al., 1992).

5 Conclusions

Our study brought to light changes in life history and demographic traits caused by forest degradation in sensitive understory tropical birds. It also highlighted the importance of studies looking beyond the many studies that clump species at the guild level: we demonstrated that only the most sensitive species within guilds displayed changes in their life history and population traits. In the secondary forest, we identified a decrease in the proportion of molting in two ant-following species and detected a higher proportion of first year birds in four species. All of the species that we identified as having alterations in their life history and population traits were also 50% less common in secondary forest (Barrie et al., in review) (Table 2) emphasizing the sensitivity of these species. A comprehensive model of population dynamics could provide further information on the impacts that limit population growth in degraded forests such as juvenile and adult survival rates and nesting success. With this information at hand, we could better explain the patterns that we observed in this study such as the higher proportion of first year birds in secondary forests. Finally, given the keystone nature of *Dorylus* ants (Peters et al., 2009), and the predicted increase in selective logging across the Afrotropics, it is critical to gain a better understanding of how selective logging and other forms of anthropogentic disturbance impact the behavior and therefore integrity of ant-following bird populations.

Data availability statement

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

Ethics statement

The animal study was approved by Institutional Animal Care and Use Committee NZP-IACUC Action on Proposal #14-34 at Smithsonian National Zoological Park. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

PN: Data curation, Formal analysis, Writing – original draft, Writing – review & editing. BK: Writing – review & editing, Data curation. PR: Writing – review & editing, Data curation. KB: Funding acquisition, Methodology, Project administration, Resources, Writing – review & editing. CT: Investigation, Resources, Writing – review & editing. JC: Writing – review & editing. JW: Data curation, Funding acquisition, Methodology, Project administration, Writing – review & editing. LP: Writing – review & editing, Funding acquisition, Methodology, Project administration, Resources, Supervision. SEM: Data curation, Writing – review & editing. SLM: Writing – review & editing, Data curation.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

Publisher's note

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Specialized insectivores drive differences in avian community composition between primary and secondary forest in Central Africa

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The human population of sub-Saharan Africa is projected to triple by 2100, drastically increasing anthropogenic pressure on biodiversity. When rainforest is disturbed by anthropogenic drivers, species respond heterogeneously; these patterns have rarely been quantified for Congo rainforest fauna. Our objective was to understand how community composition changed with human disturbance—with particular interest in the guilds and species that indicate primary rainforest. At a long-term bird banding site on mainland Equatorial Guinea, we captured over 3200 birds across 6 field seasons in selectively logged secondary forest and in largely undisturbed primary forest. Our multivariate ordination indicated a significant split between primary and secondary forest communities. We caught 47% fewer birds in secondary forest overall, with Dorylus ant-followers, mixed-species flockers and terrestrial insectivores showing at least two-fold reductions. We identified 12 species that were characteristic of primary forest. Of those, 10 were strict insectivores: terrestrial insectivores (*Sheppardia cyornithopsis, Illadopsis cleaveri, I. fulvescens/rufipennis*), mixed-flockers (*Phyllastrephus icterinus/xavieri, Elminia nigromitrata, Terpsiphone rufiventer, Pardipicus nivosus, Deleornis fraseri*), ant-followers (*Alethe castanea, Chamaetylas poliocephala*), White-bellied Kingfisher (*Corythornis leucogaster*), and Blue-headed Wood Dove (*Turtur brehmeri*). Only the kingfisher Ispidina lecontei was captured more in secondary forest. This contributes to a growing body of Pantropical literature suggesting that insectivores living on or near the forest floor are vulnerable to rainforest degradation. Notably, few species disappeared entirely in secondary forest (unlike patterns seen in the Neotropics); rather, capture rates of 12 of 30 species (40%) were significantly reduced relative to primary forest. By understanding disturbance-sensitive guilds and species, we might identify the proximate mechanisms responsible for the loss of Afrotropical birds, thus helping to manage communities as forest disturbance continues.

KEYWORDS

Afrotropics, rainforest, disturbance, ant-following birds, insectivorous birds, mixed species flocks, understory insectivores, primary and secondary forest

1 Introduction

The Congo rainforest (herein including Lower Guinea Forest) Central Africa constitutes the second largest tract of tropical rainforest on Earth (Hardy et al., 2013) and serves as a significant global carbon sink (Baccini et al., 2012; Hubau et al., 2020). Still, Afrotropical forests are experiencing increasing rates of forest loss and disturbance, mainly driven by non-mechanized, small-scale agriculture and selective logging (Potapov et al., 2017; Tyukavina et al., 2018). These drivers are linked to the increasing human population of sub-Saharan Africa (Potapov et al., 2017; Tyukavina et al., 2018), which is projected to triple to almost 3.8 billion by the end of the 21st century (Vollset et al., 2020). Industrial logging and large-scale mechanized agriculture will also likely increase in the future, which may allow increased encroachment of smallholder agriculture into previously undisturbed areas (Tyukavina et al., 2018). Given these threats and their effects on existing forests, it is essential to address gaps in our understanding of how the region's biodiversity responds to forest degradation. In Equatorial Guinea, most high-grade selective logging took place during the oil boom period of the 2000s and early 2010s, but primary forest loss has stabilized and is lower than in other central-African countries (Tyukavina et al., 2018). This provides a valuable opportunity to gather baseline data on tropical forest ecosystems which can then aid in their management and protection. Furthermore, it is important to understand the value of secondary forest in fostering biodiversity in the face of increased forest degradation and a changing climate (Poorter et al., 2016). In Western and Central Africa, primary forests only account for 38% of total forest area (Food and Agricultural Organization of the United Nations, 2020); as such, simply protecting primary forests alone may not be a realistic or effective way to conserve biodiversity and ecosystem function (Cox and Underwood, 2011; Struhsaker et al., 2005).

Afrotropical forests are particularly important for the conservation of terrestrial biodiversity (Jung et al., 2021). Despite their designation as global biodiversity hotspots and increasing pressure from population growth (Morris, 2010; Pereira et al., 2012), Afrotropical forests are disproportionately understudied compared to the Neotropics and Asian Paleotropics (Malhi et al., 2013). For example, Di Marco et al. (2017) found that, of 2,553 articles on conservation published between 2011 and 2015, only 10% focused on the Afrotropics. Of those, most focused on large mammals and several countries were omitted completely, with little focus on other terrestrial taxa, like avifauna, which can be indicators of forest health. Tropical birds also play important roles in ecosystem functioning and services (Gray et al., 2007; Newbold et al., 2013); insectivores can control agricultural pests (Whelan et al., 2008; Ferreira et al., 2023)and frugivores can aid in seed-dispersal and germination (Şekercioğlu, 2006; Wenny et al., 2011). Certain guilds—such as understory insectivores—may also act as sentinels of habitat disturbance or degradation as they show particular sensitivity to such changes in habitat conditions; however, this has rarely been investigated or quantified in the Afrotropics (Powell et al., 2015). Tropical forest birds are often used to understand the effects of forest degradation on ecological integrity, due to being a diverse, sparsely hunted, and often sensitive group, with extensive data on the morphological and ecological traits of species across communities (Şekercioğlu et al., 2012; Bregman et al., 2014). Pantropical and global literature reviews such as those of Gray et al. (2007), Newbold et al. (2013), and Bregman et al. (2014) highlight that tropical insectivores are more vulnerable than other guilds.

In general, studies from other tropical regions have shown that understory insectivores are particularly sensitive to forest fragmentation (Stouffer and Bierregaard, 1995; Robinson, 1999; Beier et al., 2002; Şekercioğlu et al., 2002; Sodhi et al., 2004; Barlow et al., 2006). In regenerating secondary forests in the Amazon, understory insectivores—particularly the terrestrial insectivores—took decades longer than other avian guilds to reach densities comparable to primary forest (Powell et al., 2013). Insectivores that participate in mixed-species flocks (species that forage and move together; Winterbottom, 1943, Morse, 1970) have shown high sensitivity to habitat degradation and disturbance; in the Asian Paleotropics, mixed-flock participants are the most sensitive group to human activity along with forest and understory specialists (Lee et al., 2005; Mammides et al., 2015). In the Neotropics, the species richness, stability and size of mixed-flocks are sensitive to habitat fragmentation (Stouffer and Bierregaard, 1995; Thiollay, 1997; Develey and Stouffer, 2001; Maldonado-Coelho and Marini, 2004; Mokross et al., 2014, 2018). It is possible that African mixed-flock species could respond differently to these threats as they appear to be less stable, with participants not defending a communal territory and with more species being opportunistic flock members (McClure, 1967).

Many insectivorous birds follow swarms of predatory ants (hereafter "ant-followers"), such as Afrotropical driver ants (*Dorylus* spp.) or the Neotropical army ant *Eciton burchellii*, and feed on the organisms that flee from the swarm (Brosset, 1969; Willis and Oniki, 1978; Chesser, 1995). Swarmraiding ants are considered keystone species that have a profound impact on ecosystems, with *Dorylus* colonies containing up to 20 million individuals (Gotwald, 1995). Neotropical ant-following birds are often among the first guilds to disappear or decrease in richness and flock size in small forest fragments (Harper, 1989; Stouffer and Bierregaard, 1995; Roberts et al., 2000; Kumar and O'Donnell, 2007). Though the Afrotropical equivalents are less well known, a handful of studies from Africa have now found that ant-followers and terrestrial insectivores decrease in species richness or abundance in response to disturbance (Waltert et al., 2005; Peters and Okalo, 2009; Jarrett et al., 2021; Miller et al., 2021).

The overall aim of this study was to describe if and how Central African bird communities differ between primary and disturbed secondary rainforest. The primary objectives were:

- To determine the degree to which understory bird communities differ between primary and secondary forest (via ordination).
- To compare capture rates of foraging guilds and species to determine the drivers of community dissimilarity between primary and secondary forests (via mixed models).
- To identify which species are "indicators" of primary forest (via indicator species analysis). Here, we define a primary forest indicator as a species that is found significantly less frequently in secondary forest in our indicator analysis and is therefore assumed to be sensitive to human disturbance.

Based on evidence from other tropical regions (Stouffer and Bierregaard, 1995; Robinson, 1999; Beier et al., 2002; Şekercioğlu et al., 2002; Sodhi et al., 2004; Barlow et al., 2006; Powell et al., 2013), we predict that the three understory insectivore guilds (terrestrial insectivores, mixed-species flockers, and ant-following birds) will have lower capture rates in secondary forest.

2 Methods

2.1 Study area

We carried out this research in lowland rainforest adjacent to the city of Ciudad de la Paz on the border between the Wele-Nzas and Centro Sur provinces of mainland Equatorial Guinea. Our

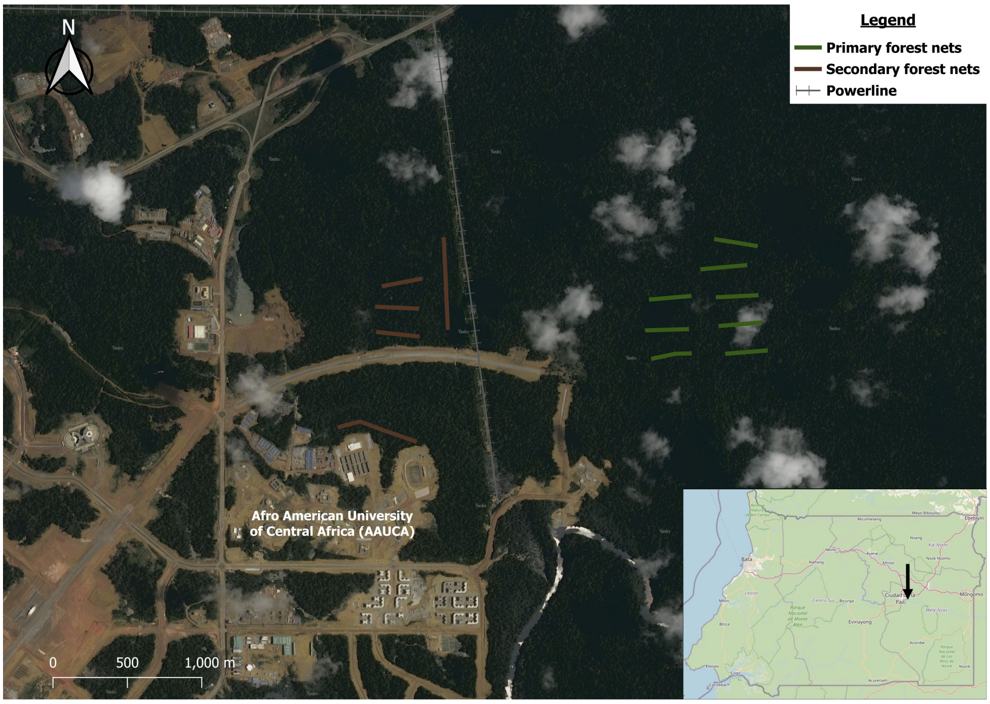

FIGURE 1
Distribution of net lanes in primary and secondary forest near Ciudad de la Paz, Equatorial Guinea. Satellite imagery: "Yandex Satellite 2022"sourced from https://core-sat.maps.yandex.net/tiles?l=sat&v=3.1025.0&x={x}&y={y}&z={z}&scale=1&lang=ru_RU using plugin "quick maps" in QGIS version 3.38.2. The inset map shows the field site location within continental Equatorial Guinea. © OpenStreetMap contributors, available under the Open Database License (see https://www.openstreetmap.org/copyright).

