

Assessing the sensitivity of avian species abundance to land cover and climate

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Abstract. Climate projections for the Midwestern United States predict southerly climates to shift northward. These shifts in climate could alter distributions of species across North America through changes in climate (i.e., temperature and precipitation), or through climate-induced changes on land cover. Our objective was to determine the relative impacts of land cover and climate on the abundance of five bird species in the Central United States that have habitat requirements ranging from grassland and shrubland to forest. We substituted space for time to examine potential impacts of a changing climate by assessing climate and land cover relationships over a broad latitudinal gradient. We found positive and negative relationships of climate and land cover factors with avian abundances. Habitat variables drove patterns of abundance in migratory and resident species, although climate was also influential in predicting abundance for some species occupying more open habitat (i.e., prairie warbler, blue-winged warbler, and northern bobwhite). Abundance of northern bobwhite increased with winter temperature and was the species exhibiting the most significant effect of climate. Models for birds primarily occupying early successional habitats performed better with a combination of habitat and climate variables whereas models of species found in contiguous forest performed best with land cover alone. These varied species-specific responses present unique challenges to land managers trying to balance species conservation over a variety of land covers. Management activities focused on increasing forest cover may play a role in mitigating effects of future climate by providing habitat refugia to species vulnerable to projected changes. Conservation efforts would be best served focusing on areas with high species abundances and an array of habitats. Future work managing forests for resilience and resistance to climate change could benefit species already susceptible to climate impacts.

Key words: Avian abundance; Bayesian hierarchical models; Central USA; climate; *Colinus virginianus*; *Helmitheros vermivorum*; land cover; latitudinal gradient; North American Breeding Bird Survey; *Setophaga discolor*; *Setophaga pinus*; *Vermivora cyanoptera*.

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INTRODUCTION

Future climate has the potential to affect species across the globe. Global projections for over

900 bird species call for greater than half their ranges to be reduced by the end of the century, with temperate regions impacted almost equally by changes in land-use and climate (Jetz et al.

2007). However, it is unclear if habitat loss or climate change is the greater contributing factor in species loss, but climate is expected to be a major driver (Pimm 2008). Understanding how landscape and climate factors contribute to species abundance is important for predicting the impacts of future climates.

Avian species are greatly affected by landscape-level influences often occurring over entire ecoregions and across political boundaries (Forcey et al. 2008). Ranges of wintering North American birds are shifting poleward (LaSorte and Thompson 2007) and similar shifts are occurring for breeding birds in North America (Hitch and Leberg 2007, Zuckerberg et al. 2009), Great Britain (Thomas and Lennon 1999), and South Africa (Hockey et al. 2011). We know very little in regards to the potential mechanisms behind these shifts. However, range shifts in birds and other organisms could lead to changes in plant and animal communities (Root et al. 2003, Visser et al. 2012), or a mismatch between available habitat and suitable climatic conditions (DeLeon et al. 2011). Ultimately, these changes have the potential to increase species extinctions (Rodenhouse et al. 2008, Sekercioglu et al. 2008).

In addition to range shifts, there is increasing evidence that climate is linked to avian survival and productivity (Rolland et al. 2011, Skagen and Adams 2012, Cox et al. 2013a, b, Jenouvrier 2013). Dybala et al. (2013) found a direct effect of winter temperature on adult survival and an indirect effect of prior rainy season on juvenile survival. This study along with others showed the importance of temperature and precipitation throughout the annual cycle (Carey 2009, Stephenson et al. 2011, Wilson et al. 2011, Dybala et al. 2013) as well as life stages (Both and Visser 2005, Albright et al. 2010b, Dybala et al. 2013, Townsend et al. 2013). In addition to winter and spring seasons, several studies found that the previous year's summer temperature and precipitation have a direct effect on both community structure (Albright et al. 2010a, 2011), and avian abundance (Forcey et al. 2007, 2014) while warmer spring temperatures can lead to species breeding earlier and double brooding more often (Townsend et al. 2013). Climate and land cover effects do not occur in isolation and often lead to conflicting impacts (Lemoine et al. 2007, Cox et al. 2013b). Cox et al. (2013a) found a direct

relationship between forest cover and an increase in nest productivity; however, as temperatures increased, so did predation, resulting in lower nest survival.

Migratory behavior may also play an important role in determining which species are affected by changes in climate (Albright et al. 2010a, Both et al. 2010, Rolland et al. 2011, Salewski et al. 2013). Winter severity is linked to the survival of resident and short-distance migrants (Salewski et al. 2013), while long-distance migrants are affected more in seasonal habitats due to their sensitivity to droughts (Albright et al. 2010b) and seasonal mismatches with food resources (Both et al. 2010). Little is known how climate effects on local survival and productivity translate to regional abundances across species ranges, but finding a way to link them is important in understanding how species may be affected by future changes.

Species distribution models have become an important tool in understanding associations between species and their environments (Guisan and Zimmermann 2000). Often, predictions of changes in avian distributions are not empirically based (McRae et al. 2008) or are based on climatic variables without incorporating other drivers such as land cover or dispersal (Pearson and Dawson 2003, Lawler 2009, Araújo and Peterson 2012). Researchers have recently used empirically based methods to incorporate effects of climate and land cover on avian abundance at broad spatial scales (Forcey et al. 2007, 2011, 2014, Jetz et al. 2007, Lemoine et al. 2007, Filloy and Bellocq 2013). Empirical models incorporating effects of climate and land cover on avian abundance allow for the estimation of the potential effects of climate change, as well as effects of changes in land cover resulting from other drivers such as urbanization, land management, and succession.

Our objective was to assess the potential individual and combined effects of climate and land cover on avian abundance across a broad latitudinal gradient to determine their extent and magnitude of influence. We hypothesized a combination of land cover and climate would be the best predictors of avian abundance, but that land cover would be a greater driver of avian abundance than the effects of temperature and precipitation. We predicted that the previous year's summer temperature and precipitation would relate to lower abundance (through their effect

on productivity and recruitment of juveniles into the following year), whereas increasing winter temperature and decreasing winter precipitation would result in higher abundance for short distance migrants and resident species (because of a decrease in mortality). While we considered winter weather effects in the U.S. for residents and short-distance migrants, we did not consider winter weather effects occurring outside the U.S. for Neotropical migrants.

METHODS

Study area

Our study area covered approximately 1.2 million km² across 19 states and four Bird Conservation Regions (BCR) within the Central United States (U.S. NABCI Committee 2000; Fig. 1). We chose this area based on the diversity in land cover and landscape features as well as its geographic extent. We used a latitudinal gradient from approximately 45°N in Minnesota to 30°N in Louisiana to capture potential future climate effects by substituting space for time (Blois et al. 2013). From 1981 to 2010, annual mean temperatures in this region ranged from approximately 7–21°C (PRISM Climate Group 2011). The general landscape features of the study area are characterized by four distinct BCRs (U.S. NABCI Committee 2000). The Eastern Tallgrass Prairie (BCR 22) covered 536,000 km² that was historically covered by tallgrass prairies and oak (*Quercus* spp.) savannas but now consist primarily of agriculture. The Central Hardwoods (BCR 24) covered approximately 303,000 km² with the Ozark Highlands west of the Mississippi River and the Low Plateaus to the east. The region is a mix of oak-hickory (*Carya* spp.) forest, agriculture, and urban areas. The West Gulf Coastal Plain/Ouachitas (BCR 25) was approximately 213,000 km² and characterized by shortleaf pine (*Pinus echinata*) forests in the north and longleaf pine (*Pinus palustris*) forest to the south. Land conversions to agriculture and commercial loblolly pine (*Pinus taeda*) plantations threaten this area's native pine forests. The Mississippi Alluvial Valley (BCR 26) covered approximately 114,000 km² and consisted primarily of bottomland hardwood forests and alluvial floodplains. Land conversion to agriculture and

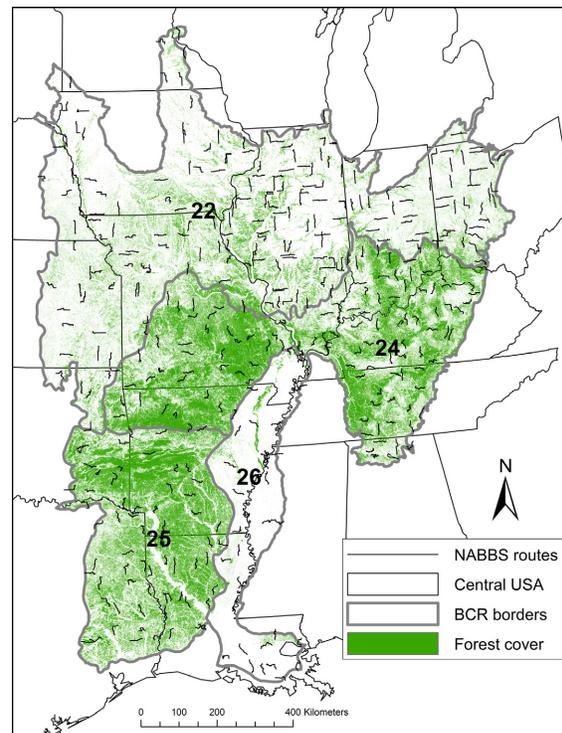


Fig. 1. North American Breeding Bird Survey (NABBS) routes ($n = 410$; black lines) and forest cover in four Bird Conservation Regions (i.e., Eastern Tallgrass Prairie, 22; Central Hardwoods, 24; West Gulf Coastal Plain/Ouachitas, 25; and Mississippi Alluvial Valley, 26) within the Central United States used to relate bird abundance to climate and landscape factors, 1997–2003.

channelization of the lower Mississippi River has reduced the forests in this BCR by 75% and regional flooding by 90% (U.S. NABCI Committee 2000).

Data

We relied on readily available data for our response and explanatory variables. The response variable was the total number of individuals of a species counted on a North American Breeding Bird Survey (NABBS) route per year (Sauer et al. 2014). NABBS routes are roadside surveys approximately 40 km in length with 50 stops situated 0.8 km apart. Trained observers count all birds seen or heard at each route stop in a 3 min period. To make predictions we used a total of 2140 route counts from 410 NABBS routes and 371 observers from

1997 to 2003. We chose these routes and years to capture variation across space as well as within and between years.

We focused on five species primarily breeding within the lower 48 states with various migration patterns and habitat preferences. We modeled three Neotropical migrants, two associated with open early successional habitats, the prairie warbler (*Setophaga discolor*) and blue-winged warbler (*Vermivora cyanoptera*), as well as the worm-eating warbler (*Helmitheros vermivorum*), a species dependent on large tracts of forests with a dense understory. In addition, we modeled the northern bobwhite (*Colinus virginianus*), a non-migratory resident dependent on patches of agriculture interspersed amongst early successional habitat, and the pine warbler (*Setophaga pinus*), a resident/short-distance migrant associated with large tracts of pine forests.

