











RESEARCH ARTICLE

Unraveling a century of global change impacts on winter bird distributions in the eastern United States

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Abstract

One of the most pressing questions in ecology and conservation centers on disentangling the relative impacts of concurrent global change drivers, climate and land-use/land-cover (LULC), on biodiversity. Yet studies that evaluate the effects of both drivers on species' winter distributions remain scarce, hampering our ability to develop full-annual-cycle conservation strategies. Additionally, understanding how groups of species differentially respond to climate versus LULC change is vital for efforts to enhance bird community resilience to future environmental change. We analyzed long-term changes in winter occurrence of 89 species across nine bird groups over a 90-year period within the eastern United States using Audubon Christmas Bird Count (CBC) data. We estimated variation in occurrence probability of each group as a function of spatial and temporal variation in winter climate (minimum temperature, cumulative precipitation) and LULC (proportion of group-specific and anthropogenic habitats within CBC circle). We reveal that spatial variation in bird occurrence probability was consistently explained by climate across all nine species groups. Conversely, LULC change explained more than twice the temporal variation (i.e., decadal changes) in bird occurrence probability than climate change on average across groups. This pattern was largely driven by habitat-constrained species (e.g., grassland birds, waterbirds), whereas decadal changes in occurrence probabilities of habitat-unconstrained species (e.g., forest passerines, mixed habitat birds) were equally explained by both climate and LULC changes over the last century. We conclude that climate has generally governed the winter occurrence of avifauna in space and time, while LULC change has played a pivotal role in driving distributional dynamics of species with limited and declining habitat availability. Effective land management will be critical for improving species' resilience to climate change, especially during a season of relative resource scarcity and critical energetic trade-offs.

KEYWORDS

Audubon Christmas Bird Count, climate change, community science, habitat-constrained, land-use change, occurrence probability

1 | INTRODUCTION

Distributions of species across diverse taxa are shifting as a consequence of human-induced global change (Freeman et al., 2018; Sirois-Delisle & Kerr, 2018). While multiple ecological factors may be contributing to distributional shifts, such as changes in predation and invasive species (Harley, 2011; Kovach et al., 2017), climate and land-use/land-cover (LULC) change are undoubtedly two dominant drivers. Independently, climate and LULC have been shown to influence the distributions of plants, mammals, birds, insects, and aquatic organisms (Brodie, 2016; Radinger et al., 2017; Termaat et al., 2019). Global change-driven range shifts pose an intensifying threat to many imperiled species (Egli et al., 2018; Gibbs et al., 2009). Substantial alterations to avian populations and communities have occurred over the past century (Princé & Zuckerberg, 2015; Rosenberg et al., 2019; Ward et al., 2018) and are projected to continue in the coming decades (Bateman et al., 2020; Sohl, 2014; Wessely et al., 2017). Quantifying the relative roles of climate and LULC in shaping bird distributions has widespread implications for management strategies and allocation of conservation resources, such as siting protected areas, prioritizing habitat restoration, and planning species reintroductions (Hannah et al., 2007; Zwiener et al., 2017). Yet analyses that simultaneously evaluate climate and LULC impacts, especially during winter, remain scarce despite repeated calls for incorporation of multiple drivers (Sirami et al., 2017), hindering our ability to develop effective management strategies across the full annual cycle.

The limited focus on climate-LULC change integration is due, in part, to insufficient data at suitably broad spatiotemporal scales that can capture the relationships between long-term environmental changes and changes in species' distributions. Because climate and land-use gradients vary at different temporal scales, and are often correlated over narrow extents of space and time (Oliver & Morecroft, 2014), detecting coherent signals of global change on species' occurrence requires expansive, long-term studies that allow for the isolation of spatial versus temporal components of environmental variables (Kelly et al., 2013; Maclean et al., 2008). As a result of these challenges, most studies have either assessed the influence of a single global-change driver, often climate, over long time periods (Amano et al., 2020; Pearce-Higgins et al., 2015; Termaat et al., 2019; Tingley et al., 2009) or have fit static models assessing the influence of multiple drivers under the assumption that species' responses will exhibit stationarity (Seaborn et al., 2021; Vermaat et al., 2017). However, species may not be in equilibrium with their environment at limited spatial and/or temporal scales (Bar-Massada & Belmaker, 2017). Thus, it is critical to investigate the ecological mechanisms that underlie occurrence dynamics, rather than simply characterize current distribution patterns.

Birds wintering in North America have long been considered sentinels of climate change due to their mobility and ability to survive high-latitude winters, and recent research shows that birds track climate change more rapidly in winter (i.e., their stationary non-breeding period) than during the breeding season (Lehikoinen et al., 2021). Yet the relationships between winter bird distributions

and climate drivers tend to focus on individual species, while group-level effects (e.g., within biomes or across families) remain poorly understood (Princé & Zuckerberg, 2015). Classifying species into groups, coupled with multispecies models, provides an opportunity to examine the influence of macroecological processes on species assemblages at large spatial scales (e.g., Pacifici et al., 2014), contributing to our understanding of multispecies responses across heterogeneous landscapes. Similarly, few studies have explored possible LULC impacts on winter bird occurrence, despite the link between LULC and resource availability, and hence, bird distribution and abundance (Meehan et al., 2004). Such associations can be particularly vital during a season of relative resource scarcity and critical energetic trade-offs (Williams et al., 2015). Understanding how species groups are differentially affected by both habitat alteration and climatic conditions can inform biodiversity projections, policy-making, and multispecies conservation efforts across ecosystems (Karp et al., 2018; Northrup et al., 2019; Reynolds et al., 2017). Thus, multidriver analyses of wintering avifauna are needed for rigorous inference on occurrence dynamics in the face of ongoing climate and land-cover changes.

Audubon's Christmas Bird Count (CBC) program provides an exceptionally rare data set for unravelling the spatiotemporal drivers of winter bird occurrence because data have been systematically collected on hundreds of species throughout North America for over a century. Here, we used CBC data to assess the relative importance of climate and LULC to spatiotemporal changes in winter occurrence of nine bird groups ($n = 89$ total species) over a 90-year period (1930–2019) across the eastern United States (east of 100th meridian). We estimated variation in multispecies occurrence probabilities as a function of site-specific, decadal variation in minimum winter temperature, cumulative precipitation, and group-specific LULC. To do this, we partitioned environmental variables into spatial (local average over the time series) and temporal (decadal anomaly relative to local, long-term average) components to improve our inferences about the processes affecting species' distributions, and thus, the potential consequences of future global change (Princé & Zuckerberg, 2015). We then compared the amount of variation in occurrence probabilities explained by different global change drivers, in isolation as well as in combination, across the nine bird groups (*sensu* Clement et al., 2019). Quantification of group-specific responses to climate and land-use changes represents a key step in understanding the role that such factors might have played in observed long-term declines of North American avifauna (Rosenberg et al., 2019).

