



Changes in potential habitat of 147 North American breeding bird species in response to redistribution of trees and climate following predicted climate change

Stephen N. Matthews, Louis R. Iverson, Anantha M. Prasad and Matthew P. Peters

S. N. Matthews (snmatthews@fs.fed.us), L. R. Iverson, A. M. Prasad and M. P. Peters, US Forest Service, 359 Main Road, Delaware, OH 43015, USA. Present address of SNM: Terrestrial Wildlife Ecology Lab, School of Environment and Natural Resources, Ohio State Univ., 2021 Coffey Road, Columbus, OH 43210, USA.

Mounting evidence shows that organisms have already begun to respond to global climate change. Advances in our knowledge of how climate shapes species distributional patterns has helped us better understand the response of birds to climate change. However, the distribution of birds across the landscape is also driven by biotic and abiotic components, including habitat characteristics. We therefore developed statistical models of 147 bird species distributions in the eastern United States, using climate, elevation, and the distributions of 39 tree species to predict contemporary bird distributions. We used randomForest, a robust regression-based decision tree ensemble method to predict contemporary bird distributions. These models were then projected onto three models of climate change under high and low emission scenarios for both climate and the projected change in suitable habitat for the 39 tree species. The resulting bird species models indicated that breeding habitat will decrease by at least 10% for 61–79 species (depending on model and emissions scenario) and increase by at least 10% for 38–52 species in the eastern United States. Alternatively, running the species models using only climate/elevation (omitting tree species), we found that the predictive power of these models was significantly reduced ($p < 0.001$). When these climate/elevation-only models were projected onto the climate change scenarios, the change in suitable habitat was more extreme in 60% of the species. In the end, the strong associations with vegetation tempers a climate/elevation-only response to climate change and indicates that refugia of suitable habitat may persist for these bird species in the eastern US, even after the redistribution of tree species. These results suggest the importance of interacting biotic processes and that further fine-scale research exploring how climate change may disrupt species specific requirements is needed.

Mounting evidence shows that a wide variety of organisms have already begun to respond to global climate change (Thomas and Lennon 1999, Walther et al. 2002, Parmesan 2006), a trend that is likely to intensify with accelerating changes in climate. Some of the most compelling evidence for species responses to climate change is being documented in bird species. These changes include shifts in migratory arrival dates (Beaumont et al. 2006, Jonzen et al. 2006), mismatches in timing of resource availability (Visser et al. 2006, Waite and Strickland 2006), and advances in nesting dates (Winkler et al. 2002, Both et al. 2005). In addition, many bird species in North America have exhibited northward expansion of wintering (La Sorte and Thompson 2007) and breeding (Hitch and Leberg 2007) limits of 1–2 km yr⁻¹ over the last 30 yr.

Projections for accelerating increases in temperatures and changes in precipitation patterns over the next century are expected to change the future distribution and population sizes across many taxa substantially (Kareiva et al. 1993).

For breeding birds, patterns of species richness in the United States reflect the importance of climate in terms of seasonality and potential evapotranspiration (Ashmole 1963, Currie 1991). Further, direct, climate-mediated influences on northern range limits of birds are linked to metabolic rate and capacity to withstand low winter temperatures (Root 1988). These associations between climate and bird distributions have led to projections of range shifts under climate change as a function of the climate envelope of birds in several continents, e.g. North America (Sorenson et al. 1998, Price and Root 2001), Europe (Virkkala et al. 2008), and Africa (Erasmus et al. 2002).

However, broad-scale bird distributions are not constrained solely by climate conditions; future tree species patterns altered by climate change are likely to have independent influences on species distributions (Root and Schneider 2002). The importance of vegetation characteristics can be linked to specific habitat requirements of bird

species and land-cover attributes that play an important role in the hierarchical nature of habitat selection for bird species (O'Connor et al. 1996, Fearer et al. 2007). Furthermore, in the eastern United States, assemblages of bird and tree species have been positively linked (Lee and Rotenberry 2005), and individual tree species data have been successfully used to model regional patterns of bird abundance (Matthews et al. 2004, Fearer et al. 2007). During historic episodes of global climate change, tree species migrated independently of each other, leading to marked changes in tree communities over time (Jacobson et al. 1987), a dynamic that is likely to continue into the future (Webb and Bartlein 1992). Contemporary models of tree species distribution highlight marked shifts in future distribution in response to projected global climate change (Thuiller et al. 2006, McKenney et al. 2007, Iversen et al. 2008). In fact, recent evidence suggests that individual tree species are already showing distributional shift pressures with saplings and mature trees showing latitudinal separation (Woodall et al. 2009). Furthermore, of the 40 species in common between actual documented shifts (Woodall et al. 2009) and projected changes (Iversen et al. 2008), 37 are in a similar direction. Thus, to address the potential effects of climate change on bird habitats, it is important to consider both climate and tree species influences under a changing climate.

We developed statistical models for the incidence (relative abundance) of 147 bird species in the eastern United States, based on a pool of 50 predictor variables including climate, elevation, and individual tree species distributions. Advances in parameterizing species and community models that address important ecological mechanisms and processes are required to build the understanding of bird responses to climate change; for example, these models will allow us to explore how changes in structural complexity through time will influence bird responses to climate change. Nonetheless, the data presented here provide a comprehensive perspective of how bird species habitat may respond to climate change and are essential as we develop new hypotheses addressing climate change impacts. Therefore, the large sample of bird species and the diverse set of potential predictors allowed us to explore potential regional changes in bird habitats and assess the ability of our predictor variables to represent contemporary bird distributions. We examined community-wide patterns of the 147 species and investigated how changes in habitat may influence different guilds of species preferences for habitat and migration strategy. Finally, we generated models, with and without the tree species information, to evaluate the importance of including the tree species information as predictor variables for the bird models.

Methods

Spatial extent

The study area encompassed the United States east of the 100th meridian. This extent matches that of the county-level analysis of Matthews et al. (2004), but the resolution of the analysis here is conducted at a finer grain (20 by 20-km grid, 400 km²) to match the latest available data used by

Iversen et al. (2008) to model tree species habitat, thus allowing us to incorporate tree species information into our modeling efforts and work from a consistent spatial grid.