We derived environmental covariates from four data sources and processed in ArcGIS v. 9.3.1, 10.2 (ESRI 2009, 2013) and FRAGSTATS v. 3.3 (McGarigal et al. 2002, Table 1). We calculated land cover composition and configuration from 30 × 30 m resolution reconciled 2001 National Land Cover Data (NLCD; Homer et al. 2007) and 2000 National Biomass and Carbon Dataset (NBCD; Kellnendorfer et al. 2011) rasters. We then reclassified NLCD and NBCD rasters into land cover and composition classes (Table 1). The NBCD is a map of estimated basal area-weighted canopy height derived from Forest Inventory and Analysis (FIA) and remote sensing data from Landsat. We reclassified the NBCD map into early successional and mature forest cover that was 0 ≤ 19 yr old and ≥ 20 yr old, respectively, using FIA data to relate forest height to age (Li et al. 2011).

In addition, we collected elevation data from 30 × 30 m resolution National Elevation Dataset (NED; Gesch et al. 2002), and 4 × 4 km resolution climate data from the PRISM Climate Group for the years 1996–2002 (PRISM Climate Group 2011). Using ArcGIS 9.3.1, 10.2 (ESRI 2009, 2013), we intersected the NED and climate grids with our routes to calculate the average elevation, temperature, and precipitation (i.e., average seasonal summer and winter temperature and precipitation) for each NABBS route.

Lastly, we calculated landscape metrics for 800 and 8000 ha scales defined by 100 and 1000 m buffers around 410 NABBS routes (Table 2). We

reasoned that these scales covered the range of detection of most species, included the home ranges of birds heard, and encompassed any immediate land cover effects on bird abundance (LeBrun et al. 2012). We used FRAGSTATS version 3.3 (McGarigal et al. 2002) to calculate landscape metrics for the buffered areas (Table 2).

Model development

We identified associations between environmental covariates and avian abundance using a hierarchical Bayesian log-linear model and iterative simulation (Markov chain Monte Carlo) in WinBUGS. We included the following random effects in each of our models to accommodate the repeated measure nature of our counts and variation in the counts not explained by our covariates: a year effect γ to account for temporal variation in bird abundance, and a route effect z to account for spatial variation among routes. While data collected by NABBS cannot separate the detection process from the state process as in standard occupancy approaches, differences in detectability are considered. For instance we used a standardized methodology to control for variation among conditions associated with observers by including a random observer effect ω to account for differences in surveying abilities among observers (Thogmartin et al. 2004) and we excluded counts by first-time observers. We constructed the Poisson model as:

$$\log[\lambda(s)] = \sum_{j=1}^n \beta_j X_j(s) + z_j(s) + \omega_j(s) + \gamma_j(s) + \epsilon_j$$

where λ represents the total route count of a species in a particular year across space (s), with β representing the change in abundance per unit change in the $j = 1$ to n year-specific counts, and X representing a matrix of the environmental fixed effects. The error term ϵ was a random effect accommodating potential overdispersion. We used non-informative priors for the initial models with mean zero and a precision equal to 10^5 for both the fixed and random effects. Models were run in three chains for 550,000 iterations, with a burn-in of 100,000 iterations; we used the Gelman-Rubin diagnostic in WinBUGS to identify multiple chain convergence during model simulation (Brooks and Gelman 1998, Lunn et al. 2000, Link et al. 2002).

Table 1. Environmental covariates included in global models for predicting abundance of prairie warbler (PRAW), blue-winged warbler (BWWA), northern bobwhite (NOBO), pine warbler (PIWA), and worm-eating warbler (WEWA) derived from 100 and 1000 m radius buffers surrounding breeding bird survey routes within the Eastern Tallgrass Prairie, Central Hardwoods, West Gulf Coastal Plain/Ouachitas, and Mississippi Alluvial Valley Bird Conservation Regions in the United States.

Type of variable	Variable	Variable description	Species
Land cover composition	Cropland (%)†	Percentage of cropland in the landscape	NOBO
	Grassland (%)†	Percentage of grassland in the landscape	NOBO, PRAW, BWWA
	Forest (%)†	Percentage of forest in the landscape (i.e., includes deciduous, coniferous, and mixed forest)	NOBO, PRAW, WEWA, BWWA
	Deciduous forest (%)†	Percentage of deciduous forest in the landscape	WEWA
	Coniferous forest (%)†	Percentage of coniferous forest in the landscape	PIWA, PRAW, BWWA
	Early successional forest (%)‡	Percentage of transitional shrub and forest cover <20 yr old	NOBO, PRAW, BWWA
	Mature forest (%)‡	Percentage of the forest >20 yr old	PIWA, WEWA
	Shrub (%)†	Percentage of shrubland in the landscape	NOBO, PRAW, WEWA
	Canopy (%)§	Percentage of canopy cover in the landscape	PIWA, WEWA
Land cover configuration	Forest patch area (ha)†	Mean patch size of forest cover (ha)	PIWA, WEWA
	Contagion (%)†	Percentage of habitat patch types (when contagion = 100 then the landscape consists of a single patch)	NOBO
Topography	Ruggedness index¶	Captures the heterogeneity of landforms and slopes in the landscape	PIWA, PRAW, WEWA
Climate	Summer precipitation (mm)#	Summer average (average June, July and August) precipitation from the year previous to when bird abundance was measured	NOBO, PIWA, PRAW, WEWA, BWWA
	Summer temperature (°C)#	Summer average (average June, July and August) temperature from the year previous to when bird abundance was measured	NOBO, PIWA, PRAW, WEWA, BWWA
	Summer maximum monthly average temperature (°C)#	Summer max monthly average (June, July and August) temperature from the year previous to when bird abundance was measured	BWWA
	Winter precipitation (mm)#	Winter average (average December, January and February) precipitation from the year previous to when bird abundance was measured	NOBO
	Winter temperature (°C)#	Winter average (average December, January and February) temperature from the year previous to when bird abundance was measured	NOBO

† 2001 and 2006 National Land Cover Data (NLCD).

‡ 2000 National Biomass and Carbon Dataset (NBCD).

§ 2001 NLCD percent tree canopy layer. It quantifies the per pixel tree canopy fraction as a continuous variable from 1% to 100% across the entire landscape.

¶ National Elevation Dataset (NED).

1996–2002 and 2006–2009 PRISM climate data.

Table 2. Mean, standard deviation (SD), minimum value (Min), and maximum value (Max) of environmental covariates used to predict abundances of five bird species in the Central United States.

Environmental variables	Mean	SD	Min	Max
Cropland (%)	54.48	27.47	0.00	94.49
Grassland (%)	3.62	9.02	0.00	79.25
Shrub (%)	5.31	11.18	0.00	84.47
Forest (%)	26.91	23.71	0.00	94.82
Deciduous forest (%)	19.87	19.35	0.00	84.50
Coniferous forest (%)	5.17	12.02	0.00	68.86
Early successional forest (%)	11.81	19.02	0.00	92.00
Mature forest (%)	24.73	22.87	0.00	98.00
Canopy (%)	23.68	20.29	0.00	84.00
Forest patch area (ha)	22.61	67.90	0.00	1019.92
Contagion (%)	66.67	14.31	27.16	97.80
Ruggedness index	4.03	3.59	0.17	22.38
Summer precipitation (mm)	101.48	31.26	31.16	356.19
Summer temperature (°C)	30.13	2.13	24.78	36.67
Summer maximum monthly average temperature (°C)	31.59	2.41	25.57	38.82
Winter precipitation (mm)	80.15	43.10	5.71	239.46
Winter temperature (°C)	-3.15	4.07	-15.98	8.82

We considered models representing a priori hypotheses containing ecologically relevant combinations of covariates and determined the most supported models for each species (Appendix S1). We hypothesized a combination of climate, and land cover variables would be the best predictor of avian abundance and climate would be a major driver of species distributions. We first tested all covariates for multicollinearity, and we found only canopy and forest cover correlated; therefore, we only used percent forest or canopy cover in any single model. We then constructed hypotheses to compare the individual and combined effects of climate vs. landscape factors on avian abundance. They included landscape hypotheses separated into composition, structure, and pattern covariates, climate hypotheses separated by temperature and precipitation, and a global hypothesis combining both landscape and climate variables. We began by considering models with a single covariate and then proceeded by considering models with combinations of supported covariates. We identified the most supported models (models ≤ 2 Δ DIC, Deviance Information Criterion units) using the DIC (Spiegelhalter et al. 2002) and used the best-supported model to make abundance predictions. Initial model runs examined a conditional autoregressive prior for the route random effect to control for potential spatial correlation among

route counts (Thogmartin et al. 2004), but these models had higher Δ DIC values than the alternative model in all cases.

Abundance maps

We mapped predicted relative abundances using ArcGIS v. 10.2 (ESRI 2013) Spatial Analyst raster calculator (Thogmartin and Knutson 2007). We created two lattices equivalent to the mean area covered by the 100-m and 1-km buffered NABBS routes, and averaged pixel values for each environmental covariate within the cells. We then estimated relative abundances across the landscape using the gridded rasters. Final predicted abundances were mapped as a 7-yr expected mean count centered on the 2001 NLCD for a given 9030-m resolution pixel (the average resolution for a 1 km buffered route). We chose 2001 for our prediction map in order to use it as the basis for future work modeling the effects of climate change 100 yr into the future.

Model validation

We tested the predictive performance of the best models on a new set of data collected after the final year of the data used to originally fit the models. First, we re-fit the top models using the beta coefficients as informative priors and made predictions of species abundance for NABBS routes across the study area using

reconciled 2006 NLCD, PRISM climate data from 2005–2008, and 2000 NBCD. We then regressed NABBS route counts collected across the study areas, but not used in model construction (i.e., 2006, 2007, 2008, and 2009), against the predicted abundance of each modeled species using RStudio 0.96.330 and R 2.12.1 (R Development Core Team 2013, RStudio Team 2014). Lastly, we calculated the adjusted R^2 and root mean squared error (RMSE) for each of the four prediction years and five avian species.

RESULTS

Most supported models were either a combination of land cover and climate or solely land cover variables (Table 3). The 8000 ha scale was consistently the best spatial scale

across species for characterizing patterns in bird abundance (Table 3, Appendix S1). Habitat affinity of bird species was an important determinant of climate sensitivity whereas migratory behavior did not appear associated with sensitivity to climate. Models for species preferring early successional habitats (i.e., prairie warbler, blue-winged warbler, and northern bobwhite) improved with the addition of climate variables, whereas models for species dependent on contiguous mature forest did not improve with the addition of climate variables (Table 3, Appendix S1).

