



Original research article

Tree species distributions modify decadal trajectories of bird species habitat suitability predicted by climate change

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ARTICLE INFO

Dataset link: <https://doi.org/10.5061/dryad.cz8w9gjhc>

Keywords:

Breeding Bird Survey
Climate change
Forest birds
Habitat suitability
Tree species

ABSTRACT

Global climate change threatens biodiversity, in part due to its effects on species distributions and habitat suitability. The ability to predict future impacts and discern variability in rates of change is critical for conservation planning. Here, we quantified the relative influence of climate and tree species metrics on contemporary and future patterns of incidence (i.e., an index of broad-scale habitat conditions and a metric of habitat suitability) associated with forest-breeding birds across the eastern USA and assessed trends in decadal trajectories of future projections. We hypothesized that potential future tree species distributions will modify decadal trajectories of bird species habitat suitability predicted by climate change, with differential outcomes associated with tree species remaining static or shifting dynamically over time. We used North American Breeding Bird Survey data and randomForest models to evaluate the incidence of 100 forest bird species and quantify the pace of predicted change based on climate alone and in conjunction with static and lagged tree distributions. For 90 forest bird species, our results showed that future tree species distributions altered either the overall trajectory ($n = 83$) or timing ($n = 50$) of changes in projections of habitat suitability expected from climate effects only. In particular, maintaining contemporary tree species distributions into the future moderated climate-associated declines in habitat suitability for 78 bird species. Decadal trajectories emphasized the importance of timing, with the greatest declines occurring for 16–30 bird species within the first three decades of the century, depending on the future scenario. Ultimately, these findings underscore the importance of climate-informed, time-sensitive conservation plans for forests and the birds breeding within them.

1. Introduction

Global climate change is among the most significant contemporary threats to biodiversity, with recent rising temperatures leading to distributional shifts in a myriad of animal taxa (Lenoir et al., 2020). To develop effective conservation plans, it is essential to generate timely, data-driven projections of species changes. However, the increasing velocity of climate change over the next century and the complexity of potential ecological interactions make it challenging to predict future shifts in species. Because of non-linear responses over time, modeling efforts require thorough consideration of temporally relevant environmental drivers, as well as

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<https://doi.org/10.1016/j.gecco.2026.e04396>

Received 17 March 2026; Received in revised form 19 July 2026; Accepted 29 August 2026

Available online 31 August 2026

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interactions among them.

Climate plays a fundamental role in shaping bird species distributions at multiple spatiotemporal scales (Jiménez-Valverde et al., 2011; Callaghan et al., 2024). The effects of climate can be direct (e.g., physiological limits) or indirect (e.g., changes to resource availability), with individual responses combining into population-level impacts. For instance, range limits are influenced by extreme low and high temperatures, as dictated by physiological tolerance thresholds, and warming temperatures can induce rapid range shifts poleward and to higher elevations (Chen et al., 2011). Interspecific variability may influence the degree of climate matching (Viana and Chase, 2022), with some bird species lacking the adaptability to respond quickly to novel climate conditions or changes in the timing of environmental cues (Beever et al., 2017). Ultimately, a considerable reshuffling of species distributions is predicted to result from projected climate change (Hitch and Leberg, 2007; Langham et al., 2015; Sorenson et al., 1998; Virkkala et al., 2008).

Beyond climate, there is clear evidence that additional environmental factors influence the realized distributions (Rich and Currie, 2018) and capture contemporary population changes of many bird species (Betts et al., 2022). For example, vegetative conditions and the presence of specific plant species that provide nesting or foraging substrates can dictate important constraints on bird species habitat suitability (Adams and Matthews, 2019). These associations occur across ecological scales, from individual-level links with floristic composition (Holmes et al., 1979) to population-level dependence. Prime examples of the latter include Kirtland's warblers (*Setophaga kirtlandii*) in north-central USA (Mayfield, 1953) and red-cockaded woodpeckers (*Dryobates borealis*) in the southeastern USA (Hooper, 1988), both of which are habitat specialists with strong ties to a specific tree species — jack pine (*Pinus banksiana*) and longleaf pine (*Pinus palustris*), respectively. In some cases, bird species rely on particular tree species within a portion of their overall breeding range (e.g., Swainson's thrushes [*Catharus ustulatus*] and red spruce [*Picea rubens*] in West Virginia; Clipp et al., 2022). Looking forward, projected range shifts due to changing climate could be significantly modified by indirect effects to habitat suitability, as bird species may track changes in vegetative composition or structure more strongly than climate (Kissling et al., 2010; Martin and Maron, 2012).

Previous efforts to model regional patterns of bird abundance have considered non-climate, habitat-related factors such as landscape change (Clipp et al., 2025) and individual tree species distributions (Fearer et al., 2007; Matthews et al., 2011), which were found to improve model performance and prediction accuracy. Tree species distributions are expected to shift in the future (Iverson et al., 2019; Prasad et al., 2025), although recent evidence suggests that tree range margins are relatively stable (Woodall et al., 2018) and tree species longevity dictates that turnover in forested ecosystems usually occurs at slower rates than projected climate shifts. Thus, incorporating predicted changes in individual tree species distributions in a lagged manner could enhance the predictive capacity of climate-driven models for bird species. In addition, recent changes in bird populations have been non-linear, with inter-specific variation in the direction and magnitude of potential change. Being able to predict variable rates of change is critical for conservation planning, as steep declines projected over the coming decades would imply the need to quickly implement targeted conservation practices. To address this research need, we built upon previous efforts to model the combined effects of both climate factors and tree species distributions under future climate scenarios (e.g., Kissling et al., 2010; Lalechère and Bergès, 2022; Triviño et al., 2011) by forecasting bird species habitat suitability at decadal timesteps throughout the 21st century.

Our goals were to quantify the relative influence of climate factors and tree species metrics on contemporary and future distributions of bird species that breed in forested ecosystems across the eastern USA (hereafter, referred to as forest birds) and assess trends in decadal trajectories of future habitat suitability. Within this framework, we tested the hypothesis that potential future tree species distributions will modify decadal trajectories of forest bird habitat suitability predicted by climate change. Specifically, we expected tree species metrics to have higher relative importance than climate factors, and we predicted that future tree species distributions would mitigate the timing and overall change in forest bird species habitat suitability, such that maintaining contemporary tree species distributions would slow the rate and reduce the total amount of projected change. To explicitly test our predictions, our objectives were to: (1) determine the value of incorporating tree species information into forest bird models of breeding habitat suitability; (2) identify which forest bird species were most strongly influenced by tree species metrics; (3) quantify the effects of static and lagged future tree distributions on overall trends and timing of decadal trajectories; and (4) compare trajectories of breeding habitat suitability among bird species. Given the likely future decoupling of climate conditions and forested ecosystems, our study will provide important insights into possible outcomes for individual and groups of forest bird species.

2. Methods

2.1. Bird data

Our study area encompassed the eastern USA (i.e., east of the 100th meridian; Peters et al., 2019) in order to leverage the critical environmental predictor space necessary to develop species distribution models for current and future habitat availability projections. We obtained data for 100 bird species that breed in forested ecosystems within the eastern USA from the North American Breeding Bird Survey (BBS) from 2000 to 2009 (Sauer et al., 2019). Considering only routes that were surveyed at least seven times across the 10-year sampling period, we used incidence as our response metric, calculated as the proportion of occasions when a given bird species was recorded on a route across the decade. Incidence approximates relative abundance and is a metric of habitat suitability (Matthews et al., 2011), but it should not be conflated with true occupancy or abundance, as it does not account for variation in detectability.