Bird data

The data for 147 individual bird species of the eastern US was obtained from the North American Breeding Bird Survey (BBS) for the years 1981 to 1990. O'Connor et al. (1996) extracted 1223 high quality routes (sampled at least seven of the ten years) across the conterminous US, and then matched the starting point of each route to the 640-km² hexagonal grid of White et al. (1992). Incidence, or the proportion of routes with the species present, was used as a measure of relative abundance (O'Connor et al. 1996, Rodenhouse et al. 2008). We used this database here as it has been extensively evaluated (O'Connor et al. 1996, Lawler et al. 2004) and it represents a consistent link to our previous research (Matthews et al. 2004, Rodenhouse et al. 2008). Therefore, we converted the bird data from hexagons to the 20 by 20 km grid (400 km²) by overlaying the two grids and calculating an area-weighted average bird incidence value for each cell with at least 50% of its area overlapping BBS hexagons. We evaluated the transformation to the finer grain by comparing the coefficient of variation for bird incidences at the two resolutions ($\beta = 0.98$, $r^2 = 0.93$, $p < 0.01$). The residuals were all < 0.2 and uninfluenced by the range size of the species, providing strong evidence that the transformation did not markedly alter the variance structure of the bird incidence values. Therefore, the response variable used in this analysis was species incidence, a continuous variable ranging from zero to one at a spatial resolution of 20 by 20 km cells across the eastern US.

Because various groups of birds may be differentially affected by climate change, we considered the migratory strategy and dominant habitat characterization of each species. For migratory strategies, we used Gough et al.'s (1998) classification of species into neotropical migrants, temperate migrants, or resident species. In our study, this classification resulted in 68 species of neotropical migrants, 43 temperate migrants, 19 residents, and the remaining 17 as unclassified (these were wetland species, as common characterization of migratory patterns were not analogous to the other species). We used Peterjohn and Sauer (1993) and Rodenhouse et al. (1995) to classify the primary habitat for each species, which yielded 53 species in forests, 28 in shrublands, 11 in grasslands, 19 in wetlands, and 36 as unclassified. While species such as American robin and blue jay could be considered forest birds, they were classified as urban, and instead of reclassifying to forest, we aggregated urban birds into the unclassified categories to maintain the previously published guilds.

Predictor variables

The independent variables used as potential predictors of bird species incidence were obtained from Iversen et al. (2008). These variables consisted of seven climate variables derived from long-term monthly averages (mean annual

temperature, mean July temperatures, mean January temperatures, total precipitation, seasonality (defined here as the difference between mean July and January temperature), mean May to September temperature, and total May to September precipitation). Elevation variables were also included as four measures: minimum, maximum, mean, and range within each 20×20 km grid cell. Finally, tree species importance values (a measure of abundance, Iverson et al. 2008) were included as predictor variables. The tree species models were derived from over 100 000 Forest Inventory and Analysis plots distributed across the eastern US. For each cell, the importance value for each species was calculated from the number of stems and basal area of each species relative to all trees in a plot. The tree species were modeled with randomForest (see model approach below) from a pool of 38 predictor variables including climate, soil type, soil characteristics and landscape variables. These data present a unique set of continuous tree species distribution models built on a rich and diverse set of predictor variables. We selected 39 of the 134 possible tree species based on initial model runs and retained a tree species as a predictor if it occurred in the top five of the most important variables for at least two bird models (see variable importance in the modeling approach section below). We also included northern red oak because it was among the ten most important variables for nine bird species, despite being among the top five only once. In the end, 36 of the 39 selected tree species had the highest model reliability (assessment of model fit and stability, Iverson et al. 2008), and the remaining three were in the moderate category, providing confidence in all the tree species distribution models used. Because the tree species models project habitat under climate change, they do not account for dispersal time lags. Iverson et al. (2004) evaluated the implications of dispersal through a heterogeneous landscape using a spatially explicit cellular automata model for five tree species and found that, over a 100-yr period, there was virtually no chance of colonization beyond 200 km from the species current range boundary. To assess the consequences of this minimal dispersal for the 39 species, we determined that the median distance from any species current range boundary out to 200 km contained over 92% of the projected future habitat under the harshest HADhi model (1st quartile = 85%). While dispersal constraints are key for the tree species models, the species used in this analysis do not suggest unrealistic outcomes.

Modeling approach

We used randomForests (RCran 2008), a statistical modeling approach that uses bootstrap sampling and a random set of predictors (Breiman 2001). This method uses regression tree analysis, in which the response variable is recursively partitioned by the predictor variables that minimizes deviance within the response variable. RandomForest uses an ensemble of regression trees (in our case 500 iterations) for robust prediction (Prasad et al. 2006, Cutler et al. 2007) and uses bootstrapping techniques where, in each iteration, 2/3 of the data are used to build the model with the remaining 1/3 held in reserve (out-of-bag training set). In addition, at each split, 1/3 of the predictors (16 in our case)

are used to identify the best split. This procedure generates a model that limits overfitting of the data (Breiman 2001). The out-of-bag training data were also used for model prediction to limit bias (Prasad et al. 2006). Furthermore, we obtained a measure of the model fit based on the mean square error (analogous to and referred to here as r^2). To evaluate the role of the predictor variables in each model, we extracted and analyzed, for all variables, the variable importance scores. Because variable importance scores can be influenced by closely related variables (Strobl et al. 2007), we present only the three top variables for discussion of the key environmental determinates for each species. This is a conservative approach to avoid over-interpretation of importance scores for all variables, but the full models are used in prediction and key determinates (often regionally important tree species) will not be reflected in the variable importance results presented here. While the randomForest modeling procedure tests the entire set of predictor variables throughout the individual runs (by selecting a subset in each iteration), the models stabilize through the iterative process and the relative variable importance is weighted to a few key variables.