Forest cover and canopy cover were the primary drivers of species relative abundance (Figs. 2–6). Species dependent on early successional habitat had abundances influenced primarily by forest cover, while canopy cover affected mature forest

Table 3. Explanatory variables, and posterior distribution means (fiftieth percentile of the simulations), lower (LCI) and upper (UCI) credible intervals included in the best competing models for predicting abundance of prairie warbler, blue-winged warbler, northern bobwhite, pine warbler, and worm-eating warbler in the Central United States, 1997–2003.

Species	Explanatory variables	Mean	95% LCI	95% UCI
Prairie warbler	Coniferous forest (%)	-0.05	-0.30	0.19
	Early successional (%)	0.28	0.08	0.53
	Forest (%)	1.90	1.56	2.23
	Grass (%)	-0.34	-0.91	0.10
	Shrub (%)	0.15	-0.15	0.45
	Average maximum precipitation (mm)	0.07	-0.03	0.16
	Average maximum summer temp (°C)	0.27	0.01	0.52
Blue-winged warbler	Average maximum summer temp squared (°C)	-0.03	-0.12	0.05
	Coniferous forest (%)	-1.65	-2.41	-0.99
	Early successional (%)	-0.44	-0.86	-0.03
	Forest (%)	2.35	2.86	3.40
	Grass (%)	-0.92	-0.86	0.09
	Max monthly average summer temp (°C)	-0.30	-0.63	0.03
Northern bobwhite	Max monthly average summer temperature squared (°C)	0.32	0.09	0.53
	Contagion (%)	-0.72	-0.94	-0.51
	Crop (%)	1.05	0.64	1.43
	Early successional (%)	-0.29	-0.52	-0.06
	Forest (%)	0.93	0.57	1.27
	Shrub (%)	-0.46	-0.73	-0.19
	Average winter precipitation (mm)	-0.02	-0.07	0.03
Pine warbler	Average minimum winter temp (°C)	0.22	0.10	0.34
	Canopy cover (%)	2.45	1.96	2.99
	Coniferous forest (%)	1.09	0.82	1.37
	Forest patch area (ha)	-0.29	-0.58	-0.03
Worm-eating warbler	Mature forest (%)	0.24	-0.05	0.53
	Canopy cover (%)	2.67	2.17	3.25
	Forest patch area (ha)	-0.14	-0.30	0.03
	Shrub (%)	-0.88	-1.37	-0.44

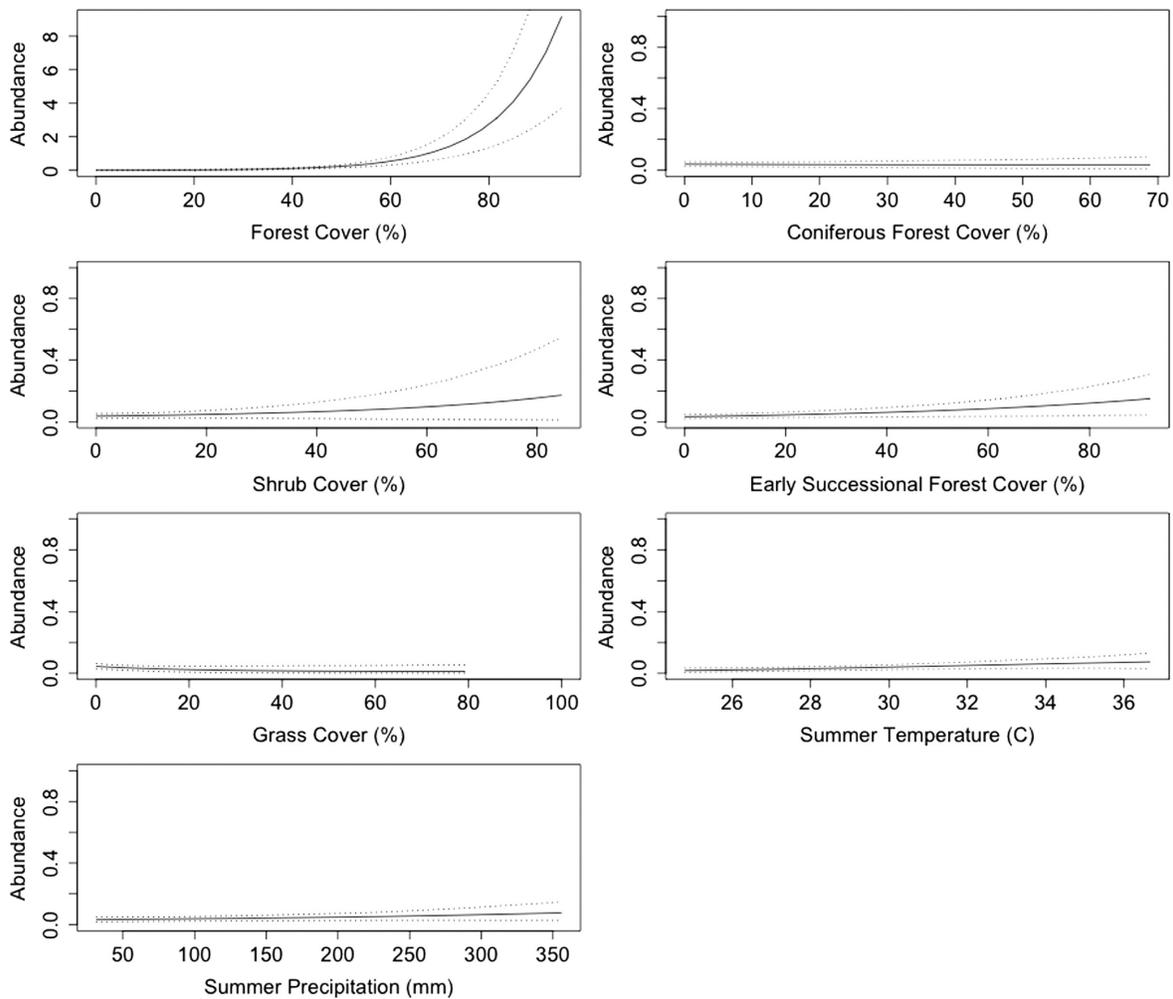


Fig. 2. The effects of the environmental covariates on prairie warbler relative abundance in the Central United States, 1997–2003. Dashed lines represent the confidence intervals around the predictions.

associated species. Prairie warbler, blue-winged warbler, and northern bobwhite increased by approximately 9, 14, and 79 birds per route, respectively, across the observed range of percent forest cover (i.e., 3, 6, and 5 times greater than the mean non-zero route counts for each species; Table 4, Figs. 2–4). In comparison, the pine and worm-eating warblers increased by 27 and six birds per route across the observed extent of percent canopy cover (i.e., two and three times greater than the mean non-zero route counts for each species; Table 4, Figs. 5 and 6). We also found northern bobwhite abundance negatively affected by increasing contagion (e.g., reduced habitat patchiness), decreasing by 36 birds per

route (i.e., two times greater than the mean non-zero route count; Table 4, Fig. 4). Similarly, pine warblers were positively affected by the percent coniferous forest in the landscape and increased by six birds per route (i.e., 10% of the maximum route count; Table 4) across the observed range of the variable (Fig. 5). Unlike the resident (i.e., northern bobwhite) and short-distance migrant (i.e., pine warbler), the three Neotropical migrants' (i.e., prairie, blue-winged, and worm-eating warblers) next most influential variables only increased abundance by <1 bird per route (Figs. 2, 3 and 6).

Models improved for prairie warbler, blue-winged warbler, and northern bobwhite with

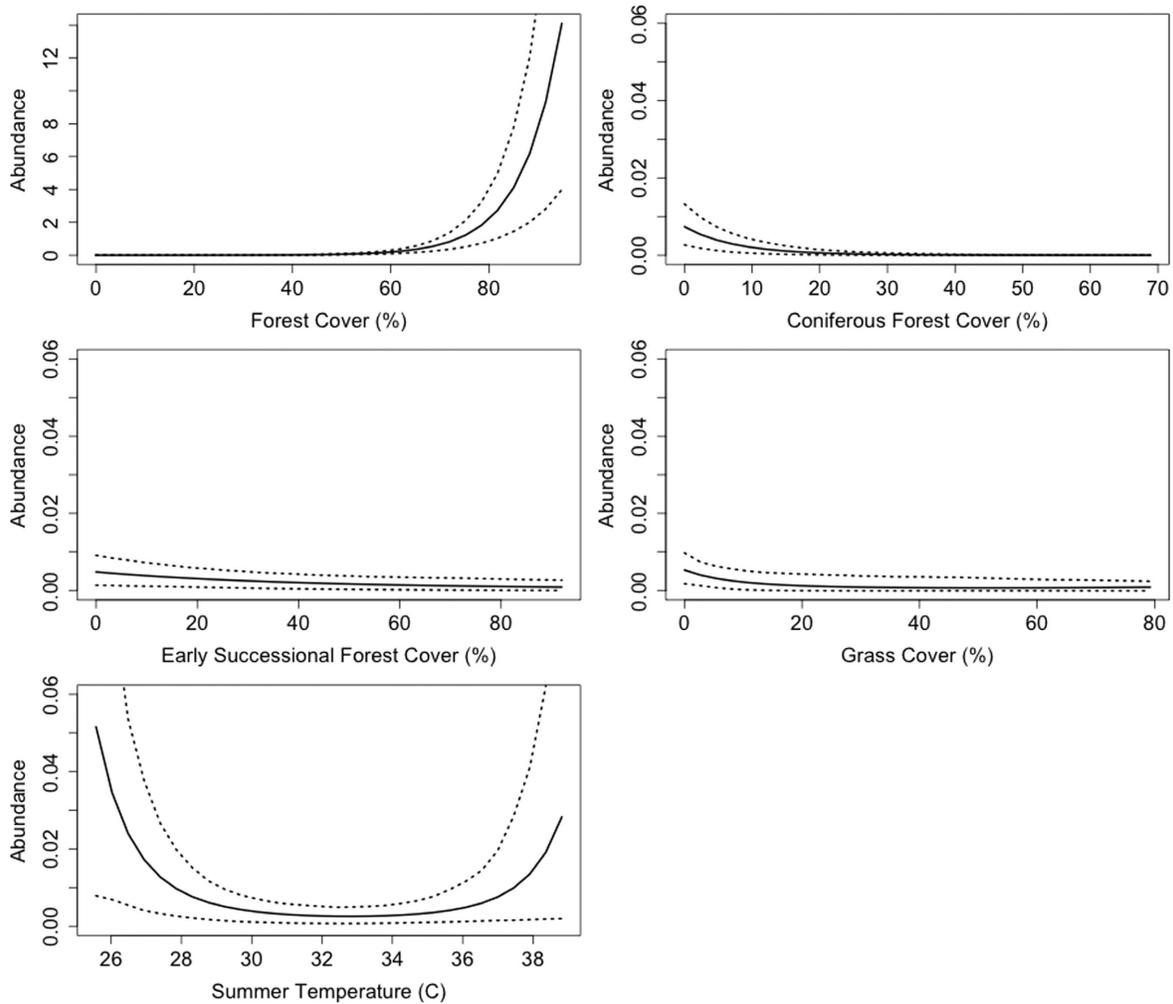


Fig. 3. The effects of the environmental covariates on blue-winged warbler relative abundance in the Central United States, 1997–2003. Dashed lines represent the confidence intervals around the predictions.

the addition of climate covariates (Appendix S1). The most significant (>1 birds/route) climate effect we observed was for northern bobwhite abundance. The northern bobwhite increased by nine birds per route (i.e., 9% of the maximum count, MC) with increasing winter temperature and increased by one bird per route (i.e., 1% of the MC) with decreasing winter precipitation (Table 4, Fig. 4). Prairie warbler abundance increased by <1 bird per route across the observed range in summer temperature and precipitation and abundance of blue-winged warblers decreased by <1 bird per route across the range of summer temperature (Figs. 2 and 3).