2 | MATERIALS AND METHODS

2.1 | Christmas Bird Count data

To reveal drivers of long-term changes in species' occurrence, we used data from the CBC, a volunteer bird monitoring program that began in 1900. In this study, we restricted CBC data spatially (east

of 100th meridian) and temporally (since 1930) to maintain consistency in protocols and count efforts. We chose to begin our study period in 1930 because this was the first decade with a robust sample of CBC sites (i.e., >50 circles) that remained active throughout the 90-year period, and standardized land cover and climate data were available for the United States from this decade forward. This time period limited our study area to a total of 119 CBC circles in the eastern United States (see map in Figure 1c). Circles in this region have been more consistently surveyed since the 1930s (i.e., $\geq 75\%$ of

circles surveyed per decade) than those in the western United States (i.e., three decades with <50% of circles surveyed) and extending the study area further west would have resulted in large regions without CBC circles. An individual CBC occurs over a 24-h period, once per year, during late December or early January. During a count, volunteers record all birds seen or heard within a defined circular study area with a 24.1 km diameter. The area covered and the amount of time spent counting birds in a given circle varies considerably across years and locations, so we standardized bird counts using annual

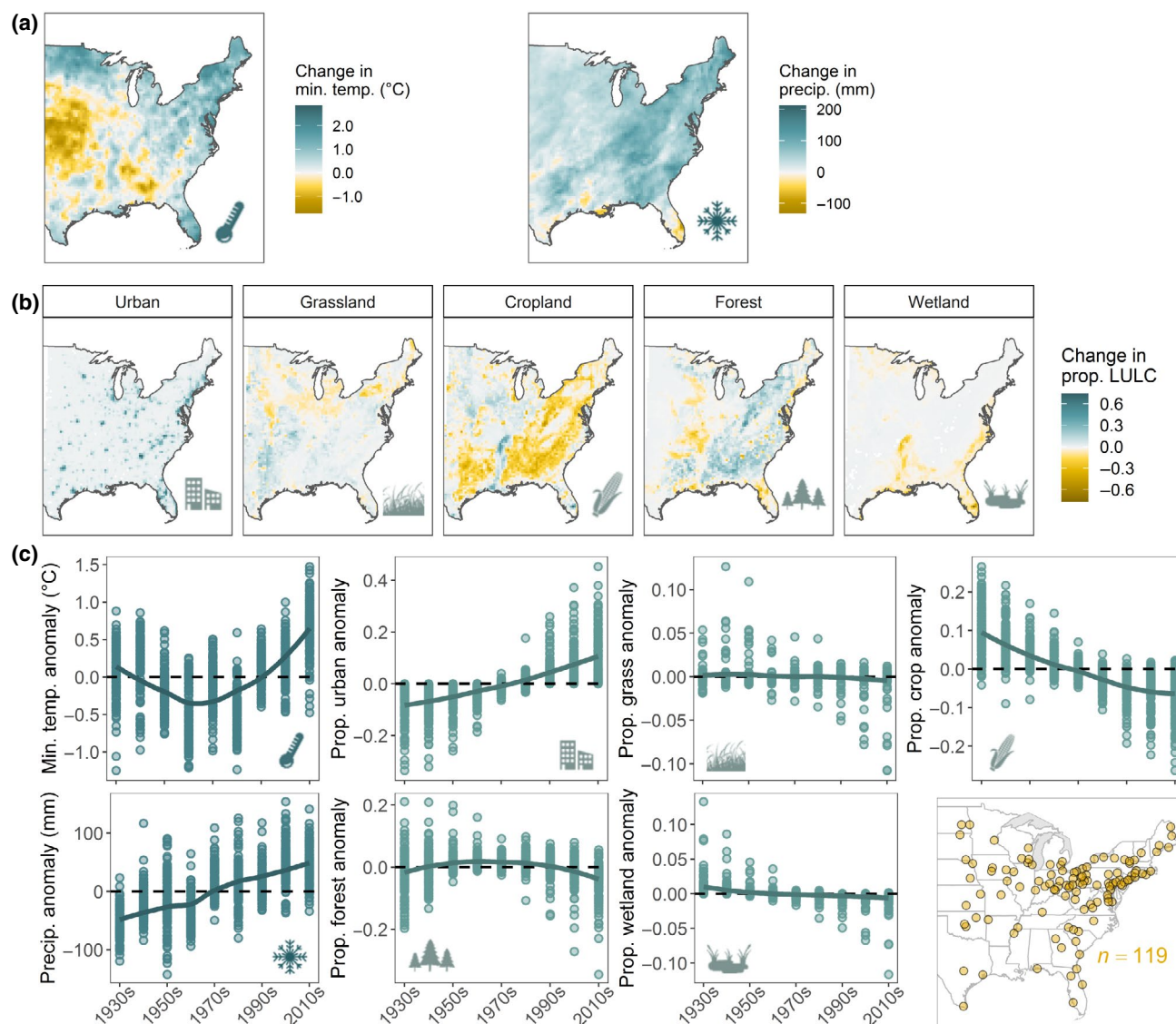


FIGURE 1 Spatial and temporal changes in climate and land-use/land-cover (LULC) during 1930–2019 across the eastern United States. (a) Spatial changes in winter climate conditions (Oct–Dec), average minimum temperature ($^{\circ}\text{C}$; left) and cumulative precipitation (mm; right), from the 1930s to the 2010s. Raw PRISM climate data are shown at a 30-km resolution, which is the scale used to capture spatiotemporal changes in climate conditions within CBC circles (see Section 2 for details). (b) Spatial changes in proportions of five LULC types from the 1930s to the 2010s. Raw LULC data from EROS are shown at a 30-km resolution, which is the scale used to capture spatiotemporal changes in group-specific LULC within CBC circles. The forest + shrubland category (used in models for mixed habitat birds and shrubland birds) is not shown because the pattern of change was consistent with that of the forest category given the scarcity of shrubland cover within our study area. (c) Decadal changes in climate (dark blue) and LULC variables (light blue), based on calculated anomalies (i.e., decadal deviation from long-term site average) per CBC circle ($n = 119$). Solid lines within each panel show a loess fit to the data, representing the overall trend over the 90-year study period. Horizontal dashed lines (black) are shown at zero to indicate no change (i.e., no deviation from long-term average). The bottom right panel in (c) shows the spatial distribution of the 119 CBC circles used in our analyses [Colour figure can be viewed at wileyonlinelibrary.com]

effort metrics (Meehan et al., 2019; Soykan et al., 2016). More details about the CBC can be found in Butcher et al. (1990) and Dunn et al. (2005).

We pooled CBC count data within each decade for subsequent analyses for three main reasons: (i) to minimize the year-to-year variability (i.e., noise) associated with both annual bird counts and annual climatic conditions (Roy et al., 2019); (ii) to align with the temporal scale at which long-term LULC and climatic changes are typically measured (Kalnay & Cai, 2003; Sohl et al., 2016); and (iii) to boost sample sizes (i.e., number of circles surveyed) and computational efficiency. In preliminary analyses, we also evaluated binning observations into 5-year increments, but sample sizes of surveyed CBC circles were more limited at this temporal resolution, particularly in the first half of the study period. For these reasons, and given our primary interest in explaining long-term distributional changes rather than short-term fluctuations, we modeled changes in multi-species occurrence probabilities as a function of decadal changes in climate and LULC (see Supporting Information for more details on the decadal time step).

2.2 | Bird species groups

We used CBC data for a total of 89 species that were selected from a suite of 565 species, primarily based on winter range overlap with the study area (see Supporting Information for full details on selection criteria). We then grouped the 89 species according to a two-step process. We first grouped species by shared habitat preferences (and thus presumably similar responses, on average, to given LULC predictors; see Section 2.4). Habitat assignments (e.g., wetland, forest, etc.) followed those of Soykan et al. (2016), which were based on the primary non-breeding habitat designations from the Avian Conservation and Assessment Database (Partners in Flight, 2021). We then subdivided habitat groups by taxonomy (i.e., order), such as wetland passerines versus waterfowl, and assumed similar responses on average to given climate predictors within these groupings based on previous work (e.g., due to similar body sizes of closely related species; Pacifici et al., 2017; Salewski & Watt, 2017; Weeks et al., 2020). We retained at least three species per group and categorized species according to similar habitat requirements and taxonomy to (i) maximize sample sizes for robust inference; (ii) minimize the impact of relationships between species' ranges and the geographic bounds of the study area (Sohl, 2014); and (iii) develop group-specific hypotheses about distributional dynamics. For example, grouping species by primary habitat affiliations provided a means of assessing the response of birds as a whole in a given habitat type, enabling comparisons among the diversity of ecosystems in the eastern United States.