Climate change scenarios

We used long-term (30-yr averages), downscaled, monthly data for current and future climates, provided by Hayhoe et al. (2006) from three general circulation model outputs: the HadleyCM3 model (hereafter abbreviated HAD) (Pope 2000), the Geophysical Fluid Dynamics Laboratory (GFDL) (GFDL CM2.1) model (Delworth et al. 2006), and the Parallel Climate Model (PCM) (Washington et al. 2000). In addition, we modeled bird habitats under two emission scenarios: the A1fi (fossil fuel intensive emissions, which assumes that the current emission trends continue for the next several decades without modification, hereafter abbreviated 'hi' when paired with a model abbreviation) and the B1 (a high level of conservation and reduction of CO₂ emissions, hereafter abbreviated 'lo'). We also averaged the three models for each emission scenario to yield an average high (AVG3hi) and average low (AVG3lo) emission set of climate predictors. We modeled with these two averages plus the PCM B1 (coolest scenario, PCMlo) and HadleyCM3 A1fi (warmest scenario, HADhi) to represent the average and extreme possible outcomes from the climate analysis. These four scenarios each project a warmer eastern US, with generally higher precipitation, and with the higher emissions scenarios resulting in much greater increases in temperature by the end of the century (Iverson et al. 2008). These warmer conditions, coupled with changes in the seasonal distribution of precipitation (e.g. drier later summers), are expected to increase drought stress for many organisms (Allen et al. 2010).

Model summarization and analysis

Considering the 147 bird species, three GCM models, two emission pathways, and multiple ways to analyze the data, we needed to select a subset of results to present here, representing the full range of outcomes, for an overview

of potential impacts of climate change on the birds of the eastern US. Additional analyses and species-by-species results and maps for all scenarios can be found at <www.nrs.fs.fed.us/atlas>. To encompass the breadth of results, we focus on change in three measures: area (defined here as simple presence/absence), weighted incidence, and mean-center of spatial distribution. We use the terms ‘change in habitat’ or ‘change in suitable habitat’ when discussing potential future incidence because of the assumptions involved in projecting distributions (see assumption section below). The change in area is a measure of gains or losses in the area of suitable habitat. The percentage change is relative to the current modeled habitat presence. Because the randomForest technique generally assigns very low values to all cells, we performed a sensitivity analysis by altering the cutoff value of 0.01, 0.05, and 0.10 and compared this to the actual BBS incidence value for each species. The cutoff value of 0.05 for a species current modeled incidence resulted in only a one percent difference in median of coefficient of variation (CV) to the actual species incidence. In contrast, the more restrictive cutoff (0.1) and liberal cutoff (0.01) under and over biased the species within range variability (median difference in CV of -10 and +20 percent, respectively). Further evidence of the bias of the 0.10 and 0.01 cutoffs was that, in both cases, the 1st and 3rd quartiles of CV differences did not cross zero. Therefore, in an attempt to limit the error in assigning an unoccupied cell as occupied, we considered cells occupied only if the modeled incidence value was >0.05. Change in area-weighted incidence incorporates both area and the relative incidence of each species; thus it is a better indicator of gains or losses in suitable habitat. For example, a species may expand its distribution but still lose suitable habitat within the occupied area. To evaluate potential change in habitat suitability, we determined the percentage change in area-weighted incidence for the current modeled distribution with that under the projected future conditions. Finally, the change in mean-center for the incidence values of each species were obtained via the spatial statistic tools ‘mean-center’ within ArcGIS 9.1 (ESRI 2005). The coordinates of the mean-center were used to calculate distance and direction of potential movement of suitable habitat, by species and by scenario. In addition, we tested for significant directional movement from random of the mean-centers using the Rayleigh test of random circular distribution (RCran 2008).

Alternative model parameterization

To evaluate the relative importance of adding tree species variables into the set of potential predictors, the individual tree species variables were removed and the 147 species models were processed with only climate/elevation variables. The two model sets were compared using the overall model fit (r^2) and the Fuzzy Kappa score, which assesses the spatial representation of modeled to actual BBS incidences (Hagen-Zanker et al. 2006). Finally, we evaluated the differences in the projected change in area-weighted incidence under the PCMlo and HADhi climate models for each alternative model set.

Assumptions

Our habitat model projections assume that 1) contemporary predictor–response relationships remain unchanged under climate change; 2) the predictors used are a comprehensive set of those ecologically relevant to birds; 3) the models of bird habitat associations are able to capture the distribution of a species and are not merely artifacts of spurious spatial associations; 4) biotic interactions such as interspecific competition or host-parasite or predator–prey relationships, which can be important in shaping species distributions (Davis et al. 1998, Hahn and O’Connor 2002), do not change outcomes in the models; and 5) while our models do consider interaction with tree species, they cannot address changes in forest dynamics. Of course, disruption of these relationships by the consequences of climate change could lead to model deficiencies. Furthermore, we have chosen to utilize a more robust modeling methodology to account for nonlinear and nonparametric realities of modeling species distributions (Prasad et al. 2006). This methodology at present limits our ability to account for and separate spatial dependences, thus we have not partitioned the species level variation explained by habitat, spatial structure, and their joint contribution (which may still have a habitat component but associated with different processes such as dispersal, Bahn et al. 2006). Given these assumptions, it is important to stress the broad-scale habitat perspective of these models. Furthermore, because we know that biotic interactions are important in shaping occupancy and use of habitats, especially at finer scales, more research is needed to describe the importance of fine-scale variability in species abundance patterns in a changing climate. The present analysis, therefore, provides projections of future bird habitats that incorporate current understanding both of future climate and future tree distributions as primary determinants of avian distributions. These projections are based on the assumption that birds do not adapt to climate change and the inherent time lag between projected changes in climate and the ability of tree species to shift to the projected future habitat in ways that do not change the bird’s contemporary relationships with climate and tree species.

Results

Modeling characteristics

Mean model fit (r^2) across the 147 bird species was 0.66 and ranged from 0.27 to 0.92. The wide range indicates the high variability in predictive capability because of variation in species–environment relationships, sample size (Schwartz et al. 2006), predictor performance, and data quality. However, because of a long left tail in the distribution, the first quartile of the data is only 0.1 units lower than the mean, i.e. only 25% of the species models have an r^2 below 0.54 (Fig. 1). The high model fit for most species indicates that these models provide a good base for projecting broad-scale habitat models under various climate change scenarios.

