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RESEARCH PAPER

Potential resilience of forest birds in the Appalachian Mountains to future climate change during the breeding season

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Abstract

Context Global climate change is predicted to cause long-term changes in bird distributions and populations. Although previous studies often prioritized understanding avian responses to shifting climate conditions, recent efforts increasingly incorporate landscape change as an additional factor.

Objectives We evaluated current and potential future effects of both climate and landscape change on the breeding distributions and relative abundance of 14 forest songbird species in the Appalachian Mountains.

Methods For each species, we compiled route-level total count data from 322 North American Breeding Bird Survey routes that were sampled between 1997–2017. Using Bayesian modeling techniques, we determined the relative influence of temperature, precipitation, and proportions of land cover types on route-level annual total species counts. We then projected future changes in relative abundance, regional occupancy, and distribution of relative abundance from 2000 to 2100, based on multiple greenhouse gas emission scenarios.

Results Our models showed that proportions of land cover types tended to be more influential and had higher effect sizes than climate variables on forest songbird relative abundance during the breeding season. In our future predictions, most changes in relative abundance and regional occupancy were modest.

Conclusions These results indicated that net projected impacts of climate change on the 14 focal forest songbird species during the breeding season were minimal at a broad scale in the Appalachian Mountains. Instead, land use changes that result in reduced forest cover and increased urban cover may pose a more immediate threat than climate change to forest songbirds breeding in this region.

Keywords Climate change · Distributions · Land cover change · North American breeding bird survey · Temperature · Precipitation

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Introduction

Global climate change is implicated as a factor in widespread declines of avian populations. Impacts to birds from global climate change can occur either directly or indirectly, resulting in altered population dynamics, phenological mismatches, shifts in distributions, and changes in abundance (Leech and Crick 2007; Oliver and Morecroft 2014; Scridel et al. 2018). Rising temperatures and increasing frequency and intensity of precipitation-related events (e.g., storms, floods, droughts) have direct fitness consequences on individuals through physiological stress impacting health, survival, and reproduction (Newton 2007). During the breeding season, increases in average maximum daily temperatures can negatively impact nest survival of certain bird species (Bonnot et al. 2018); maximum daily temperatures can also interact with factors in the landscape to further reduce breeding bird productivity and exacerbate rates of predator-induced nest failure (Cox et al. 2013a, b). Global climate change has also precipitated phenological mismatches among birds, vegetation budding dates, and emergence or peak abundances of insect prey (Visser et al. 2006; Waite and Strickland 2006). Bird species that are able to advance their pre-breeding migration or breeding phenology to track changes in climate may benefit from longer breeding periods and possibly increased recruitment, but species with limited phenological plasticity may face an increasing mismatch in the timing of food requirements vs. food availability during the pre-breeding and breeding seasons (Both et al. 2009), leading to population-level consequences. Ultimately, global climate change is posing considerable challenges to many bird species (Mayor et al. 2017; Scridel et al. 2018) and likely plays a role in declining avian populations through direct, indirect, and interactive effects (Jenouvrier 2013; Oliver and Morecroft 2014; Northrup et al. 2019), with consequences potentially greatest for long-distance migrants in seasonal habitats (Virkkala and Lehikoinen 2014, Flousek et al. 2015; Zurell et al. 2018).

Concomitant with the direct and indirect impacts to avian populations and phenology, global climate change is affecting biogeographical patterns and abundance. Plentiful evidence links long-term changes in avian distributions and geographical ranges to climate change and particularly warming average temperatures (Chen et al. 2011). Many bird species in the Northern Hemisphere have shifted their breeding and/or non-breeding ranges northward (Hitch and Leberg 2007; La Sorte and Thompson 2007; Virkkala et al. 2008). In addition, studies have documented and predicted both latitudinal and elevational shifts in bird distributions associated with increasing mean daily, July, breeding season, or annual temperatures (Rodenhouse et al. 2008; Maggini et al. 2011; Flousek et al. 2015), with high-elevation species deemed particularly vulnerable to climate change (Siegel et al. 2014; Flousek et al. 2015; Freeman et al. 2018). However, it is important to note that climate change can cause heterogeneous range shifts along elevational gradients, as increases in average annual temperatures may cause species to shift upslope, whereas higher average annual precipitation may drive them downslope (Tingley et al. 2012).

In addition, responses to global climate change are variable across species. As the climate continues to warm, certain birds may face extirpation and extinction in the most extreme cases (Sekercioglu et al. 2008; Tayleur et al. 2016; Freeman et al. 2018), but other species are predicted to expand their distributions in response to temperature increases (Tayleur et al. 2016), and resident species may benefit from warmer winters (Rodenhouse et al. 2008). In particular, habitat generalists may potentially expand their ranges and increase in relative abundance (Davey et al. 2013), whereas habitat specialists and cold-associated species are more likely to decline in numbers and be more negatively affected by higher mean annual temperatures and monthly temperatures during the pre-breeding and breeding seasons than southerly distributed species associated with warm temperatures (Pearce-Higgins et al. 2015; Tayleur et al. 2016; Freeman et al. 2018). In addition, the outcome of precipitation effects may be species-specific, as previous studies have found mixed responses by different bird species to cumulative growing season precipitation (Duclos et al. 2019) and annual precipitation (Tingley et al. 2012).

Many studies that address global change are focused solely on anthropogenic climate change, but it is important to also consider landscape change (encompassing changes in land cover and land use) and implications for habitat availability. Although

habitat specialist species may be particularly vulnerable to climate change, they are also sensitive to land cover change and respond strongly to habitat loss and degradation. For example, certain forest songbirds (e.g., forest-interior species) require extensive tracts of mature forest (Moenkkoenen and Welsh 1994), and losses in suitable forest habitat directly lead to subsequent declines or absences of associated forest songbird populations (Pimm and Askins 1995; Trzcinski et al. 1999). Conversion of forest habitat to alternative land use types in the landscape can also lead to population declines and reductions in species richness (Gaston et al. 2003; Aratrakorn et al. 2006; Zurita et al. 2006). For instance, energy development and urbanization tend to negatively impact native forest songbird communities (Er et al. 2005; Farwell et al. 2016; Margenau et al. 2019). Because land cover change can have significant impacts on bird distributions and populations (Rittenhouse et al. 2012), it is worth considering as an additive or interactive factor when evaluating avian responses to global climate change.

Changes in both climate and land cover patterns are occurring within the Appalachian Mountains of eastern North America, with ongoing consequences for regional bird assemblages. The Appalachian Mountains contain a range of elevations and primarily forested habitats, from temperate deciduous forests at lower elevations and southern latitudes to boreal coniferous forests at higher elevations and northern latitudes. The forest songbird communities in this extensive region reflect the diversity of woodland habitats, comprising species from a myriad of families. The Appalachian Mountains are a critical factor in dictating forest songbird species ranges, with forests at higher elevations in the southern Appalachians serving as the southernmost limit for many breeding songbird species (Merker and Chandler 2020). Looking forward, the Appalachian Mountains will likely play an important role in shaping future distributions of birds in eastern North America, particularly those whose regional distributions seem to be influenced heavily by elevation and concomitant climatic conditions. As the climate warms over time, the topography and elevational gradient of the Appalachian Mountains may enable them to serve as refugia for bird species (Peterson 2003; Keppel et al. 2012) or as a dispersal corridor that enables the northward migration of southerly species (Lawler et al. 2013; Zhu et al. 2021). Additionally, the extensive forested landscapes of the Appalachian Mountains could moderate the effects of climate warming for forest songbirds during the breeding season (De Frenne et al. 2013, 2019, 2021). However, the Appalachian Mountains region is also experiencing and projected to undergo rapid land cover change in some areas (Ordonez et al. 2014; Leonard et al. 2017), primarily due to energy extraction and urban development (Lawler et al. 2014). Thus, the Appalachian Mountains serve as a compelling study system to assess bird responses to the effects of global climate change and land cover change. Evaluating how avian populations and species distributions in the Appalachian Mountains have changed and could change over time will clarify their potential role as climate refugia and further our understanding of the relative importance and effects of climate change vs. land cover change in a heavily forested montane system.

Therefore, the purpose of our study was to investigate the current and potential future effects of both climate and land cover change on forest songbirds of the Appalachian Mountains during the breeding season. Using 20 years of North American Breeding Bird Survey (BBS) data from the Appalachian Mountains Bird Conservation Region (AMBCR; Fig. 1), we evaluated how climate and land cover influence contemporary and future breeding distributions of forest songbirds in the Appalachian Mountains. First, we determined the relative importance and effects of four climate and three land cover variables on the current breeding distributions and relative abundance of 14 forest songbirds during 1997–2017. Based on previous literature, we generally expected: positive relationships with increasing pre-breeding precipitation (due to potential indirect effects on vegetation growth) and increasing amounts of forest cover; negative relationships with increasing amounts of non-forest cover; diverging negative vs. positive relationships with increasing breeding season temperatures for cold-associated vs. warm-associated species, respectively; and mixed responses to breeding season precipitation and pre-breeding season temperatures (due to potential indirect effects on food availability and vegetation). Next, we explored potential future changes in breeding distributions and relative species abundance from 2000 to 2100, based on expected

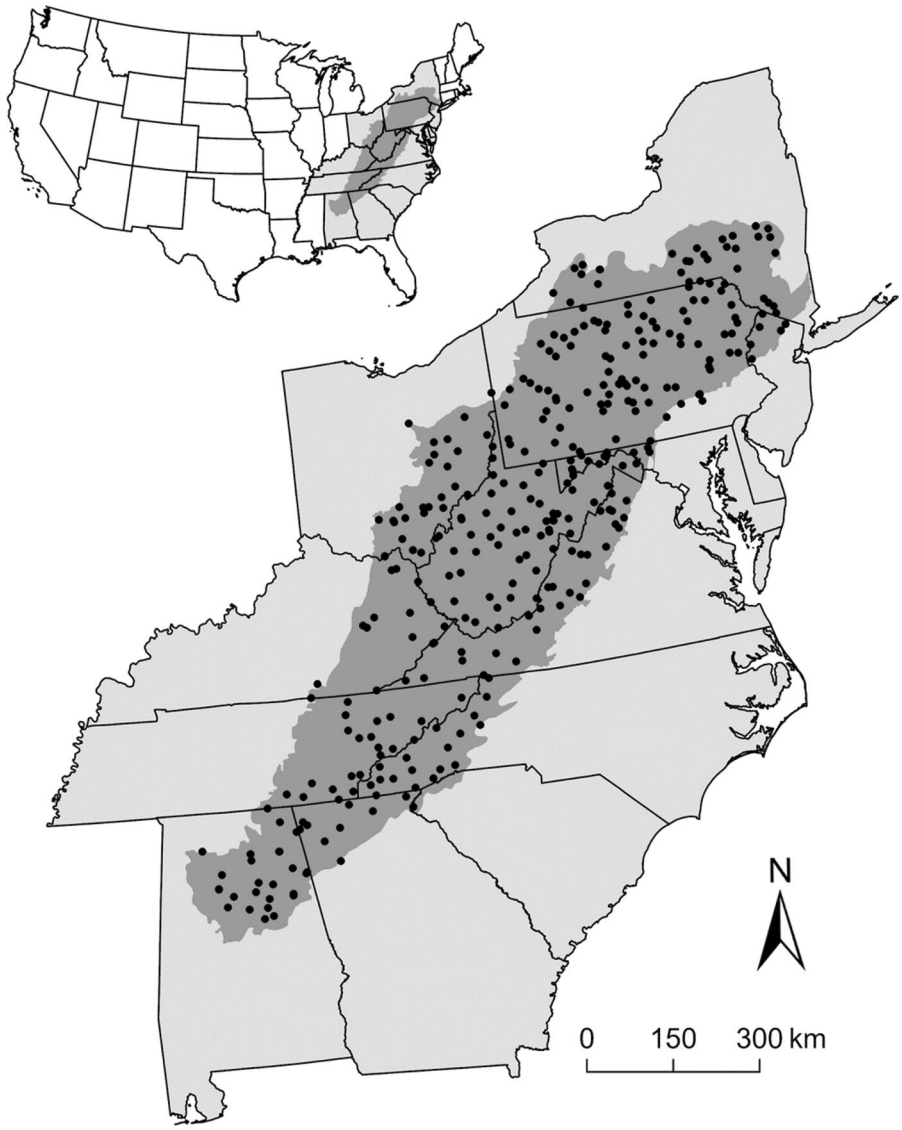


Fig. 1 Location and extent of the Appalachian Mountains Bird Conservation Region (shaded in dark gray) in the eastern United States, along with the starting point associated with 322 North American Breeding Bird Survey routes (black points; Sauer et al. 2013; Pardieck et al. 2019) within the study region

scenarios of changing climate and land cover patterns. Specifically, we quantified the differences in overall abundance and occurrence during the breeding season throughout the AMBCR, as well as shifts in distributions between 2000 and 2100.