Highest predicted abundance, for all species except the northern bobwhite, was primarily in and around areas with extensive forest cover; however, percent forest cover varied among species and across the four BCR (Figs. 7–11). Prairie warblers were primarily located in the Central Hardwoods BCR and the West Gulf Coastal Plain/Ouachita BCR. Highest prairie warbler abundances occurred mainly in the Ouachita National Forest in west central Arkansas and in portions of central Tennessee (Fig. 7). The blue-winged warbler differed from the prairie warbler and occurred mainly in the Central Hardwoods BCR with the highest concentrations in the Mark Twain National Forest within the

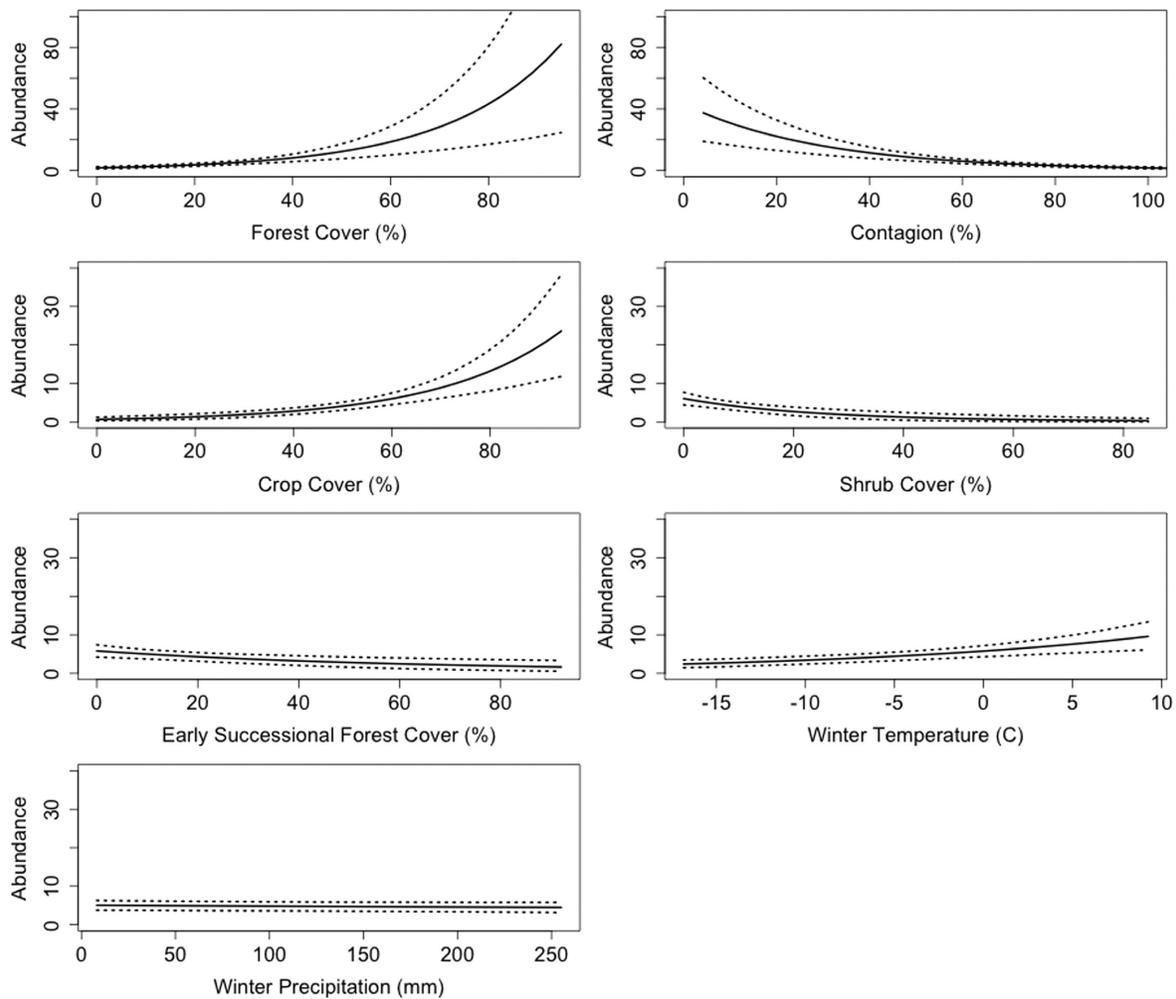


Fig. 4. The effects of the environmental covariates on northern bobwhite relative abundance in the Central United States, 1997–2003. Dashed lines represent the confidence intervals around the predictions.

Missouri Ozarks followed by portions of central Tennessee, and the Ozark National Forest in northwestern Arkansas (Fig. 8). Conversely, the previous species, the highest abundances of northern bobwhite were widely distributed across the four BCR with the highest concentrations in northeastern Missouri, southeastern Oklahoma and in eastern Kansas near the Flint Hills (Fig. 9). Similar to the prairie warbler, the pine warbler occurred in both the Central Hardwoods BCR and the West Gulf Coastal Plain/Ouachita BCR. However, pine warbler abundance was less concentrated and primarily occurred throughout the West Gulf Coastal Plain/Ouachita BCR and the western part of the Central Hardwoods BCR (Fig. 10). Finally,

the worm-eating warbler mapped abundance was low (i.e., <5 birds/8000 ha) for all four BCR, but concentrated within the Missouri Ozarks centered near the Mark Twain National Forest, and in west central Arkansas centered near the Ozark National Forest (Fig. 11).

Model validation for the most supported species models had a moderate to good fit ($R^2 = 0.36$ – 0.85) with the lowest R^2 for the worm-eating warbler and the highest R^2 for the prairie warbler in 2006 (Appendix S2). The range of R^2 values across years coincided with the amount of model uncertainty for each species (Appendices S1 and S2), however; it did not determine how well the models predicted relative abundance. We did not observe a drop in model predictability across

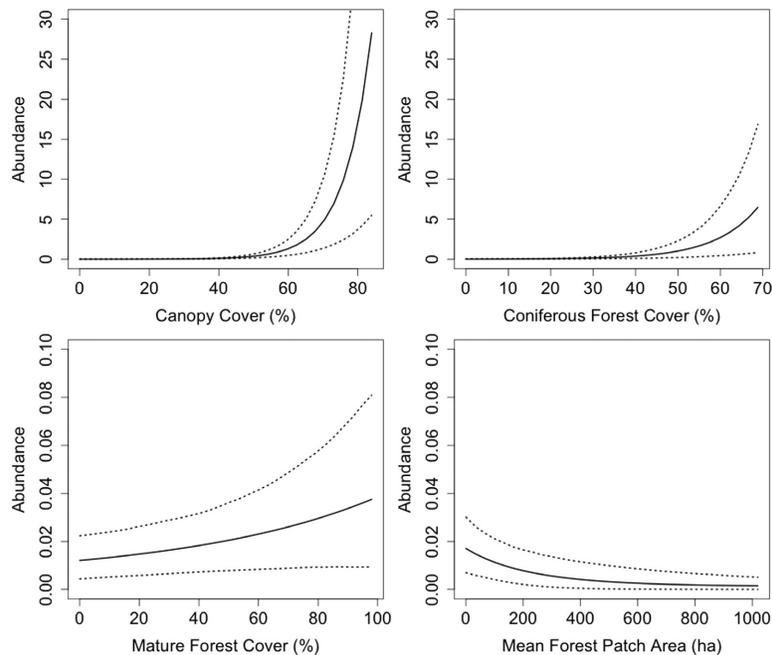


Fig. 5. The effects of the environmental covariates on pine warbler relative abundance in the Central United States, 1997–2003. Dashed lines represent the confidence intervals around the predictions.

the four validation years from 2006 to 2009 for most of the species except for the prairie warbler (decreasing from $R^2 = 0.85$ – 0.58) and the northern bobwhite (decreasing from $R^2 = 0.70$ – 0.63 ; Appendix S2). The species models fitting best were the prairie warbler (RMSE = 1.4; $n = 97$ maximum count/route; MC/R), followed by the pine warbler (RMSE = 5.1; $n = 30$ MC/R) and the northern bobwhite (RMSE = 8.68; $n = 112$ MC/R) with all having $R^2 \geq 0.6$, while the worm-eating (RMSE = 0.91; $n = 14$ MC/R) warbler and the blue-winged warbler (RMSE = 1.3; $n = 15$ MC/R) fit moderately well with $R^2 \geq 0.3$ and <0.6 . Originally, the worm-eating warbler model did a poor job of predicting relative abundance for the four validation years (e.g., $R^2 < 0.35$); however, a single site within the Missouri Ozarks acted as an outlier to the rest of the predictions. After the removal of this site across all 4 yr, model predictions increased by 15–40%.

