

Dynamic-landscape metapopulation models predict complex response of wildlife populations to climate and landscape change

THOMAS W. BONNOT,^{1,†} FRANK R. THOMPSON III,² AND JOSHUA J. MILLSPAUGH³

¹*School of Natural Resources, University of Missouri, 302 Natural Resources Building, Columbia, Missouri 65211 USA*

²*United States Forest Service, Northern Research Station, University of Missouri-Columbia, 202 Natural Resources Building, Columbia, Missouri 65211 USA*

³*Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, W. A. Franke College of Forestry and Conservation, University of Montana, Missoula, Montana 59812 USA*

Citation: Bonnot, T. W., F. R. Thompson III, and J. J. Millsbaugh. 2017. Dynamic-landscape metapopulation models predict complex response of wildlife populations to climate and landscape change. *Ecosphere* 8(7):e01890. 10.1002/ecs2.1890

Abstract. The increasing need to predict how climate change will impact wildlife species has exposed limitations in how well current approaches model important biological processes at scales at which those processes interact with climate. We used a comprehensive approach that combined recent advances in landscape and population modeling into dynamic-landscape metapopulation models (DLMPs) to predict responses of two declining songbird species in the central hardwoods region of the United States to changes in forest conditions from climate change. We modeled wood thrush (*Hylocichla mustelina*) and prairie warbler (*Setophaga discolor*) population dynamics and distribution throughout the central hardwoods based on estimates of habitat and demographics derived from landscapes projected through 2100 under a current climate scenario and two future climate change scenarios. Climate change, natural forest succession, and forest management interacted to change forest structure and composition over time, variably affecting the distribution and amount of habitat of the two birds. The resulting changes in habitat and metapopulation processes produced contrasting predictions for future populations. Wood thrush, a forest generalist, showed little response to climate-driven forest change but declined by >25% due to reduced productivity associated with existing forest fragmentation across much of the region. Prairie warblers initially declined due to loss of habitat resulting from current land management; however, after 2050 cumulative effects of climate change on forest structure created enough habitat in source landscapes to restore population growth. These species-specific responses were the result of interactions among climate, landscape, and population processes. We suggest relationships between climate change, succession, and land management are species specific and important determinants of future wildlife populations and that DLMPs are a comprehensive approach that can capture such processes to generate more realistic predictions of populations under climate change.

Key words: distribution; habitat; landscape; population dynamics; prairie warbler; wood thrush.

Received 5 June 2017; **accepted** 8 June 2017. Corresponding Editor: Debra P. C. Peters.

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† **E-mail:** bonnott@missouri.edu

INTRODUCTION

One of the most significant questions in wildlife conservation is how climate change will affect biodiversity. Biodiversity and ecosystems

are more stressed than at any comparable period of human history because they are intrinsically dependent on climate and thus impacted by its changes (Staudinger et al. 2013). Many species are at a far greater risk of extinction than in the

recent geological past (Fischlin et al. 2007). Climate change has caused significant population declines and been linked to species extinctions (Monzón et al. 2011, Selwood et al. 2015). Climate change is also causing shifts in species' distributions and phenologies, which could substantially alter ecosystem structure and function (Schneider and Root 2002, Thomas et al. 2004). The proactive actions needed to prevent such outcomes have left managers and biologists across the globe looking for approaches that can predict how species and populations will respond to climate change and other aspects of global change (Staudinger et al. 2013).

A variety of methods have been employed to address such a broad question. Correlative and mechanistic models are two approaches to predicting species impacts that have been frequently contrasted in recent years (Moritz and Agudo 2013). Correlative species distribution models (SDMs; also known as ecological niche models or bioclimatic envelope models) predict changes in the ranges of species using statistical associations between climate/environmental variables and patterns of species distribution (Guisan and Thuiller 2005, Elith and Leathwick 2009, Fordham et al. 2012). These models have seen widespread use due to the availability of methods, data, and their ability to predict climate impacts over range-wide scales (Fordham et al. 2013, Moritz and Agudo 2013). Projecting potential changes in distribution is a sensible goal for guiding future conservation, given accumulating evidence of these effects (Parmesan 2006, LaSalle and Thompson 2007, Chen et al. 2011). However, SDMs have been criticized for their inability to account for the variety of processes affecting populations (Fischlin et al. 2007, Brook et al. 2008). Although SDMs often assume that climate alone drives shifts in species distribution, it is likely that responses to other environmental threats might overshadow those related to climate (Brook et al. 2008, Swab et al. 2015). Indeed, climate change is occurring against the backdrop of a wide range of land management and other environmental and anthropogenic stressors, which have caused dramatic changes to landscapes already (Staudinger et al. 2013). The lack of a direct mechanistic basis could predispose these models to suggest more extreme responses than might actually occur (Moritz and

Agudo 2013). Most importantly, a lack of mechanistic processes in SDMs prevents modeling changes in population dynamics under climate change which would provide important information about persistence (Fordham et al. 2012). Distributional change is one of the last symptoms of species decline, allowing populations to be at risk without any shifts in range or distribution (Selwood et al. 2015).

Recent mechanistic approaches represent an increased awareness of the processes that determine how species respond to climate change. Species responses to climate change are influenced by more than changes in habitat alone. Climate has numerous effects on demographic rates and population processes (Selwood et al. 2015), and species interactions and interactions between demographic and landscape dynamics all drive populations status and trends (Keith et al. 2008, Millspaugh et al. 2009). Therefore, efforts to account for these processes and how climate affects them have resulted in more robust predictions and better capture context-dependent variability in species responses (Monahan 2009, Cheung et al. 2012, Fordham et al. 2013). Recently, some have shown that still a more complete understanding of a population impacts is possible by explicitly integrating climate with demographic processes (Keith et al. 2008, Brook et al. 2008). Dynamic-landscape metapopulation models (DLMP; *sensu* Akçakaya 2000, Larson et al. 2004) represent this approach through an integration of landscape, habitat, and metapopulation modeling. These models have experienced renewed use in recent years because of their ability to provide a spatial representation of how landscapes change through time and how species respond to this spatially and temporally variable environment (e.g., Fordham et al. 2013, Franklin et al. 2014). Because population responses to changing landscapes can be complex and sometimes counterintuitive (Bonnot et al. 2013), DLMPs have provided an important step toward realistically predicting species impacts from climate change.