Because various groups of forest bird species may be differentially affected by climate change and tree species, we assessed potential variation among taxonomic groups, life history traits, breeding distributions, and breeding habitat guilds. We used species-specific information from Billerman et al. (2025) and Partners in Flight databases to classify each bird species based on the following categories (Table S1 in Supporting Information): taxonomic family, diet, foraging method, nest substrate, migratory status,

breeding biome, breeding distribution within the eastern USA, general breeding habitat guild, and specific forest habitat type.

2.2. Environmental data and spatial grain

Environmental covariates consisted of seven climate indices, four topographical metrics, and habitat suitability of 46 tree species (Table 1), which were compiled into a 10-km and 20-km hybrid modeling grid (Peters et al., 2019). For each predictor variable, we

Table 1

List of the environmental predictor variables included in the randomForest models for the 100 focal bird species that breed in forests of the eastern USA. Relative abundance of tree species was quantified as an importance value (IV). Total number of models indicates how many models incorporated each predictor variable. Tree species were only included if their model reliability was medium or high and their range overlapped the range of the focal forest bird species.

Category	Predictor Variable	Metric	Total Models	Model Reliability
Climate	Annual precipitation	mm	100	N/A
	May–September precipitation	mm	100	N/A
	Mean annual temperature	°C	100	N/A
	Mean January temperature	°C	100	N/A
	Mean July temperature	°C	100	N/A
	Mean May–September temperature	°C	100	N/A
	Annual potential evapotranspiration	mm	100	N/A
Topography	Maximum elevation	m	100	N/A
	Mean elevation	m	100	N/A
	Elevational range	m	100	N/A
	Standard deviation of elevation	m	100	N/A
Tree Species	Balsam fir (<i>Abies balsamea</i>)	IV	86	High
	Striped maple (<i>Acer pensylvanicum</i>)	IV	98	Medium
	Red maple (<i>Acer rubrum</i>)	IV	100	High
	Sugar maple (<i>Acer saccharum</i>)	IV	98	High
	Yellow birch (<i>Betula alleghaniensis</i>)	IV	97	High
	Sweet birch (<i>Betula lenta</i>)	IV	97	High
	Paper birch (<i>Betula papyrifera</i>)	IV	91	High
	Shagbark hickory (<i>Carya ovata</i>)	IV	100	Medium
	Black hickory (<i>Carya texana</i>)	IV	73	High
	Hackberry (<i>Celtis occidentalis</i>)	IV	93	Medium
	Flowering dogwood (<i>Cornus florida</i>)	IV	98	Medium
	American beech (<i>Fagus grandifolia</i>)	IV	100	High
	White ash (<i>Fraxinus americana</i>)	IV	100	Medium
	Black ash (<i>Fraxinus nigra</i>)	IV	98	Medium
	Eastern redcedar (<i>Juniperus virginiana</i>)	IV	98	Medium
	Tamarack (<i>Larix laricina</i>)	IV	90	High
	Sweetgum (<i>Liquidambar styraciflua</i>)	IV	87	High
	Yellow-poplar (<i>Liriodendron tulipifera</i>)	IV	97	High
	Water tupelo (<i>Nyssa aquatica</i>)	IV	69	Medium
	Blackgum (<i>Nyssa sylvatica</i>)	IV	98	Medium
	Black spruce (<i>Picea mariana</i>)	IV	84	High
	Red spruce (<i>Picea rubens</i>)	IV	93	High
	Jack pine (<i>Pinus banksiana</i>)	IV	89	Medium
	Shortleaf pine (<i>Pinus echinata</i>)	IV	86	High
	Slash pine (<i>Pinus elliottii</i>)	IV	65	High
	Longleaf pine (<i>Pinus palustris</i>)	IV	67	Medium
	Pitch pine (<i>Pinus rigida</i>)	IV	94	High
	Eastern white pine (<i>Pinus strobus</i>)	IV	98	High
	Loblolly pine (<i>Pinus taeda</i>)	IV	99	High
	Virginia pine (<i>Pinus virginiana</i>)	IV	93	High
	Bigtooth aspen (<i>Populus grandidentata</i>)	IV	96	Medium
	Quaking aspen (<i>Populus tremuloides</i>)	IV	95	High
	Black cherry (<i>Prunus serotina</i>)	IV	100	Medium
	White oak (<i>Quercus alba</i>)	IV	99	Medium
	Scarlet oak (<i>Quercus coccinea</i>)	IV	99	Medium
	Chestnut oak (<i>Quercus montana</i>)	IV	99	High
	Water oak (<i>Quercus nigra</i>)	IV	74	High
	Northern red oak (<i>Quercus rubra</i>)	IV	100	Medium
	Post oak (<i>Quercus stellata</i>)	IV	89	High
	Black oak (<i>Quercus velutina</i>)	IV	99	High
	Live oak (<i>Quercus virginiana</i>)	IV	64	High
	Pondcypress (<i>Taxodium ascendens</i>)	IV	63	Medium
	Northern white-cedar (<i>Thuja occidentalis</i>)	IV	92	High
	American basswood (<i>Tilia americana</i>)	IV	100	Medium
	Eastern hemlock (<i>Tsuga canadensis</i>)	IV	97	High
	American elm (<i>Ulmus americana</i>)	IV	100	Medium

calculated the area-weighted value based on the intersection of the hybrid grid and 2-km buffers around the BBS routes. Buffering the BBS routes was necessary to account for adjacent environmental conditions that were potentially driving the occurrence of bird species detected during the BBS surveys. We considered multiple buffer distances around BBS routes (e.g., 0 km, 1 km, 2 km) but found the extracted predictor variables were generally strongly correlated; for example, when comparing the grid intersection of each BBS route to an area-weighted metric from the 2-km buffer, mean correlation was 0.93 (standard deviation [SD] = 0.089), with the lowest correlation among all predictor variables ($r = 0.61$) for range in elevation and the lowest correlation with a tree species ($r = 0.77$) for American elm. Thus, we selected the 2-km buffer to represent local to landscape-level environmental conditions adjacent to each BBS route that were associated with bird detections, while aligning with the resolution of the predictor variable datasets.

Contemporary climate conditions were summarized using annual, seasonal, and monthly temperature and precipitation metrics calculated at a resolution of 800 m across the 30-year period 1981–2010 from the PRISM dataset (Daly et al., 2008; PRISM Group, 2020). Monthly mean temperature and estimated day length (Forsythe et al., 1995) were used to calculate potential evapotranspiration (Thornthwaite, 1948). We obtained annual future climate projections for the period 2020–2099 from the NASA Earth Exchange U.S. Downscaled Climate Projections (NEX-US-DCP30) project (Thrasher et al., 2013). We opted to focus solely on the climate scenario combining the Hadley Global Environment Model—Earth System (Jones et al., 2011) and representative concentration pathway (RCP) 8.5 (Moss et al., 2008) to simplify our efforts to quantify potential decadal trajectories and highlight conservation concerns for bird species assuming a higher emissions future. We acknowledge the higher uncertainty associated with limiting our analyses to a single future climate scenario, but we note that there is a similar range of climate space across multiple prevailing future climate scenarios within the majority of our temporal window (Figure S1). To reduce bias, downscaled future climate data were used to adjust the baseline values (e.g., PRISM 1981–2010) with projected deltas (Monahan et al., 2013). For the four topographical predictor variables, elevation data obtained from the Shuttle Radar Topography Mission (Farr et al., 2007), which had a resolution of 90 m, were used to calculate the maximum, mean, range, and standard deviation.