DISCUSSION

We successfully applied Bayesian hierarchical count models to predict avian abundance across space, time, and species. Our models did just

as good or better at predicting species abundance at a regional scale compared to other studies using similar methods (Thogmartin et al. 2004, Forcey et al. 2007, 2011, Thogmartin and Knutson 2007, Murray et al. 2008, LeBrun et al. 2012). Unlike these previous studies, we modeled species abundance across a latitudinal gradient that allowed us to draw inferences concerning climate factors based on variation in climate across the region. Our average summer temperatures for this region had a range of 12°C , which is almost double the expected increase in temperature under the highest emissions scenario for the end of the century (IPCC 2007). In addition to predicting avian abundance across space, we successfully validated predictions projected into the future whereas similar studies found mixed results for models validated against either independently collected data, or from a portion of data withheld from model construction (Thogmartin et al. 2004, Murray et al. 2008, LeBrun et al. 2012). Lastly, we successfully predicted a range of species across a habitat gradient from farmland to mature forest. Based on our validations, we are confident that our results credibly identify effects of both

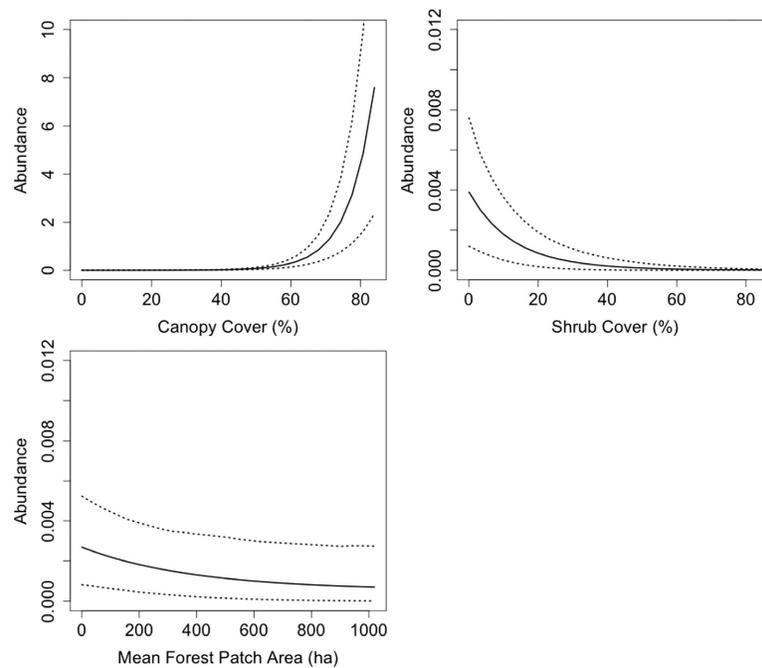


Fig. 6. The effects of the environmental covariates on worm-eating warbler relative abundance in the Central United States, 1997–2003. Dashed lines represent the confidence intervals around the predictions.

climate and land cover on species abundance over a broad geographic region.

Land cover was a primary driver for all species and only a few species performed better with the addition of climate covariates, with only one species exhibiting any significant climate effect (i.e., positive effect of winter temperature on northern bobwhite abundance). Other studies have shown that land cover and land use were stronger drivers of species abundance than climate factors in the United Kingdom (Eglington and Pearce-Higgins 2012), whereas, other research suggests

that climate may play a greater role in determining abundance (Lemoine et al. 2007, DesGranges and LeBlanc 2012, Cumming et al. 2014). These contradictory results may indicate that climate effects are habitat- and species-specific and may differ over a species annual cycle and range (Wilson et al. 2011). Species in more northerly latitudes seem to show stronger impacts associated with climate than species with ranges centered at lower latitudes, suggesting climate is a greater limiting factor closer to the poles (DesGranges and LeBlanc 2012, Cumming et al. 2014).

Table 4. Bird species summary statistics for North American Breeding Bird Survey route counts ($n = 2140$) in the Eastern Tallgrass Prairie, Central Hardwoods, West Gulf Coastal Plain/Ouachitas, and Mississippi Alluvial Valley Bird Conservation Regions in the United States, 1997–2003.

Species	Min	Mean	Max	Variance	Count sum	Total zero counts (%)	Non-zero mean	Non-zero variance
Prairie warbler	0.0	0.8	30.0	5.1	1648.0	78.2	3.5	13.4
Blue-winged warbler	0.0	0.2	15.0	0.7	392.0	92.2	2.4	4.5
Northern bobwhite	0.0	13.1	102.0	237.1	28,128.0	19.4	16.3	242.6
Pine warbler	0.0	2.9	60.0	63.5	6169.0	78.8	13.6	153.8
Worm-eating warbler	0.0	0.2	14.0	0.8	354.0	92.7	2.3	5.6

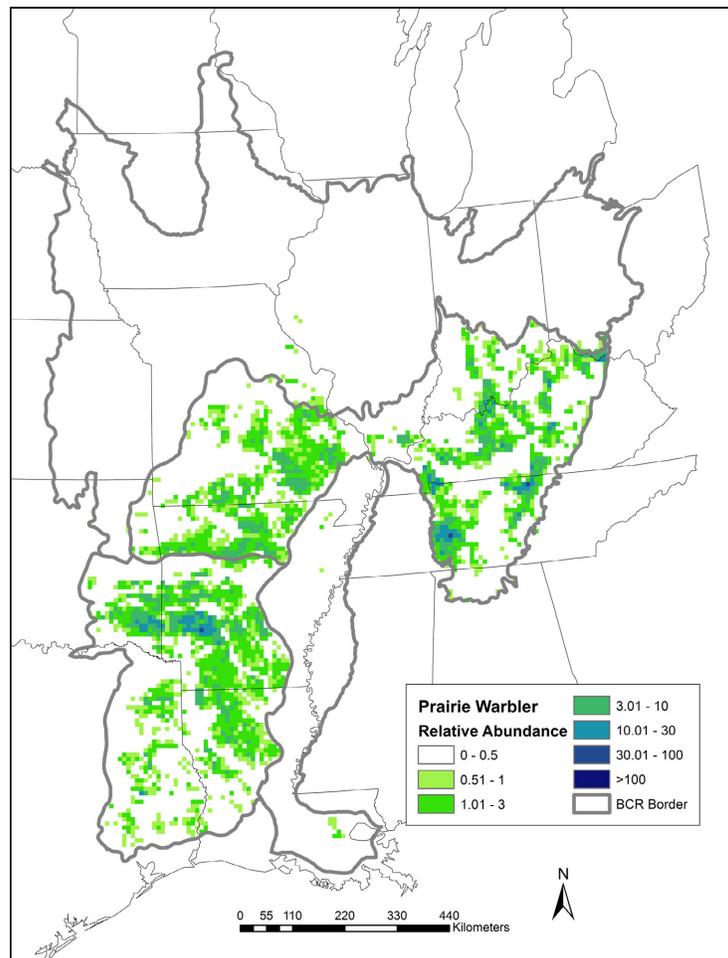


Fig. 7. Maps of 2001 predicted relative abundance for prairie warbler within four Bird Conservation Regions (BCR) across the Central United States.

However, when habitat availability is already low, climate can increase the extinction threshold of a species (Travis 2003). For several species, we studied only the southern edge of their ranges and it is possible that at higher latitudes climate will increase in significance especially in areas with greater habitat loss (Travis 2003). Ultimately it is likely that the influence of climate change over time will overtake land use as the principal driver of bird populations; there is evidence to suggest that this shift has begun in Central Europe (Lemoine et al. 2007).

One of the most significant findings from our study was that forest and canopy cover were the most influential environmental factors for determining abundance for early successional and mature forest species respectively. Even

though early successional and mature forest species differed between forest and canopy cover, we found those two covariates were highly correlated across our region. A similar study examining regional abundance support our findings of the importance of forest cover over climate factors (Fillooy and Bellocq 2013). Our results contradicted our initial hypotheses that transitional habitat (i.e., shrub and forests <20 yr old) is the primary driver of early successional species abundance. This is possibly the result of our NABBS routes averaging <12% in early-successional forest within 1 km of a route. We would likely see stronger associations if our sites were located in areas with more early-successional habitat instead of along roadways (Keller and Scallan 1999). However, recent research suggests that species

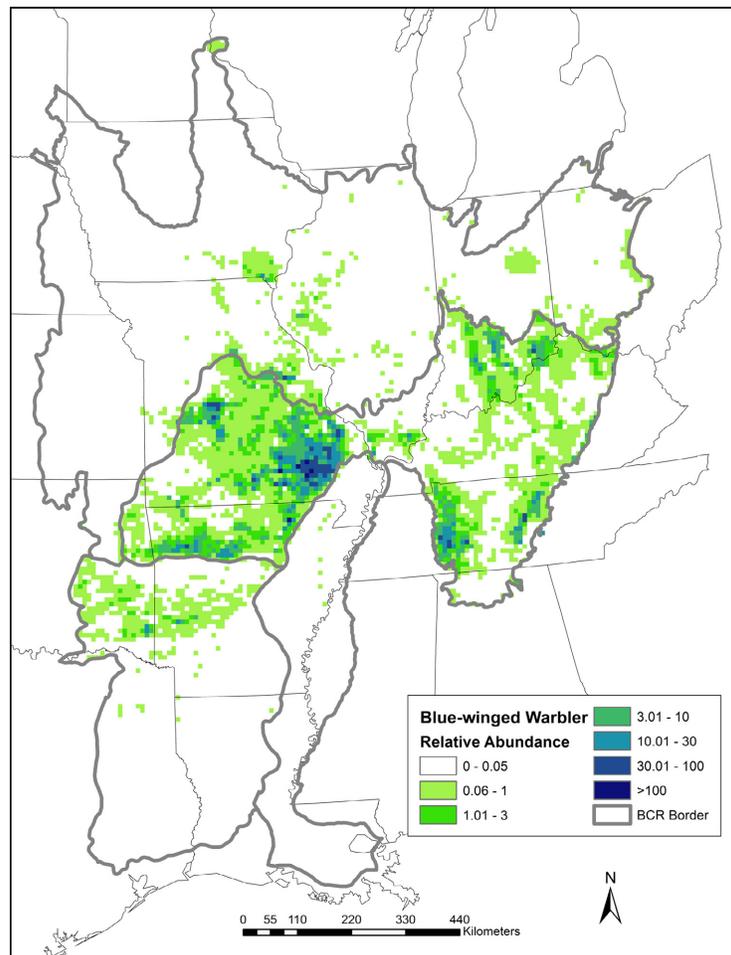


Fig. 8. Maps of 2001 predicted relative abundance for blue-winged warbler within four Bird Conservation Regions (BCR) across the Central United States.

considered early successional obligates may actually utilize forest habitat more than originally thought (Thogmartin 2010, Streby et al. 2012). Forest land cover in this region also consists of a gradient of forest communities including savanna and woodland, which are used extensively by many species considered early successional species (Reidy et al. 2014). Besides the possibility of additional use of forest cover by early successional species, forested areas are some of the only locations with significant amounts of suitable habitat in this region highly fragmented by agriculture. In this region, forested areas are primarily clustered around publicly managed lands (Bonnot et al. 2013). Management on these public lands is primarily for multiple uses including wood products, savanna woodland

restoration, and wildlife habitat (Hamilton et al. 2013). Strategic planning of forest restoration efforts in and around these publicly owned lands is key for increasing survival for some of these species (Bonnot et al. 2013).