Mechanistic approaches such as DLMPs still face limitations in complexity and scope. An ideal approach would be complex enough to model important processes driving population dynamics and distribution at the scales at which those processes interact. However, if identifying climate

effects on species' habitat or demographic rates is difficult, then spatially integrating those effects with other metapopulation processes across entire landscapes or regions is improbable. As a result, information on population dynamics provided by mechanistic approaches is limited to specific landscapes or study areas, not the regional or range-wide scales that can inform species distributions under climate change (Akçakaya and Brook 2009). Although there are more examples of DLMPs for plant species under climate change (e.g., Regan et al. 2012, Franklin et al. 2014), these models still lack important mechanisms by overlooking various ecosystem and landscape processes affecting plants (Wang et al. 2015). Characterizing wildlife habitat involves representing both the structure and composition of habitat. Therefore, modeling changes in habitat for animals compounds this problem by requiring data on climate-induced changes in entire vegetation communities through time. Forest landscape models such as LANDIS PRO can account for many of these processes to inform wildlife habitat models, but until recently have not integrated climate (Wang et al. 2015). Ultimately, achieving a comprehensive understanding of wildlife responses to climate change is going to require an approach that can integrate climate, landscape, habitat, and metapopulation processes across a range of scales to predict changes in dynamics and distributions overtime.

We advanced the capability of DLMPs to address climate change by incorporating two recent developments in landscape and metapopulation modeling. Recent efforts to extend landscape-based population modeling to regional scales provided the ability to link local habitat and demographics with population growth over tens of millions of hectares (Bonnot et al. 2011, 2013). The capability to model changes in forest structure and composition under climate change at similarly large, regional scales has provided an approach to predicting how wildlife habitat might change in the future (Wang et al. 2015, 2016). Our objective was to integrate Bonnot et al.'s (2011) regional population models with Wang et al.'s (2015) forest landscape projections to predict impacts of landscape and climate change on populations of two species of songbirds in the Central Hardwoods forest of the Midwestern United States under three future climate scenarios. We

picked two birds species, wood thrush (*Hylocichla mustelina*) and prairie warblers (*Setophaga discolor*), with contrasting demographics and habitat, to demonstrate how this approach can account for interactions among species demographics and landscape and climate change to predict population change. Furthermore, these species are a conservation concern in the Eastern United States because of long-term population declines.

METHODS

Study area

We studied a 39.5 million ha (395,519 km²) portion of the Central Hardwoods forest in the center of the United States (Fig. 1). The area encompasses a variety of vegetation, terrains, soils, and climates (Cleland et al. 2007). The topography varies from relatively flat Central Till Plains to open hills and irregular plains (e.g., Interior Low Plateau), to highly dissected Ozark Highlands. The region supported a diversity of forest ecosystems, including upland oak (*Quercus* spp.)–hickory (*Carya* spp.) forests and oak-pine (*Pinus* spp.) forests, woodlands, and savannas. While a portion of the land that was historically forested in the Central Hardwoods remains so today, glades and woodlands and other communities have been lost and dramatically altered (Fitzgerald et al. 2005). Widespread logging in the early part of the 20th century and fire suppression in subsequent decades resulted in conversion of glade, barren, and pine woodland habitats to oak or oak-pine forests. Forests in this region have also been fragmented by agriculture and urban development.

The loss of these communities as habitat combined with the effects of fragmentation has likely contributed to long-term population declines of wood thrush and prairie warblers, and conservation organizations consider them as species of concern within the Central Hardwoods (Panjabi et al. 2005, U.S. Department of the Interior Fish and Wildlife Service 2008, Sauer et al. 2017). Prairie warblers are declining by an estimated 1.98% annually (Sauer et al. 2017). Prairie warblers breed in shrubby vegetation under an open or semi-open canopy such as in glades, savannas, abandoned fields, and regenerating forests. Their decline is likely the result of loss of this habitat over much of the region and reduced productivity

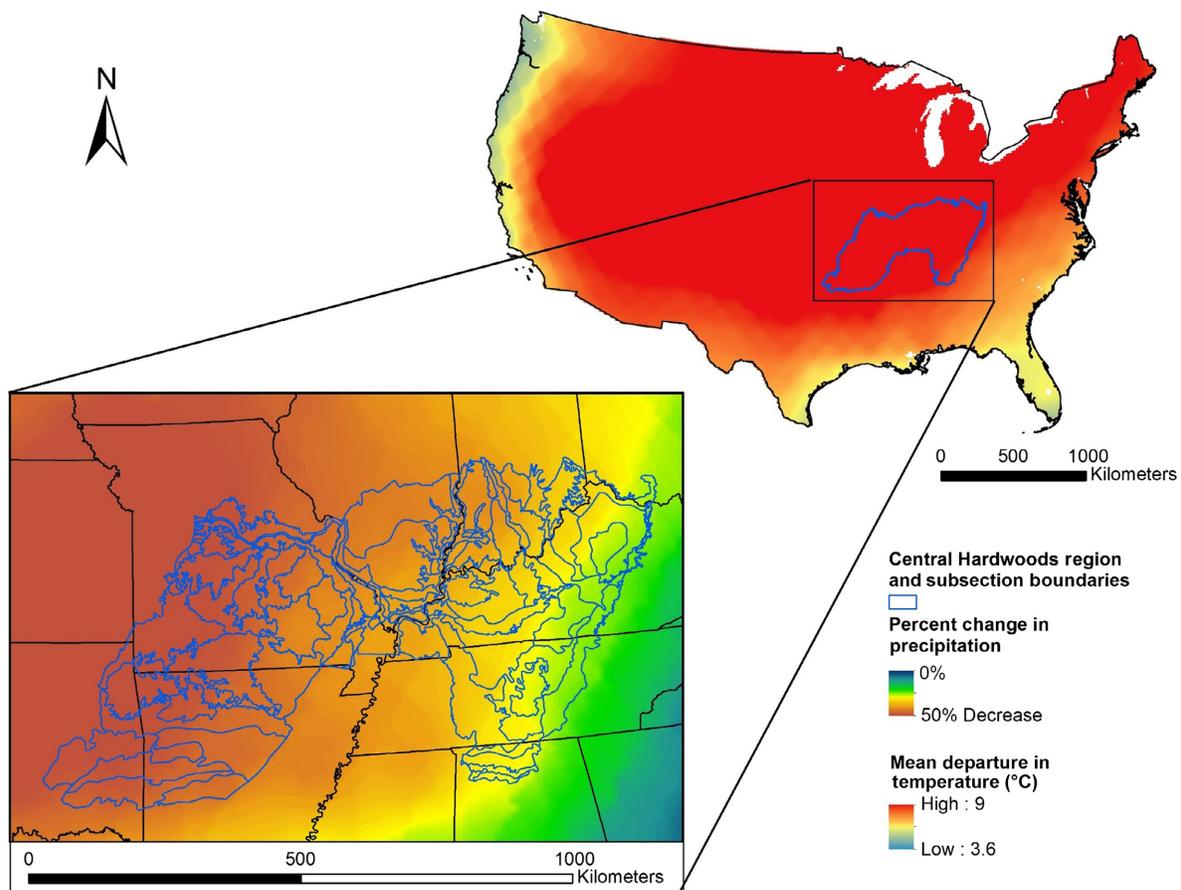


Fig. 1. Dynamic-landscape metapopulation models were developed for two species of songbirds in the Central Hardwoods forested region in central United States. The models integrate habitat with metapopulation processes to predict future changes in population dynamics and distribution throughout the region's ecological subsections. Estimates of habitat incorporated changes in the region's forest through 2100 under varying degrees of climate change, which is expected to increase temperature (main figure) and reduce summer precipitation (inset) under a GFDL-A1Fi scenario.

due to parasitism associated with fragmentation (Nolan et al. 2014). Wood thrush are much more abundant than prairie warblers because they are distributed throughout closed-canopy, mid-successional forest, which is abundant in the region (Evans et al. 2011). However, wood thrush numbers have declined 0.6% annually since 1966 (Sauer et al. 2017) and declines are at least partly due to higher predation and parasitism in fragmented forests (Robinson et al. 1995).