Methods

Study area

Our study area was the AMBCR, which includes portions of 13 states in the eastern United States (Fig. 1) and encompasses most of the Appalachian Mountains range, covering nearly 42 million ha and stretching across a latitudinal range of 1260 km. It comprises four main physiographic provinces (Appalachian Plateau, Ridge and Valley, Blue Ridge, and Piedmont) and broadly forms the Appalachian Highlands physiographic division (Fenneman 1917). Elevation within the AMBCR ranges from below sea level to ~ 2,025 m above sea level. Mean breeding season precipitation and temperature vary widely across latitudes and elevations (see Fig. S1 in the Supplementary Information).

The dominant land cover type within the AMBCR is mature forest (Fig. S2). Tree diversity reflects local and regional geology, latitude, elevation, and moisture availability. Coniferous forests with pines (*Pinus* spp.), eastern hemlock (*Tsuga canadensis*), red spruce (*Picea rubens*), and firs (*Abies* spp.) tend to dominate the northern latitudes and high elevations. At middle and lower latitudes and elevations, deciduous tree communities include mixed mesophytic, northern hardwood, oak (*Quercus* spp.)-hickory (*Carya* spp.), and oak-pine forests (Turner et al. 2003). In the southernmost reaches of the AMBCR, there are also pockets of pine stands in the lowlands (Ruefenacht et al. 2008).

Focal species

We focused on 14 forest songbird species that use mature forest as primary breeding habitat, are considered medium- or long-distance migrants, and are readily detectable via roadside surveys (i.e., > 180 individuals detected at > 110 BBS routes throughout the study period) (Table 1). Although we primarily focused on wood-warblers from the Parulidae family (N = 7), we additionally selected two species each from the Cardinalidae, Turdidae, Tyrannidae, and Vireonidae families, and intentionally included species of regional conservation concern (N = 9) when possible, given the previous selection criteria. For each species, we assigned one of the following three climate classifications based on its occurrence and general range patterns within the AMBCR: cold-associated (i.e., primarily found at higher elevations or higher latitudes; N = 5), warm-associated (i.e., primarily found at lower elevations or lower latitudes; N = 4), or climate generalist (i.e., found throughout the AMBCR; N = 5).

Table 1 List of the 14 focal forest songbird species in our study, including climate classification, common and scientific names, 4-letter species code, and taxonomic family

Climate classifications were assigned based on the species' occurrence and general range patterns within just the Appalachian Mountains Bird Conservation Region: cold-associated (i.e., primarily found at higher elevations or higher latitudes; N = 5), warm-associated (i.e., primarily found at lower elevations or lower latitudes; N = 4), or climate generalist (i.e., found throughout the study region; N = 5). An asterisk (*) following the common name indicates a species of regional conservation concern (i.e., listed as an Appalachian Mountains Joint Venture Priority Species or North American Bird Conservation Initiative's Watch List species)

Climate classification	Common name (*Scientific Name*)	Code	Family
Cold-associated	Black-throated blue warbler (*Setophaga caerulescens*)	BTBW	Parulidae
	Blue-headed vireo (*Vireo solitarius*)	BHVI	Vireonidae
	Canada warbler* (*Cardellina canadensis*)	CAWA	Parulidae
	Least flycatcher (*Empidonax minimus*)	LEFL	Tyrannidae
	Veery (*Catharus fuscescens*)	VEER	Turdidae
Warm-associated	Cerulean warbler* (*Setophaga cerulea*)	CERW	Parulidae
	Kentucky warbler* (*Geothlypis formosa*)	KEWA	Parulidae
	Summer tanager* (*Piranga rubra*)	SUTA	Cardinalidae
	Swainson's warbler* (*Limnothlypis swainsonii*)	SWWA	Parulidae
Climate generalist	Eastern wood-pewee* (*Contopus virens*)	EAWP	Tyrannidae
	Scarlet tanager* (*Piranga olivacea*)	SCTA	Cardinalidae
	Red-eyed vireo (*Vireo olivaceus*)	REVI	Vireonidae
	Worm-eating warbler* (*Helmitheros vermivorum*)	WEWA	Parulidae
	Wood thrush* (*Hylocichla mustelina*)	WOTH	Turdidae

Bird count data

We obtained count data collected between 1997–2017 for the 14 individual bird species from BBS routes located within the AMBCR (Fig. 1; Pardieck et al. 2019). The BBS is a long-term, large-scale, international avian monitoring program initiated in 1966 to track the status and trends of North American bird populations (Sauer et al. 2013). Following a rigorous protocol, BBS data are collected by thousands of participants along randomly established roadside survey routes. Each survey route is approximately 40 km long, with 50 stops separated by ~ 800 m. At each stop, a 3-min point count survey is conducted by a single observer who records every bird seen or heard within a 400-m radius. Surveys start 30 min before local sunrise and continue for 5 h. Note that 1997 is the first year for which BBS data at the individual stop-level were available.

All statistical analyses were conducted at the route-level, as point-level location data were only available for the first stop along a route (representing 2% of the points). We downloaded data from all BBS routes within the AMBCR with at least 1 year of data during the 20-year period, for a total of 322 routes. We then calculated the summed count for each of the 14 focal species from each BBS route in each year to obtain 20 years of route-level annual total species counts, which served as the response variable in our analyses.

Study design for compiling contemporary and future environmental data

We summarized all environmental data within regular hexagons with vertices that were spaced approximately 24 km from the center point of the hexagon (Fig. S3). We determined the dimensions of the sampling hexagon to ensure that the entire BBS route was fully encompassed within the hexagon (i.e., every route was completely contained within its corresponding hexagon). Hexagons were used to keep shape consistency between the first and second objectives of the investigation and because hexagonal grids have advantages over square grids when applied to ecological networks or systems at this broad scale (Kimerling et al. 1999; Birch et al. 2007; Nhancale and Smith 2011), such as reduced edge effects and better fit to curved surfaces (White et al. 1992). As part of the first study objective, we generated 322 individual sampling hexagons that were centered on the midpoint of each BBS route (Fig. S3) and then compiled the corresponding environmental data within the sampling hexagons from 1997–2017, using spatial analysis approaches in R (R Core Team 2022). Sampling hexagons were allowed to overlap to sample the representative environmental data. As part of the second study objective, we created 346 individual hexagons that formed a non-overlapping grid that encompassed the AMBCR (Fig. S3), within which we summarized contemporary (2000) and future (2100) environmental data. The hexagonal grid cells used for prediction matched the dimensions of the sampling hexagons used for model building; thus, contemporary and future environmental data were compiled and projected at the same resolution across the entire study.

Contemporary environmental data compilation

We considered nine environmental covariates as contemporary predictor variables (see Table S1 in the Supplementary Information): latitude, median elevation, mean temperature during the bird breeding season (May–June), mean temperature difference between the leaf-out period of woody vegetation (March–April) and the bird breeding season, mean total precipitation during the leaf-out period of woody vegetation, mean total precipitation during the bird breeding season, and proportions of deciduous and mixed forest (combined), conifer forest, and developed land. Latitude and elevation were included to account for their known relationships with bird occupancy and abundance. Previous studies have found that latitude and/or elevation influences bird distributions and populations, even when climate variables are considered in conjunction (Matthews et al. 2011; Currie and Venne 2017; Duclos et al. 2019; Neate-Clegg and Tingley 2023), likely due to specific associated habitat characteristics. In our models, we assumed that latitude and elevation serve as proxies of certain habitat conditions, such as particular forest communities or tree assemblages, for which we lack comprehensive data. Mean breeding season temperature and mean total breeding season precipitation were meant to assess direct climate effects on birds and were measured across the same time period that BBS data were collected. We used the mean temperature, which was strongly correlated with both

maximum and minimum breeding season temperatures, to align with future temperature data. The two climate metrics incorporating the leaf-out period of woody vegetation were included to capture potential indirect effects involving habitat and food availability. Proportions of the two forest types represent habitat cover, whereas the proportion of developed land represents non-habitat cover. Latitude and mean May–June temperature were negatively correlated ($r = -0.76$), but elevation mediates that relationship throughout much of the AMBCR (Fig. S1). All other correlations among the nine environmental covariates ranged from − 0.55 to 0.63 (Fig. S4), which is below the threshold of concern for collinearity (Dormann et al. 2013).

We used land cover data from the National Land Cover Database (NLCD; Jin et al. 2019), which had a resolution of 30 m and were available for the years 2001, 2004, 2006, 2008, 2011, 2013, and 2016. For the three land cover classes, we used combinations of eight NLCD land cover categories, such that: (1) deciduous and mixed forest was comprised of three similar NLCD land cover categories that represented all mature forest not dominated by conifer species: deciduous forest, mixed forest, and woody wetlands; (2) conifer forest corresponded directly with the NLCD land cover category of evergreen forest; and (3) developed land was comprised of four related NLCD land cover categories that represented human impacts or urban development: developed – open space, developed – low intensity, developed – medium intensity, and developed – high intensity. Additional land cover types were omitted due to collinearity issues (e.g., the proportion of non-forest [comprised of agriculture, grasslands, and wetlands] was highly negatively correlated [$r = -0.87$] with the proportion of deciduous and mixed forest). We prioritized forest and developed land cover due to their well-documented relationships with forest-breeding and forest-interior specialist species, as well as their projected future dynamics in the AMBCR (Fig. S1).

To determine the relative importance and effects of climate and land cover variables on the current distributions and relative abundance of 14 forest songbirds (i.e., first study objective), we calculated latitude of the hexagon center point and median elevation, means of the climate variables, and proportions of the land cover variables within each sampling hexagon. Central latitude and median elevation (derived from Shuttle Radar Topography Mission digital elevation data [Farr et al. 2007] with a resolution of 20–25 m; Table S1) were static across the sampling period, but climate variables were calculated from PRISM Climate Group monthly temperature and precipitation data (Daly et al. 2008) corresponding to each year and land cover variables were derived from NLCD data, using the closest year available.