We found species habitat associations were a key determinant of whether a species experienced any climate effects, while migratory behavior did not exhibit a clear connection. Species preferring more open canopy characteristics exhibited model improvement with the inclusion of temperature and/or precipitation variables to habitat models whereas forest-dependent species did not show similar model improvement. This may indicate the role that habitat, particularly complex vertical structure, has on providing shelter and protection from extreme weather

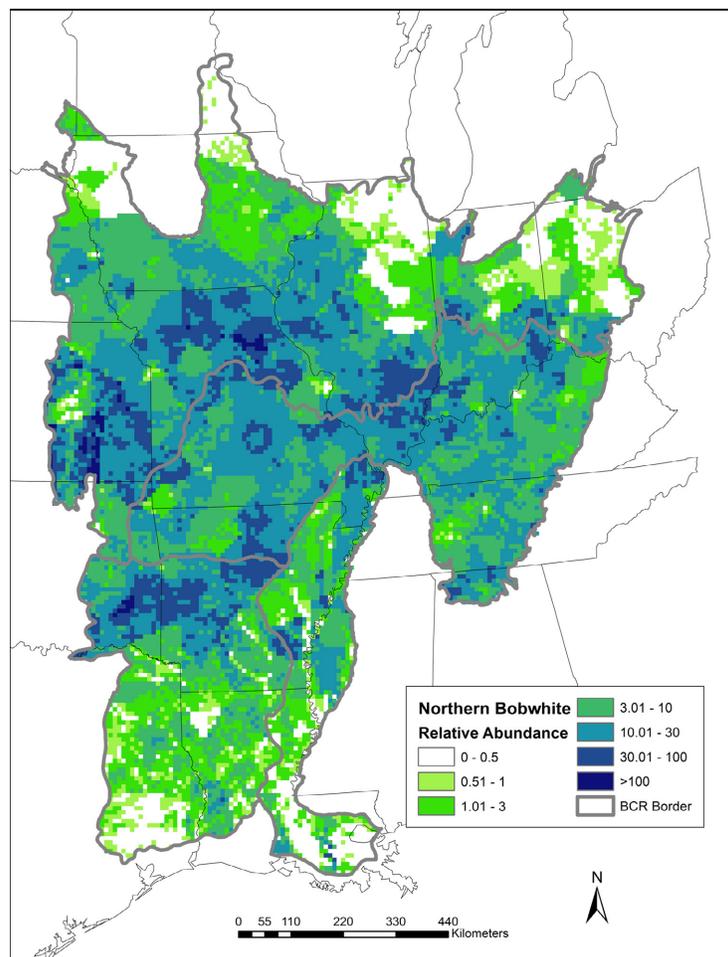


Fig. 9. Maps of 2001 predicted relative abundance for northern bobwhite within four Bird Conservation Regions (BCR) across the Central United States.

events as well as changes across microclimates (Zimmerman et al. 2009, Scheffers et al. 2014). Even though we found no clear connection between migratory pattern and climate, migratory species may be influenced more by climate factors on the wintering grounds (Wilson et al. 2011) or during migration due to changes in vegetation phenology or weather events (Gordo 2007, Jones and Cresswell 2010, Saino et al. 2011).

Climate change will affect species positively and negatively. Climate predictions for the Midwestern United States call for hot dry summers and warm wet winters (Wuebbles and Hayhoe 2004). Prairie warblers would benefit from climate warming in the region because we found their abundance increased with rising summer

temperatures to a threshold around 36°C. Northern bobwhite will likely benefit from projected warmer winter temperatures, but at the same time decrease in abundance with increasing winter precipitation. Lusk et al. (2001) found the reverse relationship between precipitation and northern bobwhite abundance; however, their study only sampled a portion of the southern end of the northern bobwhite's range. Thus, there will be winners and losers as climate changes with noticeable changes in avian abundance and distribution across the region.

Our data also provide evidence for shifting species distributions. Prairie warblers should increase along the northern border of their range as temperatures increase, and eventually

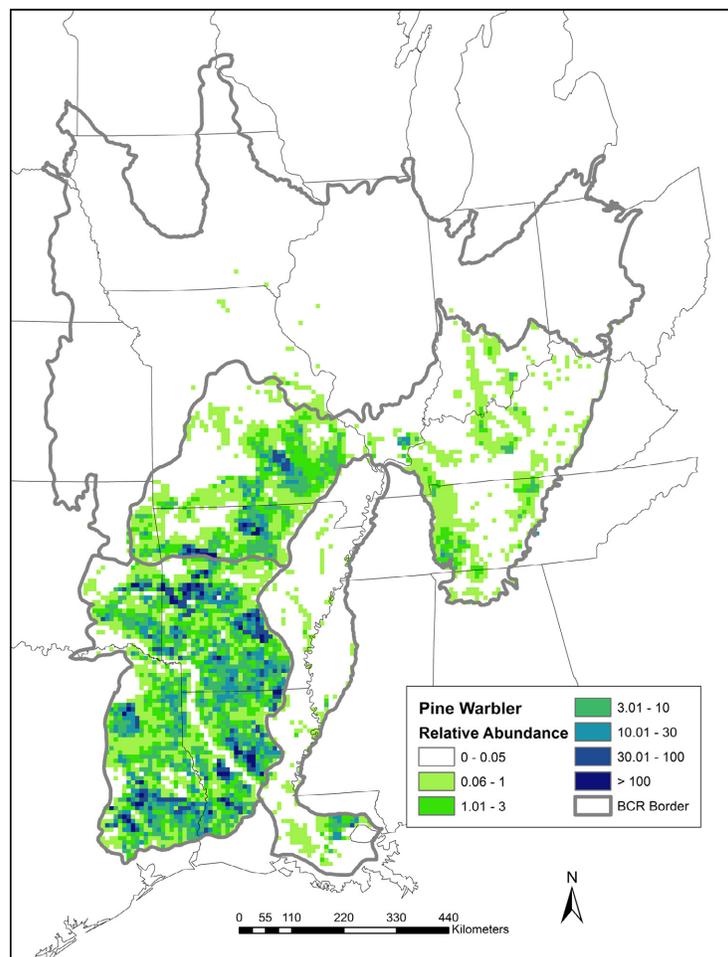


Fig. 10. Maps of 2001 predicted relative abundance for pine warbler within four Bird Conservation Regions (BCR) across the Central United States.

contract along its southern border once temperatures exceed 36°C. Hitch and Leberg (2007) found evidence to suggest both prairie warblers and blue-winged warblers have begun to shift their ranges northward as temperatures across the United States have increased. Along with Hitch and Leberg's (2007) findings of a 0.6 km/yr northward shift for the prairie warbler, our results indicate a possible time lag or slower northward shift in its range. In addition to the prairie warbler results, we found that as summer temperatures increase, blue-winged warbler abundance decreases, providing a mechanism to support Hitch and Leberg's (2007) findings of an average northward shift of around 3 km/yr. However, our results also

showed blue-winged warbler abundance increasing slightly at the highest temperatures. This conflicting response of the blue-winged warbler to the highest temperatures may indicate that the timing and duration of temperature extremes within a season is important (Bolger et al. 2005, Albright et al. 2010b, 2011). Extreme temperatures, in this region, primarily occur in late summer near the end of the breeding season and start of migration for the blue-winged warbler. Therefore, cooler temperatures during nesting and fledgling stages followed by an end of the summer heat wave may not be as detrimental to blue-winged warbler productivity. These results illustrate the complexities associated with determining the impacts of climate

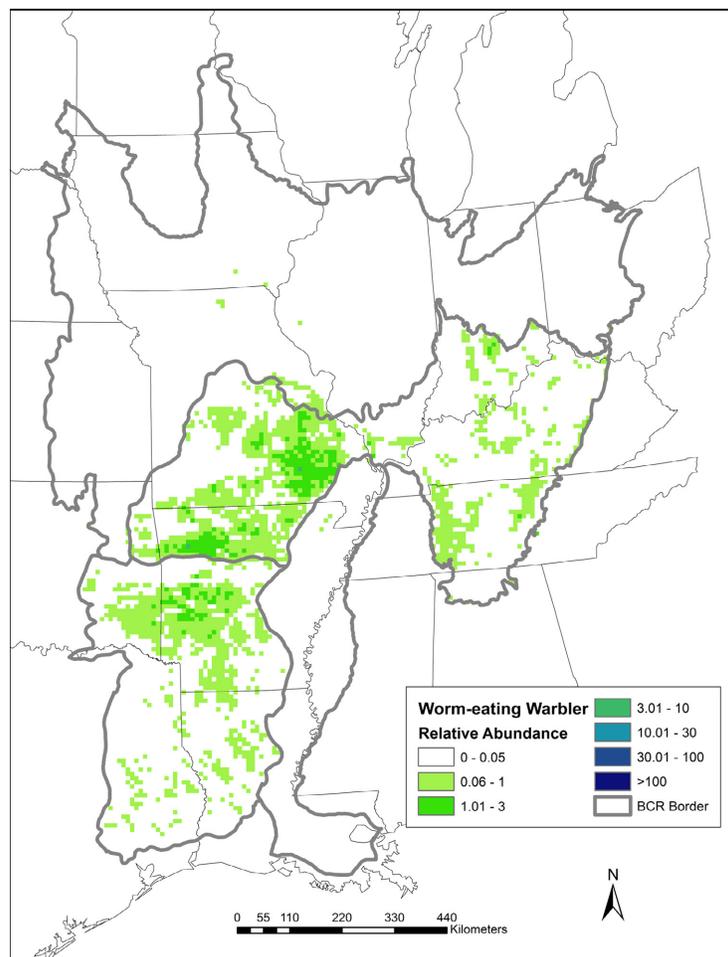


Fig. 11. Maps of 2001 predicted relative abundance for worm-eating warbler within four Bird Conservation Regions (BCR) across the Central United States.

on species abundance as well as provide rationale for range shifts already occurring.

