

NOVEL APPROACHES TO CONSERVING THE VIABILITY OF REGIONAL
WILDLIFE POPULATIONS IN RESPONSE TO LANDSCAPE AND CLIMATE
CHANGE

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CHANGE

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To my mom...I did it! I love you and miss you. To my family, thanks for your support and interest along the way.

Pryce, Rowan, and Aiden, I love you guys! Don't ever stop learning and loving nature.

To Julie, thanks for all you have done along the way! Your love and support have sustained me. I am blessed to have you beside me on my journey. I love you!

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NOVEL APPROACHES TO CONSERVING THE VIABILITY OF REGIONAL WILDLIFE POPULATIONS IN RESPONSE TO LANDSCAPE AND CLIMATE CHANGE

Thomas W. Bonnot

ABSTRACT

The proactive actions needed to prevent loss of biodiversity from global change have left managers and biologists looking for approaches that can predict how species and populations will respond to this threat and help guide conservation to address it. However, the 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. Conservation planning is also hampered by uncertainty in how species will respond to conservation actions amidst impacts from landscape and climate change and complicated by the complexities of the planning decisions, including tradeoffs among competing species objectives. Therefore, this doctoral research focused on the development of approaches that can overcome these limitations to guide conservation.

In chapter 1 we developed 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 U.S. to changes in forest conditions from climate change. Changes in habitat and metapopulation processes produced contrasting predictions for future populations of wood thrush and prairie warblers, allowing us to identify that relationships between climate change, succession, and land management are species-

specific and important determinants of future wildlife populations. Thus, DLMPs provide a comprehensive approach that can capture such processes to generate more realistic predictions of populations under climate change.

In chapter 2, we piloted a process that integrated DLMPs and Structured Decision Making to overcome the uncertainties and complexities that are inherent in the process of long-term, large-scale conservation planning. We coordinated with a team of planners from the OZHI throughout the decision process to determine choose among scenarios for habitat restoration that best meet desired endpoints for focal wildlife species in the GCPO's Ozark Highlands region under climate change and urbanization. Overall impact of restoration on focal species was positive and presented evidence to support landscape conservation design. Despite the general effectiveness of restoration, species-specific responses to individual scenarios varied in complex ways through interactions with landscape change processes such as urbanization and climate change and the demographic processes affecting each species. The planning team identified a scenario that targeted full acreage objectives on both private and protected lands, prioritized based on future landscapes as best reducing the average risk across species. This pilot project demonstrated that planning for viable populations across large scales can be achieved under global change. This approach has the potential to overcome the uncertainties and complexities that are inherent in the process of long-term, large-scale conservation planning.

Predicting the impacts of global change on populations of species for conservation planning requires approaches that are comprehensive enough to model important biological processes at the scales at which they interact with climate. We

combined individual-based and metapopulation models to estimate direct effects of climate change on daily nest survival, annual productivity, and ultimately population viability of Acadian flycatchers (*Empidonax virescens*) across the Central Hardwoods region of the U.S through 2099. The individual-based model estimated productivity based on daily nest survival that considered landscape and climatic factors such as daily temperature and precipitation. We integrated future productivity estimates into dynamic landscape metapopulation models that projected growth of the regional populations overtime. Models projected increasing declines in annual productivity and lower nest survival from increasing levels of warming under three scenarios for future climate change. Average annual productivity across the region declined by the end of the century under mild, moderate, and severe climate change scenarios, respectively. Reduced productivity drove significant population declines across a range of adult and juveniles rates indicating that climate change poses a substantial risk to ACFLs in the Central Hardwoods. These results highlight the importance of considering direct effects of climate change on demographics when assessing vulnerability of species and planning conservation.

The following chapters are formatted for individual publication in separate journals so formatting may be inconsistent.

CHAPTER 1

DEVELOPMENT OF DYNAMIC-LANDSCAPE METAPOPOPULATION MODELS TO PROJECT RESPONSES OF WILDLIFE POPULATIONS TO LANDSCAPE AND CLIMATE CHANGE

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 U.S. 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 overtime, 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. The wood thrush, a forest generalist, showed little response to climate driven forest change but declined by >25% due to reduced productivity associated with 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.

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' geographical ranges, distributions, and phenologies, which could substantially alter ecosystem structure and function (Schneider & 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.