study sites consisted of two ca. 70 ha plots in tall, closed canopy forest within walking distance of the AfroAmerican University of Central Africa (Figure 1). The plots have revealed no recent evidence of forest elephants during our work (i.e., no footprints, no camera trap images), but otherwise the full complement of Central African mammal fauna exist on the immediate landscape (Murai et al., 2013; DeGroot, 2024). The primary forest plot is in minimally disturbed primary forest that was lightly selectively logged through the 20th century and as late as the 1980s. Effectively all the lowland tropical rainforest in Equatorial Guinea has been at least lightly selectively logged, so we believe this primary forest plot to represent a reasonable baseline. The primary forest plot lies in the northernmost portion of a continuous block of several hundred thousand hectares of forest, broken only by a handful of lightly traveled roads; the closest road to this plot lies 500 m to the west. The secondary forest plot remains closed-canopy forest, but has been regularly selectively logged for decades, with the last harvests (especially of Okume *Aucoumea klaineana*) occurring in about 2017. Most of the secondary forest plot was isolated in the 2000s during the construction of the new capital city: by 4lane paved roads to the north and west, a large (~50 m wide) dirt road to the south, and high-voltage power lines to the east (~30 m wide gap with regularly trimmed vegetation ~2–3 m tall); this effectively created a forest fragment of ~250 ha with considerable edge habitat and regenerating canopy gaps (Andrews, 1990; Strevens et al., 2008). Canopy height above our nets was similar between the two plots where we netted, including average canopy height (primary: 14.1 ± 0.5 m SE; secondary 14.1 ± 0.4 m SE), and height of emergent trees (primary: 27 ± 0.9 m SE; secondary 27 ± 0.7 m SE); canopy cover and visibility through the understory were slightly higher in the primary plot (canopy cover: primary: 88 ± 1.3 m SE; secondary 83 ± 2.2 m SE; visibility: primary: 9.5 ± 0.5 m SE; secondary 7.5 ± 0.4 m SE)—which were probably a result of dense treefall gaps that were recovering from selective logging.

2.2 Data collection

We sampled understory birds using mist-nets between 2016–2023 during the sunny dry season (December–February/March), as well as once in July 2022 (the cloudy dry season). We did not sample during the rainy season due to the impracticality and animal welfare issues of carrying out fieldwork/mist-netting in heavy rain. Mist-net lanes (hereafter "lanes") run in one morning was our sample unit; these lanes consisted of linear transects of typically 20 nets (12 x 2.5 m, 36-mm mesh; Figure 1). The number of nets per lane varied somewhat due to logistical constraints, treefall gaps etc; the mean number of nets per lane was 21.29 ± 0.99 SE. We ran eight lanes in the primary forest plot (N = 160 nets); this locality accounted for 11,070 mist-net hours (hours of operation x no. mistnets). In the secondary forest plot, we ran five net lanes (N = 145 nets), which accounted for 8807 mist-net hours. These differences in net lane length and effort between plots were accounted for during the modelling (see below). We sampled each net lane for two consecutive days each year and approximately six hours per day from ca. 06h30–12h30. The number of net lanes that we sampled on any given day was dependent on the number of field crew present. We adjusted effort when faced with poor weather conditions (e.g., heavy rain). Net lanes were separated by at least 200 m to facilitate spatial independence (Hill and Hamer, 2004).

Three genera had species pairs that were challenging to identify in the hand to species level were lumped at the genus level; ongoing genetic analysis will aid future efforts. These three pairs were *Phyllastrephus icterinus/xavieri* (Icterine/Xavier's Greenbul), *Criniger calurus/ndussumensis* (Redtailed/White-bearded Greenbul), and *Illadopsis fulvescens/rufipennis* (Brown/Pale-breasted Illadopsis). For ease of communication, these species pairs are included when referring to "species" throughout. Prior to any analysis, we removed all same-day recaptures of individuals (identified via band number) from the dataset.

2.3 Statistical analysis

2.3.1 Non-metric multi-dimensional scaling

To visualize bird community differences between forest types, we conducted a nonmetric multidimensional scaling (NMDS) ordination analysis using the function "metaMDS" from the package "vegan" (Oksanen et al., 2020) in R (R Core Team, 2022). Raw count values were logtransformed to reduce spurious results driven by rare and/or hyper-abundant species. Species with less than five observations were removed from the dataset. We used Bray-Curtis distance estimates. A PERMANOVA was then conducted on the NMDS output using the function "adonis" from the package "vegan" (Oksanen et al., 2020) to determine if primary and secondary forest bird communities were significantly different.

2.3.2 Generalized linear mixed models

To determine if captures rates differed significantly between the primary and secondary forest plots, we fitted generalized linear mixed models (GLMMs) to the data in R version 4.2.1 (R Core Team, 2022). In these analyses, we included only our focal, species, which we defined as those caught >10 times such that statistical models were likely to converge. We classified these species into guilds (Table 1) based on diet composition obtained from EltonTraits1.0 (Wilman et al., 2014), field observations, and species accounts in Birds of the World (Billerman et al., 2022).

We fitted separate models to the data for each guild and species, using the package glmmTMB (Brooks et al., 2017), with a negative binomial distribution to account for overdispersion in count data. For each model, we used number of captures per net lane/per day ("capture rate") as the response variable. "Forest type" (primary vs secondary) and "Day" were included in the models as fixed effects. "Day" refers to day 1 vs day 2 of back-to-back sampling at each net lane within each field season—to account for the typical ~30% decline in capture rates that banders see on the second consecutive netting day in the same location (L.L.P., J.D.W. pers obs.). Field season was included as a random effect to account for inter-annual variation and net lane was included as a random effect to account for variation associated to specific lane location.

TABLE 1 Summary of the results of model selection for the guilds and species analysed—specifically the chi-squared value and *p*-value obtained from comparison, via likelihood ratio test, of models with and without forest type as an explanatory variable. A *p*-value of <0.05 indicates that the model containing forest type is the better fit. In nearly all cases of a significant difference between forest types, capture rate was higher in primary forest; the lone exception was *Ispidina lecontei*, which showed the opposite pattern.

Species	Guild	Chi-sq	*p*-value	Significance
	All species	7.0776	0.007805	**
	Mixed flockers	9.9841	0.001579	**
Hylia prasina		0.6765	0.4108	
Sasia africana		3.6674	0.05549	
Nicator chloris		0.0004	0.9859	
Parmoptila woodhousei		1.7464	0.1863	
Pardipicus nivosus		5.0451	0.0247	*
Terpsiphone rufiventer		5.7088	0.01688	*
Deleornis fraseri		6.3584	0.01168	*
Elminia nigromitrata		6.9157	0.008544	**
Phyllastrephus icterinus/xavieri		9.4936	0.002062	**
	Ant-followers	6.6597	0.009862	**
Criniger chloronotus		0.1725	0.6779	
Neocossyphus Rufus		3.7517	0.05275	
Neocossyphus poensis		0.1929	0.6605	
Bleda syndactylus		0.0526	0.8186	
Bleda notatus		1.3685	0.2421	
Chamaetylas poliocephala		9.7366	0.001806	**
Alethe castanea		7.5975	0.005845	**
	Terrestrial Insectivores	12.591	0.0003875	***
Stiphrornis erythrothorax		1.9848	0.1589	
Sheppardia cyornithopsis		17.662	2.639E-05	***
Illadopsis cleaveri		10.367	0.001283	**
Illadopsis rufipennis/fulvescens		16.482	4.911E-05	***
	Wattle-eyes	0.688	0.4068	
Platysteira castanea		0.0249	0.8746	
Platysteira concreta		2.9034	0.08839	
Ispidina lecontei	Insectivorous Kingfisher	10.777	0.001028	**
	Frugivore-invertivores	2.0499	0.1522	
Eurillas latirostris		2.1277	0.1447	
Eurillas virens		0.5647	0.4524	
Cyanomitra olivacea	Omnivore	2.5731	0.1087	
Spermophaga haematina	Omnivore	0.2949	0.5871	
Corythornis leucogaster	Insectivore-vertivore	11.94	0.0005495	***
Turtur brehmeri	Insectivore-granivore	6.9045	0.008598	**
Criniger calurus/ndussumensis	n/a	1.4201	0.2334	

Asterisks indicate level of significance (* for *p*-value <0.05, ** for <0.01, and *** for <0.001).

In addition to the random effect of net lane, we sought to further account for potential spatial autocorrelation between lanes by applying a penalty for lanes located near other net lanes using the "offset" function in the GLMM. In other words, we adjusted the baseline level of the response variable to be lower for lanes close to other lanes that were less spatially independent, and higher for more spatially isolated lanes. To appropriately calibrate this offset at the correct spatial scale (i.e., the scale at which birds move), we first used our georeferenced recapture data to quantify the maximum distance that individual birds typically moved. Across individuals, the mean maximum distance between recaptures was 238 ± 25 m 95% CI. From this, we conservatively took the high end of the 95% CI (263 m) and used it to draw a 263 m "buffer zone" around each net lane. For each net lane, the number of other net lanes that fell within its buffer zone (i.e., the amount of overlap) was used to create a proportion (1/overlap), which was used as the offset. Using this method, individual net lanes that were closest to each other and had more overlap with the buffer were penalized most by the offset as they had a lower baseline level for the response variable. An offset for net hours per net lane per day was also included to account for varying effort among lanes. For each guild and species, backwards stepwise model selection was carried out using likelihood ratio tests. In two cases, the random effect of field season had to be removed from models to facilitate model convergence. Thus, for *Turtur brehmeri* and *Hylia prasina*, inter-annual variation is not accounted for in the results.

2.3.3 Indicator analysis

We conducted an indicator species analysis using the package "indicspecies" (De Cáceres and Legendre, 2009) to identify the species that were significantly associated with primary and secondary forest. This test allowed us to determine the ecological "preferences" of species among a set of alternative site groups (i.e., sites within each forest type) and to associate their species distribution patterns with these groups of sites (De Cáceres and Legendre, 2009). Hence, these species can be considered as proxies to evaluate community integrity within each forest type. We calculated the association index value ("r.g") using 10,000 permutations and standardized captures by per 1000 mist-net hours. This analysis did not include data from the most recent field season.

3 Results

We captured 2090 individuals in primary forest during 11,070 net hours (0.19 birds per net hour) and 1133 individuals in secondary forest during 8807 net hours (0.13 birds per net hour). Of the 78 species captured, 22 were exclusively caught in primary forest and 15 were exclusively caught in secondary forest (Supplementary Table S1). We calculated the Shannon-Wiener Diversity Index for each plot, which was roughly equal between the two (H' = 2.98 in primary and H' = 2.89 in secondary). We carried out statistical analyses for 30 focal species caught more than 10 times (37% of all species caught and 95.5% of all captures). All species were caught in both forest types, except for *Ispidina lecontei* (African Dwarf Kingfisher), which was caught exclusively in secondary forest (although we did detect this species visually on several occasions in the primary forest plot). Only three individuals of three species—*Spermophaga haematina* (Western Bluebill), *Indicator maculatus* (Spotted Honeyguide), and *Eurillas latirostris* (Yellow-whiskered Greenbul)—moved between primary and secondary forest plots. The species not included in our analyses (i.e., those captured less than 10 times) likely included canopy or mid-story species (such as *Pogoniulus atroflavus*, *I. maculatus*, and *Stelgidillas gracilirostris*) as well as a few migrant species. Considering only these focal species, we had 1999 captures in primary forest and 1078 captures in secondary forest.