Modeling approach

We combined three components that are integral to DLMP approaches (Fig. 2; Bekessy et al.

2009). We begin with projections of the landscape into the future under forest management and climate change scenarios in the form of a series of spatial data grids that map the distribution, structure, and composition of forests at specified time steps. Next, we translated these landscape projections into species' habitat and demographics at each time step. We considered known relationships between habitat and population processes (e.g., abundance, reproduction, survival, or dispersal). Finally, we incorporated these spatially and temporally varying demographics in a metapopulation model that included stochasticity and uncertainty. The resulting model provided a

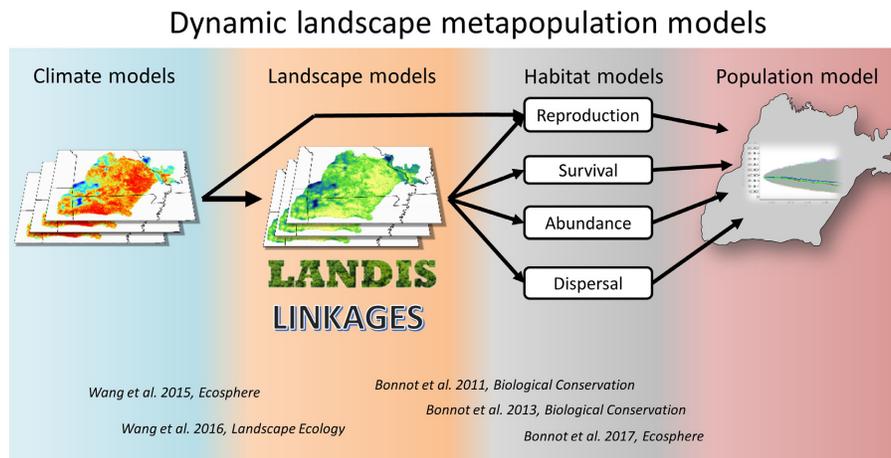


Fig. 2. Overview of dynamic-landscape metapopulation modeling approach used to project the impacts of climate change on landscapes, habitat, and wildlife populations across the Central Hardwoods region.

spatially and temporally explicit representation of habitat and population dynamics and distribution throughout the region.

Future landscape data

We used recent projections of the structure and composition of forests in the Central Hardwoods from 2000 to 2300 under three climate change scenarios (Wang et al. 2015, 2016). Wang et al. used the forest landscape model LANDIS PRO to project forest changes due to succession, harvest, and climate change. LANDIS PRO is a spatial model that operates across grid cells in a landscape, modeling cell-level processes that include species-specific seed dispersal, establishment, growth, competition, and mortality and landscape-level processes such as wind throw and tree harvest. In their scenarios, forest management reflected current patterns in tree harvest throughout the region observed from region-wide Forest Inventory and Analysis data from 1995 to 2005. Wang et al. (2015) directly incorporated changes in climate in LANDIS PRO via the early growth and establishment of different tree species and the maximum allowable tree biomass based on their attributes and cell locations. They estimated these parameters with the ecosystem model LINKAGES III, which integrates temperature and precipitation data with nitrogen availability and soil moisture to model individual tree species growth and mortality at a site (Dijak et al. 2016).

The landscapes were modeled under a current climate scenario and two climate change scenarios based on combinations of general circulation models (GCMs) and emission scenarios from the IPCC (2007). The current climate scenario used temperature, precipitation, and wind speed data for the 30-yr period from 1980 to 2009 observed throughout the region (Wang et al. 2015). The two IPCC-derived climate change scenarios CGCM.T47-A2 and GFDL-A1Fi represented alternative degrees of climate change. The GFDL-A1Fi scenario combined a more substantial and immediate increase in greenhouse gas emissions (A1Fi) with a model that is more sensitive to that increase (GFDL; IPCC 2007). Thus, the GFDL-A1Fi scenario presented more severe changes in climate relative to the CGCM.T47-A2 scenario. For example, by the end of the century the GFDL-A1Fi scenario projects a 4.5°C increase in the mean annual daily maximum temperature as well as twice the number of consecutive summer dry days as has been observed in the region (Fig. 1; Girvetz et al. 2009).

Wang et al. (2015) estimated forest projections from 2000 to 2300 at 10-yr time steps and at a 270-m resolution. The projections comprised cell-based estimates of importance values, basal area, and number and diameter at breast height (dbh) of trees by species and age cohort. Their results suggested a prolonged period (i.e., 300 yr) before substantial shifts in forest composition would

occur in response to climate change. When shifts did occur, it was toward more southern and xeric species and lesser northern and mesic species. Although there were no significant changes in overall tree species composition among current climate and climate change scenarios in the region's midterm (100 yr), forests did become more xeric as indicated by lower basal areas and tree densities. The greatest of these changes occurred in the southwest portion of the Central Hardwoods (Wang et al. 2015).

Habitat modeling

We employed habitat models to link landscapes to three demographic processes: the distribution of carrying capacity (K) and abundance, breeding productivity, and dispersal. These models are meta-analytic approaches that integrate published data and findings to quantify habitat and demographic processes (Dijak and Rittenhouse 2009). Although partly conceptual, the flexibility of these approaches allows them to incorporate processes from a range of studies and sites to model local habitat throughout entire regions.

We modeled the distribution of wood thrush and prairie warbler abundance and K using landscape-scale Habitat Suitability Index (HSI) models. Previously developed specifically for the Central Hardwoods, the HSIs indexed the suitability of 30×30 m cells based on the habitat attributes of the cell and the surrounding landscape (Tirpak et al. 2009a). Both the prairie warbler and wood thrush models have been independently verified and validated with data from the North American Breeding Bird Survey, a long-term, large-scale bird monitoring program (Tirpak et al. 2009b). The HSI models combined characteristics of land cover (as defined by the National Land Cover Data, NLCD; Fry et al. 2011), landform, and forest seral stage with additional variables that reflected the wood thrush's use of mature hardwood and mixed forests with relatively closed canopies. Prairie warblers inhabit a variety of early successional forest types as well as glades and woodlands. Therefore, an open canopy and shrubby understory were important structural components considered in the prairie warbler model. In addition, HSI models captured each species sensitivity to habitat patch size and the predominance of forest in the surrounding landscape (Tirpak et al. 2009a). See

Appendix S1 for a full description of the HSI models.