Other effects of climate may also play a significant role in determining abundance (Rodenhouse et al. 2008, Jones and Cresswell 2010, Matthews et al. 2011, Saino et al. 2011). Species not currently exhibiting impacts from temperature and precipitation, such as the worm-eating and pine warblers, may exhibit them through indirect effects associated with climate induced habitat loss (Mantyka-Pringle et al. 2012) brought on by changes in vegetation composition (Rodenhouse et al. 2008, Matthews et al. 2011) and structure (Meynard and Quinn 2008). In addition to changes to habitat composition and structure, phenological shifts resulting in the reduction of

food resources during important life stages such as breeding and migration could also affect these species (Mac Nally et al. 2009, Dybala et al. 2013, Jenouvrier 2013, Whitehouse et al. 2013). With the reduction of habitat and food resources, species are more susceptible to interactions with other species through competition for suitable habitat (Auer and Martin 2013, Urban et al. 2013) or temperature induced increases in predation (Cox et al. 2013a, b). Managing for changes in climate by maintaining and creating new habitat will be essential for mitigating these potential indirect effects of climate change.

Species-specific responses to the effects of climate present unique challenges to land managers trying to balance species management over a

variety of land covers. Landscapes with a high percentage of public lands within the Central United States are among the few remaining landscapes with high percentages of forest cover in a region dominated by agriculture. These forested landscapes act as refugia for species already vulnerable to habitat loss and will only become more important as climate and land use effects increase (Hamilton et al. 2013, 2014). In addition, where habitat availability is already low, climate change has the potential to lower the threshold at which species go extinct (Travis 2003). Species already vulnerable to the effects of climate and habitat changes (i.e., species experiencing habitat loss) will need greater attention paid to habitat management. Therefore, habitat management will be important in mitigating and adapting to the effects of climate and land use change through forest conservation, creation, and restoration (Seavy et al. 2009, Conroy et al. 2011, Bernazzani et al. 2012). Conservation efforts are likely to be more effective if concentrated around areas with high abundances and that provide an array of habitats (Reidy et al. 2014). The goal should be to maintain species diversity while maintaining and expanding habitat in and around public lands through conservation easements (Rissman et al. 2007, Mac Nally et al. 2009, Bonnot et al. 2013). Many scientists have suggested management strategies to both adapt and mitigate the effects of future changes to climate through forest management focused on resilience, adaptation, and carbon sequestration (Dale et al. 2000, Millar et al. 2007, Evans and Perschel 2009, Lawler 2009). However, only a few have attempted to implement these management strategies (Schneiderman 2015, Wang et al. 2015), and even fewer have looked at how these management activities may affect wildlife. Future work exploring management aimed at mitigating and adapting to future climate change could be beneficial to species already vulnerable to climate and habitat changes.

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LITERATURE CITED

- Albright, T. P., A. M. Pidgeon, C. D. Rittenhouse, M. K. Clayton, C. H. Flather, P. D. Culbert, B. D. Wardlow, and V. C. Radeloff. 2010a. Effects of drought on avian community structure. *Global Change Biology* 16:2158–2170.
- Albright, T. P., A. M. Pidgeon, C. D. Rittenhouse, M. K. Clayton, B. D. Wardlow, C. H. Flather, P. D. Culbert, and V. C. Radeloff. 2010b. Combined effects of heat waves and droughts on avian communities across the conterminous United States. *Ecosphere* 1:12.
- Albright, T. P., A. M. Pidgeon, C. D. Rittenhouse, M. K. Clayton, C. H. Flather, P. D. Culbert, and V. C. Radeloff. 2011. Heat waves measured with MODIS land surface temperature data predict changes in avian community structure. *Remote Sensing of Environment* 115:245–254.
- Araújo, M. B., and A. T. Peterson. 2012. Uses and misuses of bioclimatic envelope modeling. *Ecology* 93:1527–1539.
- Auer, S. K., and T. E. Martin. 2013. Climate change has indirect effects on resource use and overlap among coexisting bird species with negative consequences for their reproductive success. *Global Change Biology* 19:411–419.
- Bernazzani, P., B. A. Bradley and J. J. Opperman. 2012. Integrating climate change into habitat conservation plans under the U.S. Endangered Species Act. *Environmental Management* 49:1103–1114.
- Blois, J. L., J. W. Williams, M. C. Fitzpatrick, S. T. Jackson, and S. Ferrier. 2013. Space can substitute for time in predicting climate-change effects on biodiversity. *Proceedings National Academy of Sciences USA* 110:9374–9379.
- Bolger, D. T., M. A. Patten, and D. C. Bostock. 2005. Avian reproductive failure in response to an extreme climatic event. *Oecologia* 142:398–406.
- Bonnot, T. W., F. R. Thompson III, J. J. Millsaugh, and D. T. Jones-Farrand. 2013. Landscape-based population viability models demonstrate importance of strategic conservation planning for birds. *Biological Conservation* 165:104–114.

- Both, C., and M. E. Visser. 2005. The effect of climate change on the correlation between avian life-history traits. *Global Change Biology* 11:1606–1613.
- Both, C., C. A. M. Van Turnhout, R. G. Bijlsma, H. Siepel, A. J. Van Strien, and R. P. B. Foppen. 2010. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 277:1259–1266.
- Brooks, S. P., and A. Gelman. 1998. General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics* 7:434–455.
- Carey, C. 2009. The impacts of climate change on the annual cycles of birds. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 364:3321–3330.
- Conroy, M. J., M. C. Runge, J. D. Nichols, K. W. Stodola, and R. J. Cooper. 2011. Conservation in the face of climate change: the roles of alternative models, monitoring, and adaptation in confronting and reducing uncertainty. *Biological Conservation* 144:1204–1213.
- Cox, W. A., F. R. Thompson III, and J. L. Reidy. 2013a. The effects of temperature on nest predation by mammals, birds, and snakes. *Auk* 130:784–790.
- Cox, W. A., F. R. Thompson III, J. L. Reidy, and J. Faaborg. 2013b. Temperature can interact with landscape factors to affect songbird productivity. *Global Change Biology* 19:1064–1074.
- Cumming, S. G., D. Stralberg, K. L. Lefevre, P. Sólomos, E. M. Bayne, S. Fang, T. Fontaine, D. Mazzerolle, F. K. A. Schmiegelow, and S. J. Song. 2014. Climate and vegetation hierarchically structure patterns of songbird distribution in the Canadian boreal region. *Ecography* 37:137–151.
- Dale, V. H., L. A. Joyce, S. McNulty, and R. P. Neilson. 2000. The interplay between climate change, forests, and disturbances. *Science of the Total Environment* 262:201–204.
- DeLeon, R. L., E. E. DeLeon, and G. R. Rising. 2011. Influence of climate change on avian migrants' first arrival dates. *Condor* 113:915–923.
- DesGranges, J.-L., and M.-L. LeBlanc. 2012. The influence of summer climate on avian community composition in the eastern boreal forest of Canada. *Avian Conservation and Ecology* 7:1–11.
- Dybala, K. E., J. M. Eadie, T. Gardali, N. E. Seavy, and M. P. Herzog. 2013. Projecting demographic responses to climate change: adult and juvenile survival respond differently to direct and indirect effects of weather in a passerine population. *Global Change Biology* 19:2688–2697.
- Eglinton, S. M., and J. W. Pearce-Higgins. 2012. Disentangling the relative importance of changes in climate and land-use intensity in driving recent bird population trends. *PLoS ONE* 7:e30407.
- ESRI. 2009. ArcGIS desktop: release 9.3.1. Environmental Systems Research Institute, Redlands, California, USA.
- ESRI. 2013. ArcGIS desktop: release 10.2. Environmental Systems Research Institute, Redlands, California, USA.
- Evans, A. M., and R. Perschel. 2009. A review of forestry mitigation and adaptation strategies in the Northeast U.S. *Climate Change* 96:167–183.
- Filloy, J., and M. I. Bellocq. 2013. Spatial variation in bird species abundances: environmental constraints across southern Neotropical regions. *Basic and Applied Ecology* 14:263–270.
- Forcey, G. M., G. M. Linz, W. E. Thogmartin, and W. J. Bleier. 2007. Influence of land use and climate on wetland breeding birds in the Prairie Pothole Region of Canada. *Canadian Journal of Zoology* 85:421–436.
- Forcey, G. M., G. M. Linz, W. E. Thogmartin, and W. J. Bleier. 2008. Modeling wetland blackbird populations as a function of waterfowl abundance in the Prairie Pothole Region of the United States and Canada. *Environmental Bioindicators* 3:124–135.
- Forcey, G. M., W. E. Thogmartin, G. M. Linz, W. J. Bleier, and P. C. McKann. 2011. Land use and climate influences on waterbirds in the Prairie Potholes. *Journal of Biogeography* 38:1694–1707.
- Forcey, G. M., W. E. Thogmartin, G. M. Linz, and P. C. McKann. 2014. Land use and climate affect Black Tern, Northern Harrier, and Marsh Wren abundance in the Prairie Pothole Region of the United States. *Condor* 116:226–241.
- Gesch, D., M. Oimoen, S. Greenlee, C. Nelson, M. Steuck, and D. Tyler. 2002. The National Elevation Dataset. *Photogrammetric Engineering and Remote Sensing* 68:5–11.
- Gordo, O. 2007. Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Climate Research* 35:37–58.
- Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135:147–186.
- Hamilton, C. M., S. Martinuzzi, A. J. Plantinga, V. C. Radeloff, D. J. Lewis, W. E. Thogmartin, P. J. Heglund, and A. M. Pidgeon. 2013. Current and future land use around a nationwide protected area network. *PLoS ONE* 8:e55737.
- Hamilton, C. M., W. E. Thogmartin, V. C. Radeloff, A. J. Plantinga, P. J. Heglund, S. Martinuzzi, and A. M. Pidgeon. 2014. Change in agricultural land use constrains adaptation of national wildlife refuges to climate change. *Environmental Conservation* 42:1–8.