Despite a broad overlap in species composition and canopy cover between forest types, our NMDS ordination indicated that the community composition in primary forest was significantly different from that of secondary forest (F= 5.6936, P= 0.0035, R^2 = 0.34106, Figure 2). *Alethe castanea* (Firecrested Alethe), *Chamaetylas poliocephala* (Brown-chested Alethe), and *Illadopsis cleaveri* (Blackcap Illadopsis) were central to the primary forest NMDS ellipse, suggesting that they were most representative of the primary forest community. *Hylia prasina* (Green Hylia), *Platysteira castanea* (Yellow-bellied Wattle-eye), and *Spermophaga haematina* (Western Bluebill) were central representatives of secondary forest.

Based on a GLMM that included all species, capture rates were 47.3% lower in secondary forest overall. When modeling guild-level differences using GLMMs, we estimated that ant-followers, terrestrial insectivores and mixed-flockers had significantly higher capture rates in primary than in secondary forest, with 1.9-, 3.3-, and 2.8-times increases, respectively (Table 1). Wattle-eyes showed no significant difference in capture rate between forest types.

Several insectivorous species appeared to be driving the guild-level trends (Table 1, Figure 3). Of the ant-followers, *Alethe castanea* and *Chamaetylas poliocephala* were captured ca. 2.5 and 3 times more frequently, respectively, in primary forest than in secondary forest. Conversely the antfollowers *Bleda notatus* (Lesser Bristlebill), *Bleda syndactylus* (Red-tailed Bristlebill), *Neocossyphus poensis* (White-tailed Ant-Thrush), *N. rufus* (Red-tailed Ant-Thrush), and *Criniger chloronotus* (Eastern Bearded Greenbul) showed no such difference.

Except for *Stiphrornis erythrothorax* (Orange-breasted Forest Robin), all species of terrestrial/nearground insectivores had significantly higher capture rates in primary than in secondary forest; eleventimes higher for *Sheppardia cyornithopsis* (Lowland Akalat), nine-times higher for *Illadopsis fulvescens/rufipennis*, and three-times higher for *Illadopsis cleaveri*.

Of the mixed-flockers, *Phyllastrephus icterinus/xavieri*, *Elminia nigromitrata* (Dusky Crested Flycatcher), *Pardipicus nivosus* (Buff-spotted Woodpecker), *Terpsiphone rufiventer* (Red-bellied Paradise-Flycatcher), and *Deleornis fraseri* (Fraser's Sunbird) all had significantly higher capture rates in primary forest (five, four, three, three, and six times higher, respectively). The remaining mixed-flockers showed no significant differences in capture rates between habitats. *Turtur brehmeri* (13/15 captures in primary), a species that consumes both invertebrates and seeds, and *Corythornis leucogaster* (White-bellied Kingfisher; 26/27 captures

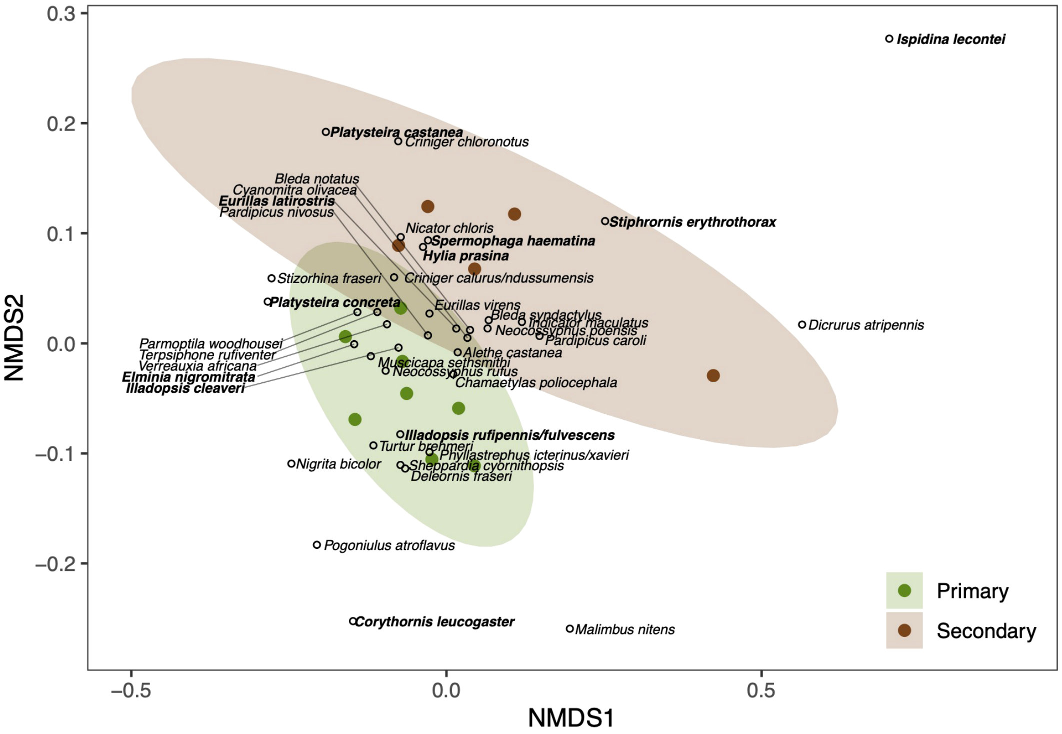

FIGURE 2
Ordination plot using non-metric multidimensional scaling that significantly separates the community into species representing primary forest and those representing secondary forest. Each open dot represents a species, and the ellipses represent the 95% confidence interval about the estimate in multivariate space. Bolded species names indicate species significant at the 5% level.

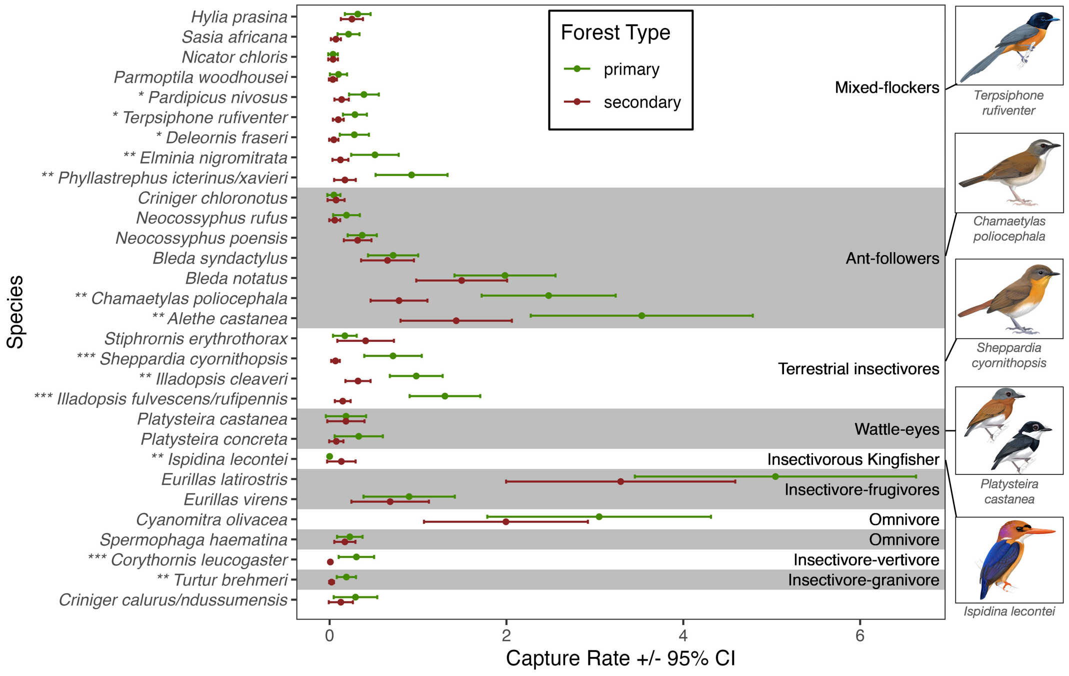

FIGURE 3
Capture rates of focal species in primary and secondary rainforest in Equatorial Guinea, based on the output of mixed models. Asterisks indicate significantly different capture rates between primary and secondary (* for *p*-value <0.05, ** for <0.01, and *** for <0.001). A *p*-value of <0.05 indicates that the model containing forest type was the better fit. Capture rate refers to number of birds captured per net lane (mean 21.29 nets per lane) per ~6 hour morning of netting. Artwork by Faansie Peacock, commissioned by Biodiversity Initiative.

in primary), a species that consumes invertebrates and fish or small ectotherms, both had significantly higher capture rates in primary forest. *Ispidina lecontei* was the only species for which we found significantly higher capture rates in secondary forest (Table 1, Figure 3).

The indicator species analysis showed that *Sheppardia cyornithopsis*, *Illadopsis cleaveri*, and *Illadopsis fulvescens* (terrestrial insectivores) as well as *Alethe castanea* (an ant-follower) were significant indicators of primary forest. One species (*Ispidina lecontei*) was a significant indicator of secondary forest (Table 2).

4 Discussion

4.1 Interpretation of results

Despite the superficial similarity of species richness between our two focal forests, the avian community responded substantially to forest disturbance in terms of relative abundances and community composition. We regularly caught more birds in the primary forest overall: we caught 85% more birds in the primary forest with just 26% more effort; correcting for effort, we caught 46% more birds in primary forest (Supplementary Table S1). Terrestrial insectivores, ant-followers, and mixed-flockers had higher captures rates in primary than in secondary forests, as did *Turtur brehmeri* (insectivoregranivore) and *Corythornis leucogaster* (insectivore-vertivore). Terrestrial insectivores appeared to be the guild most sensitive to disturbance, as indicated by the magnitude of differences in capture rates and the proportion of species driving the trend (4/5). Considering the mixed models, ordination and indicator analysis, the species that appear most representative of primary forest are the antfollowers *Alethe castanea* and *Chamaetylas poliocephala* as well as the terrestrial insectivores *Sheppardia cyornithopsis*, *Illadopsis cleaveri* and *Illadopsis fulvescens/rufipennis*. The insectivorous kingfisher *Ispidina lecontei* appears to be the lone representative of secondary forest.

There could be several mechanisms behind the response of terrestrial insectivores to disturbance and habitat degradation. Arthropod availability may be lower in secondary forest, although

TABLE 2 Results from the indicator species analysis for the 23 bird species present in the primary and secondary forest; association index value of 1 suggests a strong association with a given forest type.