To evaluate potential future changes in bird distributions and relative abundance across the AMBCR (i.e., second study objective), we used the year 2000 as the baseline (i.e., contemporary projection). Thus, we compiled data for each hexagonal grid cell using environmental metrics corresponding to just the year 2000. We calculated latitude of the center point, median elevation, means of the climate variables from 2000 PRISM data, and proportions of the land cover variables from 2001 NLCD data (i.e., closest year available for 2000).

Future environmental data

To project future distributions of bird species counts across the AMBCR, we used the same nine environmental covariates that we considered when estimating contemporary distributions (Table S1) and summarized projected conditions in the same manner as previously described. For calculations of mean climate conditions in 2100, we used long-term (30-yr average from 2070–2099), downscaled, monthly data from three general circulation model outputs (Iverson et al. 2019): the Community Earth System Model 4.0 (CCSM; Gent et al. 2011) from the National Center for Atmospheric Research, the Geophysical Fluid Dynamics Laboratory model 3.0 (GFDL; Donner et al. 2011) from the National Aeronautics and Space Administration, and Hadley GEM2-ES (HAD; Collins et al. 2011) from the UK Hadley Centre. We further considered two representative concentration pathways (RCPs), 4.5 and 8.5, that reflect lower and higher levels of greenhouse gas emissions, respectively. These data were compiled into a 10-km^2 grid (Iverson et al. 2019), from which we extracted area-weighted means for each hexagonal cell. For analysis purposes, we averaged the three circulation models for each RCP to yield an average low (AVG LOW: average 4.5 RCP) and average high (AVG HIGH: average 8.5 RCP) emissions set of climate predictors (Hayhoe

et al. 2017). In addition to the two averages, we modeled the coolest scenario (COOL: CCSM-4.5 RCP) and warmest scenario (WARM: GFDL-8.5 RCP) to represent the two extreme possible outcomes from the climate analysis (USDA Forest Service 2023).

To calculate future proportions of land cover, we used projections produced by the U.S. Geological Survey Earth Resources Observation and Science Center (Sohl et al. 2007), which used a modeling framework that forecasts scenarios of land cover change out to 2100 based on three greenhouse gas emissions scenarios. Corresponding to the two RCPs of the future climate change scenarios, we used the higher (A1b) and lower (B1) emissions scenarios for projecting land cover change (Knutti and Sedláček 2013). In both scenarios, the amount of developed land and forest cover is projected to increase and decrease, respectively, although greater magnitude changes are associated with the higher emissions scenario (Fig. S1).

Combining the projected climate and land cover data together, we focused on four future scenarios: (1) the coolest (COOL) scenario combines the CCSM general circulation model with a 4.5 RCP and land cover change based on B1 emissions; (2) the average low emissions (AVG LOW) scenario incorporates the averaged outputs of the three general circulation models with a 4.5 RCP and land cover change based on B1 emissions; (3) the average high emissions (AVG HIGH) scenario incorporates the averaged outputs of the three general circulation models with a 8.5 RCP and land cover change based on A1b emissions; and (4) the warmest (WARM) scenario combines the GFDL general circulation model with an 8.5 RCP and land cover change based on A1b emissions. Although we do not explicitly account for uncertainty in the future climate or land cover projections, we attempted to reduce the bias of variable annual climate conditions by averaging predictions over 30-year periods. In addition, the four scenarios were selected to cover a plausible range of future conditions, from the mildest potential scenario with moderate emissions to the most extreme potential scenario with high emissions. We expect that future climate and land cover change will fall within the bounds of the mildest and most extreme projections.

Data analysis

We modeled each of the 14 focal species individually, with the route-level annual total counts assumed to be a negative binomial random variable and the predictor variables consisting of the nine environmental covariates described previously. Based on species-specific *a priori* predictions of relationships, latitude was specified as an orthogonal polynomial with either one degree (i.e., linear) or two degrees (i.e., quadratic) to allow for nonlinear relationships, and elevation was specified as an orthogonal polynomial with either one degree or four degrees to allow for multimodal relationships. For species whose relationship with elevation may vary with latitude (e.g., species with trailing-edge populations in the southern Appalachian Mountains), we modeled the route-level annual total counts as a function of latitude + elevation + latitude × elevation, plus the climate and land cover variables (Table 2). For the species with widespread distributions or whose relationship with elevation was generally constant across latitudes, we modeled the route-level annual total counts as a function of latitude (two-degree polynomial) + elevation (four-degree polynomial), plus the climate and land cover variables (Table 2). For all models, the four climate variables were specified as orthogonal polynomials with two degrees to allow for nonlinear relationships and the three land cover variables were specified as orthogonal polynomials with one degree, based on an expectation for positive vs. negative linear relationships with habitat vs. non-habitat cover types, respectively. Because our data included repeated observations at each route over time, all models also included a random site effect for log expected count.

Ten of the focal species exhibited spatial structure in their distribution and required spatial models to ensure that predictions followed regional clustering patterns. To incorporate spatial relatedness among route-level annual total counts into these models, we included spatial random effects and assumed that the spatial process followed an exponential covariance structure (Banerjee et al. 2003; Royle and Wikle 2005). For the four focal species that were abundant and widespread across the study region, with overdispersed counts and non-constant variance across space, we constructed models without spatial dependence but incorporated site-level random effects for the negative binomial dispersion parameter because they

Table 2 Measures of prevalence based on North American Breeding Bird Survey data from routes surveyed in 1997–2017, model type and model fit, the number of iterations in the posterior distribution, and statistical significance of predictor variables for the 14 focal forest songbird species (comprised of 5 cold-associated, 4 warm-associated, and 5 climate generalist species; see Table 1 for species codes). "Routes" is the total number of routes across years where at least 1 individual was detected, and "Count" is the total count across years (i.e., the total number of individuals detected across all routes and years)

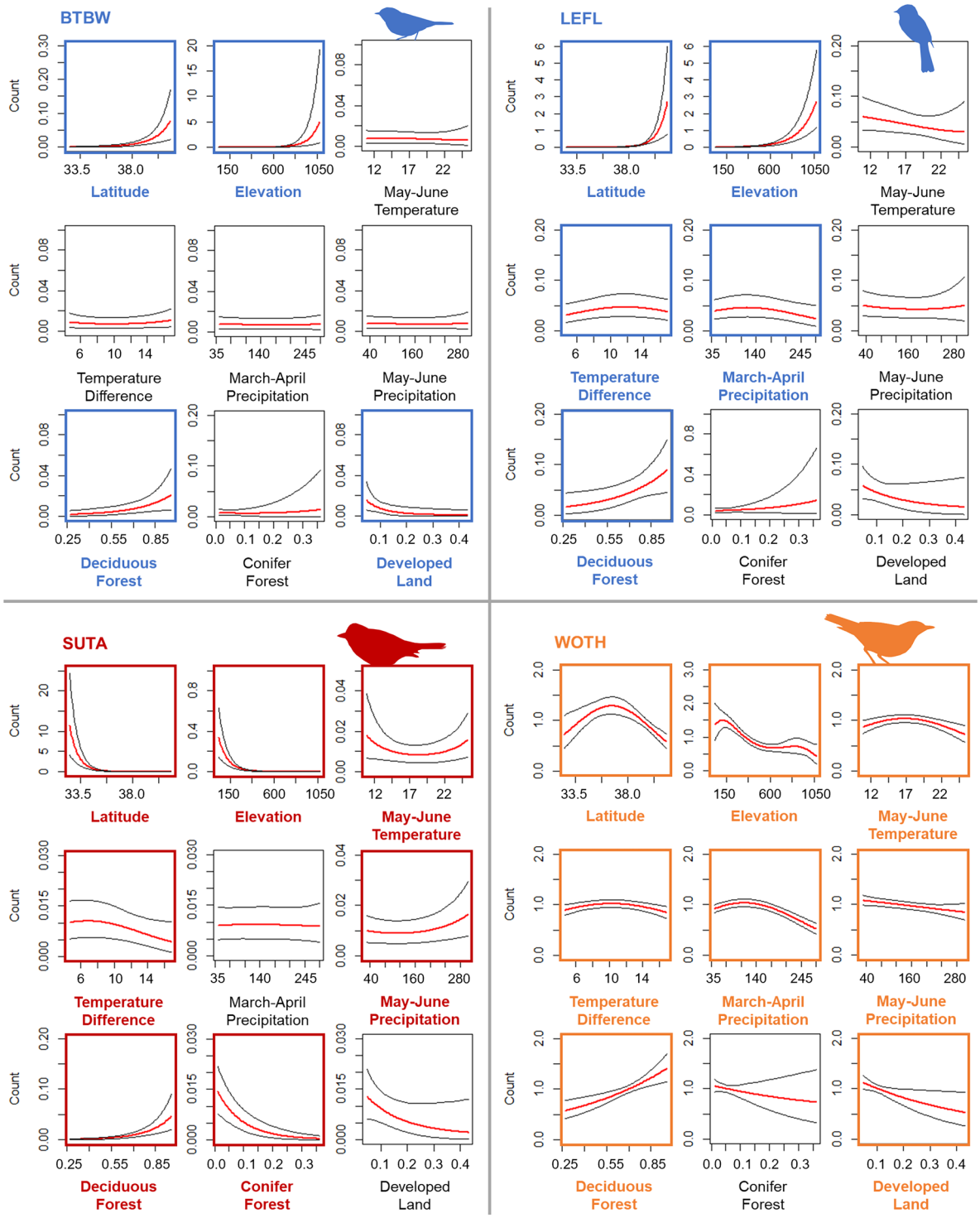
Species	Routes	Count	Model type	Model fit	Iterations	LAT	ELEV	L×E	MJT	TD	MAP	MJP	DF	CF	DL
BTBW	857	3016	1	0.73	18,000	X	X	X	0	0	0	0	X	0	X
BHVI	1768	6995	1	0.31	15,000	X	X	0	0	X	X	0	0	X	0
CAWA	411	1041	1	0.41	15,000	X	X	X	0	0	0	0	0	0	0
LEFL	1352	5299	1	0.45	21,000	X	X	X	0	X	X	0	X	0	0
VEER	1590	11,441	1	0.68	6000	X	X	X	0	0	0	X	0	0	X
CERW	904	2761	1	0.45	3000	0	X	-	X	X	0	0	X	X	0
KEWA	1317	3575	1	0.65	3000	X	X	-	X	X	0	X	X	0	0
SUTA	826	3078	1	0.84	15,000	X	X	0	X	X	0	X	X	X	0
SWWA	114	183	1	0.62	18,000	0	0	-	0	0	0	0	X	0	0
EAWP	3933	20,348	0	0.46	3000	X	X	-	X	X	0	X	0	0	X
REVI	4481	140,488	0	0.32	3000	X	X	-	0	X	X	0	X	0	X
SCTA	4034	34,152	0	0.41	3000	X	X	-	X	0	0	0	X	0	X
WOTH	4412	56,553	0	0.21	3000	X	X	-	X	X	X	X	X	0	X
WEWA	1274	3648	0	0.52	6000	X	X	-	0	0	X	0	X	0	0

Model type refers to whether the negative binomial model included spatial dependence (1) or not (0). Model fit (i.e., Bayesian *p*-value) was assessed with posterior predictive checks. Predictor variables (latitude [LAT], elevation [ELEV], interaction between latitude and elevation [L×E], mean May–June temperature [MJT], difference between mean March–April temperature and mean May–June temperature [TD], mean total March–April precipitation [MAP], mean total May–June precipitation [MJP], and proportions of deciduous and mixed forest [DF], conifer forest [CF], and developed land [DL]) are marked with an X if the 95% credible interval of their slope coefficient(s) did not overlap 0 (which indicates statistical significance) and with a 0 if their slope coefficient(s) did overlap 0

exhibited substantial regional variation in counts, and this allowed for site-level changes in count variance.