The structure of the species models reveals differences in habitat associations among the 147 bird species. When we compared the increases in mean square error from the most

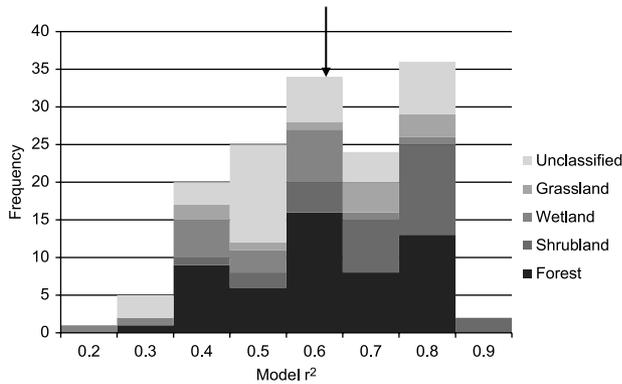


Figure 1. Predictive model fit of randomForest models (equivalent to r^2) for 147 bird species, as classified by a priori habitat characteristics. Arrow indicates the mean model r^2 across all species (0.66).

important variable (mean 23.0, SD 5.96) to the other variables in the model, we found that on average, only two additional variables constitute at least 75% of the maximum variable importance score for each species. In an examination of the three most important variables among all species, all seven climate, three of the four elevation, and 36 of 39 tree species variables were represented. Annual precipitation occurred among the top three positions for 72 models and average January temperature 41 times. The most influential tree species variables were balsam fir, red maple, and American elm, which occurred in the top three position 18, 16, and 14 times, respectively. The contribution of tree species variables as the top variables was greatest for forest birds, where 57% of the 53 species had two or three tree species variables in the top three variables (Fig. 2).

Overall distributional changes in bird habitat

When projected across the eastern US using current climate data and four scenarios of climate change, the habitat models for each bird species often show stark differences in habitat among species and across scenarios. For example, the black-throated blue warbler *Dendroica caerulescens* is

projected to have marked contraction of habitat into northern New England and along the Appalachian Mountains and far more extensive losses under a higher emissions scenario (Fig. 3). Conversely, the brown-headed nuthatch *Sitta pusilla* is projected to increase its area of suitable habitat (under high emissions extending up the Atlantic coast). However, under both high and low emission scenarios, the incidence levels are reduced in areas where it currently has the highest incidence (e.g. the piedmont of the Carolinas, Fig. 3). (Note: these maps are available for all bird species on the website, <www.nrs.fs.fed.us/atlas>, as well as tabular summaries for all species in Supplementary material Appendix 1.) These projected changes in habitat were similar in direction for each species regardless of climate change scenario (Spearman's rho correlation coefficient $r_s > 0.88$ and $r_s > 0.78$ across all models for incidence and occurrence, respectively), but the magnitude of changes varies with the severity of the projected change in climate (Fig. 4). Furthermore, across all scenarios, there was a mean projected shift in mean-center distance of 98 to 203 km and a directional movement significantly different from random, to the north-northeast for the 147 species habitat (Fig. 5, Table 1).

Habitat changes by common migratory and habitat guilds

While the overall pattern of change highlights the magnitude of potential shifts in bird species throughout the eastern US, the species modeled here represent a broad spectrum of life history strategies that may be influenced differently by climate-induced changes. We use contingency tables (chi square) to evaluate if projected changes are similar among species groups. First, the species responses under all four scenarios differed among the migratory strategies, i.e. residents, temperate migrants, and neotropical migrants (HADhi $\chi^2 = 15$, AVG3hi $\chi^2 = 23$, AVG3lo $\chi^2 = 20$, PCMlo $\chi^2 = 27$, all $p < 0.05$, $\chi^2_{n(6),p(0.05)} = 11.1$). The primary driver to this significant result is the relative greater losses projected for migrants compared to resident species (Table 2A). When species were grouped into habitat guilds (forest, grassland, shrubland, wetland, unclassified),

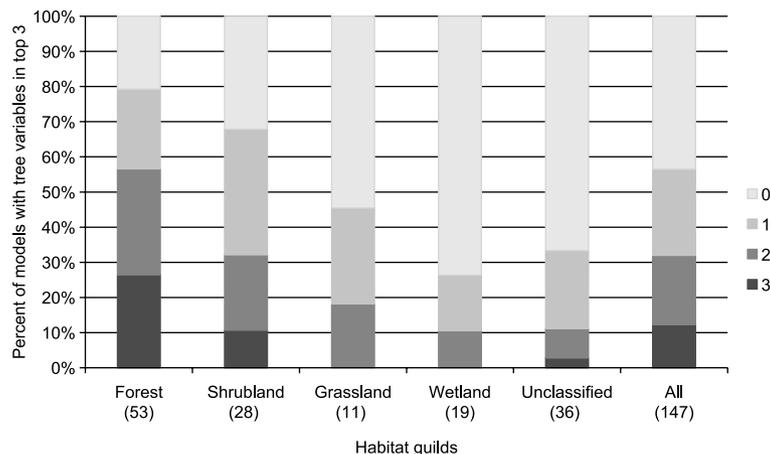


Figure 2. The occurrence and number of tree species variables in the three most influential variables in each bird species model, separated by bird habitat guild. Number in parentheses indicates the number of species models within that habitat guild.