A variety of methods have been employed to address such a broad question. However, correlative and mechanistic models are two approaches to predicting species impacts that have seen frequent contrasts in recent years (Moritz & 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 (Guissan & Thuiller, 2005; Elith & 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 (Moritz & Agudo 2013; Fordham, 2013). Projecting potential changes in distribution is a sensible goal for guiding future conservation, given accumulating evidence of these effects (Parmesan 2006; LaSorte & Thompson, 2007; Chen et al., 2011). However, SDMs have been criticized for their inability to account for the variety of processes affecting populations. 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). To the contrary, their lack of a direct mechanistic basis could predispose these models to suggest more extreme responses than might actually occur (Moritz & 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 & Thompson, 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 researchers have shown that still a more complete understanding of a population's response is attained by explicitly integrating climate with these processes in metapopulation models (Keith et al., 2008; Brook et al., 2009). 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 towards 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 rather than regional or range wide scales that better inform species distributions under climate change (Akçakaya & Brook, 2009). Although there has been greater success at developing DLMPs for plant species under climate change (e.g., Regan et al., 2012; Franklin et al., 2013), these models still lack complexity by overlooking various ecosystem and landscape processes affecting plants (Wang et al., 2015). Wildlife habitat typically involves structure and composition of entire vegetation communities, therefore modeling changes in habitat for animals compounds this problem. Forest landscape models such as LANDIS PRO can account for many of these processes to inform wildlife habitat models (He, 2009), but until recently have not integrated climate (Wang et al., 2015a). 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. Bonnot et al. (2011) extended landscape-based population modeling to regional scales, thus connecting local habitat and demographics with population growth over tens of millions of hectares. Wang et al. (2015a, b) developed the capability to model future forest landscapes under climate change at similarly large, regional scales, thus providing

estimates of how wildlife habitat might change in the future. Our objective was to integrate Bonnot et al.'s (2011) regional population models with Wang et al.'s (2015a) 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 U.S. 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 U. S. 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 U.S. (Figure 1). The area encompassed a variety of vegetation, terrains, soils, and climates (Cleland et al., 2007). The topography varied 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). 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 (US Fish and Wildlife Service, 2002; Panjabi et al., 2005; Bonnot et al., 2013).

Modeling Approach

We combined three components that are integral to DLMP approaches (Bekessy et al., 2009). We begin with projections of the landscape into the future under climate change scenarios in the form of a series spatial data grids that map the distribution, structure, and composition of forests at specified time steps (Figure 2). 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 spatially and temporally explicit representation of habitat and population dynamics and distribution throughout the region (Figure 2).

Future Landscape Data

We used recent projections of the structure and composition of forests in the Central Hardwoods from 2000–2300 under three climate-change scenarios (Wang et al. 2015a, b). Wang et al. (2015a, b) 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. Tree

harvest reflected current management of the regions forest based on Forest Inventory and Analysis data from 1995–2005. Wang et al. (2015a, b) 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 II, which integrates temperature and precipitation data with nitrogen availability and soil moisture to model individual tree species growth and mortality at a site (Wullschleger et al., 2003).

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-year period from 1980–2009 observed throughout the region (Wang, et al., 2015a). 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 (Figure 1; Girvetz et al., 2009).

Wang et al. (2015a) estimated forest projections from 2000 to 2300 at 10-year 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 years) 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 species composition among current climate and climate change scenarios in the region's midterm (100 years), 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., 2015a).

Habitat Modeling

We employed habitat models to link landscapes to three demographic processes considered by Bonnot et al. (2011): distribution and carrying capacity (K), breeding productivity, and dispersal. We modeled wood thrush and prairie warbler distribution and K using landscape-scale Habitat Suitability Index (HSI) models developed for the Central Hardwoods (Tirpak et al., 2009). We predicted suitability of habitat in cells based on their attributes and the surrounding landscape and have been verified and validated with regional abundance data from the North American Breeding Bird Survey. We incorporated forest composition through land cover (as defined by the National Land Cover Data, NLCD; Fry et al., 2011), forest structure (percent canopy cover, density of small stems, and forest seral stage), in addition to landscape variables that include forest patch size, early successional forest patch size, proximity to forest edge, and percent forest within 10 km (Table 1; Tirpak et al., 2009). The wood thrush model reflected the species' use of mature hardwood and mixed forests with relatively closed canopies (Tirpak et al., 2009). Prairie warblers inhabit a variety of early successional forest types

as well as glades and woodlands. Open canopy and shrubby understory were important structural components considered in their model. Both species are sensitive to habitat patch size and the predominance of forest in the surrounding landscape (Tirpak et al., 2009).