Incorporating habitat suitability of 46 eastern USA tree species allowed us to provide information about the contemporary and potential future relative abundance of ecologically important tree species under various projected climate scenarios. We ensured each tree species was biologically relevant (e.g., associated with food resources or nesting substrate for birds) and had either high or moderate model reliability (Peters et al., 2019). In order to align the tree species pool with each focal bird species and reduce the potential for spurious associations influencing model performance, we only included individual tree species in the set of predictor variables for bird species incidence if they overlapped in occurrence (Table 1). Modeled tree species habitat suitability (Iverson et al., 2019; Peters et al., 2019) used the same sources for climate and elevation data, along with soil information, to predict relative abundance under the same six climate scenarios used in this study at 30-year intervals (2010–2039, 2040–2069, 2070–2099). Because the tree species habitat suitability models incorporated climate data, we calculated Pearson's correlation coefficient values to check for potential collinearity and confirmed that the tree species metrics were not strongly correlated ($-0.7 < r < 0.7$) with the seven climate predictor variables in our models (Table S2).

2.3. Data analyses

To quantify the influence of climate and tree species metrics on contemporary patterns of breeding bird species incidence across the eastern USA, randomForest models (Breiman, 2001) were trained with the environmental predictor variables, using the “randomForest” package (Liaw and Wiener, 2002) in R version 4.3.1 (R Core Team, 2023). For each bird species, we assembled two different sets of predictor variables to explain incidence: (1) climate + elevation (hereafter, the abiotic model), and (2) climate + elevation + tree species (hereafter, the tree-informed model). Thus, we ran a total of 200 randomForest models for the 100 focal bird species. Each model was then used to predict bird species incidence within the 2-km buffered BBS routes at present and at decadal time intervals under three future scenarios: (S1) climate change only, (S2) climate change with static tree species distributions, and (S3) climate change with lagged tree species change (i.e., projections for a given time period used tree species data from the preceding time period, such that: the 2010–2019 and 2020–2029 projections used current modeled tree species data; the 2030–2039, 2040–2049, and 2050–2059 projections used data from the 2010–2039 tree species projection window; the 2060–2069, 2070–2079, and 2080–2089 projections used data from the 2040–2069 tree species projection window; and the 2090–2099 projection used data from the 2070–2099 tree species projection window).

Given the expansive temporal and spatial domain of our analyses, it is important to consider additional measures of model performance focused specifically on cross-validation in time and space (Roberts et al., 2017). The general accuracy of model projections was assessed by using Spearman's correlation to compare modeled trends from the model-predicted incidence (trained on 2000–2009 data) to the actual data for the decade of 2010–2019 for 1084 routes that were surveyed at least seven of the 10 years. We then quantified the slope of the relationship between observed and predicted incidence in the 2010–2019 decade for each bird species to determine the mean divergence from a 1:1 line. We also calculated the mean square error (MSE) of projecting into the new time domain. To further evaluate model performance, we implemented leave-one-out spatial block cross-validation. We partitioned the full extent of the study region into 100 evenly spaced grid cells of $\sim 2.5^\circ$ of latitude and identified 39 grid cells that contained at least 20 BBS routes used in our study. We proceeded to build models by iteratively holding out one grid cell for prediction and validation. We then compared the mean square error (MSE) values from the leave-one-out spatial block cross-validation to the MSE values from the full randomForest model.

To first determine the value of incorporating tree species information into the models, we used out-of-bag prediction to calculate a pseudo R^2 — a measure of deviance explained that indicates model performance — for each model, and compared those values between the abiotic models and tree-informed models. Specifically, we used the “t.test” function in the “stats” R package to run a paired

two-sample *t*-test, with the alternative hypothesis being that the true mean difference is greater than 0. For this and all of the following data analyses, statistical significance was determined with an alpha-level of 0.05. To compare the relative influence of climate factors and tree species metrics on bird species incidence, we used the “chisq.test” and “fisher.test” functions from the “stats” R package to run Pearson’s chi-squared tests and Fisher’s exact tests for count data, respectively, to assess trends in the most influential variables among groups of bird species, although we acknowledge that we do not explicitly account for phylogenetic non-independence among closely related species. Fisher’s exact tests for count data were used for sparse contingency tables with expected cell counts less than 5, violating the assumptions of the original Pearson’s chi-squared test.

To address the final two objectives regarding future distributions, we quantified the trajectory of projected incidence change at decadal increments spanning 2000–2099. We defined the decadal functional form by generating a loess first-degree polynomial to derive a continuous spline (with the span parameter set to 0.666 to ensure a comparable degree of smoothing across species and to avoid local minimum and maximum impacts on curve characterization) and then identifying the integral of this line to report as the cumulative projected incidence (CPI) across the 100-year time domain. Thus, the CPI is defined as the integral of a loess-smoothed incidence $\times$ time trajectory. Differences in projected incidence among future scenarios were calculated as the ratio of the CPI values corresponding to any two future scenarios (hereafter, CPI_s ratio). We used Pearson’s chi-squared tests and Fisher’s exact tests for count data to evaluate whether trends in CPI_s ratios corresponded strongly to specific sets of highly influential predictor variables or forest bird species. When necessary, we report Fisher’s simulated *p*-values, based on 2000 replicates, rather than Fisher’s exact *p*-value. For assessing the timing and overall amounts of change in projected incidence associated with a specific future scenario, we calculated the ratio of the CPI corresponding to the future scenario to the CPI corresponding to the 2000 constant (hereafter, CPI_{2099/2000} ratio), and then used the “aov” function in the “stats” R package to run one-way ANOVA tests that compared CPI_{2099/2000} ratios for bird species corresponding to different taxonomic groups, life history traits, breeding distributions, and breeding habitat guilds. When comparing among the forest bird species, we note that closely related species are not phylogenetically independent, as assumed by the statistical tests. To evaluate the pace of change, we quantified the decade at which 25%, 50%, and 75% of the total change was captured, thus indicating the general shape of the trajectory. Three bird species (blackpoll warbler, ruby-crowned kinglet, and yellow-bellied flycatcher) had CPIs that were < 5000 in 2000 and < 500 in 2099 in at least one of the future scenarios and thus were excluded from the analyses described above due to unstable, noise-dominated CPI ratios.