We used a Bayesian framework for inference and prediction, implemented with Markov chain Monte Carlo methods. For all parameters in each model, we used prior distributions which were meant to provide little information. We fit the models in JAGS (Plummer 2003) using the "jagsUI" package (Kellner and Meredith 2021) in R (R Core Team 2022). We used the "autojags" function to run three chains for each model with a burn-in of 25,000 iterations, thinning rate of 50 iterations, and iteration increment of 50,000; models iteratively ran until reasonable convergence ($\hat{R} \leq 1.1$) was achieved (Gelman et al. 2014), resulting in a range of 3000 to 21,000 posterior draws (Table 2). Model goodness-of-fit was assessed with posterior predictive checks that compared parameter sets derived from the original data with those derived for a replicate (simulated data set); significant differences between the observed and simulated data would indicate that model assumptions were not being met (Conn et al. 2018). To compare the two data sets, we used the sum of squared Pearson residuals as a test statistic; if the Bayesian p-value was between 0.05 and 0.95, we considered the model fit to be good (Gelman et al. 2014).

To determine the relative influence of climate change and land cover change on the 14 focal species, we compared variable importance and effect sizes on expected count among the climate and land cover variables. Variable importance was determined by evaluating whether 95% credible intervals (CIs) of the slope coefficient values overlapped 0 (Fig. S5); if the 95% CIs did not overlap 0, the variable was considered important. To compare the effect sizes of each climate and land cover variable overall and for each species, we calculated the absolute difference between the maximum mean expected count and minimum mean expected count across all values of each covariate (while



holding all other variables at their mean value), and additionally plotted the change in mean expected count (with 95% CIs) from the minimum value to the maximum value of the covariate (Fig. 2, Fig. S5). Because some of the focal species had higher expected counts than others, which would

◂**Fig. 2** Plots of the relationships between the predictor variables and the mean expected count (red line) for 4 of the 14 focal forest songbird species (BTBW: black-throated blue warbler, LEFL: least flycatcher, SUTA: summer tanager, WOTH: wood thrush), with 95% credible intervals (black lines). The nine predictor variables include: latitude (decimal degrees), median elevation (m), mean May–June temperature (°C), difference between mean March–April temperature and mean May–June temperature (°C), mean total March–April precipitation (mm), mean total May–June precipitation (mm), and proportions of deciduous and mixed forest, conifer forest, and developed land. When making predictions of the effect sizes of each predictor variable, all other variables were held at their mean value. Predictor variables with bolded and colorful font have statistically significant slope coefficients (i.e., 95% credible intervals do not overlap 0). The color of the 4-letter species code and plot elements indicates the climate classification of that species (blue = cold-associated, red = warm-associated, orange = climate generalist)

lead to higher absolute differences, we also calculated a proportional difference for each covariate (Table S5), which is the absolute difference between the maximum and minimum mean expected species counts across all values of the individual predictor variable, divided by the maximum mean expected species count across all predictor variables.

Once we ascertained that all the negative binomial models exhibited good fit, we used them to predict contemporary (2000) and future (2100) species counts (under each of the four different future climate and land cover combination scenarios) within each cell of the hexagonal grid covering the study area. We then quantified three indices of changes: (1) differences in the total projected count of individuals across the entire study region; (2) differences in the total number of occupied hexagonal grid cells (i.e., for which the expected count was ≥ 1) across the entire study region; and (3) shifts (measured by distance and angle) in the spatial mean-center of count distributions between 2000 and 2100 for each species, which was determined by calculating the count-weighted mean latitude and longitude values. All predicted counts were assumed to be an index of abundance. Statistical significance of the changes in total projected counts and total number of occupied hexagonal grid cells were determined by whether the 95% CI of the distribution of differences between expected counts in 2000 and 2100 overlapped 0. Statistical significance of the shifts in count-weighted mean-center of the projected distributions was determined by whether 95% isopleths around the projected 2000 and 2100 count-weighted mean-centers from the posterior iterations overlapped.

Results

Model fit for each of the 14 focal forest songbird species ranged from 0.21 to 0.84, indicating good model fit for all species (Table 2). The number of important environmental predictor variables for each species ranged from 1 for Swainson's warbler (*Limnothlypis swainsonii*) to 8 for wood thrush (*Hylocichla mustelina*) (Table 2, Fig. S5). Latitude and elevation were included to account for their known effects on the focal forest songbird species during the breeding season and indeed, they were important for all species except Swainson's warbler (for which neither were important) and cerulean warbler (*Setophaga cerulea*) (for which only elevation was important), but hereafter, we focus on the relative importance and effects of the climate and land cover variables. All predictor variables of interest (i.e., climate or land cover variables) were important for at least one of the focal forest songbird species (Table 2).

Relative importance and effect sizes of climate vs. land cover variables

Overall, land cover variables were more frequently important for the focal species than climate variables. Across all 14 species, at least one climate variable was important for 11 species, and at least one land cover variable was important for 13 species (Table 2). Across all 14 species, the most frequently important predictor variable was proportion of deciduous and mixed forest (N = 10 species), followed by temperature difference (N = 8 species). In terms of the climate classifications, at least one climate variable was important for three of the five cold-associated species, three of the four warm-associated species, and all five climate generalist species, while at least one land cover variable was significant for four of the five cold-associated species, all four warm-associated species, and all five climate generalist species. There were no apparent trends in the importance of climate vs. land cover variables for the cold-associated species, but for the warm-associated species, the proportion of deciduous and mixed forest was important for all four species, and the two temperature variables

were important for three of the four species. Among the five climate generalist species, the proportion of deciduous and mixed forest and the proportion of developed land were each important for four species.

Corresponding to the greater relative importance of land cover variables, we also found that the land cover variables had greater effect sizes compared to climate variables. For each bird species, we calculated the absolute and proportional differences between the maximum and minimum mean expected counts corresponding to each covariate (Table S5) in order to compare the individual effect sizes of the climate and land cover variables on expected count (Fig. 2, Fig. S5) and aid in determining the relative influence of climate change and land cover change. Across all 14 species, changes in the proportion of conifer forest resulted in the greatest average absolute difference in mean expected count (primarily driven by its high modeled effect size on Swainson's warbler and blue-headed vireo [*Vireo solitarius*]), followed by changes in the proportion of developed land and the proportion of deciduous and mixed forest. Changes in the proportions of conifer forest, deciduous and mixed forest, and developed land also resulted in the three highest average proportional differences, respectively. The proportion of conifer forest had a significant negative effect on two warm-associated species and a positive effect on one cold-associated species. The proportion of deciduous and mixed forest had a significant positive effect on 10 focal species (Fig. 2, Fig. S5), whereas the proportion of developed land had a significant negative effect on five of the six species for which it was an important predictor variable.

Among the five cold-associated species, changes in the proportion of conifer forest had the greatest average effect (with generally positive relationships), followed by changes in the proportion of developed land (with generally negative relationships). For two cold-associated species (blue-headed vireo and least flycatcher [*Empidonax minimus*]), changes in mean May–June temperature had greater average effects than any of the other three climate variables, but the effects were uniformly low for the remaining cold-associated species. For the warm-associated species, changes in the proportion of conifer forest also had the highest magnitude effects (with generally negative relationships). However, the model for Swainson's warbler produced a relatively high estimate for maximum mean expected count across the gradient of proportion of conifer forest, which drove the influence patterns for the warm-associated species group; excluding Swainson's warbler, the highest average absolute and proportional changes in mean expected counts for the remaining three warm-associated species were associated with changes in the proportion of deciduous and mixed forest (with positive relationships). Of the four climate variables, mean May–June temperature and May–June precipitation had the greatest average effects on cerulean warbler and Kentucky warbler (*Geothlypis formosa*) but similar effects sizes for summer tanager (*Piranga rubra*) and Swainson's warbler. Among the five climate generalist species, changes in the proportion of deciduous and mixed forest resulted in the highest average difference in mean expected counts (with positive relationships). In addition, the four climate variables had the greatest average effects on the climate generalist species compared to the cold-associated and warm-associated species.

When comparing the mean effect sizes across the four climate variables vs. the mean effect sizes across the three land cover variables, the average effects of land cover changes on the mean expected count during the breeding season had higher magnitude overall (i.e., across all species), within the three climate classifications, and for all individual species (Table S5). Across all 14 species, the average absolute differences resulting from changes in land cover proportions were 7 (excluding Swainson's warbler) to 62 (including Swainson's warbler) times higher than the average absolute differences resulting from changes in the four climate variables. The average proportional differences varied by a magnitude of 4.6–5.2 times.

Projected climate and land cover differences in 2100

The four future climate and land cover combination scenarios varied slightly in predicted mean leaf-out period and bird breeding season temperatures and precipitation amounts in 2100 (Table S5). The difference in mean temperatures between the COOL and WARM scenarios was 3.7 °C in the leaf-out period and 3.1 °C in the bird breeding season, while the difference in mean precipitation amounts was 27 mm and 22 mm in the leaf-out period and bird breeding season, respectively. The differences between the AVG LOW and AVG HIGH scenarios were less pronounced. In all four future climate and land cover

combination scenarios, mean temperatures increased, mean total precipitation amounts stayed the same or increased, and the proportion of developed land increased from 2000 to 2100 (Table S5).

Total species counts from 2000 to 2100

Projections of each species' breeding distribution in 2000 using contemporary environmental data were largely consistent with the raw results from the BBS data (Fig. 3, Fig. S5). Spatial patterns during the breeding season were captured well for the five cold-associated species with trailing-edge populations in the central and southern Appalachian Mountains and the four most populous climate generalist species, but the model for the least common species, Swainson's warbler, uniformly predicted low counts across the study region (although the model fit was good).

There were statistically significant differences in the predicted total counts during the breeding season across the entire study region between 2000 and 2100 for seven species (Table 3). Among the climate classifications, warm-associated species as a group experienced the most consistent percent declines (mean: − 3.5%, 95% CI range: − 17.8–1.5%) across the four future scenarios and in each future scenario. However, the magnitude of the average percent decline in warm-associated species was largely driven by summer tanager, which was projected to significantly decline by an average of 12.1% (95% CI range: − 17.8—6.2%) across future climate and land cover combination scenarios from 2000 to 2100. The total counts for the other three warm-associated species remained relatively stable over time. Cold-associated species declined an average of 2.0% across the four future scenarios, but there was a high amount of variation in trends among the five species. Least flycatcher was the only species projected to consistently and significantly increase in total count by an average of 6.7–11.4% (95% CI range: 1.5–22.5%) from 2000 to 2100. In contrast, black-throated blue warbler (*Setophaga caerulescens*) and veery (*Catharus fuscescens*) were projected to decline by an average of 9.5% (95% CI range: − 25.8–3.9%) and 8.1% (95% CI range: − 41.3–21.7%), respectively, from 2000 to 2100 across the four future scenarios (although their changes in expected total count were not statistically significant). Meanwhile, the trends for blue-headed vireo and Canada warbler (*Cardellina canadensis*) depended on the future scenario; for instance, Canada warbler total counts were projected to remain relatively stable in the COOL and AVG LOW scenarios but decline by an average of 5.8% (95% CI range: − 37.3–43.6%) in the AVG HIGH and WARM scenarios. For both of the warmest scenarios, three of the five cold-associated species were projected to decrease in total count from 2000 to 2100. Projections for climate generalist species, both as a group and individually, were relatively stable across all four future scenarios, with an average change of − 0.16% (95% CI range: − 2.8–1.7%) across all five species and four future scenarios.