Forest type	Species	Value	*p*-value	Significance
Primary forest	*Sheppardia cyornithopsis*	0.770	0.005	**
	Alethe castanea	0.659	0.015	*
	Illadopsis cleaveri	0.642	0.021	*
	Illadopsis fulvescens	0.589	0.042	*
	Chamaetylas poliocephala	0.569	0.054	.
	Illadopsis rufipennis	0.533	0.155	
	Phyllastrephus sp.	0.484	0.164	
	Elminia nigromitrata	0.468	0.124	
	Platysteira concreta	0.398	0.186	
	Pardipicus nivosus	0.391	0.191	
	Neocossyphus rufus	0.357	0.258	
	Sasia africana	0.284	0.375	
	Deleornis fraseri	0.260	0.433	
	Terpsiphone rufipennis	0.197	0.522	
	Bleda notatus	0.003	0.991	
Secondary forest	*Ispidina lecontei*	0.598	0.033	*
	Stiphrornis erythrothorax	0.466	0.141	
	Neocossyphus poensis	0.459	0.119	
	Spermophaga haematina	0.378	0.213	
	Platysteira castanea	0.362	0.235	
	Bleda syndactylus	0.246	0.423	
	Hylia prasina	0.239	0.444	
	Cyanomitra olivacea	0.044	0.889	

Asterisks indicate level of significance (* for *p*-value <0.05, ** for <0.01).

we cannot say this for certain as we did not measure arthropod abundance in this study. Hypothetically, arthropod availability in general may even be higher in secondary forests or may vary climatically (as Wolfe et al., 2025 suggest), for example due to a dry El Niño year, as was the case in 2016. Further investigation of arthropod abundance at our study site is ongoing, and exploration of seasonal variation would be valuable in future work (see section 4.2). Alternatively, or additionally, foraging tactics may be impacted due to changes in vegetation and light intensity or edge effects from fragmentation (Barlow et al., 2002; Laurance et al., 2002; Powell et al., 2015). For example, a denser understory in secondary forest due to increased light may make it harder for terrestrial insectivores to move along the forest floor and use specialized foraging tactics, as seen with understory insectivores in Australian tropical forests (Pavlacky et al., 2015). Stouffer et al. (2021) noted that, due to their foraging habits, Amazonian terrestrial insectivores are more restricted to specific microhabitats than other insectivores such as ant-followers. At that same site, terrestrial insectivores selected cooler microclimates (Jirinec et al., 2022b), likely exhibiting thermal niche tracking. Further, terrestrial insectivores selected forest microhabitats with denser canopy cover during the dry season (Jirinec et al., 2022a). These results suggest that microclimate warming and homogenization in degraded and fragmented forest may limit the occupancy of secondary forest by terrestrial insectivores. Again in Amazonia, Stouffer and Bierregaard (1995) found that insectivorous guilds declined in abundance and diversity after timber harvest. Additionally, they found that terrestrial insectivores did not show marked recovery over time. Our secondary forest plot could essentially be considered a ~250 ha fragment, being effectively isolated by roads and a powerline, as opposed to the primary plot which is within continuous forest. Powell et al. (2013) showed in the same system as that of Stouffer and Bierregaard (1995) that terrestrial insectivores in secondary forest fragments took the longest to recover to pre-isolation capture rates, with a projected recovery time of 61 years compared to 26 years for all 10 foraging guilds studied. Although the commonly captured terrestrial insectivores in our Afrotropical site may have broader foraging strategies than those in Amazonia and are not strictly confined to a particular stratum (for example *Illadopsis fulvescens* sometimes forages up to 12 m from the ground (Collar and Robson, 2020), they still rank among the most terrestrial species in Afrotropical forests. Disconcertingly, the impacts of forest degradation on terrestrial insectivores seen in our results may be an under-estimation of the reality. Stouffer et al. (2021) found that even in a vast block of undisturbed, continuous primary forest in the Amazon, the abundance of terrestrial insectivores was significantly lower compared to several decades prior. These concerning trends could partly be attributed to the effects of global climate change (Wolfe et al., 2025), raising the question of whether the baseline against which we are comparing is itself representative of a healthy ecosystem.

Of our focal terrestrial insectivores, the near-ground *Sheppardia cyornithopsis* showed the strongest contrast in capture rates between primary and secondary forest—just 10 of 83 captures were in the secondary forest (Supplementary Table S1). *Sheppardia cyornithopsis* typically perch 0.5–2 m from the ground and forage for insects by sallying or by sally-gleaning to the ground or tree trunks (Collar, 2020), a foraging strategy that may be inhibited by dense understories. This would reflect the findings of Arcilla et al. (2015), who found that insectivores that foraged by sallying were more sensitive to logging in the Upper Guinean Forest. Also, among terrestrial insectivores, we found that all three secretive, near-ground insectivores in the genus *Illadopsis* were quite sensitive to disturbance: *I. cleaveri*, and *I. rufipennis/fulvescens* both had significantly higher capture rates in primary than in secondary forest (only 28 of 97 captures and 16 of 115 captures were in secondary forest, respectively). Thus, *Illadopsis* may act as good indicators of changing habitat conditions and quality of tropical forest habitat in Lower Guinea Forests. We define the term "indicators" above, and consider the limitations of generalizing this in section 4.2. Unfortunately, it is very challenging to morphologically distinguish between *I. fulvescens* and *I. rufipennis*, so we grouped the two for this analysis. Similar field identification issues apply to two flocking greenbul genera: *Phyllastrephus icterinus/xavieri* and *Criniger ndussumensis/calurus*. In all three cases of difficult-to-distinguish species, the behaviors and natural histories of these congeners are quite similar (Borrow and Demey, 2014; Billerman et al., 2022), so it is reasonable to expect similar patterns of sensitivity to disturbance. Further research using molecular markers and multiple, fine-scale morphological measurements is ongoing and will aid species-specific conclusions for these six species in the future (Billerman et al., 2022).

Capture rates of the ant-followers were driven by the terrestrial Muscicapids, *Alethe castanea* and *Chamaetylas poliocephala*, both of which are often found foraging together and likely have similar natural histories and are regular followers of driver ants (genus *Dorylus;* Peters and Okalo, 2009; Craig, 2022; Rodrigues, 2024). The decline of ant-followers in secondary forest is likely driven by the abundance of driver ant swarms (Peters and Okalo, 2009). In the Neotropics, army ants (*Eciton burchellii*) and ant-following birds are sensitive to habitat degradation and fragmentation (Harper, 1989; Stouffer and Bierregaard, 1995; Roberts et al., 2000; Kumar and O'Donnell, 2007). Among the few to work on ant-following birds in Africa, Peters et al. (2008) and Peters and Okalo (2009) found that, in Kenya, ant-following birds were limited by the abundance of *Dorylus wilverthi* driver ants in fragmented landscapes (again, our secondary forest plots is effectively a forest fragment). Further, the presence of more disturbance-tolerant driver ants *D. molestus* did not compensate for *D. wilverthi* declines, suggesting that even subtle changes in driver ant communities can drive declines in specialized ant-followers. Similar mechanisms could be driving ant-follower declines at our site, possibly due to reduced foraging opportunities for birds. This could result from overall declines in arthropod prey or driver ant abundance and swarming rates due to increasingly drier conditions. Climatic factors may have an impact (Wolfe et al., 2025), as the driver ants may be exposed to higher temperatures and lower humidities in secondary forests. Alternatively, our site likely contains three main species of swarming *Dorylus* driver ants (Max P.G.T. Tercel, unpublished data), and these may have species-specific responses to disturbance. For example, Peters and Okalo (2009) found that specialized ant-followers were more dependent on *D. wilverthi*, which had more stable activity independent of humidity levels than *D. molestus*. The driver ants at our study site remain poorly understood, but future studies should focus on the distribution, behavior and foraging ecology of driver ant species in West and Central Africa, as well as their connection with forest degradation and declines of ant-following birds. The effective isolation of our secondary forest plot by roads and power lines may also contribute to the lower capture rates of ant-followers seen in secondary forest, as the thermal tolerances of *Dorylus* ants may prevent their movement into disturbed (sunny) areas. Jirinec et al. (2022b) found that light intensity (and corresponding heat) in areas of natural disturbance from treefall reached over 40 times that of the forest interior. However, it is not clear if low vegetation found under the power lines (2–3m as of 2023) or nocturnal movements could compensate for these impediments in our study area.

Other recent studies from the Afrotropics have also shown sensitivity of ant-followers to human landuse. For example, Ocampo-Ariza et al. (2019) identified an extinction threshold for ant-following birds at 24% forest cover along a disturbance gradient, with the most sensitive species disappearing below 52% cover. Jarrett et al. (2021) found that ant-followers were captured at least three times more commonly in primary forest (including our study site) compared to well-shaded cocoa plantations. Further, Miller et al. (2021) found that insectivores on Bioko Island—particularly antfollowers including *Alethe castanea*—showed reduced capture rates along roads relative to forest interiors at low elevation. Further, our own preliminary fieldwork carried out in 2014 in Nsork National Park (230 captures in 17 lanes of 6 nets), about 65km southeast of our study site, resulted in *Alethe castanea* being captured 11 times in primary forest and 3 times in secondary. Another of our primary forest indicators, *Sheppardia cyornithopsis* was captured 3 times in primary forest in Nsork but never in secondary (site description in Cooper et al., 2016; capture data unpublished). Indeed, the scope of this Nsork study was small, but together with other studies from the region, largely helps to corroborate the findings in our study here. Useful future work on ant-followers could include investigation of home range sizes and whether this contributes fragmentation sensitivity as is the case for ant-following birds in the Neotropics (Ferraz et al., 2007).

The effects of forest degradation on mixed-flock species shown in our results were practically as stark as those for ant-followers and terrestrial insectivores. Five of seven focal species showed significantly more captures in primary forest, with the largest effect sizes found in the flycatcher *E. nigromitrata* and the greenbul *P. icterinus/xavieri*. In contrast, Powell et al. (2013) found that in Amazon rainforest recovering from fragmentation, mixed-flock species were relatively quick to reach pre-isolation capture rates in comparison to sensitive guilds such as terrestrial insectivores. There are few mixed-flock studies from the Afrotropics (but see Cordeiro et al., 2015, 2022), thus most of our understanding of mixed-flock systems is from the Neotropics. There, species richness, and size and stability of flocks, decreases with forest fragment size and increases with mean vegetation height, with flocks being reluctant to cross open roads or enter open areas (Stouffer and Bierregaard, 1995; Thiollay, 1997; Develey and Stouffer, 2001; Maldonado-Coelho and Marini, 2004; Mokross et al., 2018). Also, flock interaction networks are sensitive to fragmentation and increasing proportions of secondary forest (Mokross et al., 2014). In Asia mixed-species flocks are sensitive to human-land use and are particularly dependent on the flock leader species (Lee et al., 2005; Mammides et al., 2015). These ecological dynamics are poorly known and ripe for future investigation with Afrotropical mixed-flockers.

The only species we captured significantly more often in secondary forest was the insectivorous kingfisher *Ispidina lecontei*. These kingfishers are generally found in secondary forest, at forest edges, as well as in other open areas such as forest clearings. They forage by diving from a low perch and catching their prey in flight or on the ground (Woodall, 2020). This species was also caught more often in cocoa plantations than in mature forest in Cameroon and Equatorial Guinea, corroborating our findings (Jarrett et al., 2021).

Several previous studies have found that nectarivores, frugivores and granivores tend to be positively affected by forest degradation (Waltert et al., 2005; Holbech, 2009), probably due to the increased light levels promoting the production of flowers, fruit and grains. We captured relatively few members of these guilds so had little power to test these predictions in the Afrotropics. These low capture numbers were likely due (at least partly) to a bias against the capture of species that are typically located in the canopy or in between stratum, as these species are less likely to be captured in mist-nets. This applies not only to frugivores but any species that are not exclusive to lower strata. A reliable comparison of capture rates between primary and secondary forest for such species would require additional surveying using other methods such as point counts and acoustic surveys. The dove *Turtur brehmeri* (an insectivore-granivore) was captured significantly less in secondary forest. Three widespread, common and versatile species—*Eurillas latirostris* (Yellow-whiskered Greenbul), *Eurillas virens* (Little Greenbul) and *Cyanomitra olivacea* (Olive Sunbird)—showed no significant differences in capture rate between primary and secondary forest. Future studies should use point counts and acoustic recording devices to properly evaluate the responses of these guilds to forest degradation.

Finally, we provide strong evidence that overall, fewer birds are captured in secondary forest (47.3% less), with few species appearing to disappear entirely; rather, many were simply caught much less frequently. The species that did disappear entirely from primary forest were all caught less than ten times, suggesting the pattern in those less-captured species is driven by sample size. This pattern hints that the local extirpation of many of these species may be more gradual in Central Africa compared to Amazonia, where the most sensitive species often disappear entirely with disturbance (Stouffer et al., 2021). However, it is important to note that our study only compares two study plots, and only by pairing our results with those from other similar studies (see above) can we begin to determine if our results are broadly generalizable. We speculate that this potential difference in sensitivity from Amazonian birds may have to do with biogeographical context: Amazonian birds have spent at least the last 2.6 million years (i.e., through the Pleistocene) evolving in a vast expanse of tropical rainforest (Bush, 1994; Rull, 2008); conversely, their African counterparts have had to adapt (or not) to the repeated Pleistocene ebb and flow of rainforest and savanna on their continent (Maley, 1996; Voelker et al., 2010). African rainforests may have shrunk into a few isolated refugia dozens of times during this epoch—creating an evolutionary filter unlikely to favor the rainforestrestricted species. An alternative, but not mutually exclusive explanation is that these differences could have derived from the management history of the secondary forest. The secondary forest at our site was repeatedly selectively logged and fragmented by roads and a powerline-cut (the powerline left ~2–3m vegetation underneath), and left many large trees and a closed canopy within the plot; in contrast, the secondary forest at the Biological Dynamics of Forest Fragments Project—where much Amazonian research was performed, regrew from abandoned clearcuts that once created hard barriers to animal movement (e.g., Stouffer et al., 2021). Future work should carefully consider the effect of secondary forest management and fragmentation per se when quantifying effects on the bird community.