This process resulted in nine bird groups, which we refer to by the majority of species included in each designation: large-bodied forest birds ($n = 4$ species), forest passerines ($n = 21$ species), grassland birds ($n = 4$ species), mixed habitat birds ($n = 11$ species), waterbirds ($n = 12$ species), shrubland birds ($n = 10$ species), waterfowl

($n = 13$ species), wetland passerines ($n = 6$ species), and woodpeckers ($n = 8$ species); see Table S1 for the complete list of species and group assignments. We designated each species group as habitat-constrained (grassland birds, wetland passerines, waterfowl, waterbirds) or unconstrained (large forest birds, forest passerines, woodpeckers, mixed habitat birds, shrubland birds) based on the availability of preferred habitats in our study area (Figure S1). We hypothesized that changes in occurrence probabilities of habitat-unconstrained groups would be associated primarily with climate, whereas occurrence of habitat-constrained groups would be more responsive to changes in LULC (Correll et al., 2019).

While we designed our analyses to estimate average relationships with climate and LULC variables across the species included in each group-specific model, we note that individual species may vary in their responses, and some species were more or less likely to occur in the CBC than others (see Tables S2–S10 for species-specific occurrences), and thus were more or less likely to contribute to overall inferences (see Supporting Information). In preliminary analyses, we explored further refinement of group designations by functional traits, including diet and migratory strategy. Based on these exercises, we found that our conclusions regarding the relative impacts of global change drivers (e.g., climate vs. LULC; spatial vs. temporal) on bird occurrences were robust to variation in both group size and species composition. Ultimately, we opted for the coarser designations of groups to maximize sample sizes, share information across species, and keep inference comparable across groupings (see Supporting Information for more details on species group designations and sensitivity analyses).

2.3 | Climate and land-use/land-cover data

For calculating climate and LULC covariates, we specified a 30-km diameter circle around each of the 119 CBC centroids, which includes a buffer distance around the standard 24.1 km count circle because we assumed that birds detected within the circle (and at circle edges) may also be responding to environmental conditions outside of the circle's immediate vicinity. To measure the influence of climate conditions on multispecies occurrence probabilities, we calculated two covariates that were included in all group-specific models: average minimum winter (Oct–Dec) temperature (*Tmin*) and cumulative winter (Oct–Dec) precipitation (*Precip*) annually, which we then averaged within 10-year increments to produce decadal metrics. We also included two LULC variables in each group-specific model: one for the primary habitat type used by the represented species (i.e., forest, forest/shrubland, grassland, wetland; *LULCHab*), and one for the anthropogenic land use (i.e., cropland, urban; *LULCAnthro*) that was most predictive of occurrence (Table S1). For the latter, we evaluated support for either *Urban* or *Cropland* as the *LULCAnthro* predictor in an initial analytical step by fitting two models with a single bivariate smooth effect for each variable (see Section 2.4 for details on GAMM structures). We retained the most supported variable in subsequent model fitting, according to the p -value of the

smooth term. For all groups except grassland birds, *Urban* was the top-supported LULCAnthro variable; *Cropland* was included as the LULCAnthro variable in grassland bird models. These results are biologically reasonable, as the primary driver of grassland loss in North America is agricultural conversion (Lark et al., 2020), while urbanization has been one of the primary drivers of both forest and wetland loss in the eastern U.S. (Curtis et al., 2018; Stedman & Dahl, 2008). Although agricultural changes may be associated with changes in occurrence of species other than grassland birds, and urbanization may also be associated with grassland bird occurrence, we limited models to inclusion of two LULC predictors to (i) balance with the climate predictors, since three LULC variables (i.e., one LULCHab and two LULCAnthro) would together likely explain more variation in bird occurrence than the two climate variables, biasing analysis of deviance (ANODEV) results toward LULC impacts and (ii) minimize overparameterization of models for less data-rich groups (i.e., those with fewer species or less frequently observed species).

These predictors are not exhaustive, but we selected them as logical, general mechanisms that might underlie avian responses to climate and land-cover change. We reasoned that changes in the amount of suitable (i.e., primary habitat type) and potentially unsuitable (i.e., anthropogenic) habitat locally available during the non-breeding season could be associated with changes in bird occurrence probabilities because of relationships between LULC and resources (e.g., food and shelter) for overwintering birds (Allen et al., 2019). Further, we expected that the parsimoniousness of our variables for each group would reduce our chances of obtaining statistically significant results by chance, and thus, would be consistent with the hypothetico-deductive method of reducing the Type 1 error rate (Anderson et al., 2001; Ioannidis, 2005). See Supporting Information for additional details on variable selection and how each covariate was measured and calculated.

2.4 | Statistical analyses

2.4.1 | Generalized additive mixed models

Our goal was to assess the relative importance of climate and LULC to changes in winter occurrence probabilities of nine bird groups during 1930–2019. To do this, we estimated climate and habitat relationships using generalized additive mixed models (GAMMs) with a decadal time step. We chose GAMMs because we expected relationships with variables to be nonlinear and GAMMs can model complex, nonlinear patterns by averaging multiple regressions with varying coefficients (Wood, 2017). Our mixed modeling framework allowed us to estimate an average, group-level relationship with each climate and LULC variable by sharing information across species (Dorazio & Royle, 2005), while also accounting for species-level variation in occurrence probability from the group-level mean (via random species effects; e.g., Blackburn & Duncan, 2001; Elith et al., 2006; Pedersen et al., 2019; Zuur et al., 2009). If species were analyzed independently, limited sample sizes (e.g., during the early

decades of the study) would preclude their inclusion in analyses, greatly limiting the scope of inference across the diversity of species observed during CBC surveys. Thus, our mixed modeling approach enabled us to (i) include data-poor species in modeling fitting and (ii) extend the temporal scope for 30–40 years longer than most other large-scale analyses of avian data sets (e.g., Breeding Bird Survey) that extend back no further than the mid-1960s (Rosenberg et al., 2019; Sauer & Link, 2011).

For our response variable, we collapsed annual CBC counts of the 89 focal species into occurrence (0 or 1, absence [i.e., non-detection] or presence; Wood, 2017; Fletcher et al., 2019) $y_{j,t,s(g)}$ at site j ($j = 1, \dots, 119$) in decade t ($t = 1, \dots, 9$) for species s ($s = 1, \dots, n$) in group g ($g = 1, \dots, 9$). In a first step, we fit spatiotemporal GAMMs (i.e., no climate or LULC covariates) to the occurrence data, assuming a binomial distribution with a logit-link function. We used these as baseline models to understand and visualize spatiotemporal changes in multispecies occurrence probabilities within each group in the absence of global change drivers (sensu Oedekoven et al., 2017). In these baseline GAMMs, we included a space-time smoother (Wood et al., 2013), a smooth effect for effort (i.e., log of total distance [km] covered) per decade, as well as random effects of site and species (Princé & Zuckerberg, 2015; see Supporting Information for more details). We used the fitted values from baseline GAMMs to predict occurrence to a standardized grid (at 0.5° resolution) across our study area for each of the nine bird groups during each of the nine decades. Here, we mapped the results as group-specific differences in expected occurrence probabilities between the first and last decades (i.e., 1930s and 2010s) for ease of interpretation and to illustrate long-term changes, although we acknowledge that this masks any nonlinear patterns over time; see Table S11 for mean estimates per decade.