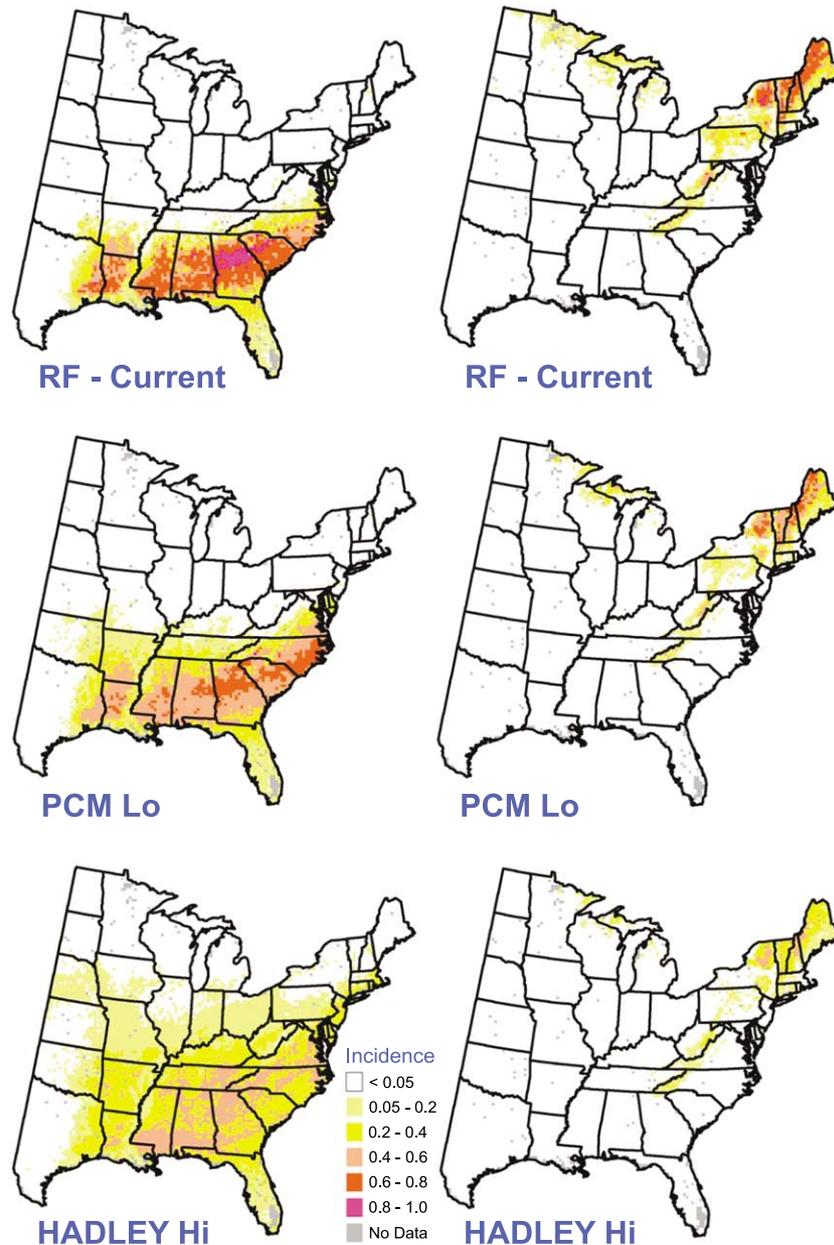


Figure 3. The current modeled distribution (RF-current) of the brown-headed nuthatch (left column) and black-throated blue warbler (right column) and projected suitable habitat under HADhi and PCMlo climate change scenarios.

all scenarios except HADhi showed a pattern of potential losses or gains significantly different from chance (HADhi $\chi^2 = 11$, AVG3hi $\chi^2 = 22$, AVG3lo $\chi^2 = 20$, PCMlo $\chi^2 = 21$, $\chi^2_{n(8),p(0.05)} = 15.5$, Table 2B). In this case, a greater-than-expected proportion of wetland species were projected to increase and a less-than-expected proportion of losses from the unclassified species were strong contributors to the significant result.

Relative importance of tree species variables in model outcomes

When we modeled each bird species using only climate/elevation variables and compared them to the full models that included the 39 tree species variables, we found

reduced predictive power (Wilcoxon signed rank $t = 840$, $p < 0.001$). However, the mean difference in goodness-of-fit (r^2) was only 3%, highlighting the ability of climate/elevation space to describe the distribution of many birds. In addition, the Fuzzy Kappa scores between the two model sets differed little (mean difference of 5%), further indicating that the models did not differ markedly in their ability to capture the spatial correspondence of the actual data. However, when the climate/elevation-only models were projected onto the climate change scenarios, the projected change in suitable habitat was more extreme in 63 and 60% of the bird models under the HADhi and PCMlo scenarios, respectively (Fig. 6). The differences were most dramatic for birds projected to decline from our initial analysis and for those species models with more tree species variables in the

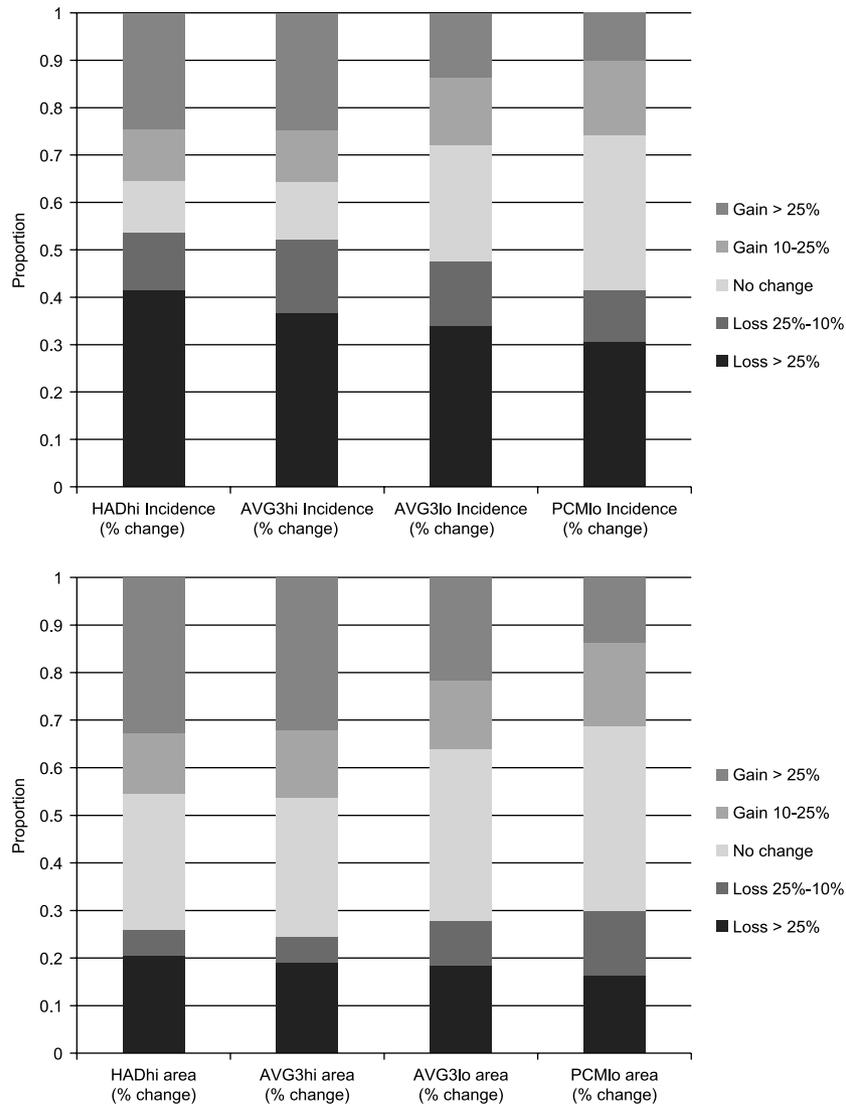


Figure 4. Change in species area-weighted incidence and total area occupied in the eastern US based on shifts in suitable habitat under four climate change scenarios.

top three positions (Fig. 7). Therefore, without the added habitat-specific information, the projected species changes are constrained only by projected changing climate conditions, resulting in a substantial divergence in the two model approaches.