Among the cold-associated species, three of the five species showed a similar regional pattern of changes in expected species counts during the breeding season across the study region (Fig. 4, Fig. significantly decline by an avera). For black-throated blue warbler, blue-headed vireo, and least flycatcher, the steepest declines were concentrated in the southern portion of their range and the highest increases were concentrated in the northern portion of their range. There did not appear to be a consistent regional trend for the warm-associated species, but three of the five climate generalist species (scarlet tanager [*Piranga olivacea*], red-eyed vireo [*Vireo olivaceus*], and wood thrush) exhibited a distinct pattern of declines along the edges of the southern half of their ranges, particularly the southeastern edge.

Species occurrence and spatial distributions from 2000 to 2100

There were no statistically significant differences for any species regarding the total number of occupied hexagonal grid cells during the breeding season across the entire study region between time periods (Table 4). In addition, no consistent trends in this metric emerged among the three climate classifications. The largest expansion (an average 6.5% gain [95% CI range: − 1.6–25.0%] across the four future scenarios) was projected for black-throated blue warbler, but the other four cold-associated species showed either no net change in range or a net gain / loss of only one hexagonal grid cell. The most contraction (an average of − 2.9% loss [95% CI range: − 9.8–2.5%] across the four future scenarios) was projected for summer tanager. For the remaining warm-associated species and four of the five climate generalist species, the

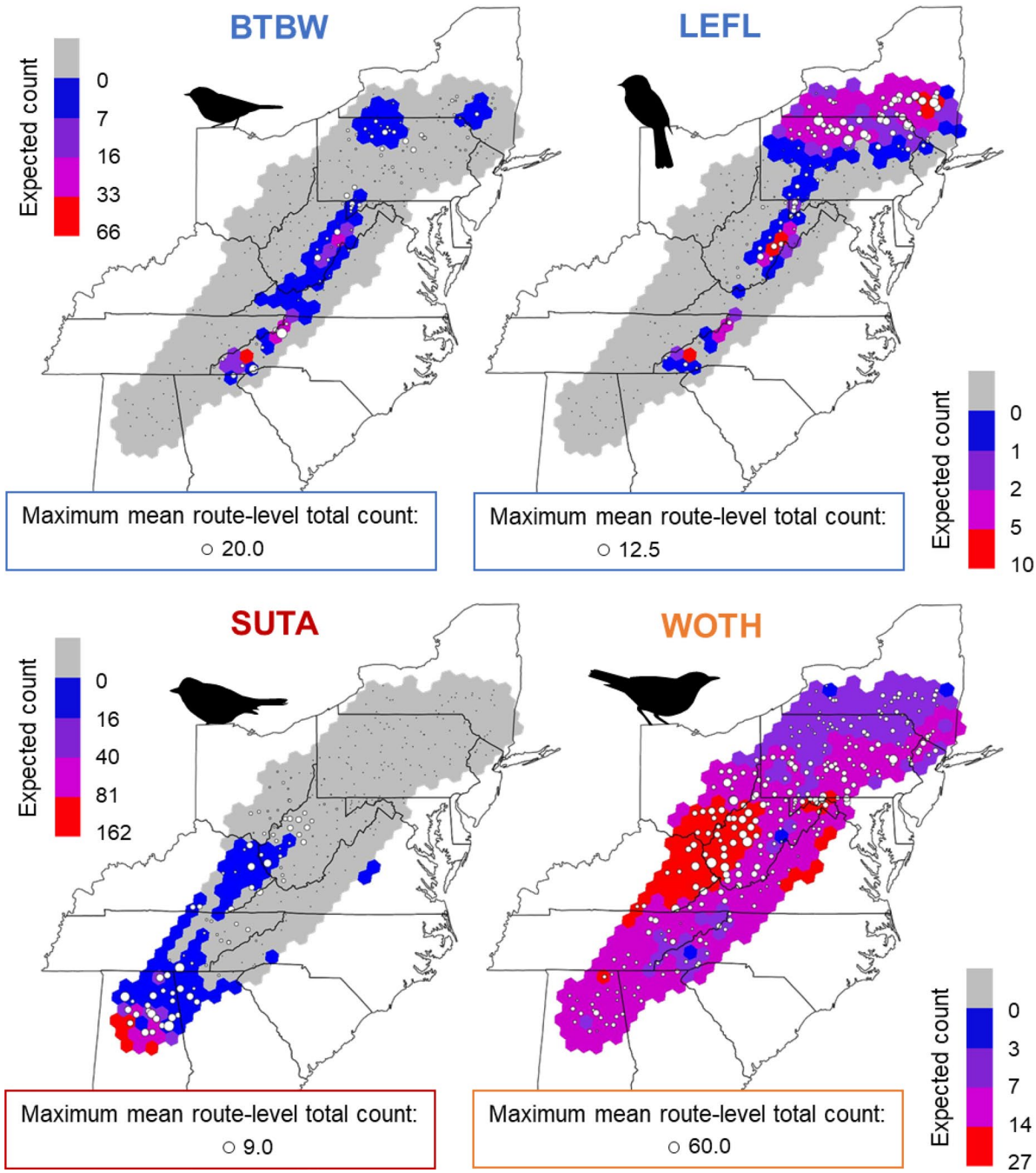


Fig. 3 Maps of the projected contemporary (2000) distribution across the study region for 4 of the 14 focal forest songbird species (BTBW: black-throated blue warbler, LEFL: least flycatcher, SUTA: summer tanager, WOTH: wood thrush), overlaid with white circles representing the 322 North American Breeding Bird Survey routes. The color of each hexagonal grid cell reflects the expected count from the model corresponding to each species (see Table 2 for model details), and the size of the white circles reflect the mean route-level total counts across years, with the maximum value presented for each species. The color of the 4-letter species code and Fig. elements indicates the climate classification of that species (blue = cold-associated, red = warm-associated, orange = climate generalist)

Table 3 Mean and 95% credible intervals (CI) of the projected total count ("Count") for each of the cold-associated (N = 5), warm-associated (N = 4), and climate generalist (N = 5) species (see Table 1 for species codes) across the entire study region in 2000 and 2100, based on the four future climate and land cover combination scenarios (COOL: CCSM-4.5 RCP, AVG LOW: average of lower emissions, AVG HIGH: average of higher emissions, and WARM: GFDL-8.5 RCP), as well as the mean and 95% CI for percent change ("%") from 2000 to 2100. Bolded text indicates a statistically significant (i.e., the 95% CI does not overlap 0) difference between years

Species	Metric	2000	COOL		AVG LOW		AVG HIGH		WARM	
		Count	*Count*	*%*	*Count*	*%*	*Count*	*%*	*Count*	*%*
BTBW	*Mean*	471	416	− 9.2	417	− 8.8	410	− 9.7	408	− 10.1
	95% CI	(69, 1587)	(68, 1333)	(− 19.6, 1.0)	(68, 1336)	(− 19.0, 1.3)	(68, 1587)	(− 25.7, 3.9)	(68, 1280)	(− 25.8, 3.0)
BHVI	*Mean*	711	696	− 1.9	695	− 2.0	762	**+6.8**	736	+3.3
	95% CI	(388, 1241)	(384, 1202)	(− 5.5, 1.1)	(385, 1196)	(− 5.3, 0.6)	(408, 1356)	**(1.6, 13.7)**	(399, 1295)	(− 1.4, 9.1)
CAWA	*Mean*	2048	2071	+1.4	2072	+0.8	1855	− 6.1	1891	− 5.4
	95% CI	(47, 16,556)	(47, 15,605)	(− 15.8, 26.3)	(47, 15,617)	(− 15.7, 27.0)	(46, 12,740)	(− 37.3, 39.7)	(46, 13,203)	(− 36.0, 43.6)
LEFL	*Mean*	348	374	**+6.7**	375	**+7.2**	379	**+8.2**	391	**+11.4**
	95% CI	(119, 720)	(122, 807)	**(1.5, 13.5)**	(123, 811)	**(2.4, 13.8)**	(124, 831)	**(2.1, 17.9)**	(127, 854)	**(4.2, 22.5)**
VEER	*Mean*	1179	1015	− 10.7	1014	− 10.5	1098	− 5.7	1100	− 5.3
	95% CI	(335, 3880)	(329, 3312)	(− 41.0, 2.8)	(331, 3286)	(− 41.3, 2.8)	(337, 3951)	(− 39.3, 21.7)	(339, 3938)	(− 38.8, 20.8)
CERW	*Mean*	72	71	− 1.0	71	− 0.6	71	− 0.3	72	− 0.1
	95% CI	(66, 82)	(66, 81)	(− 2.7, 0.0)	(66, 82)	(− 1.5, 0.0)	(66, 82)	(− 1.4, 1.4)	(66, 82)	(− 1.4, 1.5)
KEWA	*Mean*	110	108	**− 1.5**	108	**− 1.8**	109	**− 0.8**	109	**− 1.1**
	95% CI	(93, 135)	(92, 132)	**(− 3.1, 0.0)**	(92, 132)	**(− 2.9, − 0.9)**	(92, 134)	**(− 1.8, 0.0)**	(92, 134)	**(− 2.5, 0.0)**
SUTA	*Mean*	1393	1206	**− 13.0**	1244	**− 10.3**	1189	**− 14.2**	1236	**− 10.9**
	95% CI	(579, 3074)	(517, 2641)	**(− 17.7, − 8.4)**	(533, 2718)	**(− 14.5, − 6.2)**	(513, 2581)	**(− 17.8, − 10.6)**	(530, 2685)	**(− 14.7, − 7.1)**
SWWA	*Mean*	1	1	0.0	1	0.0	1	0.0	1	0.0
	95% CI	(1, 2)	(1, 2)	(0.0, 0.0)	(1, 2)	(0.0, 0.0)	(1, 2)	(0.0, 0.0)	(1, 2)	(0.0, 0.0)
EAWP	*Mean*	1194	1195	0.0	1194	− 0.1	1194	0.0	1192	− 0.2
	95% CI	(1166, 1231)	(1166, 1231)	(− 0.1, 0.2)	(1165, 1229)	(− 0.2, 0.1)	(1166, 1230)	(− 0.2, 0.2)	(1164, 1227)	(− 0.4, 0.1)
REVI	*Mean*	8057	8057	0.0	8057	0.0	8057	0.0	8059	0.0
	95% CI	(7900, 8259)	(7898, 8260)	(− 0.1, 0.1)	(7898, 8261)	(0.0, 0.1)	(7898, 8258)	(− 0.1, 0.0)	(7899, 8264)	(− 0.1, 0.1)
SCTA	*Mean*	1839	1838	0.0	1837	− 0.1	1837	− 0.1	1833	**− 0.3**
	95% CI	(1782, 1911)	(1781, 1910)	(− 0.2, 0.1)	(1782, 1909)	(− 0.2, 0.0)	(1782, 1909)	(− 0.2, 0.0)	(1780, 1902)	**(− 0.6, 0.0)**
WEWA	*Mean*	197	198	+0.5	197	− 0.1	197	− 0.3	195	**− 1.4**
	95% CI	(164, 250)	(165, 252)	(− 0.5, 1.7)	(164, 250)	(− 0.8, 0.6)	(164, 249)	(− 1.0, 0.5)	(163, 246)	**(− 2.8, 0.0)**
WOTH	*Mean*	3550	3551	0.0	3541	**− 0.2**	3544	**− 0.1**	3525	**− 0.7**
	95% CI	(3449, 3670)	(3449, 3671)	(− 0.1, 0.2)	(3443, 3659)	**(− 0.4, − 0.1)**	(3445, 3663)	**(− 0.3, 0.0)**	(3430, 3640)	**(− 1.0, − 0.4)**