We derived habitat variables from LANDIS PRO outputs through geoprocessing in ArcGIS 10.2 (Environmental Systems Research Institute, Redlands, California, USA). We identified NLCD land cover classes by comparing the relative importance values (Smith and Smith 2001) estimated by LANDIS PRO for deciduous versus coniferous species. We classified cells as deciduous forest if the combined importance of deciduous species surpassed 65% and coniferous forest if such species comprised >47% of the cell's importance value. Forested cells not classified as either deciduous or coniferous were assigned to the mixed forest type. We further classified deciduous forest cells as woody wetlands for any cells with this original NLCD class. We used the 65% and 47% thresholds because they produced land cover estimates for the initial (2000) landscape proportional to actual NLCD classes for the same region. We grouped classes into either forest or nonforest to estimate forest patch sizes and the percent forest cover within 1 km and 10 km. We classified forest seral stage as shrub/seedling, sapling, pole, or saw based on quadratic mean tree diameter calculated from LANDIS PRO projections of basal area and tree density according to Tirpak et al. (2009a). We also calculated total tree stocking, from which we estimated canopy closure based on empirical associations between stocking and canopy closure (Johnson et al. 2009, Blizzard et al. 2013). We used the density of all tree species in the 0–10 age cohort output by LANDIS PRO to approximate the density of small stems (<2.54 cm dbh) because most hardwood species take ~10 yr to reach 2.54 cm dbh (Johnson et al. 2009).

We modeled habitat at a 30-m resolution by resampling outputs from Wang et al. (2015) and augmenting gaps in habitat characteristics using spatially explicit, remotely sensed data from ancillary sources. We used 2001 canopy cover estimates from the Multi-Resolution Land Characteristics Consortium (Homer et al. 2004). We obtained data on dbh and small-stem density from efforts integrating Forest Inventory and Analysis data and MODIS imagery (Wilson et al. 2012). For these cells, we held values constant over time.

We followed Bonnot et al.'s (2013) approach to estimating K for cells through a relationship

between HSI and densities of prairie warblers and wood thrush found in the literature (Table 1). In the absence of data, we assumed densities of birds reached their maximums at HSI = 1 and declined linearly with HSI. We then scaled density by the area of cells and spatially filtered areas of the landscape that could not support at least one territory given maximum territory sizes for each species. This process more realistically captured the interaction between spatial and resource limitations inherent in estimating K than simply summing K across all cells (see Donovan et al. 2012). Shifts in distribution of habitat over time due to the effects of climate and management were captured by subsequent changes in the distribution of K . We estimated wood thrush and prairie warbler initial distributions in year 2000 throughout the region as a percentage of K (Table 1). We modeled breeding productivity of wood thrush and prairie warblers

throughout the Central Hardwoods over time using a Relative Productivity Index model (RPI; Bonnot et al. 2011). This index of reproductive success of birds ranges 0–1 and is based on the fragmentation paradigm that success is lower in fragmented landscapes and proximate to edge. This concept has a strong basis based on the original studies reporting these effects (Donovan et al. 1995, Robinson et al. 1995, Thompson et al. 2002, Cox et al. 2013) and subsequent reviews and meta-analyses (Chalfoun et al. 2002, Stephens et al. 2004, Lloyd et al. 2005). We estimated RPI for each 30-m cell using the amount of forest cover in a 10 km radius and edge within 200 m. We applied RPIs to the maximum possible productivity identified for each species from the literature to estimate fertility values throughout the region (see Appendix S1 for specific methods).

Finally, we used the dispersal model of Bonnot et al. (2011) to estimate cell-based movements

Table 1. Demographic parameters used in dynamic-landscape metapopulation models for wood thrush and prairie warblers in the Central Hardwoods in the Midwestern United States.

Parameter	Wood thrush		Prairie warbler	
	Estimate	Source	Estimate	Source
Carrying capacity (pairs/ha) at HSI = 1	0.50	Thompson et al. (1992), Roth et al. (1996), Gram et al. (2003), Wallendorf et al. (2007)	1.00	Fink (2003)
Initial abundance (% of carrying capacity)	0.12	Thompson et al. 1992), Gram et al. (2003), Wallendorf et al. (2007)	0.50	Thompson et al. (1992), Fink (2003), Brito-Aguilar (2005), Wallendorf et al. (2007)
Maximum maternity (fem/fem/year)	1.45	Donovan et al. (1995), Anders et al. (1997), Ford et al. (2001)	1.55	Fink (2003), Nolan et al. (2014)
Adult survival	0.61	Conway et al. (1995), Donovan et al. (1995), Powell et al. (2000), Simons et al. (2000)	0.60	Lehnen and Rodewald (2009), Nolan et al. (2014)
Juvenile survival	0.29	Anders et al. (1997)	0.32	Nolan et al. (2014)
Parametric uncertainty (SD)				
Maternity	0.25	Roth et al. (1996)	0.36	Roth et al. (1996)
Adult survival	0.005		0.005	
Juvenile survival	0.005		0.005	
Environmental stochasticity (CI)				
Fertility	0.27	Roth et al. (1996)	0.27	Roth et al. (1996)
Juvenile survival	0.25	Brown and Roth (2004), Schmidt et al. (2008)	0.15	Larson et al. (2004)
Adult survival	0.10	Brown and Roth (2004)	0.10	Brown and Roth (2004)
Demographic stochasticity	Yes		Yes	
Density dependence	Modified ceiling		Modified ceiling	
Percentage of juveniles dispersing annually	90%	Evans et al. (2011)	90%	Nolan et al. (2014)
Percentage of adults dispersing annually	10%	Evans et al. (2011)	20%	Nolan et al. (2014)

Note: Parameter uncertainty and environmental stochasticity are specified by standard deviation (SD) and coefficient of variation (CI), respectively.

of dispersing individuals to the surrounding landscape based on a negative exponential function of distance between cells, weighted by K of the destination cell. Weighting by carrying capacity allowed changes in future dispersal movements to reflect shifts in the distribution of habitat in the region over time. See Appendix S1 for a full description of all habitat modeling.

Population modeling

We modeled regional population growth of wood thrush and prairie warblers through 2100 based on landscapes by treating ecological subsections as subpopulations in a metapopulation model and summarizing their demographics for each subsection over time. The region contained 71 subsections which we delineated into 87 unique subpopulations that ranged in size from 5 to 24,000 km² (Fig. 1; Cleland et al. 2007).

For each subpopulation, we summarized results of the habitat models to obtain estimates of initial abundance and K at each decade. We averaged cell fertilities in each subpopulation, weighted by their K , so that estimates of productivity for subpopulations reflected areas where breeding occurred. We derived relative rates of dispersal among subpopulations by combining assumptions about the proportion of birds dispersing with relative estimates of the cell-based movements of those dispersers to the surrounding landscape (Bonnot et al. 2011). We calculated yearly values of demographics by linearly interpolating between decadal estimates because the landscape projections were for 10-yr time steps. Although landscape projections were available through 2300, we only modeled the first 100 yr given the uncertainty associated with predicting population growth.