Discussion

Our results provide a broad-scale perspective of how the habitat of bird species' distributions may respond to projected climate change, by including both climate-based associations and information about current and potential tree species habitats. Across all 147 species, greater changes in species incidence are projected than of total area of habitat, with a higher proportion of species showing the potential for losses of incidence throughout their eastern US range. Thus, for many species, the peak of the species' incidence may shift toward the tails within a relatively more stable eastern US range. Habitat may become less suitable

to sustain high incidences for some species like the black-throated blue warbler, while other species are projected to expand into new areas, e.g. the brown-headed nuthatch extending into Tennessee (Fig. 3). In addition to the distribution-wide shifts in habitat as summarized by percentage changes, it is important to consider that these species are broadly distributed in a spatial array across the eastern US, and patterns of movements are another key to understanding potential climate change impacts. The mean-centers of the habitats for 147 species are projected to move, on average between 98 and 203 km to the north-northeast by the end of the century, depending on the climate change scenario. Both scenarios show species-specific variation (Fig. 5, Table 1). A distributional shift of this magnitude is comparable to the annual rates of change recently being observed in winter range limits and breeding northern bounds within North America (Hitch and Leberg 2007, La Sorte and Thompson 2007). Furthermore, the spatial extent of Hitch and Leberg (2007) also covered the eastern US, and ten of their 13 species with significant distribution

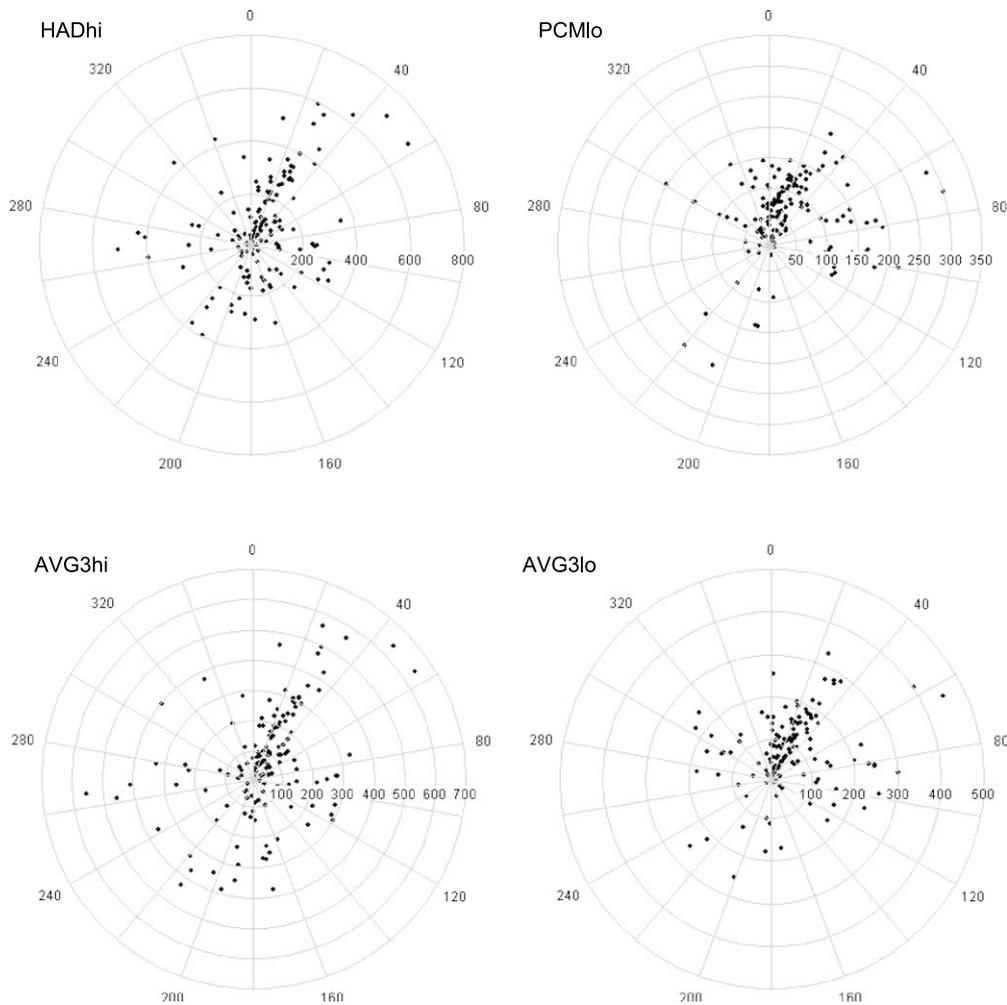


Figure 5. Potential changes in distance (km) and direction (degrees) of mean-centers of suitable habitat for 147 species for AVG3lo (note distance scale from 0 to 500 km), PCMIo (0–350 km), AVG3hi (0–700 km), and HADhi (0–800 km).

shifts and included in our models showed similar trends (e.g. northern movement of summer tanager and hooded warbler).

Bird species observed here respond individually as they adapt to changing climatic conditions or shift toward new territories. This pattern of individually based shifts in species distributions arises because of different combinations of driving climate and tree species variables. Therefore, as climate shifts and tree assemblages change as they have in the past (Webb and Bartlein 1992), birds also would likely experience extensive mixing that would, in turn, influence interspecific interactions. Understanding how species may interact and how this influences their

ability to track habitat changes will be important to evaluate bird species responses to climate change, but is predicated in part on knowing the broad-scale patterns of where species may find suitable habitat.