Both climate and LULC vary spatially and temporally, and each process could impact bird distributions. As such, we partitioned spatial and temporal variation in covariates into the local average value over the full time series (i.e., long-term average) and the local, decadal deviation (i.e., anomaly) from that average, respectively. In this way, the averaged covariate x_j represents spatial variation only, while the anomaly covariate $\Delta x_{j,t}$ represents temporal variation only (Clement et al., 2019). Building off the baseline model structure, we removed the space-time smoother because the need for this term is reduced by including covariates that are varying in space and time (Oedekoven et al., 2017). Instead, we included four bivariate smooth effects for the spatial and temporal components of two climate variables (temperature, precipitation) and two group-specific LULC variables (Table S1). Thus, we incorporated interactions between space and time for all global change drivers via bivariate smooth effects (i.e., accounting for potential nonstationarity in relationships). Estimation of covariate effects using a single, common (global) smoother is a common GAMM structure (Pedersen et al., 2019); here, the estimated global smoother represents the average relationship with the given predictor across the range of species included in the group-specific model. This approach did not allow us to estimate species-specific relationships with covariates, which may

differ from the average (group-level) relationships, but known estimation issues with fitting both global and individual-level smoothers (i.e., group and species-level smoothers; Pedersen et al., 2019) precluded us from estimating species-specific responses to climate and LULC. Because our hypotheses were posed at the group level, and thus inferring climate and LULC associations with occurrences of particular species was not the focus of the present study, we limited our interpretation of species-specific results (see Supporting Information).

We retained the smooth effect for effort from the baseline model and kept a bivariate smooth effect for longitude and latitude to account for spatial autocorrelation. We also retained the random effects of species and site, and added a random effect of decade to account for any residual temporal variation that was not explained by anomalies. This global (i.e., fully parameterized) model structure can be expressed as:

$$\begin{aligned} \text{logit}(y_{j,t,s(g)}) \sim & \text{Binomial}(S(\log_effort_{j,t}) + S(lon_j, lat_j) \\ & + S(Tmin_j, \Delta Tmin_{j,t}) + S(Precip_j, \Delta Precip_{j,t}) \\ & + S(LULCHab_j, \Delta LULCHab_{j,t}) + S(LULCAnthro_j, \Delta LULCAnthro_{j,t}) \\ & + \epsilon_j + \epsilon_t + \epsilon_s), \end{aligned}$$

where $S()$ refers to smooth terms, and ϵ_j , ϵ_t , and ϵ_s are the random effects for site, decade, and species, respectively. The model describes the temporal change in occurrence as a combination of smooth anomaly components ($\Delta Tmin_{j,t}$, $\Delta Precip_{j,t}$, $\Delta LULCHab_{j,t}$, $\Delta LULCAnthro_{j,t}$) and a random component ϵ_t . Likewise, the spatial change in occurrence is described as a combination of smooth average components ($Tmin_j$, $Precip_j$, $LULCHab_j$, $LULCAnthro_j$) and a random component ϵ_j . As an example, for forest passerines, the *LULCHab* and *LULCAnthro* terms were represented by *Forest* and *Urban*, respectively. Results from the global models were used to infer the significance, direction, and magnitude of climate and LULC bivariate smooth effects on multispecies occurrence within each of the nine groups. We assessed the significance of smooth effects for each group via p -values from chi-square test statistics in GAMM outputs, and considered $p < .05$ to indicate statistically significant predictors. See Supporting Information for full details on model fitting, goodness-of-fit, and results from global GAMMs.

2.4.2 | Analysis of deviance

We used analysis of deviance (ANODEV; Clement et al., 2019; Skalski, 2011) to evaluate the relative importance of climate and LULC, as well as their temporal and spatial components, to changes in multispecies occurrence probabilities for each bird group (see Supporting Information for more details). To do this, we compared the amount of deviance explained by subsets of global GAMMs, $\text{Dev}(\text{Mod}_{\text{sub}})$, with the deviance explained by the fully parameterized (i.e., global) model, $\text{Dev}(\text{Mod}_{\text{global}})$, by calculating R^2_{Dev} (analogous to marginal R^2 for generalized linear mixed models; e.g., Howard et al., 2020):

$$R^2_{\text{Dev}} = \frac{\text{Dev}(\text{Mod}_{\text{null}}) - \text{Dev}(\text{Mod}_{\text{sub}})}{\text{Dev}(\text{Mod}_{\text{null}}) - \text{Dev}(\text{Mod}_{\text{global}})}.$$

Higher values of R^2_{Dev} (%) indicate greater explanatory power, with 0% indicating no power and 100% indicating power equal to that of the fully parameterized model. $\text{Dev}(\text{Mod}_{\text{null}})$ refers to the deviance of a null model with the same structure as $\text{Mod}_{\text{global}}$, but without the four bivariate smooth effects for climate and LULC predictors (i.e., Mod_{null} is nested within $\text{Mod}_{\text{global}}$).

For each species group, we evaluated the relative importance of climate versus LULC ($R^2_{\text{Dev,CLIM}}$ vs. $R^2_{\text{Dev,LULC}}$) by calculating deviance explained by fitting two models (Mod_{sub}) with the same structure as Mod_{null} and with either (i) bivariate smooth effects for minimum temperature and precipitation only, or (ii) bivariate smooth effects for only the two group-specific LULC variables (i.e., Mod_{null} is nested within Mod_{sub} and Mod_{sub} is nested within $\text{Mod}_{\text{global}}$). We evaluated the relative importance of spatial versus temporal processes ($R^2_{\text{Dev,SPAT}}$ vs. $R^2_{\text{Dev,TEMP}}$) by calculating the deviance explained by two models (Mod_{sub}) fit with either (i) univariate smooth effects for $Tmin_j$, $Precip_j$, $LULCHab_j$, and $LULCAnthro_j$ (i.e., averages), or (ii) univariate smooth effects for $\Delta Tmin_{j,t}$, $\Delta Precip_{j,t}$, $\Delta LULCHab_{j,t}$, and $\Delta LULCAnthro_{j,t}$ (i.e., anomalies). We further differentiated between the importance of spatial climate versus spatial LULC ($R^2_{\text{Dev,SPCLIM}}$ vs. $R^2_{\text{Dev,SPLULC}}$), as well as temporal climate versus temporal LULC ($R^2_{\text{Dev,TECLIM}}$ vs. $R^2_{\text{Dev,TELULC}}$), by calculating the deviance explained by two models (Mod_{sub}) fit with either (i) univariate smooth effects for $Tmin_j$ and $Precip_j$ or (ii) univariate smooth effects for $LULCHab_j$ and $LULCAnthro_j$, as well as two models fit with either (i) univariate smooth effects for $\Delta Tmin_{j,t}$ and $\Delta Precip_{j,t}$ or (ii) univariate smooth effects for $\Delta LULCHab_{j,t}$ and $\Delta LULCAnthro_{j,t}$. We also used likelihood ratio tests (LRTs) as a means of measuring performance of nested models to further quantify the improvements in model fit attributed to global change drivers (Table S12).