We developed female-only, Lefkovich matrix models comprising adult and juvenile stages in R v3.0.1 (R Core Team 2016). We set adult and juvenile survival in prairie warblers and wood thrush at 0.60/0.32 and 0.61/0.29, respectively, and assumed a post-breeding census (Table 1). We redistributed dispersers among the subpopulations according to multinomial distributions with probabilities equal to the relative dispersal rates for that year. We modified the commonly referred to ceiling density dependence (Akçakaya 2000) such that individuals over K in a population were prohibited from breeding but could remain in the

population or disperse (Bonnot et al. 2013), as nonbreeding “floater” adults are relatively common in passerine populations (Smith 1978, Bayne and Hobson 2002).

To quantify viability or risk under the climate scenarios, we used Monte Carlo simulations to induce parameter uncertainty and stochasticity in our population dynamics. We simulated parameter uncertainty by sampling a different survival and fertility rate in each of the 1000 iterations from beta and gamma distributions, respectively, with means equal to their overall estimates and corresponding error, derived from the literature (Table 1; McGowan et al. 2011). In each iteration, the rates drawn were used to construct beta and lognormal distributions, from which annual survival and fertility rates could be drawn. Patterns in annual survival rates were correlated among subpopulations based on a negative exponential relationship with the distances among them (Bonnot et al. 2011). We based variances for these distributions on the amount of temporal variation empirically observed in survival or reproduction (Table 1). In each year, we modeled demographic stochasticity by drawing the number of survivors and the number of young produced in each stage each year from binomial and Poisson distributions, respectively. An example of the R code for these models can be found in Data S1.

RESULTS

Complex shifts in the roles of forest succession and management relative to climate change differentially affected habitats for the two species over the course of the next century. The dominant processes affecting forest change in the first 50 yr were succession and management that produced an aging forest. As a result, wood thrush habitat increased the first 50 yr under all climate scenarios (Fig. 3a). Increases in habitat and, consequently, K leveled off the latter half of the century with K for the two climate change scenarios <5% lower than for current climate (current: 7,581,855 females; CGCM.T47-A2: 7,364,356 females; GFDL-A1FI: 7,266,566 females). The distribution of wood thrush habitat remained mostly constant across subpopulations, with most habitat occurring in the Ozarks subsections of south-central Missouri. Counter to wood thrush, prairie

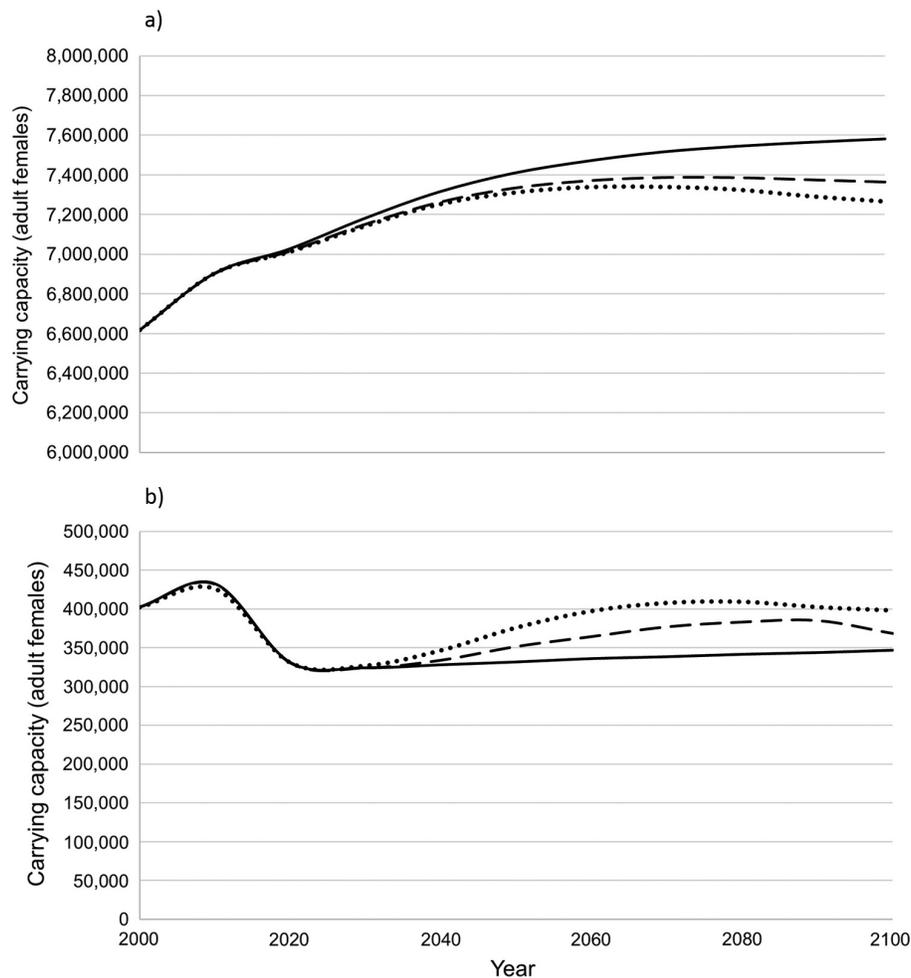


Fig. 3. Impacts of landscape change from climate change on (a) wood thrush and (b) prairie warbler habitat in the Central Hardwoods as indicated by their carrying capacities under a current climate scenario (solid), a moderate CGCM.T47-A2 climate change scenario (dashed), and an extreme climate change GFDL-A1Fi scenario (dotted).

warbler K declined sharply across the region over the first three decades for all scenarios (Fig. 3b). However, while K increased only slightly under the current climate after 2030, K increased more under both climate change scenarios as increasing effects of climate change resulted in more open forests in southwestern subsections. Carrying capacity increased as much as 88% after 2040 in these subsections causing a significant shift in the distribution of habitat under climate change and a >20% rise in K under the GFDL-A1Fi scenario than the current climate (Fig. 3b).