4.2 Study limitations and further research

There are several limitations to this study which could impact interpretation of the results, and present avenues to explore further in future research. Firstly, we only carried out sample collection in the dry seasons due to practical and ethical considerations, as explained in Section 2.2. Future work could examine patterns across seasons and climatic variables, potentially using different methods such as point counts. We catch negligible numbers of Palearctic migrants at our study site but work across seasons could help us adjust for local seasonal movements and intra-Africa migrants. Our study also only consisted of two plots, meaning that our ability to generalize our findings hinges on comparisons to other studies as discussed above. For similar reasons and because we only sampled two habitat types, we limited in making inferences about species as potential “indicators”. The methods that we used (mist-netting at near-ground level) also present limitations and potential bias in the species caught. Canopy species (such as certain frugivorous—especially hornbills—and nectarivorous species) and large ground-dwelling birds (e.g., francolins) are surely under-represented in our samples, and so we cannot make reliable conclusions about these groups. Future work using additional methods such as point counts or acoustic surveys would allow for further investigation of these species. We collected much acoustic data while netting but due to logistical constraints, we did not analyze those data here. Our net lanes were separated by at least 200m, which certainly reduced spatial autocorrelation (Hill and Hamer, 2004), but did not eliminate it as some individuals could certainly travel farther than this distance. However, we believe we appropriately accounted for this autocorrelation by systematically decreasing the influence of especially autocorrelated net lanes in our analysis (see methods). Further, we also grouped some morphologically similar species that could not be distinguished in the field (e.g. *Phyllastrephus icterinus and P. xavieri*). DNA barcoding combined with high resolution morphological data be a useful tool to avoid any potential dilution of species-specific effects. Finally, although we have proposed and discussed potential mechanisms driving the patterns seen here, we did not measure variables such as arthropod abundance, microhabitat vegetation structure, or environmental variables (temperature, light intensity etc.), thus would be valuable to explore these hypothetical drivers in future studies.

4.3 Conservation and management

Overall, our study indicates that the threat posed by forest degradation may be disproportionately high for certain bird guilds, such as terrestrial insectivores, ant-followers, and mixed-species flockers. Given that deforestation rates are still extremely high in the Congo Basin, it is essential to improve our understanding of consequences for biodiversity and potential mitigation measures. For example, 1,899,000 hectares of forest per year were removed between 2015–2020 in Western and Central Africa (Food and Agricultural Organization of the United Nations, 2020), The species and guilds that we have identified here as being particularly sensitive could potentially act as indicator species for forest quality in this region with their absence. However, further study across other sites and habitats are needed to investigate this further. The absence of these “indicators” signals a loss of habitat quality that could negatively impact not only birds, but the entire ecosystem upon which they depend (e.g. keystone *Dorylus* ants). Other research supports our findings with respect to indicator species, most of which have ranges that extend across much of Central Africa, so we believe our results are mostly generalizable across a poorly studied region. Future work should focus on determining what specific mechanism is driving these declines, be that climate food availability, vegetation and microhabitat structure, depredation risk, light regime, or a combination of these. Further work on demography (see Nikolaou et al., 2024 in this Research Topic) would allow investigation beyond capture rates to understand population dynamics and thus infer habitat quality among forest types. With the knowledge of the sensitive species presented here and a better understanding of the mechanisms for these declines, concrete conservation actions can be taken to mitigate the negative anthropogenic effects of continuous forest degradation and disappearance.

Data availability statement

The original contributions presented in the study are publicly available. This data can be found here: FigShare, https://figshare.com/articles/dataset/Data_for_analysis_in_Barrie_et_al_2025_/29114960.

Ethics statement

The animal study was approved by The Institutional Animal Care and Use Committee (IACUC) (17-18.W.06-A.) at Humboldt State University. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

EB: Conceptualization, Formal Analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. BK: Conceptualization, Formal Analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. CJ: Formal Analysis, Investigation, Visualization, Writing – original draft, Writing – review & editing. DF: Formal Analysis, Writing – original draft, Writing – review & editing. PR: Conceptualization, Formal Analysis, Investigation, Methodology, Writing – review & editing. SLM: Investigation, Writing – review & editing. SEM: Investigation, Writing – review & editing. AA: Project administration, Writing – review & editing. CA: Project administration, Writing – review & editing. KB: Investigation, Writing – review & editing, Conceptualization, Methodology, Project administration. JC: Investigation, Writing – review & editing. JW: Project administration, Writing – review & editing, Conceptualization, Funding acquisition, Investigation, Methodology. LP: Project administration, Writing – original draft, Writing – review & editing, Conceptualization, Formal Analysis, Funding acquisition, Investigation, Methodology, Supervision, Visualization.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2025.1504350/full#supplementary-material

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Avian turnover at Harvard Forest, Massachusetts, USA, 1948-2016

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Multi-decadal datasets from systematic surveys of birds are rarely published, despite their potential to yield important information about local changes in the environment over time. I compare bird surveys at Harvard Forest in central Massachusetts, USA, between 1993 and 2016 with two unpublished annotated bird checklists from the area (1948 and 1970), along with data from other long-term bird survey sites in New England, and regional community science data. While a handful of breeding species at the Harvard Forest are common each year, species turnover has been constant, with roughly a third of bird species found one survey year and not the other. I list 18 species that have apparently colonized Harvard Forest as breeding species after 1948, and 16 that have declined since then, including two to the point of extirpation. I also note several examples of phylogenetic replacements in the recent vs. historical avifauna. More colonizing species than declining species are at their northern range limit rather than their southern limit in southern New England, and more migratory species appear to be declining than colonizing. More colonizing species favor forest interior than declining ones, and nearly all declining species are associated with edge/early-successional habitats or are considered habitat generalists. The majority of species to have colonized Harvard Forest since 1948 show positive statewide population trends, and none showed a loss in the number of breeding bird atlas blocks occupied between the 1970s and the 2000s. I identify three declining or extirpated species, Ruffed Grouse, Eastern Whip-poor-will, and Olive-sided Flycatcher, as particularly deserving of conservation attention. Long-term, site-scale monitoring is essential to detect the impact of local forest management techniques, which at Harvard Forest has included the creation of experimental clear-cuts, the loss of conifer plantations, and the continued maturation of the mixed hardwood forest.

KEYWORDS

change, avian, Massachusetts, community, time

Introduction

Long-term datasets are key to understanding ecological change over time, and can help clarify our role in effecting these changes (Magurran et al., 2010, Knapp et al., 2012). Conspicuous and diverse, birds make ideal subjects for long-term monitoring and detection of environmental change (Collins, 2001). Studies of species turnover and other measures of community change done on various spatiotemporal scales have long provided insight into the patterns to be expected from ongoing fluctuations and shifts in climate and vegetation succession and management (e.g., Holmes, 2007; Hitch and Leberg, 2007; DeLuca and King, 2017; Neate-Clegg et al., 2021; Craig, 2023). They may also be used to develop restoration priorities and goals for projects attempting to restore lost habitats (e.g., Cooper, 2008). In North America, regional and continent-scale avian monitoring programs such as the USGS Breeding Bird Survey ("BBS"), and more recently, community-science programs such as eBird have been used to detect continent-scale population change (e.g., James et al., 1996; Goetz et al., 2014; Schipper et al., 2016; Rosenberg et al., 2019). Each of these methods has different drawbacks; those reliant on passive data collection rather than standardized methodology tend to have records clustered near populated areas and popular birding sites, though with enough participation spread across a large enough region, these issues can be statistically overcome. Data from standardized, longitudinal population surveys are rare for all but a handful of taxa and sites, but have the advantage of providing quantitative data based on repeated observations by trained observers, even where early data are fragmentary (Curtis and Robinson, 2015).

Though many excellent short-term avian-habitat studies have been made in the forested habitats of the Northeastern U.S. (e.g., DeGraaf et al., 1998), longer-term datasets from this ecoregion are few. Among the exceptions are work by ornithologists at Hubbard-Brook Experimental Forest in central New Hampshire who pioneered research on neotropical migrant birds in the 1960s (e.g., Holmes and Sherry, 1988, 2001), which continues today. Elsewhere, McNulty et al. (2008) compared bird survey results from the 1950s from Huntington Wildlife Forest in New York's Adirondack Mountains with contemporary surveys, and bird monitoring at Yale-Myers Forest in northeastern Connecticut has been ongoing since the 1980s (see Hanle et al., 2020; Craig, 2023). Such site-based studies are essential to validate regional population trends (Walsh and Servison, 2017), and to detect contrasting patterns that can be explained by local land use, informing management.

Continent-wide analyzes have suggested that in recent decades, woodland birds have been generally increasing and grassland birds decreasing, with declines in abundance driven by drops in numbers of the most abundant species (Schipper et al., 2016). The Northeastern U.S. has seen widespread and continued reforestation in rural areas such as around Harvard Forest (Foster et al., 1998), which would presumably favor forest-interior species. However, this has occurred alongside the proliferation of both insect pests (Tingley et al., 2002; Barker Plotkin et al., 2024) and non-native understory plants in the region (Jenkins et al., 2008) which continue to transform this landscape. These habitat changes have impacted avian trends, but inconsistently so. For example, from surveys in Connecticut and Rhode Island, 2001-2008, Craig (2017) reported forest interior species more associated with increases, and edge/successional species with declines. However, in a longer-term study of breeding birds in Connecticut, Craig et al. (2022) found that the "seven most strongly increasing species were variously distributed forest interior and edge/successional-associated species". Furthermore, the differing survey and analytical methods and timeframes used for local studies have confounded interpretation.

Regional trends surely play a role in habitat-associated population changes, but directionality is inconsistent, and trends often contradictory at the local level, or between study sites (see Craig, 2023). For example, at Hubbard-Brook Experimental Forest in New Hampshire, Holmes and Sherry (2001) reported an overall numerical decline of breeding birds since the late 1960s, and reported far more forest-associated species decreasing than increasing. In their upstate New York study area, McNulty et al. (2008) also found more species to exhibit a drop in relative abundance than an increase since the 1950s. Yet, Craig et al. (2022) found that overall population density *increased* between their survey years (1985 to 2019), even as diversity levels remained constant.

It is also unclear how much habitat – or our interpretation of habitat – can impact bird populations, and on what scale. Increasingly, population trends are framed as species' hypothesized response to climate change (e.g., Walsh and Servison, 2017), rather than as a response to habitat change (which has long dominated bird conservation narratives). While climatic warming appears to have an impact on many certain species' distributional shifts, the effect has been inconsistent across taxa (Martins et al., 2024). Still, patterns may be detected at the local level; Craig et al. (2022) reported the "five most strongly declining species" between 1985 and 2018/2019 in Connecticut survey sites were "northerly distributed", suggesting a retreat toward cooler climes.

Despite a long and productive publication record on forest ecology, information on the avifauna (and vertebrates in general) from Harvard Forest is lacking. During the summer of 1993, while in the Research Experience for Undergraduates (REU) program, I conducted the first systematic baseline breeding bird survey at Harvard Forest in north-central Massachusetts. Since the initial effort, I returned to Harvard Forest as a Visiting Researcher three more times to repeat the survey, in 2011, 2013 and 2016. My dataset may be compared directly with two historical, unpublished annotated lists of birds observed at the Harvard Forest and vicinity dating to the 1940s (described below). More recent data from the Massachusetts Breeding Bird Atlas project (Massachusetts Audubon Society (MAS), 2008) and the Breeding Bird Survey (Sauer et al., 2020), plus community science data such as that uploaded to online platforms such as eBird (www.ebird.org), can all be used to augment findings from Harvard Forest over the past 80 years.

Specifically, my study asks:

- Has overall avian species diversity at Harvard Forest increased or decreased over time?
- What bird species have been gained/lost over the past decades, and why?
- Are these trends similar to those found at comparable forest sites in the region, and are they reflective of regional trends?

Insight from this work may be compared with data from more established local bird-monitoring sites, as well as community-science (observational) data to inform ongoing and future habitat manipulation to benefit birds and avian diversity at Harvard Forest and elsewhere in the region.