3. Results

3.1. Model performance

The models performed well in predicting incidence during the decade immediately following model-building (mean Spearman’s $\rho = 0.7$, SD = 0.11, Figure S2), with minimal overall differences across bird species (mean MSE = 0.03, SD = 0.01) and slope estimates near the 1:1 line (mean = 1.14, SD = 0.25). Only two species (blackpoll warbler and mourning dove) had poor correlation values ($\rho < 0.3$ in either or both time steps), while ruby-crowned kinglet was the only species to have a slope estimate above 2. The leave-one-out spatial block cross-validation supported adequate overall model performance (Figure S3), with MSE values from the cross-validation only slightly elevated (mean across all bird species = +0.01) compared to the full model. In addition, models incorporating the 46 tree species metrics tended to explain slightly more variation in bird species incidence compared to climate-only models. Performance of the tree-informed models (mean pseudo R^2 value = 0.68, SD = 0.16, range = 0.25–0.90) was statistically significantly higher ($t = 13.80$, df = 99, $p < 0.001$) than the abiotic models (mean = 0.63, SD = 0.17, range = 0.16–0.89), although the mean difference

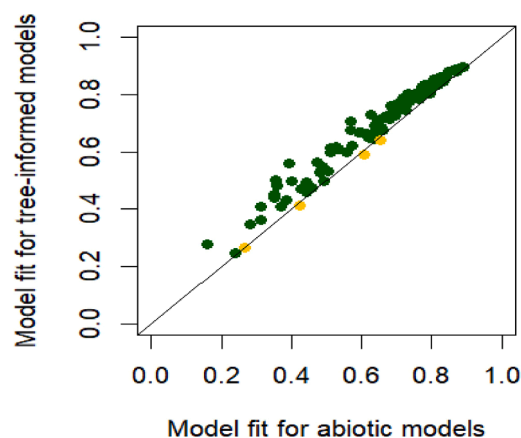


Fig. 1. Plot of pseudo R^2 values — a measure of deviance explained that indicates model fit— corresponding to the two sets of predictor variables (abiotic: climate + elevation vs. tree-informed: climate + elevation + tree species) used in the 200 randomForest models for the 100 forest bird species. Each point corresponds to a bird species, and its color indicates whether the model fit was improved by adding tree species (green) or not (gold). The diagonal line represents a 1:1 relationship (i.e., no difference in pseudo R^2 values).

was only +0.05 and therefore may not necessarily signify ecological importance. In total, model fit for 96 of the 100 forest bird species was slightly to moderately improved when tree species were included as predictor variables (Fig. 1). Excluding a single outlier, in which the pseudo R^2 values for the two eastern whip-poor-will models increased by ~73% from 0.16 (abiotic) to 0.28 (tree-informed), the average relative change in pseudo R^2 values was +8.8% (SD = 8.8%, range = -3.1%–42.1%).

3.2. Variable importance

Variable importance values (calculated as percent increase in MSE) indicated that the most influential predictors of bird species incidence were temperature and tree species. The top variable in the 100 tree-informed models was consistently either a temperature metric ($n = 43$ bird species; primarily mean July temperature [$n = 16$] or mean January temperature [$n = 13$], which were both highly correlated with each other [$r = 0.89$], mean annual temperature [$r = 0.94$ – 0.99], mean May–September temperature [$r = 0.93$ – 0.99], and annual potential evapotranspiration [$r = 0.91$ – 0.95]) or a tree species metric ($n = 43$ bird species; most frequently red maple [*Acer rubrum*; $n = 8$], balsam fir [*Abies balsamea*; $n = 5$], or loblolly pine [*Pinus taeda*; $n = 5$]). The relative influences of temperature and tree species metrics on incidence was also comparable when looking at the top five variables for each bird species; the majority of the top five variables were temperature or tree species metrics for 45 and 43 bird species, respectively. In addition, when we examined the entire set of top five variables associated with each bird species ($n = 500$ variables), the greatest proportion were tree species metrics ($n = 221$ variables; most frequently red maple [$n = 21$]), followed by temperature metrics ($n = 161$ variables; primarily mean May–September temperature [$n = 50$] or mean July temperature [$n = 49$]) and precipitation metrics ($n = 77$ variables; most frequently annual precipitation [$n = 32$]).

Trends in variable importance differed significantly by general breeding habitat guild (General Habitat Type 1: expected cell counts < 5, Fisher's exact $p = 0.02$; General Habitat Type 2: expected cell counts < 5, Fisher's exact $p < 0.001$; see Table S1 for category distinctions) and specific forest habitat type (expected cell counts < 5, Fisher's exact $p = 0.02$). Temperature metrics were generally most important in explaining the incidence of bird species that are temperate forest generalists or breed in open-country habitat mosaics, open woodlands, scrub-shrub habitat, or early-successional habitat (e.g., common yellowthroat [*Geothlypis trichas*]). In contrast, tree species metrics were generally most important in explaining the incidence of bird species that breed in boreal forests (e.g., black-throated blue warbler [*Setophaga caerulescens*]) or are considered forest-interior specialists (e.g., ovenbird [*Seiurus aurocapilla*]).

3.3. Comparing overall trajectories of species incidence predicted by three future scenarios

For 83 of the 97 bird species for which we assessed trends in CPI ratios, the overall expected change in incidence (i.e., the total difference from 2000 to 2099, without regard to decadal timing) was impacted by whether the future scenario included tree species metrics (Table 2). Notably, the majority ($n = 81$) of those bird species had lower predicted incidence (i.e., $CPI_{S1/S3}$ ratio < 0.90) from

Table 2

The total number of bird species that followed specific overall trends in incidence and specific temporal trends in decadal trajectories of incidence from 2000 to 2099, corresponding to the three future scenarios: (S1) climate change only, (S2) climate change + static tree species, and (S3) climate change + lagged tree species change. Overall trends in incidence were determined based on loess-derived cumulative projected incidence (CPI) ratios, such that a $CPI_{2099/2000}$ ratio > 1.10 was considered an increase, a $CPI_{2099/2000}$ ratio < 0.90 was considered a decline, a $CPI_{2099/2000}$ ratio < 0.50 was considered a severe decline, and a $CPI_{2099/2000}$ ratio < 0.50 plus CPI_{50} achieved in the first third of the century was considered a rapid severe decline. Three bird species were excluded from analysis due to instability in their CPI ratios. The three distinctive temporal trends in decadal trajectories of incidence included: Immediate Short-Term Change (ISTC), where the greatest amount of change occurred in the first third of the century; Early Extended Change (EEC), where change was greatest across the first two-thirds of the century; or Linear Change (LC), where change was relatively steady over the entire century. The final row indicates the total number of bird species that followed the same trends regardless of future scenario.