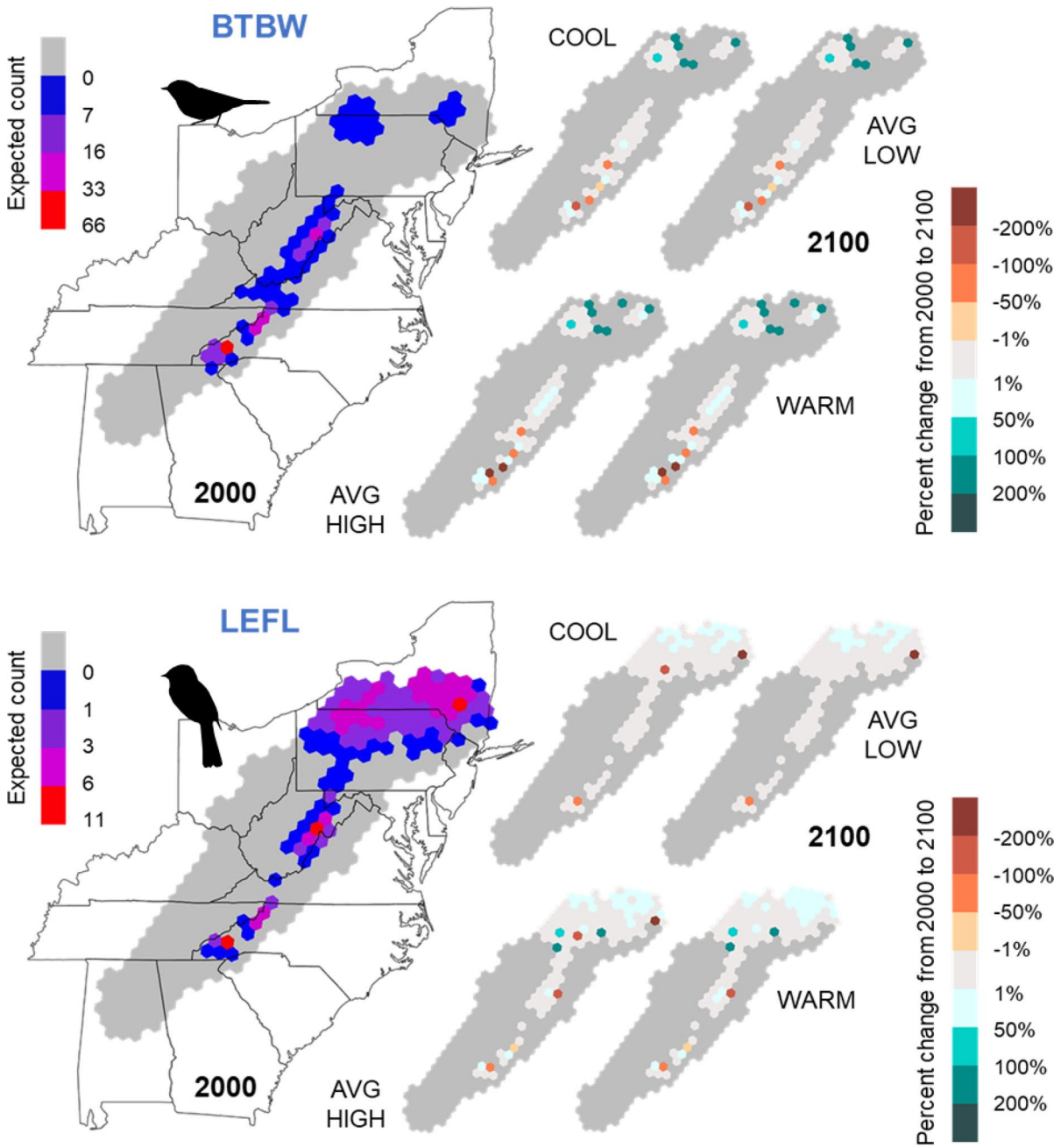


Fig. 4 Maps of the percent differences in projected contemporary (2000) and future (2100) distributions across the study region for 4 of the 14 focal forest songbird species (BTBW: black-throated blue warbler, LEFL: least flycatcher, SUTA: summer tanager, WOTH: wood thrush). Future distributions were modeled based on four future climate and land cover combination scenarios, the coolest (COOL) and warmest (WARM) scenarios and the average low (AVG LOW) and average high (AVG HIGH) emission scenarios. The color of each hexagonal grid cell reflects the expected count in 2000 on the left and the percent changes in the expected counts from 2000 and 2100 on the right. The color of the 4-letter species code indicates the climate classification of that species (blue = cold-associated, red = warm-associated, orange = climate generalist)

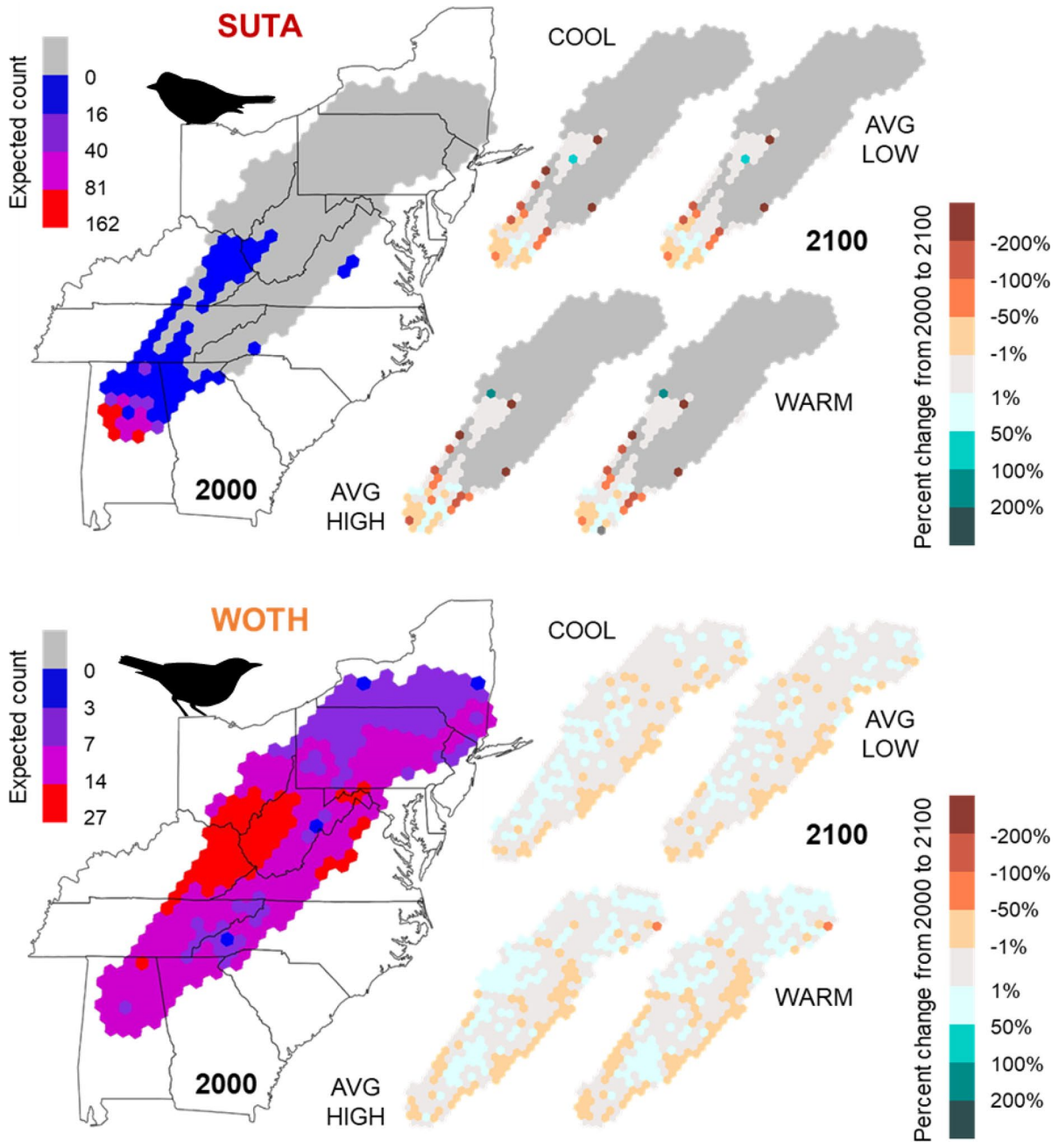


Fig. 4 (continued)

total number of occupied hexagonal grid cells did not change at all.

There were also no statistically significant shifts in the count-weighted mean-center of the projected species distributions during the breeding season from 2000 to 2100 (Table 5). However, there were a few notable trends when comparing among the climate classifications. Cold-associated species as a group had the greatest shift distances (mean: 39 km, 95% CI range: 1–381 km) across the four future scenarios), with consistent movement in the northeastern or northern direction for four of the five species. In

Table 4 Mean and 95% credible intervals (CI) of the total number of occupied hexagonal grid cells (i.e., where projected species count ≥ 1; "Cells") for each of the cold-associated (N = 5), warm-associated (N = 4), and climate generalist (N = 5) species (see Table 1 for species codes) across the entire study region in 2000 and 2100, based on the four future climate and land cover combination scenarios (COOL: CCSM-4.5 RCP, AVG LOW: average of lower emissions, AVG HIGH: average of higher emissions, and WARM: GFDL-8.5 RCP), as well as the mean and 95% CI for percent change from 2000 to 2100 ("%"). There were no statistically significant differences between years