Methods

Study area

The Prospect Hill Tract of the Harvard Forest lies within the Quabbin Reservoir Watershed (Massachusetts Department of Conservation and Recreation, 2007), covering 364 hectares/900 acres in Worcester County, north-central Massachusetts, US (Figure 1). Established in 1907, Harvard Forest supports a mix deciduous and coniferous woods, including oak-maple forest, conifer plantations, and natural spruce and hemlock bogs, with a variety of small, scattered wetlands (Jenkins et al., 2008). It is nearly encircled by disused dirt logging roads, and crisscrossed with footpaths and old stone walls, a reminder of its history as a complex of farms, pastures and woodlots. Since the early 1800s, when most of the land was cleared, these areas have grown back to contiguous woodland. While most of the land is forested, wetlands provide limited open habitat, as does an area of c. 8.5 ha/21 acres maintained as pasture lawn, or ornamental landscaping around the Forest headquarters, and several experimental clearings where trees have been selectively removed as part of forest manipulation experiments since the 1990s. It is now a combined LTER/NEON site (Parizek, 2018); the "Long-term Ecological Research" (LTER) program was launched in 1980 by the National Science Foundation to support long-term research projects in Ecology, and now boasts 28 sites, mainly in North America, including four in the northeastern U.S (LTER Network, 2022). NSF introduced the related "National Ecological Observation Network" (NEON) program in 2011, which now has 81 sites across the U.S (SanClements et al., 2020).

Major landuse changes at Harvard Forest include the Hurricane of 1938, which resulted in widespread tree blow-down throughout New England (Spurr, 1956), including at Harvard Forest. In the decades since the hurricane, plantations of non-native conifers, mainly red pine (*Pinus resinosa*), were established, such that by the early 2000s, 125 acres/50 ha of plantations remained. By the time of my 1993 survey, red pine was a dominant tree on the Prospect Hill Tract, recorded on 13 of 67 (19.4%) survey points sampled, and the 4th-ranked tree by biomass (as measured by trunk diameter), after red maple (*Acer rubrum*), "snag" (various dead trees), and red oak (*Quercus rubra*). In 2008, Harvard Forest released a plan to begin harvesting (selectively logging) 80 acres/32 ha of the remaining 125 acres of pine plantation, which was accomplished between 2008-2010 (O'Keefe et al., 2008). This resulted in the appearance of three discrete brushy clearings (of 1, 3 and 6 ha) just prior to my 2011 resurvey, which were being used as study plots by researchers. These logged areas regenerated quickly, with most supporting young forest at various stages of regrowth by the 2016 survey; six survey points were within 100 meters of these clearings, so their impact may have been detected on the post-2008 bird surveys. Vegetation surveys were not repeated in subsequent bird surveys due to time limitations.

Historical bird data from Harvard Forest

Contemporary surveys may be compared with a unique data source, a 1948 annotated checklist (unavailable online or published) by Earl E. Smith of birds observed by the author and his wife (Rhea Smith) from 12 June to 30 Nov. 1948[1]. Smith used a larger study area than mine, taking in several large ponds and swamps outside the Prospect Hill Tract. A second historical dataset was produced by Hopkins and Hopkins[2], another couple who recorded birds on the forest from Oct. 1, 1968 to Aug. 2, 1969. However, as they explain in their manuscript, they arrived unfamiliar with North American birds, having spent the prior 13 years in Africa. Still, their observations of certain (easily-identified) species serve some use for comparison.

Smith's observations from Harvard Forest in 1948 were from a landscape that had been decimated by a major hurricane just ten years prior. His account of Chestnut-sided Warbler (*Setophaga pensylvanica*) is illustrative of this. Terming it "the most common warbler of the Forest", Smith noted "the large areas of brush which cover the blow-down of the hurricane make an ideal habitat for this species." Chestnut-sided Warblers were still present and likely breeding during my surveys, but were detected at fewer than 15% of survey points each survey year (1993-2016), and outnumbered in detection frequency by *eight* other wood-warbler species during the same period. Similarly, Wood Thrush (*Hylocichla mustelina*) was noted by Smith as being a "summer resident of the forest" with "the three thrushes, hermit, wood and veery, during June and the first part of July would join in an evening chorus of pure melody." By 1993, Wood Thrush was recorded only around the Forest headquarters, in 2011 it was found just incidentally, and it was missed altogether in 2016. These qualitative observations are crucial in understanding the nuance of community change beyond numerical counts.

Contemporary bird and plant surveys

In 1993, I established and surveyed 82 fixed-radius points spread across the entire Prospect Hill tract, selected to cover as much accessible area of the forest as possible, using rock wall and trail intersections as markers. Points were situated 100–350 meters apart, and visited three times at least a week apart between 5:00 and 9:30 am from 8 June to 9 July. Counts lasted 10 minutes each, and birds heard or seen were only counted once (to the extent possible), and classified as being in "Zone A" (<50 meters of the observer) or "Zone B" (50–100 meters away from the observer). Birds detected >100 meters away, those flying over, and those encountered between points that were not recorded on survey points were recorded in incidental notes for each survey (due to the dense structure of the forest, far more birds were heard than seen while

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[1] Smith, E.E. 1948. Preliminary list of birds of the Harvard Forest. Earl E. Smith, Harvard Forest, Nov. 30, 1948.

[2] Hopkins, B. and J. Hopkins. 1970. Some notes on the birds of Harvard Forest. January 1970. Unpublished report.

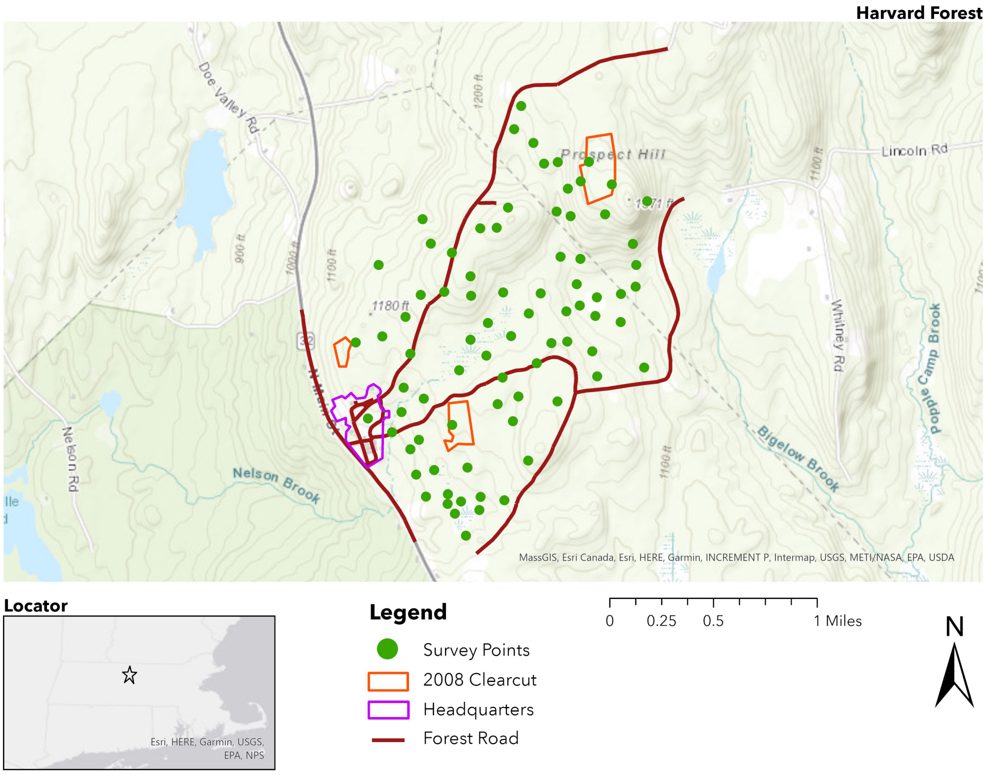

FIGURE 1
Location of survey points within the Prospect Hill Tract of Harvard Forest used 1993-2016. Not all points were used every year (depending on local conditions), and some were dropped or added (see text).

conducting point counts). All data was single-observer (Cooper), and because most avian detections were aural, and I felt confident in my identification abilities, I did not calculate visual vs. non-visual detections separately, but pooled all observations from all points (within Zone A) for this analysis.

This survey was repeated three more times, in 2011, 2013 and 2016, following the same protocol as faithfully as was feasible, but with only June visits in these years. Due to time constraints, surveys only employed 2 visits in 2011 (76 points) and 2013 (76 points), and single visits to each of 70 points in 2016. Unless noted, I dropped counts made in July (only done in 1993) because only June counts were conducted in subsequent years, and many bird species truncate their singing by mid-summer, focusing instead on raising young. I include notes on single-visit point count surveys of the adjacent former Petersham Country Club (Motzkin, 2014) from 2016 to inform my analysis of species turnover.

In 1993, I conducted vegetation surveys at 67 points. A 0.1-acre circle was established at each point using two 22-meter ropes crossed at the center/survey point. Within this circle, I recorded the diameter at standard height (DSH) of every tree with DSH of more than 4 cm (other measurements were taken, such as canopy cover, but those data have been lost and are not included in this analysis). A total of 5,174 trees and large shrubs were measured on the vegetation surveys, comprising 37 species (an additional three "species" cannot be identified and may have been mis-spellings; the full names are unknown).

Species richness and community composition

Though no single standard exists for calculating change in bird species diversity of a site over time, several comparative efforts involving repeated summer bird surveys of managed forests spanning more than one decade (e.g., Holmes and Sherry, 2001; Curtis and Robinson, 2015; Craig et al., 2022). For comparing species diversity over time, I used the R package "vegan" (v. 2.6-8) to compare overall species diversity across years (n=4 years) using the Shannon-Weaver index, which tends to be more sensitive to the gain and loss of rare species, and thus may pick up differences influenced by newly-colonizing and nearly-extirpated taxa. I calculated detection frequency for each survey year, based on the percentage of points surveyed that year where each species was recorded, expressed as a value from 0-1. This approach did not factor in a species' abundance at each point, due to the variation in number of visits per point each year (n = 1–3 visits/point), and the brevity of each visit.

Species trends over time

I analyzed individual species trends over time in two main ways. Qualitatively, I compared historical accounts from the area (notes from E. E. Smith, 1948 and those of Hopkins and Hopkins, 1970) with detection frequency and incidental observations from the 1993–2016 surveys (including my own observational data from the Petersham Country Club). I also compared these results to community science data from the Massachusetts BBA (which includes regional trends from BBS data over the past c. 60 years) and eBird records.

To quantify change in relative abundance over time, I identified a group of the most frequently-recorded species as those detected on a minimum of 10% of the survey points (n = 7 points per year) in at least one year to analyze. I used linear regression to compare slopes of detection frequency across the four years of the survey, and compared these findings to those from comparable study sites in the region. Bird species nomenclature follows Chesser et al. (2024).

Results

The four seasons of contemporary point counts (1993, 2011, 2013 and 2016) yielded 5,712 records of 84 bird species, and an c. 10 additional species were observed incidentally (see Supplemental Data). Restricting the point count data to only those species detected within 50 m of the survey point ("Zone A") and dropping July counts yielded c. 2,924 records of 72 species, which comprise the dataset used for analysis here. A total of 94 species have been recorded on eBird checklists from the "Harvard Forest" Hotspot based on 54 submitted checklists as of 2 Sept. 2024[3]. The five most frequently-encountered birds on the Harvard Forest point counts (1993-2016) were: Ovenbird (*Seiurus aurocapilla*) (detected at a mean of 87.8% of survey points per year), Red-eyed Vireo (*Vireo olivaceus*) (59.9%), Pine Warbler (*Setophaga pinus*) (34.9%), Black-capped Chickadee (*Poecile atricapillus*) (30.0%) and Scarlet Tanager (*Piranga olivacea*) (29.3%). Two additional species made the top 10 most common species in each of the four survey years: Black-throated Blue Warbler (*Setophaga caerulescens*) (29.2%) and Black-throated Green Warbler (*Setophaga virens*) (26.6%). An additional 30 species were recorded on surveys in all four years, which comprise the "core breeding songbird community" at Harvard Forest (see Supplementary Table S1 in Supplementary Material for complete list).