Future scenario	Overall trend in incidence	Temporal trend in trajectory	Timing of CPI_{50}
(S1) Climate change only	Increasing: 6 Declining: 80 Severe decline: 41 Rapid severe decline: 33	ISTC: 25 EEC: 48 LC: 15	≤ 2033: 57 > 2066: 7
(S2) Climate change + Static tree species	Increasing: 19 Declining: 54 Severe decline: 9 Rapid severe decline: 7	ISTC: 30 EEC: 41 LC: 20	≤ 2033: 44 > 2066: 5
(S3) Climate change + Lagged tree species change	Increasing: 31 Declining: 49 Severe decline: 14 Rapid severe decline: 12	ISTC: 16 EEC: 51 LC: 25	≤ 2033: 40 > 2066: 4
(S1) & (S2) & (S3)	Increasing: 6 Declining: 49 Severe decline: 9 Rapid severe decline: 7	ISTC: 12 EEC: 25 LC: 8	≤ 2033: 33 > 2066: 1

2000 to 2099 under the climate change only scenario compared to the scenario with climate change and lagged tree species change, and there was a more than twofold difference (i.e., $CPI_{S1/S3}$ ratio < 0.50) in the predicted incidence for 38 bird species (Table S3). Comparing the three future scenarios, bird species exhibited one of the following trends in incidence (Fig. 2): (1) No Difference ($n = 14$), where there was little to no difference (i.e., CPI_S ratio = 0.90–1.10) among the three future scenarios; (2) Tree Difference ($n = 48$), where there was a large difference (i.e., CPI_S ratio < 0.90 or CPI_S ratio > 1.10) between the climate change only scenario and the two scenarios involving trees; (3) Tree Static High Incidence ($n = 15$ bird species), where there were large differences among all three future scenarios and the highest incidence over time was predicted for the scenario with static tree species; and (4) Tree Change

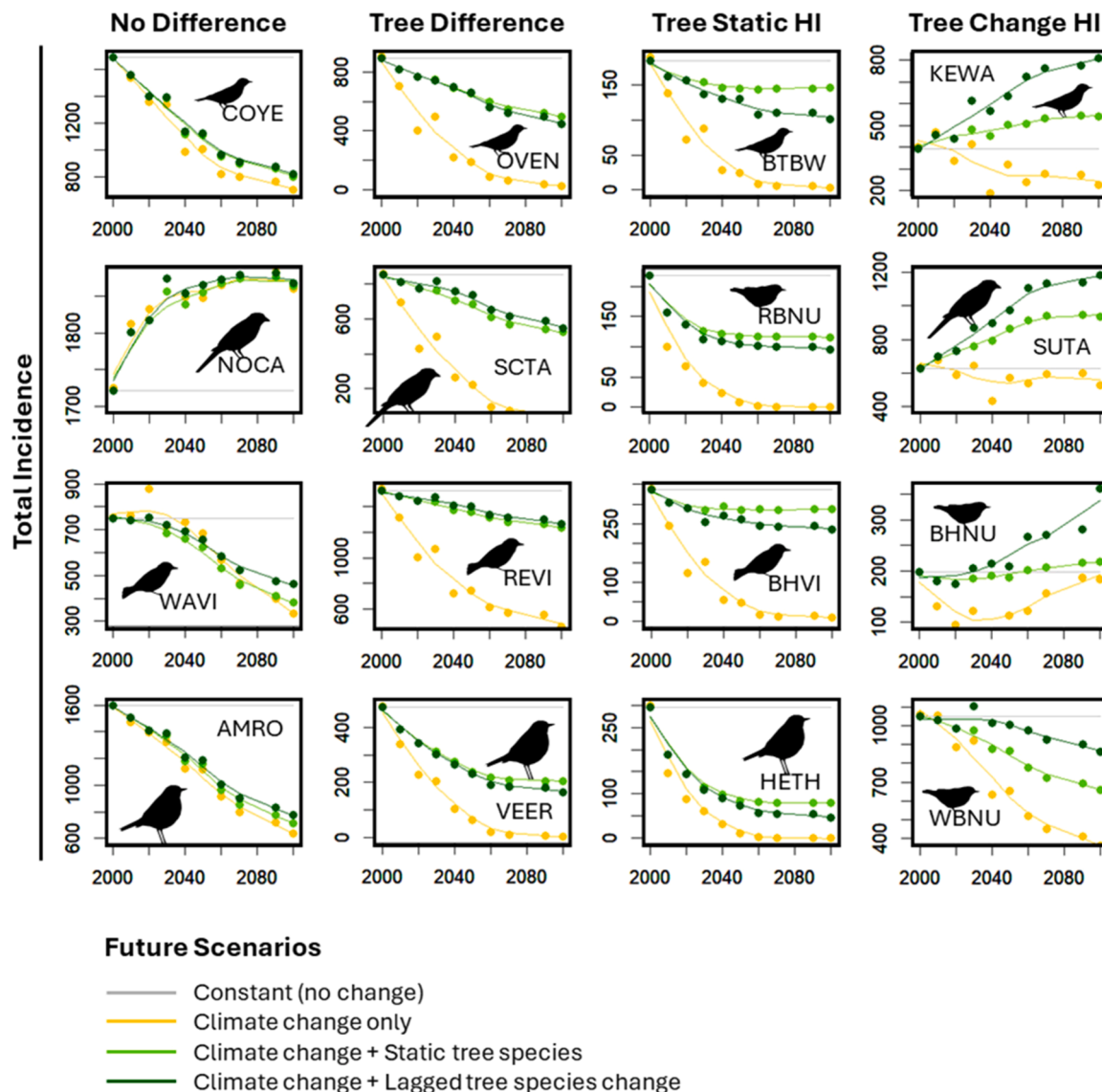


Fig. 2. Plots of the decadal trajectories of total incidence (y-axis) from 2000 to 2099 (x-axis) predicted by three future scenarios for 16 bird species (COYE = common yellowthroat, OVEN = ovenbird, BTBW = black-throated blue warbler, KEWA = Kentucky warbler, NOCA = northern cardinal, SCTA = scarlet tanager, RBNU = red-breasted nuthatch, SUTA = summer tanager, WAVI = warbling vireo, REVI = red-eyed vireo, BHVI = blue-headed vireo, BHNU = brown-headed nuthatch, AMRO = American robin, VEER = veery, HETH = hermit thrush, WBNU = white-breasted nuthatch). Note that the x-axis is held constant across all plots, but the y-axis varies, as the primary purpose of the plots is to illustrate and compare the shape of the decadal trajectories (rather than magnitude of change). Comparing the future scenarios, there were four commonly observed trends: (1) No Difference, where there was little to no difference (i.e., CPI_S ratio = 0.90–1.10) among the three future scenarios; (2) Tree Difference, where there was a large difference (i.e., CPI_S ratio < 0.90 or CPI_S ratio > 1.10) between the climate change only scenario and the two scenarios involving trees; (3) Tree Static High Incidence (HI), where there were large differences among all three future scenarios and the highest incidence over time was predicted for the scenario with climate change and static tree species; and (4) Tree Change High Incidence (HI), where there were large differences among all three future scenarios and the highest incidence over time was predicted for the scenario with climate change and lagged tree species change. Bird silhouettes indicate shared taxonomy of closely related species (either same genus or same family).

High Incidence ($n = 20$), where there were large differences among all three future scenarios and the highest incidence over time was predicted for the scenario with lagged tree species change. Among the four trends, there was a significant difference in the most influential predictor variables (top variable: expected cell counts < 5 , Fisher's exact $p < 0.001$; majority of the top five variables: expected cell counts < 5 , Fisher's simulated $p < 0.001$). Bird species following the No Difference trend and Tree Change High Incidence trend were particularly influenced by temperature metrics and tree species metrics, respectively. There were also significant differences among the four trends based on breeding biomes (expected cell counts < 5 , Fisher's simulated $p < 0.001$), breeding distributions (expected cell counts < 5 , Fisher's simulated $p < 0.001$), and breeding habitat guilds (General Habitat Type 1: expected cell counts < 5 , Fisher's simulated $p < 0.001$; General Habitat Type 2: expected cell counts < 5 , Fisher's exact $p = 0.006$; Forest Habitat Type: expected cell counts < 5 , Fisher's simulated $p < 0.001$). Bird species with widespread breeding ranges tended to follow the No Difference trend; those that are temperate forest generalists or breed in the Nearctic biome tended to follow the Tree Difference trend; those that breed in the northern region of the eastern USA or in boreal forests tended to follow the Tree Static High Incidence trend; and those that breed in the south-central region of the eastern USA tended to follow the Tree Change High Incidence trend.