- Hitch, A. T., and P. L. Leberg. 2007. Breeding distributions of North American bird species moving north as a result of climate change. *Conservation Biology* 21:534–539.
- Hockey, P. A. R., C. Sirami, A. R. Ridley, G. F. Midgley, and H. A. Babiker. 2011. Interrogating recent range changes in South African birds: confounding signals from land use and climate change present a challenge for attribution. *Diversity and Distributions* 17:254–261.
- Homer, C., J. Dewitz, J. Fry, M. Coan, N. Hossain, C. Larson, N. Herold, A. Mckerrow, J. N. Vandriel, and J. Wickham. 2007. Completion of the 2001 National Land Cover Database for the conterminous United States. *Photogrammetric Engineering and Remote Sensing* 73:337–341.
- IPCC. 2007. Climate change 2007: synthesis report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R. K. Pachauri, and A. Reisinger, editors.]. IPCC, Geneva, Switzerland.
- Jenouvrier, S. 2013. Impacts of climate change on avian populations. *Global Change Biology* 19:2036–2057.
- Jetz, W., D. S. Wilcove, and A. P. Dobson. 2007. Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology* 5:1211–1219.
- Jones, T., and W. Cresswell. 2010. The phenology mismatch hypothesis: Are declines of migrant birds linked to uneven global climate change? *Journal of Animal Ecology* 79:98–108.
- Keller, C. M. E., and J. T. Scallan. 1999. Potential roadside biases due to habitat changes along Breeding Bird Survey routes. *Condor* 101:50–57.
- Kellndorfer, J., W. Walker, L. LaPoint, J. Bishop, T. Cormier, G. Fiske, K. Kirsch and J. Westfall. 2011. NACP aboveground biomass and carbon baseline data (NBCD 2000), U.S.A., 2000. Data set. ORNL DAAC, Oak Ridge, Tennessee. Available on-line <http://daac.ornl.gov>.
- La Sorte, F. A., and F. R. Thompson III. 2007. Poleward shifts in winter ranges of North American birds. *Ecology* 88:1803–1812.
- Lawler, J. J. 2009. Climate change adaptation strategies for resource management and conservation planning. *Annals of the New York Academy of Sciences* 1162:79–98.
- LeBrun, J. J., W. E. Thogmartin, and J. R. Miller. 2012. Evaluating the ability of regional models to predict local avian abundance. *Journal of Wildlife Management* 76:1177–1187.
- Lemoine, N., H.-G. Bauer, M. Peintinger, and K. Böhring-Gaese. 2007. Effects of climate and land-use change on species abundance in a Central European bird community. *Conservation Biology* 21:495–503.
- Li, A., C. Huang, G. Sun, H. Shi, C. Toney, Z. Zhu, M. G. Rollins, S. N. Goward, and J. G. Masek. 2011. Modeling the height of young forests regenerating from recent disturbances in Mississippi using Landsat and ICESat data. *Remote Sensing of Environment* 115:1837–1849.
- Link, W. A., C. Emmanuelle, J. D. Nichols, and E. G. Cooch. 2002. Of bugs and birds: Markov chain Monte Carlo for hierarchical modeling in wildlife research. *Journal of Wildlife Management* 66:277–291.
- Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. WinBUGS—a Bayesian modelling framework: concepts, structure, and extensibility. *Statistics and Computing* 10:325–337.
- Lusk, J. J., F. S. Guthery, and S. J. DeMaso. 2001. Northern bobwhite (*Colinus virginianus*) abundance in relation to yearly weather and long-term climate patterns. *Ecological Modelling* 146:3–15.
- Mac Nally, R., A. F. Bennett, J. R. Thomson, J. Q. Radford, G. Unmack, G. Horrocks, and P. A. Vesk. 2009. Collapse of an avifauna: climate change appears to exacerbate habitat loss and degradation. *Diversity and Distributions* 15:720–730.
- Mantyka-Pringle, C. S., T. G. Martin, and J. R. Rhodes. 2012. Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Global Change Biology* 18:1239–1252.
- Matthews, S. N., L. R. Iverson, A. M. Prasad, and M. P. Peters. 2011. Changes in potential habitat of 147 North American breeding bird species in response to redistribution of trees and climate following predicted climate change. *Ecography* 34:933–945.
- McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS v3: Spatial pattern analysis program for categorical maps. University of Massachusetts, Amherst, Massachusetts, USA.
- McRae, B. H., N. H. Schumaker, R. B. McKane, R. T. Busing, A. M. Solomon, and C. A. Burdick. 2008. A multi-model framework for simulating wildlife population response to land-use and climate change. *Ecological Modelling* 219:77–91.
- Meynard, C. N., and J. F. Quinn. 2008. Bird metacommunities in temperate South American forest: vegetation structure, area, and climate effects. *Ecology* 89:981–990.
- Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. *Ecological Applications* 17:2145–2151.
- Murray, L. D., C. A. Ribic, W. E. Thogmartin, and M. G. Knutson. 2008. Accuracy assessment of predictive

- models of grassland bird abundances in the Prairie Hardwood Transition Bird Conservation Region. *Condor* 110:747–755.
- Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecology and Biogeography* 12:361–371.
- Pimm, S. L. 2008. Biodiversity: climate change or habitat loss—Which will kill more species? *Current Biology* 18:R117–R119.
- PRISM Climate Group. 2011. PRISM Climate database. <http://www.prism.oregonstate.edu>
- R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reidy, J. L., F. R. Thompson III, and S. W. Kendrick. 2014. Breeding bird response to habitat and landscape factors across a gradient of savanna, woodland, and forest in the Missouri Ozarks. *Forest Ecology and Management* 313:34–46.
- Rissman, A. R., L. Lozier, T. Comendant, P. Kareiva, J. M. Kiesecker, M. R. Shaw, and A. M. Merenlender. 2007. Conservation easements: biodiversity protection and private use. *Conservation Biology* 21:709–718.
- Rodenhouse, N. L., S. N. Matthews, K. P. McFarland, J. D. Lambert, L. R. Iverson, A. Prasad, T. S. Sillett, and R. T. Holmes. 2008. Potential effects of climate change on birds of the Northeast. *Mitigation and Adaptation Strategies for Global Change* 13:517–540.
- Rolland, V., J. A. Hostetler, T. C. Hines, H. F. Percival, and M. K. Oli. 2011. Factors influencing reproductive performance of northern bobwhite in South Florida. *European Journal of Wildlife Research* 57:717–727.
- Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421:57–60.
- RStudio Team. 2014. RStudio: integrated development environment for R (version 0.98.1091). RStudio, Inc., Boston, Massachusetts, USA.
- Saino, N., et al. 2011. Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 278:835–842.
- Salewski, V., W. M. Hochachka, and W. Fiedler. 2013. Multiple weather factors affect apparent survival of European passerine birds. *PLoS ONE* 8:e59110.
- Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Jr Ziolkowski, and W. A. Link. 2014. The North American Breeding Bird Survey, results and analysis 1966–2012. Version 02.19.2014. USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.
- Scheffers, B. R., D. P. Edwards, A. Diesmos, S. E. Williams, and T. A. Evans. 2014. Microhabitats reduce animal's exposure to climate extremes. *Global Change Biology* 20:495–503.
- Schneiderman, J. E. 2015. Climate change in the Missouri Central Hardwood Region: consequences for forest landscapes, and management strategies. Dissertation. University of Missouri, Columbia, Missouri, USA.
- Seavy, N. E., T. Gardali, G. H. Golet, F. T. Griggs, C. A. Howell, R. Kelsey, S. L. Small, J. H. Viers, and J. F. Weigand. 2009. Why climate change makes riparian restoration more important than ever: recommendations for practice and research. *Ecological Restoration* 27:330–338.
- Sekercioglu, C. H., S. H. Schneider, J. P. Fay, and S. R. Loarie. 2008. Climate change, elevational range shifts, and bird extinctions. *Conservation Biology* 22:140–150.
- Skagen, S. K., and A. A. Yackel Adams. 2012. Weather effects on avian breeding performance and implications of climate change. *Ecological Applications* 22:1131–1145.
- Spiegelhalter, D. J., N. G. Best, B. P. Carlin, and A. van der Linde. 2002. Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society: Series B, Statistical Methodology* 64:583–639.
- Stephenson, J. A., K. P. Reese, P. Zager, P. E. Heekin, P. J. Nelle, and A. Martens. 2011. Factors influencing survival of native and translocated mountain quail in Idaho and Washington. *Journal of Wildlife Management* 75:1315–1323.
- Streby, H. M., J. P. Loegering, and D. E. Andersen. 2012. Spot-mapping underestimates song-territory size and use of mature forest by breeding golden-winged warblers in Minnesota, USA. *Wildlife Society Bulletin* 36:40–46.
- Thogmartin, W. E. 2010. Modeling and mapping golden-winged warbler abundance to improve regional conservation strategies. *Avian Conservation and Ecology* 5:12.
- Thogmartin, W. E., and M. G. Knutson. 2007. Scaling local species-habitat relations to the larger landscape with a hierarchical spatial count model. *Landscape Ecology* 22:61–75.
- Thogmartin, W. E., J. R. Sauer, and M. G. Knutson. 2004. A hierarchical spatial model of avian abundance with application to Cerulean Warblers. *Ecological Applications* 14:1766–1779.
- Thomas, C. D., and J. J. Lennon. 1999. Birds extend their ranges northwards. *Nature* 399:213.
- Townsend, A. K., T. S. Sillett, N. K. Lany, S. A. Kaiser, N. L. Rodenhouse, M. S. Webster, and R. T. Holmes. 2013. Warm springs, early lay dates, and double

- brooding in a North American migratory songbird, the black-throated blue warbler. *PLoS ONE* 8:e59467.
- Travis, J. M. J. 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 270:467–473.
- Urban, M. C., P. L. Zarnetske, and D. K. Skelly. 2013. Moving forward: dispersal and species interactions determine biotic responses to climate change. *Annals of the New York Academy of Sciences* 1297:44–60.
- U.S. NABCI Committee. 2000. North American bird conservation initiative: bird conservation region descriptions. U.S. NABCI Committee, Arlington, Virginia, USA.
- Visser, M. E., L. te Marvelde, and M. E. Lof. 2012. Adaptive phenological mismatches of birds and their food in a warming world. *Journal of Ornithology* 153:S75–S84.
- Wang, W. J., H. S. He, F. R. Thompson III, J. S. Fraser, B. B. Hanberry, and W. D. Dijak. 2015. The importance of succession, harvest, and climate change in determining future forest composition. *Ecosphere* 6:277.
- Whitehouse, M. J., N. M. Harrison, J. Mackenzie, and S. A. Hinsley. 2013. Preferred habitat of breeding birds may be compromised by climate change: unexpected effects of an exceptionally cold, wet spring. *PLoS ONE* 8:e75536.
- Wilson, S., S. L. LaDeau, A. P. Tøttrup, and P. P. Marra. 2011. Range-wide effects of breeding- and nonbreeding-season climate on the abundance of a Neotropical migrant songbird. *Ecology* 92:1789–1798.
- Wuebbles, D. J. and K. Hayhoe. 2004. Climate change projections for the United States Midwest. *Mitigation and Adaptation Strategies for Global Change* 9:335–363.
- Zimmerman, G. S., R. J. Gutiérrez, W. E. Thogmartin, and S. Banerjee. 2009. Multiscale habitat selection by ruffed grouse at low population densities. *Condor* 111:294–304.
- Zuckerberg, B., A. M. Woods, and W. F. Porter. 2009. Poleward shifts in breeding bird distributions in New York State. *Global Change Biology* 15:1866–1883.

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