Differences in migratory strategies

Changes in habitat distributions are not anticipated to occur equally across all species groups. The migratory strategies of species examined here provide one classification of birds that might be expected to behave differently to climate change (Ahola et al. 2007). Year-round occupancy

Table 1. Mean distance (km) and standard deviation of the change in mean-center (center of gravity of species distribution), change (degrees), and bootstrap 95% confidence intervals in mean-center, for distributions of 147 bird species in the eastern US. Test statistic: Rayleigh test of random circular distribution.

	Distance change (km)		Directional change (degrees)		p
	Mean	SD	Mean	95% CI	
HADhi	203	145.0	36.7	18.82–57.12	<0.01
AVG3hi	201	137.9	40.2	25.55–58.13	<0.01
AVG3lo	130	80.2	31.2	22.38–39.86	<0.01
PCMIo	98	55.9	20.9	12.55–29.16	<0.01

Table 2. Contingency table of the number of species projected to have changes in area-weighted incidence of at least 25% under two scenarios of climate change for A) migratory guilds and B) habitat guilds.

A) Migratory guild	AVG3hi Loss >25%	No change	Gain >25%	AVG3lo Loss >25%	No change	Gain >25%	n
Neotropical	27	26	15	23	36	9	68
Temperate	19	19	5	20	20	3	43
Resident	2	11	6	1	16	2	19
Other	6	1	10	6	5	6	17
Total	54	57	36	50	77	20	147

B) Habitat guild	Loss >25%	No change	Gain >25%	Loss >25%	No change	Gain >25%	n
Forest	24	20	9	22	25	6	53
Grassland	4	6	1	6	4	1	11
Shrubland	14	9	5	11	15	2	28
Wetland	7	1	11	7	6	6	19
Other	5	21	10	4	27	5	36
Total	54	57	36	50	77	20	147

of resident birds directly exposes them to yearly variations in climate. Short-distance or temperate migrants move to avoid physiological challenges of year-round occupancy of their breeding ground but remain near these locations. Neotropical migrants move great distances between breeding and tropical wintering grounds but balance the energy expenditure of migrating to match seasonal abundance of resources. The impacts of climate change could be dramatic for each group but may ultimately be acting on different components of their life history. Our results suggest generally greater increases in habitat for resident species than for short-distance and neotropical migrants, indicating that migratory species may be at greater risk under climate change (Lemoine and Böhning-Gaese 2003). In addition, resident species typically show a strong northern boundary limit to winter temperature (Root 1988) and colder climates. Therefore, under increased temperatures, range expansion of residents would be more likely to occur. Other components of migrant life history may place additional pressures on these species with climate change, such as mismatches in migratory timing, e.g. with food supplies (Visser et al. 2006), and increased variability of weather events during migration (Hedenström et al. 2007).

The value of tree species information in modeling bird distributions

An important contribution of this analysis is that it includes both climate and tree species as potential predictors of the individual bird species patterns, as we try to understand how bird species habitats may shift in the face of climate change. Although Thuiller et al. (2004) found that land-cover variables (e.g. percent forest) did not markedly improve presence/absence models for European birds, Stralberg et al. (2009), working at a finer resolution within California, showed that land-cover information was important in considering potential climate change impacts. Our data provide additional evidence that indicates the importance of including tree species variables when modeling relative abundance for North American breeding bird species. Because the tree species models included edaphic and landscape determinates in addition to climate, they

produce models that are more representative of potential limiting factors of trees species than climate-only models can accommodate (Lo et al. 2010). They do have their limitations, but the additional variables and rich database limit the extent of wild extrapolations and produce models that capture the contemporary distributional patterns of trees. This lends confidence to using the most reliable tree species models as predictors to capture additional environmental dimensions of bird distributions.

Habitat guilds: we evaluated similarities and differential patterns among the 147 bird species by first classing them into habitat guilds, and then comparing the guilds. For many bird species, there are close corresponding associations between their occurrence and the distributions of a particular tree species, as with the brown-headed nuthatch's use of loblolly pine for nesting and foraging. In other cases, a broadly distributed species such as the wood thrush *Hylocichla mustelina* is likely to show association with red maple (the most widely distributed tree and a species that indicates the presence of forest). Thus, we might expect that the inclusion of tree species variables would improve models

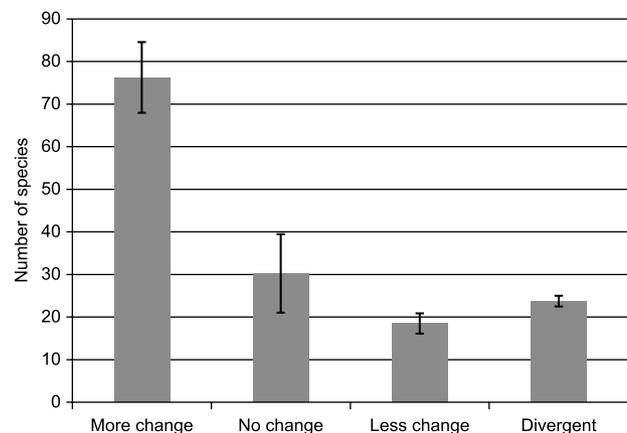


Figure 6. The mean number of species from the four scenarios (with SD) in which the species model without vegetation resulted in a greater projection of change, no change, less change, or divergent results from the species model when tree species were in the pool of predictor values.