3.4. Overall trends in species incidence from 2000 to 2099

To assess the modeled overall trajectories of bird species incidence from 2000 to 2099, we calculated $CPI_{2099/2000}$ ratios of incidence associated with the future scenario with lagged tree species change. We found significant differences in $CPI_{2099/2000}$ ratios among breeding biomes ($F = 15.55$, $df = 3$, $p < 0.001$), breeding distributions ($F = 22.59$, $df = 7$, $p < 0.001$), and general breeding habitat guilds ($F = 9.86$, $df = 3$, $p < 0.001$), with the steepest declines in incidence projected for bird species that breed in the northern forest biome (mean $CPI_{2099/2000}$ ratio = 0.66), the northern and north-central regions of the eastern USA (mean $CPI_{2099/2000}$ ratios = 0.49 and 0.65, respectively), or the boreal forest (mean $CPI_{2099/2000}$ ratio = 0.58) and the greatest average increase in incidence projected for bird species that breed in the south-central and southern regions of the eastern USA (mean $CPI_{2099/2000}$ ratios = 1.50 and 2.32, respectively), relative to other groups in each category. Additionally, individual bird species with the greatest rates of change tended to follow particular trends in CPI_s ratios of incidence and were primarily influenced by different predictors. The 10 bird species with the lowest CPI_C ratios (range: 0.28–0.47) mostly followed the Tree Static High Incidence trend ($n = 7$), and their incidence tended to be strongly influenced by temperature metrics. In contrast, the 10 bird species with the highest $CPI_{2099/2000}$ ratios (range: 1.52–3.33)

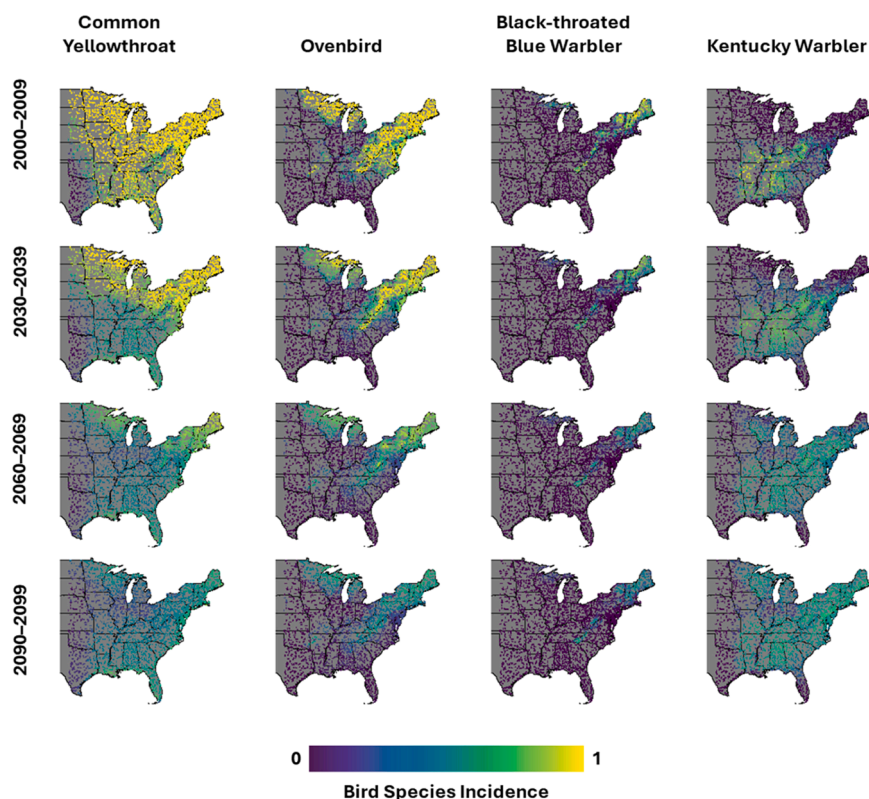


Fig. 3. Maps of the incidence of four bird species (common yellowthroat, ovenbird, black-throated blue warbler, and Kentucky warbler) across the eastern USA within 2-km buffered routes from the North American Breeding Bird Survey, showing contemporary (2000–2009) and projected future species habitat suitability for three decadal timesteps (2030–2039, 2060–2069, and 2090–2099). These projections of incidence were predicted by the future climate change + dynamic tree species change scenario, where modeled tree species habitat suitability is lagged.

mostly followed the Tree Change High Incidence trend ($n = 8$), and their incidence tended to be strongly influenced by tree species metrics.

3.5. Comparing decadal trajectories of species incidence predicted by the three future scenarios

The decadal timing of changes in bird species incidence varied depending on the future scenario (Figs 3, S4). We observed three distinctive temporal trends in decadal trajectories (Fig. 4): (1) Immediate Short-Term Change, where the greatest amount of change occurred in the first third of the century, followed by limited change in the following two-thirds; (2) Early Extended Change, where change was steady over the first two-thirds of the century, followed by a relatively level period of limited change in the final third; or (3) Linear Change, where change was relatively steady over the entire century. Among the three future scenarios, we found differences in the number of bird species following each of the temporal trends (Table 2) and in how quickly incidence reached the 50th percentile of the CPI (hereafter, CPI₅₀). In the future scenario considering climate change only, 57 bird species reached their CPI₅₀ within the first 33 years, whereas that number was lower for the future scenarios with static tree distributions ($n = 44$ bird species) and lagged tree species change ($n = 38$ bird species). Cumulatively, the inclusion of tree species metrics in the future scenario shifted the timing or rate of expected changes in incidence projected to occur between 2000 and 2099 substantially enough to result in a different temporal trend for 50 bird species.