3 | RESULTS

3.1 | Climate and land-use/land-cover changes

Between the 1930s and 2010s, minimum winter temperatures generally warmed, winter precipitation increased (Figure 1a), and there were substantial LULC changes (Figure 1b) across the eastern United States. While the vast majority of the study area experienced wetter winters over time, changes in temperature showed more spatial variation, with areas of the central United States experiencing $\geq 1^\circ\text{C}$ decreases in minimum temperature over the 90-year period (Figure 1a). According to decadal anomalies, cooling winter temperatures dominated CBC sites in the 1960s–1980s (anomaly range: -0.52 to -0.08°C) but were followed by warming temperatures in the last three decades (anomaly range: 0.13 – 0.66°C ; Figure 1c). Mean changes in precipitation anomalies increased steadily from -56.5 mm (drier) in the first decade to 46.6 mm (wetter) in the last decade (Figure 1c). When averaged across the study area, we detected no

temporal trends in grassland or wetland habitat availability within CBC circles (Figure 1c). However, there were considerable spatial patterns in habitat change, where grasslands experienced the greatest losses at northern latitudes (e.g., Midwest) and wetlands showed the largest declines along the Atlantic and Gulf coasts since the 1930s (Figure 1b). Urbanization became more pronounced during the 1990s–2010s, with a mean increase of 10% within CBC circles during the last decade (Figure 1c). Conversely, cropland declined from a mean anomaly of 9% (gaining cropland) in the 1930s to –6% (losing cropland) in the 2010s across the study area (Figure 1c), although there were substantial increases in cropland cover across the upper Midwest since the 1930s (Figure 1b). Gains in forest were greatest during the 1950s–1980s (anomaly range: 0.5%–2%) and concentrated in the Southeast and Northeast (Figure 1b); mean forest cover within CBC sites has declined in recent decades by up to –4% (Figure 1c).

3.2 | Changes in winter bird occurrence probabilities

We first fit baseline GAMMs (spatiotemporal, effort-corrected models with no climate or LULC covariates; see Section 2) and predicted to a standardized 0.5° grid to understand and visualize spatiotemporal changes in occurrence probabilities in the absence of specific global change drivers. We found that the mean expected occurrence

probabilities across the eastern United States increased somewhat from the 1930s to 2010s for three groups (albeit 95% confidence intervals [CIs] overlapped; see Table S11 for detailed results): mixed habitat birds (0.57 to 0.82), waterbirds (0.28 to 0.48), and waterfowl (0.37 to 0.64). The latter two groups exhibited multidirectional spatial changes in occurrence, with waterfowl decreasing in occurrence probability across the Prairie Potholes, Ozarks, mid-Atlantic, and southern Florida while stable or increasing in occurrence probability elsewhere, and waterbirds decreasing in occurrence probability along the southern Mississippi River watershed (Figure 2). Forest passerines (0.66 to 0.71), grassland birds (0.32 to 0.37), and large forest birds (0.92 to 0.99) showed small increases in mean occurrence probabilities (with overlapping CIs; Table S11), with already-widespread large forest birds (e.g., hawks) increasing in occurrence probability at northern latitudes (Figure 2). Spatial changes in occurrence probabilities for grassland birds and forest passerines were multidirectional, although notably, both groups declined in expected occurrence at southernmost latitudes (e.g., Florida; Figure 2). Mean occurrence probabilities of shrubland birds (0.69) and wetland passerines (0.01) remained unchanged between the first and last decades (Figure 2), albeit shrubland bird occurrence probability did increase mid-study period (Table S11). Woodpeckers were the only group that marginally decreased in mean expected occurrence probability (0.57 to 0.56), owing to an overall shift in occurrence towards the northern bounds of our study area (Figure 2). See Figure S2 for

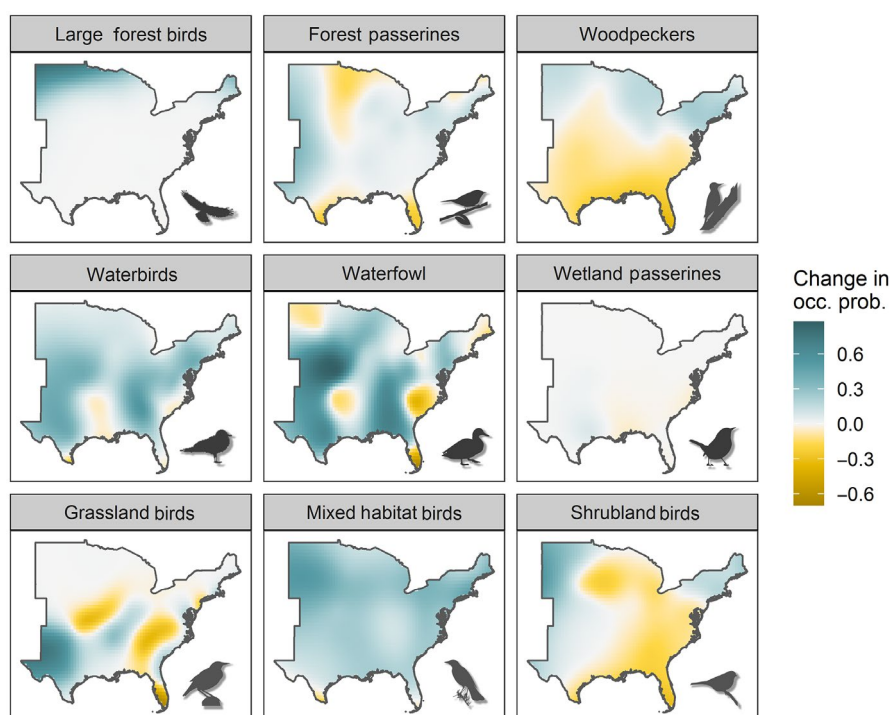


FIGURE 2 Change in winter occurrence probabilities (occ. prob.) from the 1930s to the 2010s for nine bird groups, as estimated from Christmas Bird Count data for 89 species. Positive values (blue) indicate greater occurrence probabilities during the 2010s compared with the 1930s, whereas negative values (yellow) indicate lower occurrence probabilities during the 2010s. No change in occurrence probability is shown in white. Estimates are based on fitting baseline (i.e., no climate or land-use/cover covariates) generalized additive mixed models (GAMMs) and predicting to a standardized 0.5° grid across the study area. See Section 2 for more details on baseline GAMMs and Table S11 for group-specific mean expected occurrence probabilities per decade estimated across the study area [Colour figure can be viewed at wileyonlinelibrary.com]

fitted values per decade estimated from baseline GAMMs (i.e., expected occurrence probabilities per CBC circle, decade, and species within each group).

3.3 | Relative importance of global change drivers

From our global GAMMs, which included climate and LULC covariates (see Section 2), we identified climate and land-use associations