Species turnover since 1948

As summarized in Table 1, Harvard Forest has seen 18 species colonize as breeders since 1948; during the same period, nearly as many have declined or become extirpated here (n=16) (see also Supplementary Table S1). Overall species turnover at Harvard Forest between survey years (as measured by Craig et al., 2022) was fairly high (mean = 0.315; 17–23 species gained or lost of a total of 55–69 present in the species pool each of the four survey years), and this value has varied little since 1993 (range: 0.302-0.333). Based on species representation on the survey points (presence/absence), overall species diversity has been stable across the study area since 1993, with Shannon-Weaver indices similar from year to year (range: 3.243 – 3.509). This stability is reflected in phylogenetic groups, in that a similar number of representatives have colonized vs. declined for several groups, including Galliformes (i.e., Wild Turkey *Meleagris gallopavo* colonized, Ruffed Grouse *Bonasa umbellus* declined), Accipitrids, Corvids and Parulids (Table 1). Other groups were off by just one or two species in this phylogenetic replacement (e.g., two Picids colonized, one declined).

The relationship of habitat preference, geographic position within range, and migratory status of species increasing or declining resists generalization, as counter-examples abound. However, some patterns since 1948 include the preponderance of species at their northern range limit in southern New England among the colonizing species (n=6), vs. those facing declines or extirpation here (n=1, Eastern Towhee *Pipilo eurythrophthalmus*). Species at their southern range limit were represented in both the colonizing/increasing and the declining/extirpated species (Table 1).

More migratory species at Harvard Forest appear to have declined than colonized since 1948 (12 vs. 7, long-distance and short-distance migrants combined; Table 1). Looking at habitat association, more colonizing species at Harvard Forest favor forest interior (n=9) than declining/extirpated ones (n=2), and nearly all declining/extirpated species are associated with edge/early-successional habitats, or are considered habitat generalists (Table 1). However, looking at point count data since 1993, forest-interior species show both positive and negative trends, and those associated with early-successional habitat appear to have generally increased in this latter timeframe, with just two (Common Yellowthroat *Geothlypis trichas* and Song Sparrow *Melospiza melodia*) having declined (Table 2).

Comparing Harvard Forest data with regional patterns, most breeding bird species to have colonized Harvard Forest since 1948 were also found to be increasing statewide, as measured both by range expansion (i.e., change in Atlas blocks since the 1970s) as well as in numerical abundance, as shown by BBS data (both summarized in species accounts in BBA2[4]) (Table 1). They include taxa expanding into central Massachusetts from various directions, and associated a variety of habitat types, defying easy generalization (e.g., Wild Turkey, Red-bellied Woodpecker *Melanerpes carolinus*, Brown Creeper *Certhia americana*, and Northern Cardinal *Cardinalis cardinalis*). Some of these trends have been watched for decades (Veit and Petersen, 1993), while others, such as the (re-)invasion of Red-bellied Woodpeckers in the region, are much more recent (mid-1990s on).

Colonizing species show a mean 46.2% increase in occupied atlas blocks since the 1970s, and none showed a loss in the number of blocks occupied between the 1970s and the 2000s. Conversely,

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[3] See https://ebird.org/hotspot/L1239372; note that the Hotspot location shown in eBird (as of Sept. 2024) is pinned several km to the south of the Harvard Forest headquarters and Fisher Museum, which has probably reduced the number of checklists submitted from the Forest due to confusion over its location.

[4] Species accounts published online: https://www.massaudubon.org/our-work/birds-wildlife/bird-conservation-research/breeding-bird-atlases/find-a-bird.

TABLE 1 Species turnover at Harvard Forest since 1948 (see Supplementary Table S1, and Supplemental Material for complete notes).

	BBA	BBS	Range/Migratory Status	Habitat
COLONIZED SINCE 1948				
Wild Turkey (*Meleagris gallopavo*)	97.9	+	Core/Resident	Edge/successional
Red-shouldered Hawk (*Buteo lineatus*)	29.2	+	Northern limit/Resident	Forest interior (Generalist)
Ruby-thr Hummingbird (*Archilochus colubris*)	41.7	+	Core/LDM	Generalist
Common Raven (*Corvus corax*)	70.8	+	Southern limit/Resident	Generalist
Tufted Titmouse (*Baeolophus bicolor*)	60.4	+	Northern limit/Resident	Generalist
Red-breasted Nuthatch (*Sitta canadensis*)	33.3	+	Southern limit/Resident	Forest interior
White-br. Nuthatch (*Sitta carolinensis*)	16.7	+	Core/Resident	Forest interior
Brown Creeper (*Certhia americana*)	33.3	+	Southern limit/Resident	Forest interior
Golden-cr. Kinglet (*Regulus satrapa*)	10.4	+	(Southern limit)/Resident	(Forest interior)
House Finch (*Carpodacus mexicanus*)	52.1	+	(Northern limit)/Resident	(Generalist)
No. Waterthrush (*Parkesia noveboracensis*)	29.2	+	Southern limit/LDM	Forest interior
Pine Warbler (*Setophaga pinus*)	81.3	+	Core/SDM	Forest interior
Northern Cardinal (*Cardinalis cardinalis*)	56.3	+	Northern limit/Resident	Edge/successional
Indigo Bunting (*Passerina cyanea*)	12.5	n/a	(Core)/LDM	(Edge/successional)
COLONIZED SINCE 1993				
Yellow-b. Sapsucker (*Sphyrapicus varius*)	66.7	+	Southern limit/SDM	Generalist (Forest interior)
Red-b. Woodpecker (*Melanerpes carolinus*)	66.7	+	Northern limit/Resident	Forest interior (Generalist)
Great Crested Flycatcher (*Myiarchus crinitus*)	37.5	n/a	Core/LDM	Generalist
Prairie Warbler (*Setophaga discolor*)	35.4	–	(Northern limit)/LDM	(Edge/successional)
DECLINED SINCE 1948				
Ruffed Grouse (*Bonasa umbellus*)	39.6	–	Southern limit/Resident	Edge/successional
Red-tailed Hawk (*Buteo jamaicensis*)	31.3	+	Core/Resident	Edge/successional
E. Whip-poor-will (*Caprimulgus vociferus*)	4.2	–	Core/LDM	Edge/successional
Northern Flicker (*Colaptes auratus*)	6.3	–	Core/SDM	Edge/successional
Olive-s. Flycatcher (*Contopus cooperi*)	-2.1	–	(Southern limit)/LDM	(Edge/successional)
Least Flycatcher (*Empidonax minimus*)	6.3	–	Southern limit/LDM	Edge/successional
American Crow (*Corvus brachyrhynchos*)	12.5	+	(Core)/Resident	(Generalist)
Gray Catbird (*Dumetella carolinensis*)	0	+	Core/SDM	Edge/successional
Wood Thrush (*Hylocichla mustelina*)	-4.2	–	Core/LDM	Forest interior (Edge/successional)
American Robin (*Turdus migratorius*)	2.1	–	Core/SDM	Edge/successional
Purple Finch (*Carpodacus purpureus*)	8.3	–	Southern limit/Resident	Edge/successional
Eastern Towhee (*Pipilo eurythrophthalmus*)	0	–	Northern limit/SDM	Edge/Successional
American Redstart (*Setophaga ruticilla*)	-10.5	n/a	Core/LDM	Edge/successional
Magnolia Warbler (*Setophaga magnolia*)	4.2	+	Southern limit/LDM	Generalist (Forest interior)
Chestnut-s, Warbler (*Setophaga pensylvanica*)	2.1	–	Southern limit/LDM	Edge/Successional
Rose-br. Grosbeak (*Pheucticus ludovicianus*)	18.8	–	Core/LDM	Edge/successional

Abbreviations include "BBA" [Massachusetts Breeding Bird Atlas, indicating % change between 1974 and 2011 (MAS 2008)], "BBS" (Breeding Bird Survey Results, also available in Massachusetts Audubon Society (MAS), 2008), "LDM" (long-distance migrant) and "SDM" (short-distance migrant).

TABLE 2 Detection frequency and regression slope of the most widespread species (>10% of points per year) detected on Harvard Forest point counts (Zone A, June only, 1993-2016; % of points where detected, per survey year, visits pooled).

Species	1993	2011	2013	2016	Slope (SE)	HWF	HB	YMF	Ecological notes
Pine Warbler	12.2	44.7	50	32.9	0.802 (0.393)	n/a	n/a	Increasing	I, SDM
Red-eyed Vireo	45.1	61.8	71.1	61.4	0.552 (0.210)	0.000	-0.010*	Increasing	I, LDM
Ovenbird	78	85.5	94.7	92.9	0.401 (0.133)	-0.021***	0.013*	Increasing	I, LDM
Yellow-bellied Sapsucker	0	13.2	7.9	14.3	0.345 (0.111)	-0.028**	-0.028	Increasing	G, SDM
Scarlet Tanager	22	32.9	38.2	24.3	0.234 (0.262)	-0.023***	-0.023**	Increasing	I, LDM
Blackburnian Warbler	19.5	23.7	21.1	28.6	0.166 (0.113)	-0.002	-0.056**	Decreasing	I, LDM
Hairy Woodpecker	1.2	10.5	7.9	4.3	0.152 (0.129)	0.033**	-0.014	Decreasing	G, R
Chestnut-sided Warbler	8.5	9.2	14.5	12.9	0.119 (0.082)	-0.192***	n/a	Increasing	ES, LDM
Cedar Waxwing	3.7	10.5	9.2	4.3	0.094 (0.126)	n/a	n/a	Decreasing	ES, SDM
Gray Catbird	4.9	3.9	11.8	5.7	0.069 (0.139)	n/a	n/a	Increasing	ES, SDM
Black-thr. Blue Warbler	25.6	35.5	34.2	21.4	0.067 (0.275)	-0.005	0.002	Increasing	I, LDM
Eastern Towhee	4.9	2.6	7.9	7.1	0.048 (0.092)	n/a	n/a	Increasing	ES, R
Veery	17.1	2.6	17.1	24.3	0.031 (0.373)	n/a	0.009	Increasing	I, LDM
Blue Jay	12.2	22.4	7.9	12.9	0.024 (0.250)	-0.011	n/a	No trend	G, R
Brown Creeper	19.5	18.4	18.4	20	-0.008 (0.032)	0.102***	0.013	Decreasing	I, R
Hermit Thrush	13.4	9.2	25	5.7	-0.030 (0.344)	-0.006	-0.017	Decreasing	I, SDM
Common Yellowthroat	15.9	18.4	14.5	11.4	-0.063 (0.111)	n/a	n/a	Increasing	ES, SDM
Downy Woodpecker	7.3	2.6	11.8	1.4	-0.069 (0.190)	n/a	-0.055***	No trend	G, R
Tufted Titmouse	7.3	3.9	7.9	2.9	-0.077 (0.086)	n/a	n/a	Increasing	G, R
White-br. Nuthatch	7.3	11.8	9.2	0	-0.066 (0.204)	-0.008	-0.023*	No trend	I, R
Black-thr. Green Warbler	29.3	28.9	21.1	27.1	-0.105 (0.138)	-0.001	-0.023***	Decreasing	I, LDM
Northern Waterthrush	7.3	1.3	1.3	5.7	-0.107 (0.101)	n/a	n/a	No trend	I, LDM
Song Sparrow	7.3	3.9	3.9	2.9	-0.112 (0.009)	n/a	n/a	Increasing	ES, R
Canada Warbler	13.4	6.6	6.6	8.6	-0.166 (0.062)	-0.077***	n/a	Increasing	I, LDM
Winter Wren	13.4	5.3	11.8	5.7	-0.167 (0.124)	0.008	-0.012	No trend	I, R
Eastern Wood-pewee	25.6	18.4	21.1	18.6	-0.179 (0.054)	-0.082***	n/a	Increasing	I, LDM
Yellow-rumped Warbler	29.3	14.5	26.3	15.7	-0.299 (0.222)	0.033**	0.039**	Decreasing	I, SDM
Red-br. Nuthatch	24.4	13.2	17.1	14.3	-0.269 (0.084)	0.029*	n/a	Decreasing	I, R
Black-capped Chickadee	41.5	35.5	32.9	10	-0.562 (0.404)	-0.002	n/a	Decreasing	G, R
Black-and-white Warbler	37.8	7.9	19.7	17.1	-0.613 (0.277)	-0.042*	n/a	No trend	G, LDM
Blue-headed Vireo	39	11.8	28.9	7.1	-0.691 (0.367)	0.048***	-0.002	Decreasing	I, SDM

Abbreviations include “HWF” [Huntington Wildlife Forest Natural Area, Newcomb, NY (regression slopes from point count surveys 1954-63 and 1990-2000; see McNulty et al. 2008)], “HB” [Hubbard-Brook Experimental Forest, NH (regression slopes from area search survey 1969-1998; Holmes and Sherry, 2001)] and “YMF” [Yale-Myers Forest, Tolland and Windham counties, CT (trends from transect surveys in 1985, 2018 and 2019; Craig et al. 2022)].