Species	Metric	2000	COOL		AVG LOW		AVG HIGH		WARM	
		Cells	*Cells*	*%*	*Cells*	*%*	*Cells*	*%*	*Cells*	*%*
BTBW	*Mean*	55	57	5.9	58	6.6	58	6.4	58	6.9
	95% CI	(22, 86)	(23, 86)	(− 1.6, 20.6)	(23, 87)	(− 1.3, 22.9)	(23, 86)	(− 3.1, 23.1)	(23, 86)	(− 2.9, 25.0)
BHVI	*Mean*	142	142	0.1	142	0.4	143	0.9	143	1.1
	95% CI	(132, 152)	(132, 152)	(− 2.8, 3.4)	(133, 152)	(− 2.8, 3.6)	(132, 154)	(− 2.8, 4.4)	(133, 154)	(− 2.7, 5.0)
CAWA	*Mean*	75	76	0.3	76	0.1	74	− 1.6	74	− 1.7
	95% CI	(20, 120)	(19, 123)	(− 11.4, 7.6)	(19, 123)	(− 12.2, 7.4)	(19, 121)	(− 14.3, 6.2)	(19, 121)	(− 15.9, 6.9)
LEFL	*Mean*	108	108	0.6	108	0.8	108	0.7	108	1.1
	95% CI	(76, 127)	(78, 128)	(− 2.6, 4.9)	(78, 128)	(− 2.4, 5.1)	(78, 128)	(− 3.3, 5.6)	(79, 128)	(− 3.2, 6.5)
VEER	*Mean*	135	134	− 1.0	134	− 0.6	134	− 0.5	134	− 0.4
	95% CI	(119, 151)	(116, 151)	(− 4.0, 1.7)	(117, 152)	(− 3.3, 2.1)	(117, 151)	(− 3.7, 2.1)	(117, 151)	(− 3.3, 2.4)
CERW	*Mean*	2	2	− 6.3	2	− 5.3	2	− 1.9	2	0.3
	95% CI	(0, 21)	(0, 16)	(− 100.0, 40.1)	(0, 19)	(− 100.0, 11.1)	(0, 20)	(− 100.0, 66.7)	(0, 21)	(− 80.5, 66.7)
KEWA	*Mean*	63	63	− 0.6	63	− 1.2	63	− 0.5	63	− 1.0
	95% CI	(45, 86)	(45, 84)	(− 6.7, 5.6)	(44, 85)	(− 6.7, 3.4)	(45, 85)	(− 4.9, 4.4)	(45, 85)	(− 5.8, 3.4)
SUTA	*Mean*	80	78	− 2.8	78	− 2.3	77	− 3.4	78	− 2.9
	95% CI	(67, 93)	(66, 89)	(− 7.0, 1.3)	(67, 90)	(− 6.3, 1.4)	(64, 89)	(− 9.8, 1.4)	(64, 89)	(− 9.1, 2.5)
SWWA	*Mean*	0	0	0.0	0	0.0	0	0.0	0	0.0
	95% CI	(0, 0)	(0, 0)	(0.0, 0.0)	(0, 0)	(0.0, 0.0)	(0, 0)	(0.0, 0.0)	(0, 0)	(0.0, 0.0)
EAWP	*Mean*	346	346	0.0	346	0.0	346	0.0	346	0.0
	95% CI	(344, 346)	(344, 346)	(0.0, 0.0)	(344, 346)	(0.0, 0.0)	(344, 346)	(0.0, 0.0)	(344, 346)	(0.0, 0.0)
REVI	*Mean*	346	346	0.0	346	0.0	346	0.0	346	0.0
	95% CI	(346, 346)	(346, 346)	(0.0, 0.0)	(346, 346)	(0.0, 0.0)	(346, 346)	(0.0, 0.0)	(346, 346)	(0.0, 0.0)
SCTA	*Mean*	346	346	0.0	346	0.0	346	0.0	346	0.0
	95% CI	(344, 346)	(344, 346)	(0.0, 0.0)	(344, 346)	(0.0, 0.0)	(344, 346)	(0.0, 0.0)	(344, 346)	(0.0, 0.0)
WEWA	*Mean*	154	153	− 0.9	153	− 0.9	153	− 0.5	151	− 2.0
	95% CI	(116, 186)	(115, 184)	(− 4.1, 1.8)	(115, 184)	(− 3.4, 1.2)	(116, 185)	(− 3.2, 1.9)	(113, 183)	(− 6.3, 1.2)
WOTH	*Mean*	346	346	0.0	346	0.0	346	0.0	346	0.0
	95% CI	(346, 346)	(346, 346)	(0.0, 0.0)	(346, 346)	(0.0, 0.0)	(346, 346)	(0.0, 0.0)	(346, 346)	(0.0, 0.0)

Table 5 Mean and 95% credible intervals (CI) of the distance ("Km") in kilometers and angle (consisting of the degree, where 0 is directly east and 90 is directly north, and corresponding cardinal direction) of the shift in count-weighted mean-center of the projected distribution for each of the cold-associated (N = 5), warm-associated (N = 4), and climate generalist (N = 5) species (see Table 1 for species codes) from 2000 to 2100, based on the four future climate and land cover combination scenarios (COOL: CCSM-4.5 RCP, AVG LOW: average of lower emissions, AVG HIGH: average of higher emissions, and WARM: GFDL-8.5 RCP). There were no statistically significant differences between years

Species	Metric	COOL		AVG LOW		AVG HIGH		WARM	
		Km	Angle	Km	Angle	Km	Angle	Km	Angle
BTBW	*Mean*	37	46 (NE)	38	45 (NE)	46	46 (NE)	47	46 (NE)
	95% CI	(19, 57)	(43, 47)	(20, 58)	(43, 47)	(21, 66)	(42, 50)	(22, 68)	(43, 49)
BHVI	*Mean*	7	61 (NNE)	9	54 (NE)	6	84 (N)	9	64 (NNE)
	95% CI	(1, 14)	(46, 201)	(1, 16)	(46, 80)	(1, 12)	(45, 226)	(1, 17)	(42, 226)
CAWA	*Mean*	22	157 (WNW)	23	164 (WNW)	36	112 (NNW)	37	119 (NNW)
	95% CI	(1, 72)	(22, 286)	(1, 76)	(23, 295)	(2, 109)	(40, 227)	(2, 116)	(35, 239)
LEFL	*Mean*	23	41 (NE)	21	42 (NE)	26	39 (NE)	29	35 (NE)
	95% CI	(11, 43)	(36, 45)	(9, 41)	(38, 46)	(12, 50)	(29, 47)	(10, 54)	(23, 42)
VEER	*Mean*	69	205 (WSW)	69	205 (WSW)	120	213 (WSW)	112	212 (WSW)
	95% CI	(4, 236)	(157, 223)	(4, 236)	(159, 224)	(10, 381)	(194, 223)	(5, 371)	(188, 225)
CERW	*Mean*	15	30 (ENE)	6	33 (ENE)	7	30 (ENE)	6	118 (NNW)
	95% CI	(4, 27)	(22, 40)	(2, 11)	(6, 331)	(2, 13)	(15, 51)	(2, 15)	(2, 358)
KEWA	*Mean*	7	56 (NE)	7	40 (NE)	3	78 (NNE)	4	98 (N)
	95% CI	(2, 16)	(32, 151)	(3, 12)	(30, 51)	(1, 6)	(32, 166)	(1, 10)	(2, 357)
SUTA	*Mean*	7	20 (ENE)	6	21 (ENE)	8	26 (ENE)	7	51 (NE)
	95% CI	(5, 9)	(9, 30)	(4, 8)	(11, 30)	(6, 10)	(2, 357)	(4, 9)	(1, 359)
SWWA	*Mean*	11	111 (NNW)	8	103 (NNW)	9	83 (N)	25	63 (NNE)
	95% CI	(1, 32)	(6, 350)	(1, 27)	(14, 335)	(1, 26)	(16, 216)	(2, 75)	(32, 216)
EAWP	*Mean*	3	195 (WSW)	1	98 (N)	2	178 (W)	1	117 (NNW)
	95% CI	(1, 6)	(144, 206)	(0, 2)	(44, 198)	(1, 3)	(137, 199)	(0, 3)	(6, 355)
REVI	*Mean*	1	208 (WSW)	1	214 (SW)	1	219 (SW)	3	219 (SW)
	95% CI	(0, 3)	(201, 222)	(0, 2)	(199, 223)	(1, 2)	(200, 240)	(1, 5)	(210, 225)
SCTA	*Mean*	2	203 (WSW)	1	69 (NNE)	1	126 (NW)	3	54 (NE)
	95% CI	(0, 4)	(18, 277)	(0, 2)	(45, 145)	(0, 2)	(58, 181)	(1, 5)	(46, 72)
WEWA	*Mean*	5	209 (WSW)	2	168 (WNW)	2	131 (NW)	4	71 (NNE)
	95% CI	(1, 13)	(7, 1349)	(0, 5)	(22, 313)	(1, 5)	(25, 197)	(1, 12)	(37, 186)
WOTH	*Mean*	3	195 (WSW)	3	46 (NE)	1	128 (NW)	5	35 (NE)
	95% CI	(1, 5)	(177, 202)	(2, 4)	(42, 51)	(1, 2)	(79, 164)	(3, 7)	(30, 39)

addition, higher emissions scenarios (AVG HIGH and WARM) resulted in larger projected shift distances compared to the lower emissions scenarios (COOL and AVG LOW) for four of the five cold-associated species. Warm-associated species had an average shift distance of 9 km (95% CI range: 1–75 km) in a northeastern or northern direction across the four future scenarios. Climate generalist species had the lowest average shift distance of 2 km (95% CI range: 0–13 km) across the four future scenarios.

Discussion

Here, we conducted a study to explore the potential effects of both climate and land cover change on forest songbirds of the Appalachian Mountains during the breeding season. We first quantified the relative influence of climate change vs. land cover change on the breeding distributions and abundance of 14 forest songbirds. We then explored differences between their contemporary and future breeding distributions, using

four projections of climate and land cover conditions in 2100. At a broad spatiotemporal scale, the net projected impact of climate change on forest songbirds within the Appalachian Mountains during the breeding season was modest. Based on the importance and effect sizes of land cover variables in this study, land use changes that result in reduced forest cover and increased urban cover may pose a more immediate and proximate threat than climate change to forest songbirds that breed in this region. Thus, conservation efforts for forest songbirds during the breeding season might be better focused on landscape-scale strategies to maintain and manage mature forest habitat rather than implementing climate change adaptation strategies for individual species.

Looking towards the future, the magnitude and direction of differences between breeding distributions projected in 2000 vs. 2100 varied by species, but there were some consistent trends within the climate classifications. As a group, cold-associated species were projected to experience slight declines in relative abundance during the breeding season, with the steepest declines concentrated in the southern portion of their ranges within the AMBCR (Fig. 4, Fig. S8), coinciding with areas where the proportion of urban cover was expected to increase and the proportion of deciduous and mixed forests was expected to decrease (Fig. S2). Correspondingly, the mean-center of projected distributions for cold-associated species shifted the greatest average distance from 2000 to 2100; although not statistically significant, movements were somewhat consistently in the northeastern and northern direction. Another study projecting future relative abundance of bird species in eastern North America also predicted shifts in a north-northeast direction (Matthews et al. 2011). Meanwhile, the relative abundance and ranges for warm-associated species during the breeding season either declined or remained similar in the future, with limited (and non-significant) distribution shifts in the northeastern or northern direction. Climate generalist species appeared to be least affected by future climate and land cover changes; there was little to no change in overall projected relative abundance or range, and very little to no shifts in their distribution; however, there was a distinct regional pattern of declining relative abundance during the breeding season along the edges of the southern half of their ranges within the AMBCR, again aligning with areas with projected increases in the proportion of urban cover and decreases in the proportion of deciduous and mixed forests (Fig. S2).