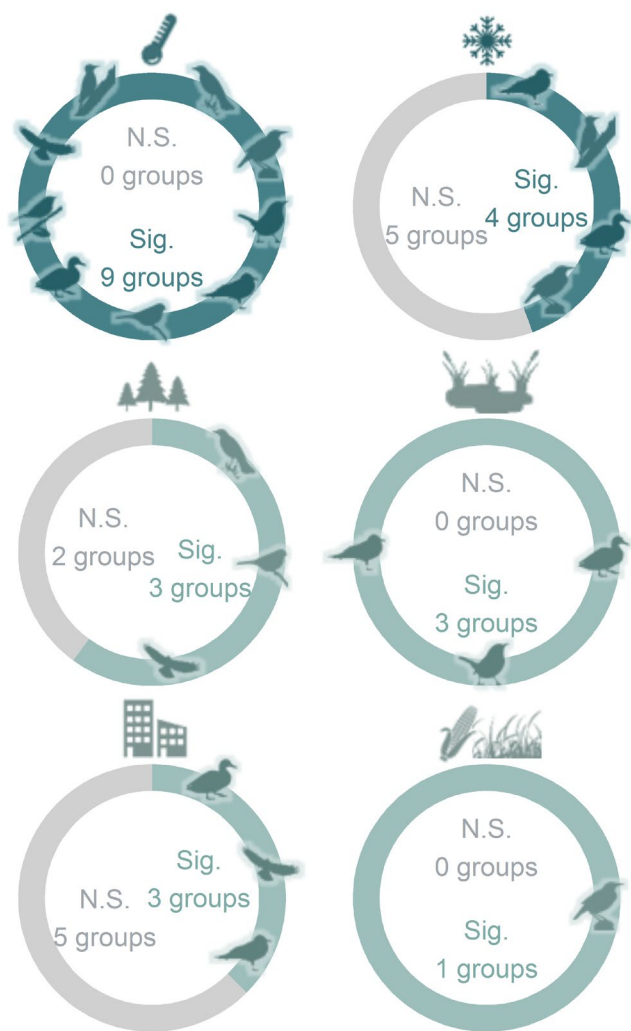


FIGURE 3 Proportions of bird species groups for which the given bivariate smooth effect was considered significant (Sig.; $p < .05$) in global GAMMs using Christmas Bird Count data for 89 species from 1930 to 2019. The total number of groups represented in each plot differ based on group-specific model structures (see Section 2 for more details); the proportion of groups with nonsignificant effects (N.S.) is indicated in gray. Bivariate smooth effects of two climate (dark blue) and four land-use/land-cover (LULC) covariates (light blue) are shown (top to bottom): minimum winter temperature, cumulative precipitation, forest (or forest + shrubland) cover, wetland cover, urban cover, and grassland and cropland cover (latter two variables were included in grassland bird GAMMs only). See Figure 2 for bird group silhouette symbology [Colour figure can be viewed at wileyonlinelibrary.com]

with bird occurrence probabilities for all nine groups (Figure 3; see Tables S13–S21 for more details on general directions of covariate relationships). We then used ANODEV to evaluate the relative importance of climate and LULC, as well as their spatial and temporal components, to changes in occurrence probabilities. On average across groups, combined spatial and temporal variation in climate explained nearly twice the variation in bird occurrence probability ($81.4 \pm 13.9\%$ of the change in deviance on average \pm standard deviation [SD]) than combined spatial and temporal variation in LULC ($41.9 \pm 19.0\%$; Figure 4a). This pattern was primarily driven by four habitat-unconstrained groups (i.e., forest passerines, mixed habitat birds, shrubland birds, and woodpeckers), with an average change in deviance of 89.5% with inclusion of climate covariates versus only 25.3% with inclusion of LULC covariates. For habitat-constrained groups (i.e., the three wetland-associated groups and grassland birds), the relative deviance explained by climate was 80.2% on average, compared with 51.4% by LULC (Tables S22–S24). Comparing spatial versus temporal processes, we found that spatial variation in climate and LULC explained more of the variation in bird occurrence probability ($86.5 \pm 15.1\%$ of the change in deviance on average) than temporal variation (i.e., decadal anomalies) for all groups ($19.5 \pm 11.7\%$; Figure 4b). The groups for which temporal variation explained the most change in deviance ($>30\%$) were large forest birds, waterbirds, and waterfowl; for all others, adding temporal variation to the model had a smaller effect (Figure 4b; Tables S22–S24).

We then isolated the spatial and temporal components of variables to further partition the spatiotemporal processes underlying distributional dynamics. For three habitat-unconstrained groups (i.e., forest passerines, mixed habitat birds, and shrubland birds), decadal changes in climate and LULC were each relatively equal contributors to explained variation in occurrence probabilities over the 90-year period (Figure 5), and both comparably improved model fit based on LRTs (Table S12). In contrast, for all four habitat-constrained groups (i.e., grassland birds, waterfowl, waterbirds, and wetland passerines), temporal variation in occurrence probabilities was primarily associated with decadal changes in LULC compared with decadal changes in climate (Figure 5; Table S12). Change in minimum temperature was an important temporal predictor of occurrence probabilities for five out of nine groups and, with the exception of mixed habitat birds (i.e., generalists that use multiple habitat types), temporal variation in at least one LULC variable was also a significant predictor of bird occurrence across groups (Figure 5). Finally, when evaluating spatial climate versus spatial LULC contributions, we found that spatial variation in climate improved model fit considerably for all groups ($74.1 \pm 19.8\%$ of the change in deviance on average), compared with minimal gains in model fit when species' occurrence was modeled as a function of spatial LULC variation alone ($29.0 \pm 11.7\%$; Table S12).

4 | DISCUSSION

Efforts to trace the fingerprint of global change have focused on distributional and phenological changes for individual species,

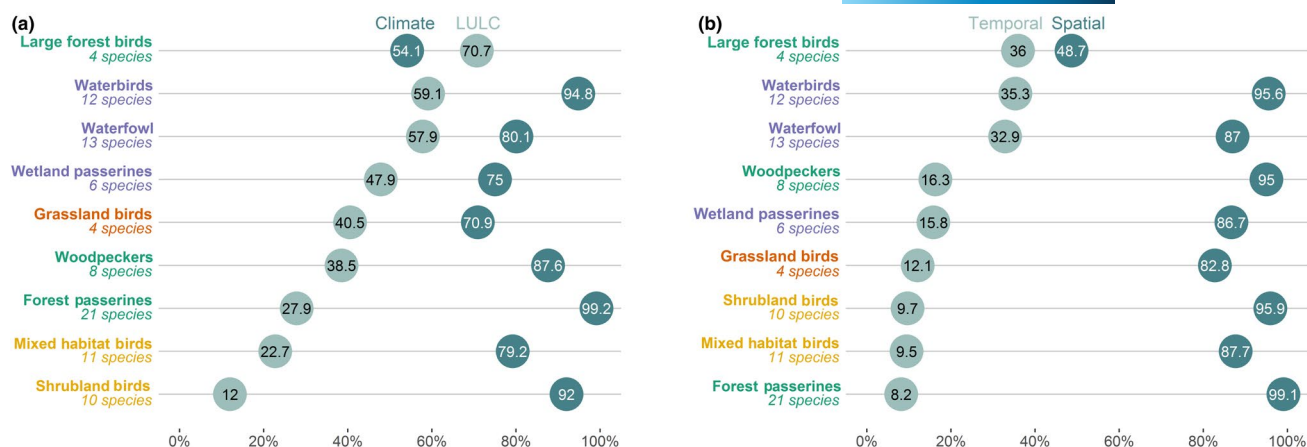


FIGURE 4 Relative change (%) in deviance (R^2_{Dev}) explained by global change drivers for nine bird groups (number of species within each group shown below group names) from generalized additive mixed models (GAMMs) describing spatiotemporal changes in winter occurrence probabilities for 89 species during 1930–2019. (a) Deviance explained by climate (dark blue) versus land-use/cover (LULC; light blue), and (b) deviance explained by spatial (dark blue) versus temporal (light blue) processes. Species groups are color-coded by shared LULC covariates (see Table S1). Estimates are from an analysis of deviance (ANODEV) approach in which we compared the amount of deviance explained by global GAMM subsets (Mod_{sub}) with the deviance explained by the fully parameterized model (Mod_{global}); hence, percentages in each row do not sum to one. See Section 2 for more details on ANODEV [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

particularly during the breeding season (Marra et al., 2015). Yet little is known about whether groups of species vary in their responses during winter, a period that is generally longer, typically resource-restricted, and more limiting to survival for temperate-zone birds (Forsman & Mönkkönen, 2003). By leveraging a spatially expansive, uniquely long-term data set, we revealed that the two most pervasive components of global change, climate and land-use change, have together shaped the winter distributional dynamics of nine bird groups over a 90-year period across the eastern United States. Spatial variation (i.e., distributional boundaries) in bird occurrence probabilities was mainly explained by spatial variation in climate, while temporal variation (i.e., decadal changes) in bird occurrence probabilities over the last century was primarily associated with temporal variation in LULC (Figure 5), most prominently for habitat-constrained species.