The changes in habitat resulted in equally complex effects on population dynamics and

distribution. Wood thrush population dynamics were unaffected by climate change. Despite increasing habitat in the region, we projected >25% declines in wood thrush abundance from the initial estimate of 794,321 adult females under all climate scenarios by 2100 (Fig. 4a). Projected declines averaged <1% per year for all scenarios, but annual dynamics of the regional population ranged between a 3.8% drop to 2.5% growth from year to year (Table 2). These declines were driven by low reproduction in many subsections resulting from habitat fragmentation; however, subpopulations in the Missouri Ozarks grew more than 50%, which concentrated the distribution of wood

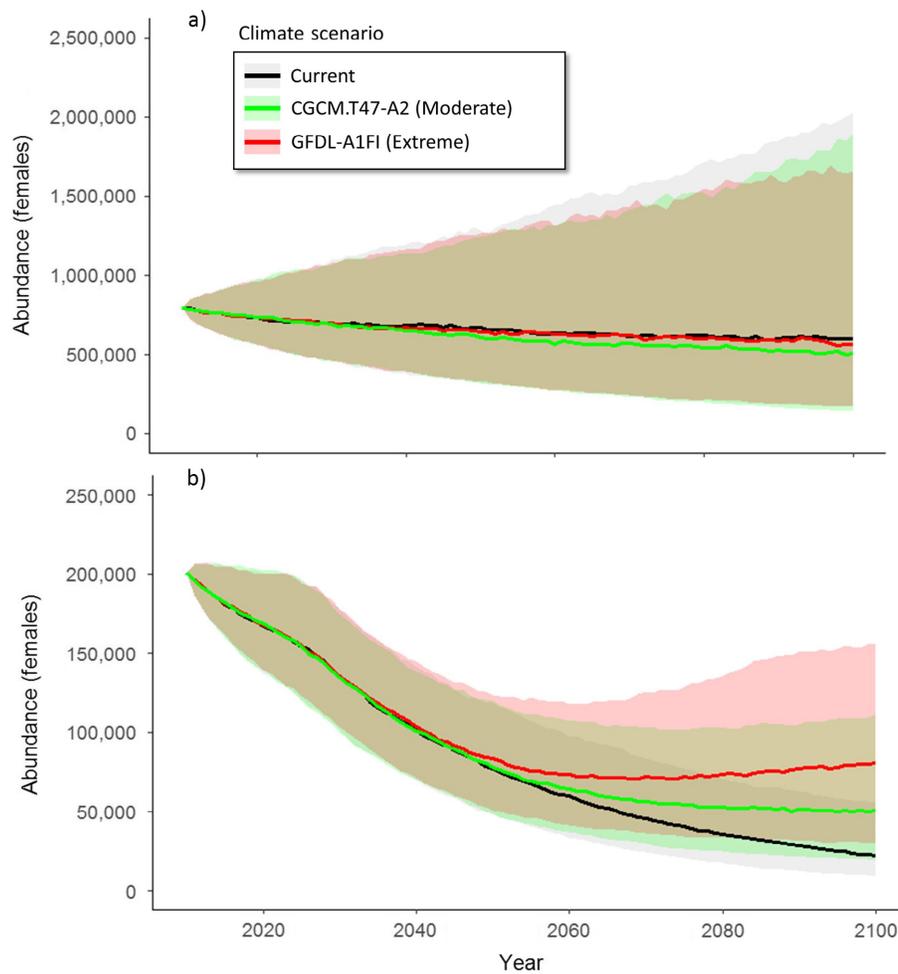


Fig. 4. Projected population dynamics of (a) wood thrush and (b) prairie warblers in the Central Hardwoods based on landscape change under three future climate change scenarios. Shaded regions indicate 85% credible intervals.

Table 2. Predicted dynamics and viability of wood thrush and prairie warbler populations in the Central Hardwoods region of the United States based on future landscapes projected under the current climate and moderate (CGCM.T47-A2) and severe (GFDL-A1Fi) climate change scenarios.

Population parameter	Prairie warbler			Wood thrush		
	Current	CGCM.T47-A2	GFDL-A1Fi	Current	CGCM.T47-A2	GFDL-A1Fi
Initial N [†]	201,161			794,321		
N in 2100 (median)	19,270	55,490	85,616	579,456	467,395	566,841
Percent change (2000–2100)	–90%	–72%	–57%	–27%	–41%	–29%
Projected average annual trend	–2.32%	–1.28%	–0.85%	–0.31%	–0.53%	–0.34%
Observed BBS trends for Central Hardwoods (1966–2015) [‡]	–1.98%			–0.62%		
Risk of 50% decline from initial N	65%	56%	48%	21%	23%	22%

[†] N, abundance of adult females.

[‡] Breeding Bird Survey (BBS) results, Sauer et al. (2017)

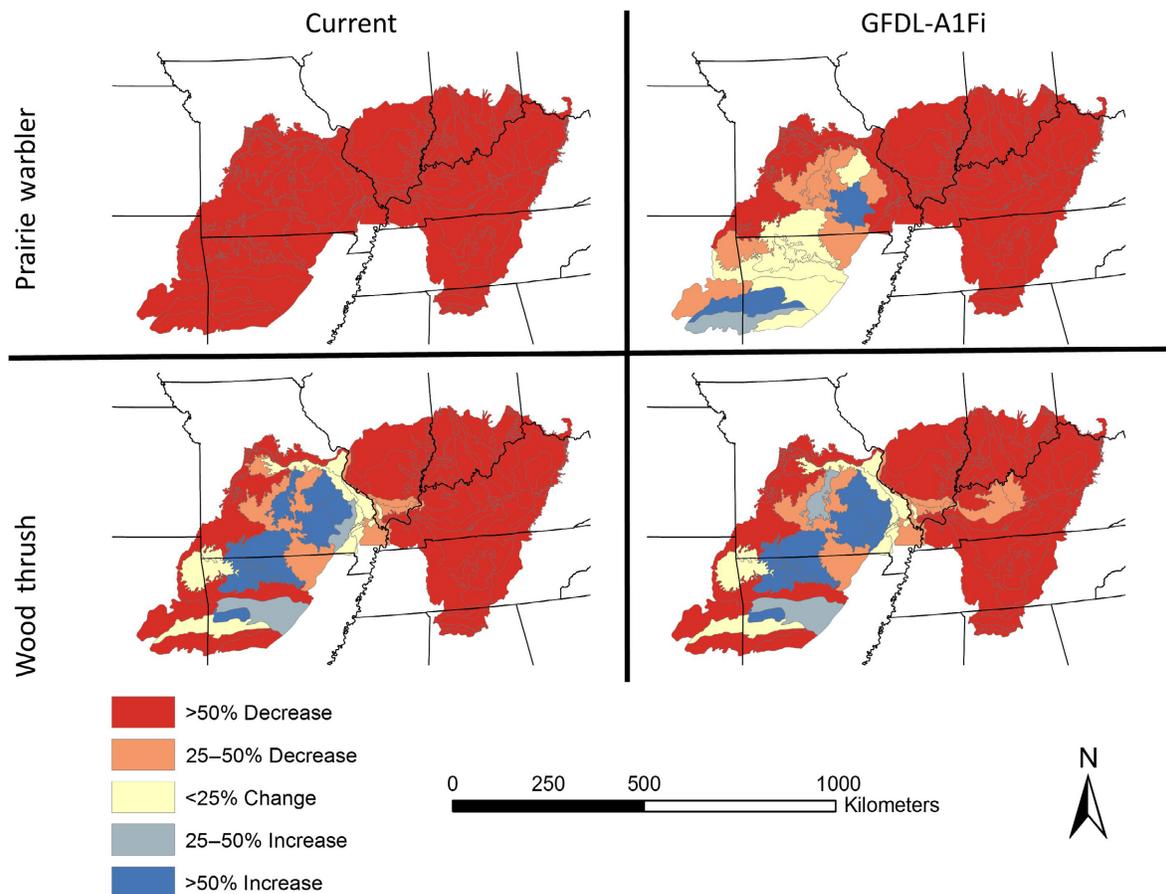


Fig. 5. Predicted changes in distribution of wood thrush and prairie warbler across the Central Hardwoods under a current climate scenario and the extreme (GFDL-A1Fi) climate change scenario. Shifts in distribution are apparent through the projected increases or decreases from initial bird abundances by 2100 across the region's ecological subsections.

thrush in these areas (Fig. 5). Projections for wood thrush were not only similar among scenarios, but they also displayed great uncertainty as the population under any scenario was less than half or more than double the initial abundance (based on 80% confidence intervals). As a result, the risk of decline for wood thrush in the Central Hardwoods was nearly identical under all three future climate scenarios (Fig. 6).