Species order follows slope values (at Harvard Forest) from positive to negative. Please refer to Supplementary Table S1 for Latin names. Abbreviations include “I” (forest interior), “G” (generalist), ES (edge/successional habitat), and “R” (resident).

*$P < 0.05$ **$P < 0.01$ ***$P < 0.0$ (from McNulty et al., 2008).

species that have been extirpated from Harvard Forest, or with apparent declines since 1948, show a much lower mean of increase in occupied blocks (7.4%), with many seeing a negative change in occupied blocks since the 1970s (and several with negative statewide population trends).

Comparisons with other sites

In comparison with other New England sites with long-term bird data, the core breeding bird community at Harvard Forest closely matches that reported from Yale-Myers Forest

(Goodale et al., 2009). Many of the population trends over time reported from Yale-Myers also match those of Harvard Forest, with similar species increasing (Yellow-bellied Sapsucker, Red-eyed Vireo, Ovenbird, Pine Warbler, and Scarlet Tanager) and decreasing (Blue-headed Vireo, Red-breasted Nuthatch, Black-capped Chickadee, Yellow-rumped Warbler).

By contrast, while both Hubbard-Brook Experimental Forest in New Hampshire and Huntington Wildlife Forest in New York shared some of the common breeding species with Harvard Forest, the trends of all three sites rarely matched (Table 2). It is possible that because both Hubbard-Brook and HWF reported their last surveys from 1998 and 2000, respectively, more contemporary trends may be different. Indeed, Holmes and Sherry (2001) noted that several of the most numerous species at Hubbard-Brook from 1969–1998 experienced significant negative population change through the 1990s, including Least Flycatcher and American Redstart (see also Holmes, 2007), leaving Ovenbird and Red-eyed Vireo as the most abundant breeding birds over multiple recent decades here (both Least Flycatcher and American Redstart are fairly rare at Harvard Forest today).

Discussion

The finding that overall species diversity (if not species makeup) has remained fairly constant at Harvard Forest since the mid-1900s, with a similar number of colonized vs. extirpated breeders (18 vs. 16), conforms to findings of Craig et al. (2022) in nearby northeastern Connecticut. The low annual rate of species turnover found at Harvard Forest – below that reported by Craig et al. (2022) for the Yale-Myers Forest – suggests even more stability over time here. Predicted northward expansion of southerly species due to climate change (see Walsh and Servison, 2017) appears to be underway, with more species near the northern edge of their range colonizing, rather than declining (of those where either pattern was noted). The suggestion that migratory species would be particularly vulnerable to extirpation (Holmes, 2007; McNulty et al., 2008), is supported by the finding that of the migratory species that have *either* colonized or declined at Harvard Forest, many more have declined or have become extirpated altogether.

The finding that more *colonizing* species at Harvard Forest since 1948 favor forest interior (n=9) than declining/extirpated ones (n=2), and nearly all of the latter group are associated with edge/early-successional habitats or are considered habitat generalists, is supported by research from other New England sites where forest interior species increased in the latter part of the 20th Century (e.g., Holmes and Sherry, 2001). However, habitat-associated trends at Harvard Forest since 1993 appear to be much more mixed, with forest-interior species showing both positive and negative trends. Several of the species with the most pronounced recent declines at Harvard Forest (Table 2) are conifer-dwelling species (e.g., Blue-headed Vireo *solitarius* and Yellow-rumped Warbler *Setophaga coronata*) that may be responding to more recent local loss/succession of conifer plantations to hardwoods, and possibly the death of eastern hemlocks due to wooly adelgid invasion (see Tingley et al., 2002). Since 1993, several species with positive trends are associated with edge/successional habitat (Table 2); however, the two declining (since 1993) species associated with these early-successional habitats, Common Yellowthroat and Song Sparrow, are both strongly associated with water and emergent wetland vegetation. Thus, it is possible that neither benefitted from the experimentally logged plots as much as upland species like Gray Catbird and Eastern Towhee.

Those species that appear to have declined at the Harvard Forest and that *also* show statewide negative (or non-positive) population trends could be candidates for continued monitoring, and as targets for future habitat management. These include Ruffed Grouse, Eastern Whip-poor-will (*Caprimulgus vociferans*), Northern Flicker (*Colaptes auratus*), Olive-sided Flycatcher (*Contopus cooperi*), Least Flycatcher (*Empidonax minimus*), Wood Thrush (*Hylocichla mustelina*), American Robin (*Turdus migratorius*), American Redstart (*Setophaga ruticilla*), Chestnut-sided Warbler (*Setophaga pensylvanica*), Eastern Towhee, Rose-breasted Grosbeak (*Pheucticus ludovicianus*), and Purple Finch (*Haemorhous purpureus*). While most of these species are still persisting in the vicinity of Harvard Forest, they tend to be restricted to early-successional habitat such as old field vegetation and the forest-clearing ecotone (including at the former Petersham County Club, Cooper, unpubl. data). However, both Eastern Whip-poor-will and Olive-sided Flycatcher, appear to be essentially extirpated as breeders from the larger Petersham area (various sources), and the former is considered a sensitive species at the state level[5]. Of the Ruffed Grouse, Smith wrote: "Many of these fine birds are present on the Forest and rarely is a trip in the field concluded without seeing or hearing several. Three broods were flushed in the summer consisting of 5 to 10 young." This decline of grouse may be fairly recent; in 1993, I noted that this species was seen "throughout", with an active nest (with eggs) on 5 June. However, by 2011, only a single bird was encountered, and it went unrecorded in 2013 and 2016 (eBird and iNaturalist only show a handful of records from the Petersham area). While not explicitly surveyed-for, the Eastern Whip-poor-will seems to have declined even earlier. It was recorded by Smith in 1948 as being "heard throughout the summer", yet none was heard during my surveys, despite spending several weeks each year staying in the same area of the Forest headquarters and taking regular dusk walks and being out pre-dawn for the point count surveys.

Of particular interest are those species with mixed trends across sites in New England, as local studies can elucidate subtle trends not detected on statewide or regional monitoring programs. From a management perspective, these may also be those species most responsive to changes in forest management, such as species that may move into experimentally logged tracts, or which may be persisting in unusual habitats such as red pine plantations surrounded by extensive hardwood forest. Examples of species showing increases at Harvard Forest over time, yet declines or

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[5] https://www.mass.gov/info-details/list-of-endangered-threatened-and-special-concern-species#birds.

static trends statewide, include Great Crested Flycatcher (*Myiarchus crinitus*), Indigo Bunting (*Passerina cyanea*) and Prairie Warbler (*Setophaga discolor*), all of which have increased at the Forest in the past decades, likely aided by local experimental habitat manipulation. See Supplementary Table S2 for notes on regional trends.

Of course, with such different methodologies employed (transects vs. point counts vs. territory mapping), it may not be possible to generalize and extract numeric trends from one study and expect it to match the other. Analysis of different datasets can also present significant analytical challenges within the same study; for Harvard Forest data, the different numbers of points visited in different years, the low number of years (n = 4), and the different number of visits per year (1, 2 or 3), limit the interpretation of actual abundance and trends. As with any such study, a trade-off exists between dropping points and visits to increase standardization and avoid bias (e.g., if a particular microhabitat type was better represented one year vs. others), or retaining them to increase the amount of available data to interpret, and to capture rare species that might be particularly data-rich (e.g., a bird associated with an age-class of clearing that might be nearing extirpation as the forest grows in and matures).

It is also possible that more species have increased at Harvard Forest, but the brief descriptions (i.e., without numerical counts) from the pre-1993 period (e.g., "summer resident in forest") make this determination is difficult. "Observer perception" can influence impressions of abundance, and may have influenced the Smith (1948) dataset; for example, any guest at Harvard Forest staying at the headquarters will hear American Robins singing continuously from well before dawn to sunset; yet away from developed areas, robins are rare in the forest interior and the natural wetlands, as seen in the point count data. So, while they may (still) seem like a "common resident of the forest", determining exactly where they were common, and how numerically common they were, is not possible from the data. Of note, Smith's references to "the Forest" included large expanses of wooded swamp habitat (e.g., Tom Swamp), as well as large clearings and other habitats and other open habitats lacking on the Prospect Hill Tract. And, a relatively large number of species were recorded (this study) in very small numbers in each year, in some cases with only a single pair or two likely present around the main headquarters, which (now) provides the largest open habitat approximating the early pasture habitat in the area (horse-grazed through summer) (Supplementary Table S1).

Finally, some increases and colonizations may be unreliable as trends in cases where the number of territorial birds continues to be small, such as with Alder Flycatcher (*Empidonax alnorum*), found on territory in 2011 and 2013, but on only two points located at a unique swamp habitat; or Nashville Warbler (*Leiothlypis ruficapilla*) and Northern Parula (*Setophaga americana*), recorded as territorial singletons in 1993 and 2016, respectively, but seemingly not fully colonized as breeders. Still, while colonizations are usually fairly straightforward – either the species was listed by earlier authors, or detected on point counts, or not – declines and even extirpations are less clear-cut, since a rare species may be persisting, and may even be common, in areas not visited on modern surveys (particularly given that the "study area" in 1948 extended well beyond the boundaries of the Prospect Hill tract used as the 1993–2016 study area). This is particularly true for species found in secondary growth and open areas, given how the forest has matured in and around the study area in the seven decades since the 1948 accounts of Smith.

From a management perspective, replicating these open habitats could be a way to encourage historically-present species to return, or to augment their populations (assuming this is a goal). The experimental forest clearings established since the initial 1993 survey may have led to the "bounce-back" of species like Least Flycatcher and Chestnut-sided Warbler, as well as the arrival of species like Prairie Warbler and Indigo Bunting which were not found as breeders historically. Assuming these interventions do not remove sensitive/rare habitats (particularly if they remove non-native plantations), they could be expanded as a management tool to create a more complex mosaic of habitats of different age classes. Habitat data was not a major component of this study, and I hope this publication may raise awareness of these important data sets for future analysis.

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 approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because this study was based on passive (listening) surveys of birds in a forest; no close contact with animals was involved.

Author contributions

DC: Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2025.1511265/full#supplementary-material

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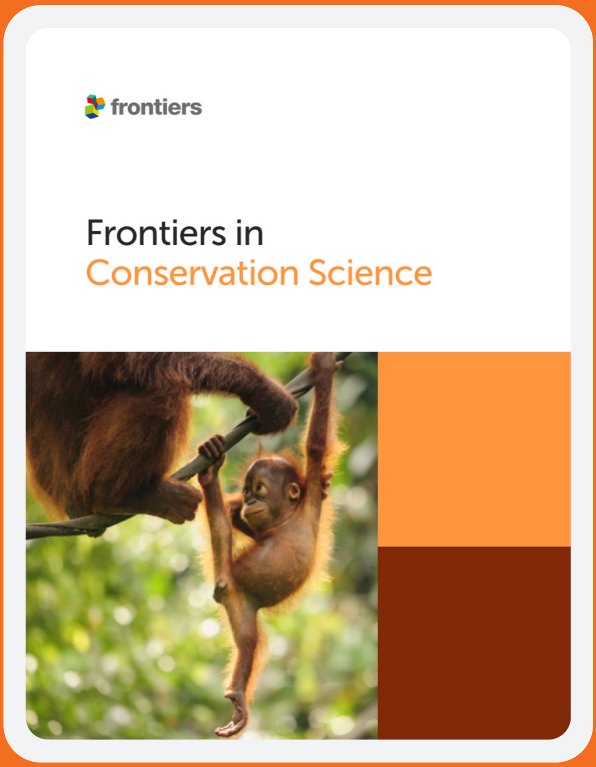
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