Declines in North American birds (Rosenberg et al., 2019) and avifauna globally (Allinson, 2018) suggest that multiple, likely simultaneous, threats are operating across biomes and families. Because the occurrence and abundance of species tend to be linked (Gaston et al., 2000; Kéry, 2010), our results bring us one step closer to disentangling the relative impacts of ongoing threats to avian biodiversity in eastern North America. Understanding group-specific sensitivities to habitat loss or alteration versus changing climatic conditions can help guide land management and climate change adaptation strategies across ecosystems, ultimately improving species' resilience to future change (Bateman et al., 2020). For example, we provide evidence that long-term changes in climate and LULC have comparably affected distributions of habitat-unconstrained species, whereas distributions of habitat-constrained species—many of which are in steep decline (e.g., grassland birds, shorebirds, waterbirds; Rosenberg et al., 2019)—have been more responsive to LULC alterations than climatic changes. Hence, we suggest that coordinated and proactive land use planning aimed at maintaining or

restoring habitat for these species groups be an essential component of state and federal land protection goals (e.g., 30% land protection by 2030) to enhance avian community resilience specifically within these biomes.

We found that spatial patterns were more predictive of variation in bird occurrence probability than temporal processes on average across groups (Figure 4b). This relationship was driven by spatial variation in climate (e.g., minimum temperature; Figure S3), which explained more variation in occurrence across all groups than spatial variation in LULC. These results indicate that species' range limits are primarily constrained by climate in winter, although these bioclimatic relationships can be modified by land use (Zuckerberg et al., 2011). Indeed, we found that species track the availability of their preferred habitats within their climatic boundaries over time. More than half (55%) of the species in our data set are passerines (Table S1), which are small-bodied and hence, more likely to be limited by their thermoregulatory ceiling (Weeks et al., 2020). This relationship may partially account for the overall greater influence of climate, compared with LULC, for nearly all groups (Figure 4a). For example, expected occurrence probabilities of forest passerines, mixed habitat birds, shrubland birds, and large forest birds were greatest at colder sites, on average, during warmer winters (Figure S3), consistent with previous studies showing northward winter range expansions by southerly-distributed species in eastern North America following the signature of warming temperatures (Kelly & Goulden, 2008; LaSorte & Thompson, 2007; Princé & Zuckerberg, 2015; Smith et al., 2019).

Decadal anomalies in climate and LULC together explained 20% of the temporal variation in occurrence probability on average across groups, while it explained >30% for large forest birds, waterfowl, and waterbirds. This stronger association between occurrence and temporal variation in covariates for these three groups suggests that

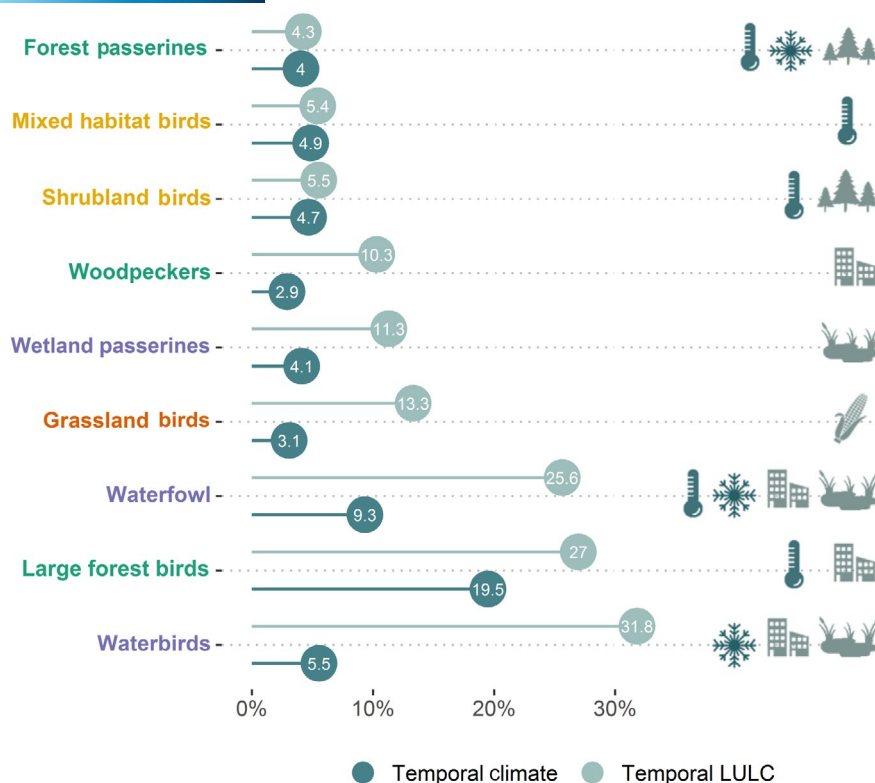


FIGURE 5 Relative change (%) in deviance (R^2_{Dev}) explained by the temporal component (i.e., decadal anomaly) of climate (dark blue) versus the temporal component of land-use/land-cover (LULC; light blue) across nine bird species groups during 1930–2019. Species groups are color-coded by shared LULC covariates (see Table S1). Estimates are from an analysis of deviance (ANODEV) approach in which we compared the amount of deviance explained by two Mod_{sub} (i.e., Temporal Climate, Temporal LULC) to the deviance explained by Mod_{global} . Temporal Climate refers to a GAMM including only climate anomalies (minimum temperature and precipitation), whereas Temporal LULC refers to a GAMM including only group-specific LULC anomalies (e.g., Wetland and Urban for wetland passerines, waterfowl, and waterbirds). Symbols in each row (right) represent significant ($p < .05$) covariates for each group; see Figure 1 for variable symbology [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

distributions of these species exhibited more dynamism, on average, in response to a century of global change. Across groups, we found that decadal changes in LULC explained more than twice the temporal variation in occurrence probability, on average, than decadal changes in climate ($14.9 \pm 10.5\%$ vs. $6.4 \pm 5.2\%$, respectively), possibly because of the pace of land conversion compared with climatic changes (Bateman et al., 2016). This pattern was largely driven by species that rely on relatively scarce habitats (Figure S1), such as grassland birds and wetland-associated birds (i.e., waterbirds, waterfowl, wetland passerines), suggesting that the magnitude of land use change (e.g., habitat loss and fragmentation) over the past 90 years has proven to be a more powerful force in driving their occurrence dynamics than climate change. Of the few studies that have examined the effects of both climate and LULC changes on species' distributions, none concluded that only climate change had an impact (Sirami et al., 2017). This suggests that the lack of integration of climate and LULC drivers is currently limiting our understanding of the impacts of global change on species' distributions (i.e., underestimating effects within climate change-only frameworks). Thus, our findings represent a notable advancement in our knowledge of the mechanisms underlying distributional dynamics for birds within human-dominated landscapes.