Considering the overall results and comparing the projected relative abundance, regional occupancy, and shifts in the distribution of relative abundance of the 14 focal forest songbird species during the breeding season in 2000 vs. 2100, we noted that most species experienced limited changes within the AMBCR. Thus, at a broad scale, the findings from this study indicate that changes in mean temperatures and total precipitation during the leaf-out period of woody vegetation and bird breeding season, along with land cover change, may not greatly impact the distribution and relative abundance of breeding forest songbirds within the Appalachian Mountains region over the next 80 years. The minimal to modest responses of the 14 focal bird species to future changes in climate and land cover may be explained by the contemporary comparative range of conditions experienced across the entire study region relative to the projected differences in those conditions in the future. Across the AMBCR, mean breeding season temperatures ranged 12.7 °C, from 13.6 °C to 23.4 °C in 2000, with the lowest temperatures in the north or at high elevations and the highest temperatures in the south at low elevations (Fig. S1). Meanwhile, under the warmest scenario, the maximum mean breeding season temperature in 2100 was 28.5 °C and the maximum increase in mean breeding season temperatures in any given area within the AMBCR from 2000 to 2100 was 6.7 °C (Table S2). Thus, there was a rise in absolute temperature, but for many locations within the AMBCR, any increase was likely within the contemporary temperature range of most of the species, particularly those with larger latitudinal gradients. In fact, for all temperature, precipitation, and land cover metrics considered in this study, the maximum absolute value in 2100 may have increased from 2000, but the maximum difference in that value in 2000 vs. 2100 in any given area within the AMBCR was always less than the regionwide range of values (Table S2). It seems probable that most changes in these metrics in 2100 across the study region were still within a tolerable range for the focal forest songbird species, whose relatively large geographic distributions suggest correspondingly wide climatic niches (Barnagaud et al. 2012; Jarzyna et al. 2015, 2016) and tolerance for thermal stress (Jiguet et al. 2006).

In addition, forests and montane regions may have the capacity to buffer the impacts of climate warming compared to open habitat or lowlands. Multiple studies have found that forest bird species are affected less by climate change than open habitat species (e.g., Chamberlain et al. 2013; Jarzyna et al. 2016), and there is some evidence that old growth forests have the capacity to buffer the negative effects of climate change for bird species that are sensitive to temperature increases (Frey et al. 2016; Betts et al. 2018; De Frenne et al. 2019). Trees intercept solar radiation and reduce direct sunlight below the canopy (De Frenne et al. 2021); therefore, thermal conditions beneath forest canopies are typically less extreme than those in open habitats (Suggitt et al. 2011; Betts et al. 2018), and canopy cover is associated with warmer minimum and cooler maximum temperatures (Gilbert et al. 2022). Dense forest canopies may moderate the impact of macroclimate warming by facilitating cooler microclimatic conditions during the summer (Suggitt et al. 2011; De Frenne et al. 2013, 2019, 2021). In fact, surface temperatures in the spring and summer decline as the proportion of forest increases, especially in landscapes with spatially extensive forests (Wickham et al. 2013). Specifically, old growth forests in montane regions appear to have a strong, thermally insulating (i.e., cooling) effect on under-canopy air temperatures during the avian breeding season (Frey et al. 2016). Thus, the expansive mature forests of the Appalachian Mountains may provide microclimates that are uncoupled from regional thermal regimes and thus exert a modulating effect from changing climatic conditions in the future (Jarzyna et al. 2016; Betts et al. 2018; De Frenne et al. 2019). In addition, the forest habitats in the Appalachian Mountains are comprised of tree species with relatively long average life spans; with this inherent inertia, or lag in how quickly they will respond to changing climatic conditions, the long-lived nature of these forests may additionally enable them to serve as a buffer for species under rapid climate changes in the future (Duclos et al. 2019). A further element to consider is the elevational gradient of the Appalachian Mountains, since cooler temperatures at higher elevations may allow species to track their climatic niches by moving upslope (Tingley et al. 2012; Freeman et al. 2018). Certain regions within mountain ranges can provide climate refugia for cold-associated bird species in the future (Stralberg et al. 2015; Brambilla et al. 2022). Sites identified as climate refugia are likely to preserve suitable ecological conditions and thus allow the persistence of species and habitats at risk from climate change (Morelli et al. 2020). Indeed, regions within the Appalachian Mountains have been identified by Stralberg et al. (2018) as prime locations for microrefugia for songbirds in the eastern United States. However, the potential for AMBCR forests to moderate the effects of rising temperatures in the future hinges on maintaining extensive forest cover within the region.

Our study reinforces how critical it is to investigate the long-term potential effects of global climate change and land cover change simultaneously on bird distributions and abundance. Based on variable importance and their effect sizes on expected species counts, both climate and land cover covariates were important in shaping forest songbird distributions during the breeding season. However, the proportions of land cover types tended to be more influential and had higher effect sizes than temperature or precipitation amounts across all species and across the three climate classifications. The higher relative influence of land cover change on breeding season abundance was mostly driven by the importance of the proportion of deciduous and mixed forest to most of the focal forest songbird species, which highlights the need to maintain mature forest cover in the landscape. In support of our findings regarding the relative influence of climate vs. land cover metrics, there is evidence for strong effects of land cover change on avian species richness, abundance, and population trends (Eglington and Pearce-Higgins 2012; Rittenhouse et al. 2012). Other studies that also used North American Breeding Bird Survey data have consistently found that land cover variables influence distributions and impact population dynamics of forest songbird species (LeBrun et al. 2017; Betts et al. 2019; Northrup et al. 2019).

In addition, among the four future climate and land cover combination scenarios, there were differences in the effect size between the two low greenhouse gas emissions scenarios (COOL and AVG LOW) compared to the two high greenhouse gas emissions scenarios (AVG HIGH and WARM). For most species, regardless of climate classification, changes in relative abundance and overall range during the breeding season from 2000 to 2100 tended to have higher magnitude under the high emissions

scenarios, and the shift distances projected for the high emissions scenarios tended to be greater than those for the low emissions scenarios. These findings are consistent with previous research efforts and predictions, which indicate that higher greenhouse gas emissions scenarios could elicit stronger forest bird responses and result in larger changes in distributions, greater losses in bird species richness, and more species with declining ranges and declining incidence within the Appalachian Mountains (Matthews et al. 2004; Rodenhouse et al. 2008; Ralston and Kirchman 2013). Importantly, the loss of forest cover and the expansion of developed land is expected to be more severe and widespread within the AMBCR under a high emissions scenario, with particularly large reductions in forest projected along the eastern edge of the region and adjacent to large metropolitan cities (Fig. S2). Concerted efforts to lower greenhouse gas emissions and maintain forest cover into the future may mediate the negative impacts projected by our models and benefit long-term avian conservation in this region. Alternatively, if future changes are more pronounced than what was projected under the WARM scenario, then the impact of climate and land cover change may be correspondingly greater than expected from our model predictions.

We acknowledge certain limitations to this study that contextualize our findings. Like many other studies that cover such a large geographic region within the United States, we used count data from the North American Breeding Bird Survey, which has known biases due to its roadside methods (Keller and Scallan 1999; Betts et al. 2007; Harris and Haskell 2007) and serves as an index of abundance rather than true abundance. It is also important to note that our model projections make the same assumptions as any other species distribution model (Heikkinen et al. 2006): (1) historical predictor–response relationships remain constant through time; (2) the predictors used are comprehensive and ecologically relevant to birds; (3) the models of bird–habitat associations are able to capture the distribution of a species rather than spurious spatial associations; and (4) biotic interactions with other species do not change the outcomes. Furthermore, we emphasize that our study was conducted at broad spatiotemporal scales and assumed that bird species counts from the linear Breeding Bird Survey routes were systematically related to the environmental data compiled within the sampling hexagons.

There were multiple sources of uncertainty involved in our modeling approach. Although we attempted to reduce bias from any given year or individual grid cell by averaging the future climate conditions over time and space, forecasting to the end of the century still introduces uncertainty into the future estimates of climate and land cover change. We did not directly account for that source of uncertainty within the models, which can lead to artificial precision and limit interpretation of the results; however, we did incorporate assessments of uncertainty by calculating 95% credible intervals for the relationships with the predictor variables and the differences between mean projections of bird species relative abundance in 2000 and 2100. There was also uncertainty introduced by extrapolating the results of our models to predict future scenarios in which certain metrics exceeded the values used to fit the models. It is possible that thresholds could exist or complex nonlinear relationships could manifest beyond the range of data that we used to parameterize species responses to predictor variables. A potential solution could be to supplement the data by sampling from areas outside the AMBCR, but this approach poses its own complications. For the cold-associated species, our study area already encapsulates their southernmost range limits, and for warm-associated and climate generalist species, expanding beyond the AMBCR introduces novel forest types and other environmental factors associated with distinct ecosystems of the southeastern United States. Ultimately, it is important to remember that all organisms have limits in their tolerance of habitat conditions. It is possible that future temperature, precipitation, or land cover conditions may surpass biological thresholds and cause avian responses to deviate from our predictions, particularly if climate and land cover change are accelerated or exceed the conditions associated with the climate projection models and future scenarios used in our study.

Certain elements of this study would benefit from further investigation. Our analyses were focused solely on the effects of mean temperatures and total precipitation during the woody vegetation leaf-out period and the bird breeding season on relative species abundance during the latter period. However, previous research has documented significant effects on bird populations from additional climate metrics and habitat factors (e.g., Matthews et al. 2011; Illán

et al. 2014), as well as from different periods of a bird's annual life cycle, including the non-breeding season (Bateman et al. 2020). We also assumed that latitude and elevation were serving as proxies of habitat conditions, such as specific forest types or tree assemblages, and we did not model changes in those metrics over time. Looking forward, future studies could build on our efforts by taking a more comprehensive or finer-scale approach that incorporates a different set of climate metrics that reflect more acute stressful conditions (e.g.,Taff and Shipley 2023; Chen and Khanna 2024), local habitat factors that may modify the responses of habitat specialists (Matthews et al. 2011), indirect effects of climate on forest habitat (Duclos et al. 2019; Ceresa et al. 2021), and/or carryover effects from the non-breeding season (Rushing et al. 2020; Cooper et al. 2024).

Conclusions and implications for conservation

Efforts to develop effective conservation plans and plan management actions benefit from knowledge of predicted climate and land cover changes, the role of additive and interacting factors, and how those changes could affect species at multiple spatiotemporal scales. This study serves as an example of a broad-scale analysis addressing these research needs for forest songbirds breeding in a heavily forested montane system. We found that the impact of projected climate change during the woody vegetation leaf-out period and bird breeding season was modest and may be mediated in the Appalachian Mountains by their mature forests and elevational gradient, which potentially buffer the impacts of climate warming for forest songbird species during the breeding season. Considering the greater relative importance and higher effect sizes of land cover change on the breeding distributions and abundance of the focal species, it may be prudent for forest songbird conservation efforts in the Appalachian Mountains and potentially other montane regions to incorporate prioritizing, preserving, and promoting extensive forest habitat to mitigate impacts from land use change.

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Author contributions H.L.C., C.T. R., and P.B.W. contributed to the study conception and design. Data compilation and/or curation was performed by H.L.C., S.N.M., and M.P.P., while C.T. R. helped to develop the methodology for statistical analyses. H.L.C. analyzed the data, wrote the main manuscript text, and prepared the figures and tables. All authors reviewed the final manuscript.

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Data availability North American Breeding Bird Survey data are freely available from the U.S. Geological Survey at https://www.sciencebase.gov/catalog/item/52b1dfa8e4b0d9b325230cd9. Climate data are freely available from the PRISM Climate Group at https://prism.oregonstate.edu/. National Land Cover Database data are freely available from the Multi-Resolution Land Characteristics Consortium at https://www.mrlc.gov/data. Additional datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing Interest The authors have no relevant financial or non-financial interests to disclose.

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