Unlike wood thrush, population dynamics for prairie warblers appeared closely linked to climate-driven increases in habitat over time. We predicted declines exceeding 3% per year through 2050, likely as a result of the decline in K (Table 2). By midcentury, the prairie warbler population was estimated at <50% its initial total of

201,161 females (Fig. 4b). While negative growth continued under the current climate scenario following 2060 (overall 90% loss), the decline slowed under the CGCM.T47-A2 scenario and was ultimately reversed under the GFDL-A1Fi scenario. The positive response of prairie warblers under climate scenarios, however, was primarily seen in the western and southwestern subpopulations (Fig. 5). The shifts in prairie warbler distribution under the two climate change scenarios corresponded with the increase in habitat in these landscapes. No distributional shifts occurred for prairie warblers under the current climate. The beneficial effects of climate change on prairie warbler habitat also translated in improved viability for the regional populations, lowering the risk of

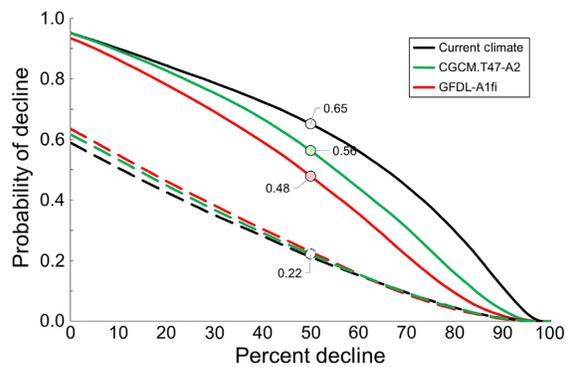


Fig. 6. Projected risk to prairie warbler (solid lines) and wood thrush (dashed lines) populations in the Central Hardwoods from 2000 to 2100 based on dynamic-landscape metapopulation modeling. The probabilities that a population will experience different levels of decline during the simulation are plotted for three future climate scenarios: a current climate scenario, a moderate CGCM.T47-A2 climate change scenario, and an extreme climate change GFDL-A1fi scenario. Model projections suggest a 17% less chance of prairie warblers declining by half (50% decline) in landscapes under extreme climate change than under a current climate.

a 50% decline sometime during the next century by 17% (Fig. 6).

DISCUSSION

The complex and contrasting responses of prairie warbler and wood thrush populations to climate change demonstrated the importance of mechanistic approaches, such as of DLMPs, that can incorporate important processes. Climate change is predicted to have less effect on the region's forests through 2100 than tree harvest and succession (Wang et al. 2015, 2016). Thus, wood thrush, whose habitat comprises a wider range of forest conditions, saw only slight effects on habitat under climate change and no effect on their population dynamics. Rather, existing landscape-level fragmentation of habitat was responsible for the declines in the population. The shift in distribution to the southwestern subsections stemmed from greater productivity in those less fragmented landscapes, a finding similar to Bonnot et al. (2011), who did not consider climate change. Prairie warbler habitat consists of a

narrow range of forest conditions that include early successional forests or woodland and glade communities that have low canopy closure and high ground and shrub cover. Declines in prairie warbler habitat the first 50 yr under all scenarios were due to forest succession resulting in older, closed-canopy forest, which is consistent with current habitat and population trends in the region (Franzreb et al. 2011). However, by the latter half of the century, reduced precipitation and elevated temperatures in the southwestern portion of the region under the climate change scenarios began to alter forest structure by reducing tree stocking in these areas (Wang et al. 2015). Lower tree stocking resulted in lower canopy cover and more open forest structure that created prairie warbler habitat. These changes occurred in subsections that had poor or droughty soils, which also tended to be areas with a larger proportion of forest land cover because they were less suitable for agricultural land uses. Therefore, climate change created prairie warbler habitat in landscapes with high potential productivity because they had lower levels of fragmentation. Thus, while prairie warblers declined regionally under the current climate, changes in forest structure in Missouri, Arkansas, and Oklahoma from climate change resulted in greater populations because of increased habitat in landscapes with high reproduction. Therefore, while wood thrush were affected little by the effects of climate change on habitat and instead declined from other threats, prairie warblers declined from loss of habitat due to succession but began to recover with the creation of habitat under climate change. The differences between species responses arrived from the interaction of climate, habitat, and demographic process. Without the means to account for these interactive processes, other less mechanistic approaches would have likely produced different predictions that might lead to alternative conservation efforts under climate change.

Our assessment of how two regional songbird populations responded to landscape change from climate warming provides a stark contrast with predictions from less mechanistic approaches. Langham et al. (2015) used SDMs based on climatic variables and projected wood thrush to lose >80% of their summer range, including much of the range in Missouri. While such a

prediction seems extreme, it is supported by others who have forecasted major range losses and extinctions of birds and other animals globally, under climate change (Thomas et al. 2004, Warren et al. 2013). The omission of species habitat and ecology by directly predicting distribution from climate forces SDMs to assume that these processes track climate or that climate is the primary determinant of species range (Keith et al. 2008). We are not the first to question these assumptions (Ralston et al. 2016). It can take long periods for habitat and wildlife populations to respond to climate during which time geological, ecological, and landscape processes could preclude or alter those responses. However, given recent evidence of range expansions and the potential for direct effects of climate change on bird demographics still not accounted for in our models, the true responses likely lie in between. Other SDMs have incorporated habitat with climate and projected similar changes to ours (Matthews et al. 2011). However, the declines we predicted in Wood Thrush were not due to climate, but instead continue the recent trend of studies that show that multiple processes in addition to climate determine the populations' dynamics and distribution (e.g., Swab et al. 2012, Fordham et al. 2013, Franklin et al. 2014). Therefore, because all approaches currently fall short in their ability to fully predict species responses to climate change and other threats, it is wise to base planning on multiple approaches, each with contrasting strengths and weaknesses (Millspaugh et al. 2009, Iverson et al. 2016).