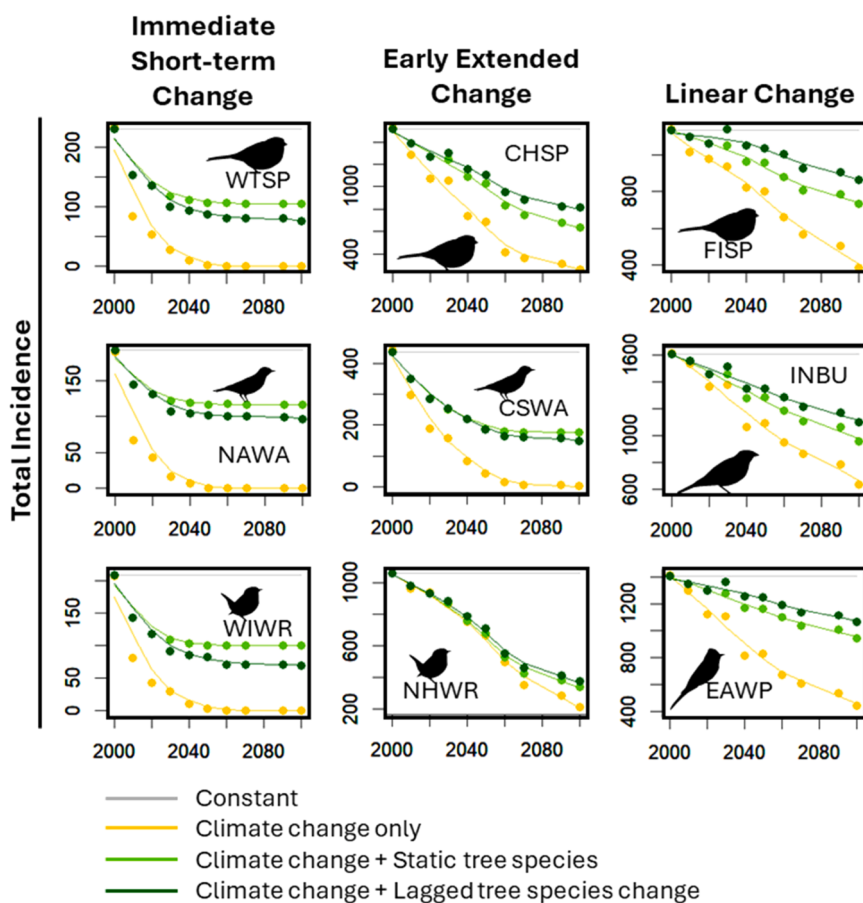


Fig. 4. Plots of the decadal trajectories of total incidence (y-axis) from 2000 to 2099 (x-axis) predicted by the future climate change + lagged tree species change scenario (dark green points and line) for 9 bird species (WTSP = white-throated sparrow, CHSP = chipping sparrow, FISP = field sparrow, NAWA = Nashville warbler, CSWA = chestnut-sided warbler, INBU = indigo bunting, WIWR = winter wren, NHWR = northern house wren, EAWP = eastern wood-pewee). Note that the x-axis is held constant across all plots, but the y-axis varies, as the primary purpose of the plots is to illustrate and compare the shape of the decadal trajectories (rather than magnitude of change). Looking at the timing of when incidence reached the 25th, 50th, and 75th percentiles of the CPI, there were three distinct temporal trends: (1) Immediate Short-Term Change, where the greatest amount of change occurred in the first third of the century; (2) Early Extended Change, where change was greatest across the first two-thirds of the century; or (3) Linear Change, where change was relatively steady over the entire century. Bird silhouettes indicate shared taxonomy of closely related species (either same genus or same family).

3.6. Decadal trends in declining species incidence from 2000 to 2099

Modeling the incidence trajectories of 97 bird species at decadal timesteps revealed interspecific differences in the timing of declines. Of the 49 bird species predicted to experience declines in incidence (i.e., $CPI_{2099/2000}$ ratio < 0.9) from 2000 to 2099 under the future scenario with lagged tree species change, incidence for 27 bird species reached the CPI_{50} in the first third of the century, and incidence for the remaining 22 bird species reached it in the middle third of the century. In addition, 13 of the 49 bird species followed the Immediate Short-Term Change trajectory, 28 bird species followed the Early Extended Change trajectory, and 8 bird species followed the Linear Change trajectory. Notably, all of the bird species following the Immediate Short-Term Change trajectory breed in either the northern or north-central portions of the eastern USA and are associated with forest habitat (as opposed to open woodlands or scrub-shrub habitat), and most of them belong to the northern forest breeding biome (69%), breed in boreal forest (92%), or are associated with forest-interior habitat (69%).

4. Discussion

Our study demonstrates the important influence of tree species on contemporary and future patterns of breeding bird distributions across the eastern USA, particularly in the context of future expectations for high greenhouse gas emissions. Although we based our results on a single climate scenario and we acknowledge the associated uncertainty, we nonetheless establish a replicable approach to test hypotheses regarding the relative contributions of climate and tree species to bird species habitat suitability and to predict potential bird species trajectories into the future at decadal timesteps. For example, despite some variation among bird species, our results support the hypothesis that potential future distributions of tree species can modify decadal trajectories of bird species habitat suitability predicted by climate change. In addition, for 84% of the focal forest bird species under consideration, the projected magnitude of decline in future habitat suitability due to direct climate effects was mitigated by tree species, with different results and timing in decadal trajectories predicted for the scenarios in which contemporary tree species distributions are maintained into the future vs. allowed to shift (Figures 3, S2). By distinguishing the roles of climate and forest habitat, it becomes clear that accounting for changes in both factors will be important in habitat conservation efforts for bird species, especially given the projected emergence of non-analog forest assemblages arising from future climate conditions (Gougherty et al., 2024).

Compared to the abiotic models, incorporating tree species information into the habitat suitability models slightly to moderately improved performance for 96% of the forest bird species (Objective 1). Previous studies also affirm the importance of including individual tree species into predictive models (Lalechère and Bergès, 2022; Matthews et al., 2011), as well as taking into account how time-lagged tree species changes may affect bird communities (Kissling et al., 2010). Tree species models may be more representative than climate factors of overall habitat conditions that support breeding populations of specific bird species, such as forest cover (Clipp et al., 2025; LeBrun et al., 2016), or they may act as surrogates for other environmental covariates (Matthews et al., 2011). In addition, bird species can have strong associations with particular tree species, which may be preferentially used for nesting or foraging, or forest types (Clipp et al., 2022).

While the inclusion of tree species tended to improve models, their relative importance compared to climate factors varied by bird species (Objective 2). Both sets of temperature variables and tree species metrics had the highest influence on 43–45% of the focal bird species, but temperature was particularly influential for those that breed in open, low-vegetation, or young forest habitat (similar to the findings of LeBrun et al. 2016), whereas trees tended to have greater relative importance in models for bird species that breed in forest-interior habitat, which is generally associated with mature (i.e., mid- to late-successional) forest, and are linked to regionally dominant tree species in many cases. In our study, rankings of variable importance reflected predictive contribution to the models and do not necessarily imply causal ecological mediation. However, previous studies have also found a significant relationship between bird and tree species assemblages in the forests of eastern North America (Lee and Rotenberry, 2005). Within this region, certain forest-breeding bird species are likely more sensitive to tree species presence and forest cover than climate factors (Clipp et al., 2025).

Future tree distributions influenced the overall trends and timing of decadal trajectories of bird species habitat suitability (Objective 3). By evaluating both static and lagged changes in tree species distributions, we aimed to consider a range of potential outcomes, as the actual migration of tree species is expected to lag behind changes in climate conditions, due to the long-lived nature of mature individuals and generally slow dispersal rates; for instance, contemporary change in dominant forest tree species in eastern North America have demonstrated lagged responses to accelerating climate change (Sittaro et al., 2017; Zhu et al., 2012). In alignment with our expectations, the overall change in future incidence due to direct climate effects was altered by incorporating tree species distributions for approximately 83% of the focal bird species. Considering the 48 bird species that followed the Tree Difference trend (where there was a large difference between the climate change-only scenario and the scenarios involving trees), the future scenarios with tree species metrics resulted in higher predicted bird species habitat suitability in all but two cases. Similarly, other studies that projected bird species presence or abundance within the conterminous USA based on future scenarios of climate change and land cover change found more modest impacts than those predicted by climate change alone (Clipp et al., 2025; Sohl, 2014). Studies from beyond North America also suggest that forest quantity and quality can positively affect forest birds separately from the influence of climate change (Ram et al., 2017).