The increased occurrence of waterfowl and waterbirds (including gulls) in some regions can be attributed, in part, to a positive association with urban land cover, which grew steadily throughout the study period. Expected occurrence probabilities of these two groups were also greatest at wetland-rich sites and at drier-than-average sites during wetter decades (Figures S4 and S6). Both groups exhibited multidirectional, rather than poleward, changes in occurrence (Figure 2), and when we isolated temporal components, we found that change in precipitation was a significant predictor of occurrence probability (Figure 5). While previous work has linked multidirectional changes with precipitation variables (Bateman et al., 2016; VanDerWal et al., 2013), we hypothesize that this result could also be a function of climate niche expansion (Ralston et al., 2017) by species with increasing population trends in both groups (Meehan et al., 2021), including Double-crested Cormorant (*Phalacrocorax auritus*; waterbird group) as well as several ducks and geese in the waterfowl group (Rosenberg et al., 2019; see Tables S2–S10 for CBC occurrence trends). These results, coupled with the high relative importance of both temporal and LULC processes in explaining model deviance (Figure 4), are consistent with previous findings that waterfowl and waterbirds are particularly responsive to decadal fluctuations in wetland availability and/or inundation (e.g., McKenna

et al., 2021). Given the relative scarcity of wetlands across the study area (Figure S1), we suggest that conservation programs aimed at restoring wetland habitats on private lands (e.g., National Resource Conservation Service's Wetland Reserve Program, U.S. Fish and Wildlife Service's Partners for Fish and Wildlife Program) become an essential adaptation strategy for ensuring that wetland-reliant species are able to locate appropriate habitats as climate variability becomes more extreme (Benson et al., 2018). These efforts are particularly important in regions like the Prairie Potholes, which support high waterfowl densities despite declines in occurrence, and are projected to lose critical wetland basins under climate change scenarios (McKenna et al., 2021).

Like waterfowl, raptors have increased in abundance since the 1970s (Rosenberg et al., 2019), which may have enabled them to geographically track climate change more closely than declining groups (Ralston et al., 2017). Raptors are known to respond to climate change by remaining farther north during warmer winters (Kim et al., 2008). Our results for large forest birds corroborate this pattern (Figure S3) and indicate that this behavior has led to long-term northward range expansions (Figure 2). Evidence also suggests that hawks are adapting to urban environments because of increased food availability from human activities (Duerr et al., 2015; Rullman & Marzluff, 2014), which may explain their greater occurrence at CBC sites that are becoming more urbanized (Figure S7).

Mean occurrence probability of grassland birds slightly increased in our study area (albeit certain species declined in occurrence during the second half of the study period; see Table S4), with the greatest increases in Texas and the greatest decreases east of the Mississippi River since the 1930s (Figure 2). This result could be a manifestation of westward and northward wintering range shifts (Jaster et al., 2020; Jones & Cornely, 2020; LaSorte & Thompson, 2007) by species like Eastern Meadowlark (*Sturnella magna*) and Vesper Sparrow (*Pooecetes gramineus*) due to grassland loss in both the eastern United States and Mexico's Chihuahuan grasslands (Brennan & Kuvlesky, 2005; Pool et al., 2014). CBC circles in the Texas region, on average, now have more grassland and less cropland, as well as became drier and cooler over time, all of which were associated with increased occurrence probability of grassland bird species (Figures S3, S4 and S8). We found that expected occurrence probability was greatest in agriculturally-rich areas and those that were gaining grassland cover over time (Figure S8). Together with the greater sensitivity of this group to LULC change relative to climate change (Figure 5), these results highlight the need to maintain and restore natural grasslands within US agricultural landscapes, especially in the face of increasing commodity and energy production. Although our study area does not include the Chihuahuan wintering grounds in Mexico, grassland restoration should also be prioritized in this region, given that rapid cropland expansion in the Chihuahuan is considered to be among the primary drivers of North American grassland bird population declines (e.g., Pool et al., 2014).

The only group for which mean occurrence probability marginally decreased during our study was that of woodpeckers (but CIs of decadal mean estimates overlapped; Table S11), which

increased in occurrence probability at northern latitudes along the study area boundary but decreased in occurrence probability at southern latitudes (Figure 2). Consistent with this pattern, we found that woodpecker occurrence probability was greatest at colder CBC sites, on average, during decades with warmer winters (Figure S3). Northward winter range shifts have been documented for several woodpecker species (LaSorte & Thompson, 2007; Walsh et al., 2019), and may reflect unmodeled interactions between natural habitat changes and anthropogenic influences, in addition to warming temperatures and changing fire regimes. For example, the isolation of temporal components revealed that change in urban cover was an important contributor to the explained variation in woodpecker occurrence (Figure 5), suggesting that local-scale changes at urban/suburban sites (e.g., supplemental food availability, habitat fragmentation) played a role in driving woodpecker distributions over the last century (Princé & Zuckerberg, 2015).

Despite repeated calls, the combined effects of multiple global change drivers on species' distributions remain under-investigated, serving as a major impediment to accurate projections of biodiversity and effective multispecies conservation (Braunisch et al., 2014; Hockey et al., 2011; Titeux et al., 2016). Looking forward, our findings suggest that climate change may influence future distributional boundaries for many bird species overwintering in the eastern United States (Bateman et al., 2020), with implications for migratory strategies, phenology, and population dynamics (Socolar et al., 2017; Youngflesh et al., 2021). We also present evidence for the pivotal role of LULC change in driving distributional dynamics of bird species with limited and declining habitat availability, indicating that effective land management will be critical for improving these species' resilience to climate change, especially during the winter season of limited food resources and energy-intensive weather conditions. Future efforts should focus similar, multidriver analyses on western U.S. bird species, which may differ in their responses to climate and LULC given the diverse stressors (e.g., fire, timber harvest, drought) operating in western landscapes (Betts et al., 2019). We note that the bird group designations and variables used here were specified and evaluated based on our study area and questions of interest; alternative approaches to both grouping species (e.g., based on management or life history traits) and selecting ecological predictors may be appropriate in other studies, depending on the focal geographies and hypotheses posed. Nevertheless, our sensitivity analyses (see Supporting Information) suggest that our overarching findings are robust to these choices. More broadly, this hierarchical, group-specific approach to quantifying ecological drivers can facilitate future work aimed at unraveling the spatio-temporal processes that underpin species' occurrence dynamics in a rapidly changing world.

ACKNOWLEDGMENTS

We are grateful to all the CBC participants and various donors over the last 90 years that have made the CBC the longest-running community science bird project. Thank you to E. Zipkin, B. Haest, and

an anonymous reviewer for insightful comments that improved the manuscript.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHOR CONTRIBUTIONS

Chad B. Wilsey, Timothy D. Meehan, and Joanna X. Wu conceived of the research; Sarah P. Saunders and Timothy D. Meehan designed the analysis with input from all authors; Brooke L. Bateman, Joanna Grand, Lotem Taylor, Henrik Westerkam, and Joanna X. Wu collected and extracted data; Sarah P. Saunders and Timothy D. Meehan conducted analyses; Sarah P. Saunders, Timothy D. Meehan, William DeLuca, Jill L. Deppe, Geoffrey S. LeBaron, and Nicole L. Michel contributed to interpretation of results; and Sarah P. Saunders wrote the paper with editorial contributions from all authors.

DATA AVAILABILITY STATEMENT

Data and code are available in Audubon's GitHub repository (https://github.com/audubongit/long_term_CBC_analysis) and permanently archived in the Zenodo digital repository: <https://doi.org/10.5281/zenodo.5784365> (Saunders, 2021).

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How to cite this article: Saunders, S. P., Meehan, T. D., Michel, N. L., Bateman, B. L., DeLuca, W., Deppe, J. L., Grand, J., LeBaron, G. S., Taylor, L., Westerkam, H., Wu, J. X., & Wilsey, C. B. (2022). Unraveling a century of global change impacts on winter bird distributions in the eastern United States. *Global Change Biology*, 28, 2221–2235. <https://doi.org/10.1111/gcb.16063>