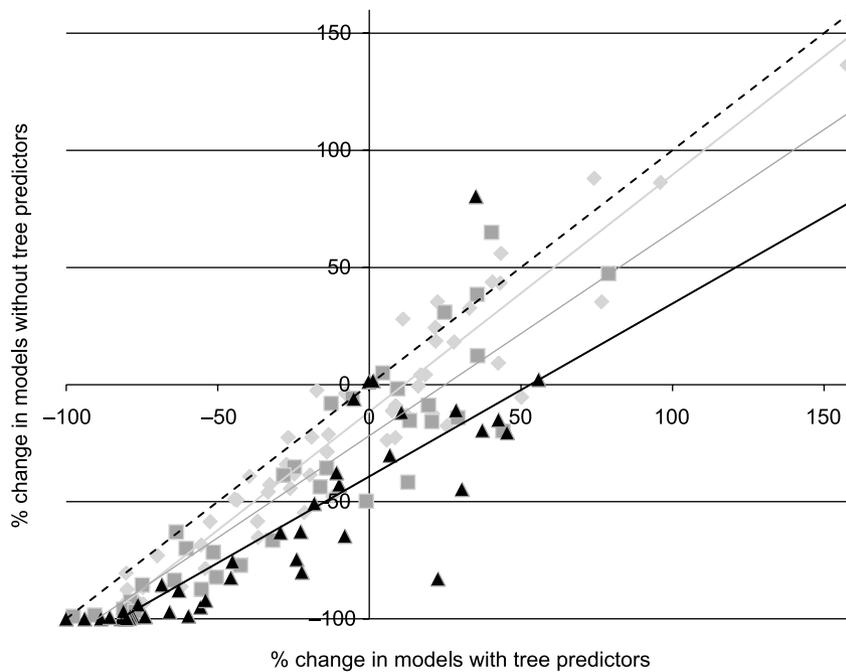


Figure 7. Projected change in habitat for species with and without vegetation variables in the predictor set. Black triangles indicate models where there were two or three tree species in the top three variables, dark gray squares indicate only one variable in the top three, and light gray diamonds indicate species models without tree species in the top three variables. Lines of the same shading are simple linear regressions by groupings with no tree species, one tree species, and > two tree species in top three variables with r^2 values of 0.94, 0.90, and 0.86, respectively, and the dashed 1:1 line for reference. Ten species have changes >160% and are not shown.

for forest bird species. Indeed, our results do suggest that many forest and shrubland species had better models (e.g. higher r^2) than the average of the 147 species models, and that these forest bird models were more likely to rely on tree variables as the most informative in describing the species habitat. For nonforest species, the occurrence of tree species variables in the model may still be important by acting as surrogates for other environmental information. In addition, these results point to the need for additional data that would allow us to consider other potentially important variables for other groups of species (e.g. to track changes in grassland or wetland birds under climate change).

Our models suggest that relatively more forest and shrubland species are projected to decrease in habitat, while many nonforest species tend to show increases in potential future habitat. The challenges faced by forest birds have been demonstrated to increase under climate change (Leech and Crick 2007), not to mention the sensitivity of these species to other forms of land-use change that reduce forest area or quality. A clear example from the results here can be found in the occurrence of American elm in the bird species model. While the elm has been devastated by Dutch Elm Disease over much of the eastern US, it still has the 4th highest importance value of the 134 tree species evaluated in the eastern US when both basal area and number of stems are considered (Iverson et al. 2008). Therefore, its persistence as small but numerous trees on the landscape, and its continued risk of infection moving forward, may exemplify multiple interacting disturbances for birds that show associations to tree species. In part, the potential

future changes for forest-associated species arise from a strong dependence on both climate conditions and trees. This double constraint on bird species generally results in a smaller area of potential suitable habitat to occupy following climate change, and this area may be further constrained by the time lags required for the tree species to redistribute (Pacala and Hurtt 1993).

Differences from climate/elevation-only models: to consider how bird species habitat might change under various climate change scenarios, it becomes important to assess the differences between models processed with and without tree species variables as potential predictors. When we relied only on climate/elevation variables, we produced poorer models of the current bird habitat distributions. These relatively poor models, in turn, often lead to models that project greater potential change for individual species. Therefore, while models without tree species may appear to portray a current species distribution quite well (without comparison to alternative models), they lack a great deal of landscape-level information, which makes them more susceptible to predicting larger changes in bird habitat. For forest and shrubland birds, whose models used the most tree species information, we see the greatest difference when models do not include tree species in the candidate set. In practice, because of the long-lived nature of trees, vegetation distributions will change at a slower rate than the projected shifts in climate that are anticipated in this century. Therefore, species that show a strong association with tree species may show a refugia effect, where habitat may not be optimal in terms of climate but the tree species continues to

provide suitable habitat for the species. These results suggest that by including information on the distribution of tree species (now and into the future), we gain a finer understanding of how suitable habitat for birds might shift under climate change.

Conclusions

For 99 to 131 of the 147 eastern US birds evaluated in this analysis, we found strong evidence for at least a 10% change in suitable habitat with the climate changes expected by 2100. With bird species already demonstrating measurable responses of behavior (Both and Visser 2005) and distributional patterns (La Sorte and Thompson 2007) to climate change, our results provide insight into how species could shift their distributions under the more intensive and rapid changes in climate conditions predicted to occur over the coming century.

Of course, any modeling exercise into an unknown future carries uncertainty, and we must ensure that results are framed in the proper light as well as provide a foundation for further deductive inquiry into climate change impacts. One pathway towards reducing model uncertainty will be the development of methods that allow the use of robust statistical models (e.g. randomForest), while accounting for and projecting how spatial dependence may change. This step will require a better understanding of the ecological processes that give rise to spatial dependences and their association with environmental determinants (Bahn et al. 2008). We must also refine our research questions to explore other components of species interactions and climate change impacts. For example, based on the associations and potential changes in bird habitats identified here, that bird communities show strong responses to the maturation and structural development of forests (Holmes and Sherry 2001), and the evidence of current shifting in tree distributions (Woodall et al. 2009), we can hypothesize how birds might interact and respond to these changes as climate distribution intensifies.

Our analyses give a broad-scale representation of the habitat conditions that are likely to be associated with eastern US bird species. This approach allows us to encapsulate important habitat requirements of the species and identify where habitats may be suitable in the future. Once these areas are identified, finer scale patterns of habitat (e.g. forests within a heterogeneous landscape) and individual-mediated responses (interspecific competition) will likely govern the realized occurrence of species. It will also be important to generate models derived from mechanistic relationships (such as Rodenhouse 1992, Anders and Post 2006) to capture additional dimensions of climate change impacts (Lo et al. 2010). In the end, it will be likely at the merger of statistical and mechanistic approaches that we can increase understanding and begin to reduce further uncertainty around climate change impacts. In the case of modeling forest bird species patterns, our results show that including climate and tree species abundance are vital to generate representative models of contemporary bird distributions and advancing our understanding of potential future bird species habitats.

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Supplementary material (Appendix E6803 at <www.oikosoffice.lu.se/appendix>). Appendix 1.