In addition, there were differences in overall change in bird species habitat suitability between maintaining contemporary tree species distributions into the future and allowing them to shift dynamically under future climate change for approximately 37% of the focal bird species. We expected static tree species distributions to reduce the total amount of projected change in future habitat suitability associated with direct or indirect climate effects, but we observed this for only 15% of the focal bird species, which were associated with the Tree Static High Incidence trend. Furthermore, the timing of changes in habitat suitability differed among the two

future scenarios with tree species metrics for approximately 30% of the focal bird species. We originally expected that static tree species distributions would slow the rate of projected change in future bird species habitat suitability, but it appeared to have a moderating effect (e.g., extended the CPI_{50} by at least 5 years) on the rate of change compared to lagged tree species distributions for only 5% of the focal bird species.

Our final objective was to compare overall and decadal trajectories of habitat suitability among bird species, and indeed, one of the distinctive contributions of this study was the consideration of trajectories at decadal timesteps. Notably, the temporal pattern of changes in habitat suitability differed among the future scenarios for 52% of the focal bird species, as tree species tended to delay or extend declines over longer periods. Similar to our results, Raymundo et al. (2024) predicted that the abundance of boreal landbird species will change later in the century as opposed to the first 20–30 years. Few other studies have predicted changes in bird species distributions or abundance at multiple time intervals, and thus rates of change are typically estimated for a single time period. Nonetheless, the variability in trajectories among bird species and declining overall trajectories in habitat suitability for bird species that breed in boreal forests or in the northern region of the eastern USA are well-supported by previous studies (Clipp et al., 2025; Matthews et al., 2011; Rodenhouse et al., 2008). For example, 9 of the 10 bird species with the highest projected losses in habitat suitability from our study were also assigned a climate sensitivity status of “Climate Threatened” at the scale of North America by Langham et al. (2015). Building upon these established expectations for declines, our study advances understanding by estimating a potential timeline and highlighting when the greatest rates of change are predicted to occur for climate-threatened forest bird species, assuming a future with high greenhouse gas emissions.

4.1. Conservation implications

By comparing decadal trajectories of habitat suitability among individual and groups of bird species, our study has important implications for the management and conservation of bird species in the eastern USA. Using our model results, decision-makers can: (a) identify bird species projected to lose suitable habitat in the future (e.g., $CPI_{2099/2000}$ ratio < 0.90); (b) distinguish the bird species for which climate change is the key driver of suitable habitat (e.g., temperature metrics have greatest variable importance values and/or follow the No Difference trend); (c) determine the bird species for which maintaining contemporary tree species distributions is critical to buffer the effects of climate change (e.g., tree species metrics have greatest variable importance values and/or follow the Tree Static High Incidence trend); (d) ascertain the bird species for which suitable habitat is predicted to persist and allowing shifting tree species distributions is critical to buffer the effects of climate change (e.g., follow the Tree Change High Incidence trend); and (e) pinpoint critical time periods for projected change in bird species habitat suitability (e.g., when the CPI_{50} is reached, Immediate Short-Term Change trajectory vs. Linear Change trajectory).

Based on our results, there is reasonable cause for conservation concern, particularly if climate change is accurately predicted by the future climate model that we used. We found that at least 49 of the 100 focal bird species are at risk of losing suitable habitat by 2099, regardless of the future scenario, and at least 7 bird species, most of which are considered forest-interior specialists or breed in boreal forest or in the northern or north-central regions of the eastern USA, are projected to experience rapid and substantial decreases in habitat suitability (e.g., loss of $\geq 50\%$ within the first three decades of the century; Table 2). Overall decreases in habitat suitability appear to be driven primarily by climate factors for 6 of those 7 bird species, but for others, tree species appear to play an important mediating role in climate change effects. The future scenario with static tree species resulted in the shallowest declines in habitat suitability for 15 of the 49 declining bird species, most of which are either forest-interior or forest-gap specialists and breed in the northern forest biome, boreal forest, or northern or north-central regions of the eastern USA.

Although the model results are specific to a single future climate scenario, they point to sensitivity to tree species and the importance of considering change over time, as well as recognizing the potential disequilibrium of climate change and disturbances that will shape future species distributions (Pang et al., 2026). Future research should consider ensemble projections to capture a range of temporal habitat changes, using a suite of alternative climate change scenarios. Results from such ensemble models may indicate varying timelines and lead to new insights; however, we anticipate that they will likely uphold our consistent findings that the greatest and most immediate risks to habitat suitability in the eastern USA are for bird species that breed in boreal forests and that maintaining contemporary tree species distribution may be critical for their conservation. Ultimately, such outcomes support contemporary efforts to actively manage forests for resilience and adaptability. National networks such as Adaptive Silviculture for Climate Change (Nagel et al., 2017) are testing silvicultural treatments to facilitate forest change to match future conditions, alongside treatments to enhance resilience of contemporary forests, which aligns strongly with our results. Forest communities will be an important consideration for maintaining future habitat availability for birds, and we can leverage new tools that provide robust assessments of potential tree species changes.

5. Conclusions

Tree species distributions are likely to have greater influence than climate on the future of certain forest-breeding bird species. In addition, potential future tree species distributions may alter the timing and overall change in projected bird species habitat suitability due to direct climate effects. For boreal forest bird species that are projected to experience steep decreases in habitat suitability under future climate change, maintaining current distributions of tree species may moderate those declines. Decadal trajectories also emphasize the importance of timing in declines, with the greatest declines in habitat suitability occurring within the first three decades of the century. These findings can guide habitat conservation efforts and identify groups of bird species that require time-sensitive management considerations. Ultimately, our study emphasizes the value of incorporating tree species distributions into climate

adaptation strategies, avian conservation efforts, and forest management plans for bird species in the eastern USA.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the thousands of volunteers across the United States and Canada who annually coordinate and participate in the North American Breeding Bird Survey. **Funding:** Hannah L. Clipp was supported by the U.S. Department of Agriculture (USDA) Forest Service Resource Assistants Program and by an appointment to the USDA Forest Service Research Participation Program administered by the Oak Ridge Institute for Science and Education (ORISE) through an interagency agreement between the U.S. Department of Energy (DOE) and USDA. ORISE is managed by ORAU under DOE contract number DE-SC0014664. Stephen N. Matthews was supported by USDA Forest Service Northern Research Station (23-JV-11242306–086). The findings and conclusions in this publication are those of the individual authors and do not necessarily reflect the policies and views of USDA, DOE, ORAU/ORISE, or the Forest Service.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2026.e04396](https://doi.org/10.1016/j.gecco.2026.e04396).

Data availability

Research Link Provided

<https://doi.org/10.5061/dryad.cz8w9gjhc> (Dryad:)

Data for trees and additional predictors are available in the USDA Research Data Archive at: <https://doi.org/10.2737/RDS-2019-0029>.

Bird data are available from the North American Breeding Bird Survey at: <https://www.pwrc.usgs.gov/bbs/rawdata/>.

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