The projected declines of wood thrush and prairie warblers in the Central Hardwoods are good illustrations of the importance of current, anthropogenic, and ecological drivers of change relative to those expected from climate change. The drop in early successional forests in the first three decades that spurred prairie warbler losses occurred because levels of disturbance and timber harvest did not offset habitat losses due to succession. Positive responses of prairie warblers to the formation of open, woodland communities under climate change scenarios further reflect the loss of these natural habitats in the Central Hardwoods from forest management over the past century, which drove much of their declines. The projected declines of both species across most of the region were also due to impaired reproduction resulting

from forest fragmentation/parasitism. Such results highlight the long-held view that anthropogenic habitat loss and fragmentation continue to be a predominant threat to terrestrial species decline (Sala et al. 2000). Nonetheless, even seemingly minor climate impacts on forests created prairie warbler habitat that caused shifts in and reversed declines of an entire regional population. Some have suggested that a key factor in the resiliency of species during past climatic changes has been absence of human-caused impacts (Moritz and Agudo 2013). Indeed, our work suggests that addressing current threats such as habitat loss and fragmentation could be key to resiliency of these species. Ultimately, however, the prairie warbler projections also remind us that impacts from climate change are likely to overwhelm even these processes over the long term; Wang et al. (2015) determined the contribution of climate change to forest landscape change in the region increased substantially from 100 to 300 yr in the future.

Although we achieved more realistic predictions by increasing the number of processes modeled, many processes are still unaccounted for that could change projections. Incorporating the influence of climate change on landscapes and habitat is an important step in modeling future viability of wildlife populations (Fordham et al. 2013). However, the degree to which predictions are improved over other less mechanistic approaches depends on how well our models replicate the actual processes. For example, the landscape projections from Wang et al. (2015) that underlie our results do not incorporate effects of climate on disturbances such as fire, insect outbreaks, and drought, which could be exacerbated by climate change and would provide direct sources of tree mortality. The resiliency of Central Hardwoods forests over the next 100 yr stemmed from the longevity of its trees. Therefore, including mortality from large-scale disturbances would most likely accelerate changes to the forests, species' habitats, and ultimately population dynamics. As a means to isolate the effects of climate change on the landscape, Wang et al. (2015) also maintained current harvest management practices over the duration of their simulations. It is possible that public land managers will adapt forest management under a changing climate, which, given the relative impact of forest management in the near term,

could affect predictions. However, much of the current forest management on public lands targets the same conditions brought on by climate change (e.g., opening of forest canopies to restore woodlands). Furthermore, the majority of forests in the Central Hardwoods are privately owned and may not see substantial changes in forest management.

Our models only begin to address the myriad of pathways climate can affect an entire species or population. For example, our DLMPs do not currently incorporate direct effects of climate change on bird demographics, despite knowledge of such relationships (Cox et al. 2013, Bonnot et al., *unpublished manuscript*). While we are currently working to incorporate these demographic processes, preliminary modeling suggests that under future climate change this mechanism could overwhelm the current responses to habitat and drive severe population declines in some species (Bonnot et al., *unpublished manuscript*). Changes in phenology, novel assemblages and invasive species, disease, physiological stress, and food availability are other examples that have been investigated (Thomas et al. 2004, Reed et al. 2013, Selwood et al. 2015, Hache et al. 2016). A century is a long time for animals to evolve in response to environmental change, and adaptations could play a role in how species persist over the long term (Alberti et al. 2017). Finally, our predictions describe impacts to the Central Hardwood's population of these birds and do not account for changes in habitat and other processes outside of the region and throughout the rest of their range. Increasing the comprehensiveness of this approach will require integrating these processes. Therefore, we must continually remain aware and transparent in our uncertainty about predictions, realizing that while our models will always be wrong to some degree, they can still be useful (Box 1979).

Relatively few examples of modeling both distributions and dynamics together under climate change exist. As a result, a dichotomy appears to have evolved where species distribution is the focus at regional and range-wide scales, while a focus on population dynamics occurs at smaller scales. However, the coupling of climate, habitat, and population dynamics is being made easier by advances in modeling and is an emerging area of research that is breaking down this dichotomy.

We showed that the distribution of a population is not solely determined by climatic or even habitat niches but is also the manifestation of the population dynamics that occur throughout its distribution. Likewise, population dynamics are influenced by the climate, habitat, and demographic processes where it is distributed. This link explains both the shifts we projected in bird distributions and the resulting population growth. The inability to address this interdependency risks leaving species threatened by local processes when relying on SDMs or, in the case of population models, larger distributional shifts when focusing on impacts at smaller scales. Therefore, it will be important to build on this study and the works of others (e.g., Hunter et al. 2010, Fordham et al. 2012, 2013, Regan et al. 2012, Franklin et al. 2014) and continue striving for more comprehensive approaches that can model important processes that drive population dynamics and distribution at the scales at which those processes interact with climate.

Because they link local habitat and demographic processes to large-scale population growth, DLMPs address two major conservation planning needs. They combine the ability to predict the impacts of landscape and climate change on populations and simultaneously evaluate the effectiveness of conservation activities to mitigate those impacts. The popularity of DLMPs arises from their ability to incorporate many processes that are important to predicting species responses to climate change (McMahon et al. 2011). As new climate change, habitat, and demographic processes are identified, or current processes are better understood, they are readily integrated to better reflect the complex reality of how climate will affect species. Such adaptability is critical where knowledge of trait-based vulnerabilities of species to climate increasingly exists, but the framework in which to quantify their effects on populations does not (Swab et al. 2012, Fordham et al. 2013, Moritz and Agudo 2013). We have also shown the importance of accounting for threats other than climate, such as land-use change and fragmentation. Further, DLMPs are scalable across species, taxa, and geographies (Jones-Farrand and Bonnot 2014, Bonnot 2016). In DLMPs, planners also have a powerful tool for Strategic Habitat Conservation (National Ecological Assessment Team 2008, Fitzgerald et al. 2009).

By altering projected landscapes or species demographics to simulate habitat restoration or other conservation measures, planners can predict how species will respond to conservation amidst global change when deciding plans. Simultaneously conveying responses of wildlife populations to conservation scenarios and the risk associated with those responses provides managers with a more intuitive and defensible way of comparing plans for species. (Drechsler and Burgman 2004, Bonnot 2016). As DLMPs become increasingly comprehensive, their potential to provide a unifying approach to conserving species in the face of global change grows.

ACKNOWLEDGMENTS

We thank J. S. Fraser, H. S. He, W. J. Wang, Todd Jones-Farrand, and W. D. Dijak for data and input on the study. Funding was provided by the Gulf Coastal Plains and Ozarks Landscape Conservation Cooperative, the Department of Interior USGS Northeast Climate Science Center graduate and post-doctoral fellowships, and the U.S.D.A. Forest Service Northern Research Station. The contents of this paper are solely the responsibility of the authors and do not necessarily represent the views of the United States Government.

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Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1890/full>