We derived habitat variables from LANDIS PRO outputs through geoprocessing in ArcGIS 10.2 (Environmental Systems Research Institute, Redlands, CA, USA). We identified NLCD land cover classes by comparing the relative importance values (Smith & Smith, 2001) estimated by LANDIS PRO for deciduous versus coniferous species. We classified cells as deciduous forest if the combined importance of deciduous species > 65% and coniferous forest if such species comprised > 47% of the cell's importance. 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 landcover estimates for the initial (2000) landscape proportional to actual NLCD classes for the same region. Following the estimation of landcover types 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. (2009). 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 approximately 10 year to reach 2.54 cm DBH (Johnson et al., 2009).

We modeled demographics 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, B. unpublished data; see also Wilson et al., 2012). For these cells we held values constant over time.

We estimated local bird demographics throughout the region based on habitat. We followed Bonnot et al.'s (2013) approach to estimating K for cells by assuming a linear relationship between HSI and maximum densities found in the literature (Table 1). We then scaled density by the area of cells and spatially filtered areas of the landscape that could not support at least one territory, constrained by a maximum territory size found in the literature. This process more realistically captured the interaction between spatial and resource limitations inherent in estimating K. We estimated wood thrush and prairie warbler initial distributions throughout the region as 12% and 50% K in year 2000, respectively (Table 1; Bonnot et al., 2011). Shifts in distribution over time due to the climate's effect on habitat were captured by subsequent changes in K. We used the Relative Productivity Index (RPI; Bonnot et al., 2011) model to link breeding productivity to habitat. The RPI index (0–1) modifies reproductive success of birds breeding in fragmented landscapes and proximate to edge based on the amount of forest cover in a 10-km radius and edge within a 200-m radius. Finally, we used the dispersal

model of Bonnot et al. (2011) to estimate cell-based movements of dispersing individuals to the surrounding landscape based on a negative exponential function of distance between cells, weighted by K of the destination cell. Thus, changes future dispersal movements reflected shifts in the distribution of birds in the region.

Population Modeling

We linked the regional populations of wood thrush and prairie warblers to landscapes by treating ecological subsections as subpopulations and summarizing their demographics for each subsection. The region contained 71 subsections which we delineated into 87 unique subpopulations (Figure 1; Cleland et al., 2007). For each subpopulation we summarized results of the habitat models to obtain estimates of initial abundance (year 2000) and K at each decade. We averaged cell RPI's in each subpopulation, weighted by their K in each decade, so that productivity estimates reflected any changes in distribution of birds over time. For each decade dispersal movements were summarized by subpopulation and standardized to obtain relative rates of dispersal from each subpopulation to surrounding ones (Bonnot et al., 2011). Because we ultimately modeled population dynamics annually, we calculated yearly values of spatial demographics by linearly interpolating between decadal estimates and stored them in spatio-temporal arrays.

We programmed the population models in R v3.0.1 (R Core Team, 2015) because of its efficient vector-based computation and widely available statistical functions. We used a female only, Lefkovitch matrix model comprising adult and juvenile stages (Caswell, 2001). We specified adult and juvenile survival rates from the literature and assumed a post-breeding census (Table 1). We multiplied RPI's with published estimates

of wood thrush and prairie warbler maternity to obtain population-specific fertility estimates in each decade. We specified adult and juvenile breeding and natal dispersal, respectively, that determined the proportion dispersing each year and redistributed them among the subpopulations according to multinomial distributions with probabilities equal to the relative dispersal rates for that year. We used a modification to the commonly referred to ceiling density dependence (Akçakaya & Brook, 2009) such that individuals over K in a population were prohibited from breeding but could remain in the population or disperse.

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 1,000 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 the supplementary information (Appendix A).

RESULTS

Complex shifts in the roles of forest succession and management relative to climate change over the course of the next century differentially affected habitats for the two species. The dominant process affecting forest change in the first 50 years was succession and management, which resulted in an aging forest. As a result, wood thrush K increased the first 50 years under all climate scenarios (Figure 3a). Increases in K leveled off the latter half of the century and K for the two climate change scenarios < 5% lower than for current climate (CGCM.T47-A2: 7,364,356 females; GFDL-A1FI: 7,266,566 females; Current: 7,581,855). The distribution of wood thrush habitat remained mostly constant across subpopulations, with most habitat occurring in the Ozarks subsection of south-central Missouri. Counter to wood thrush, prairie warbler K declined sharply across the region over the first 3 decades for all scenarios (Figure 3b). However, while K increased only slightly under the current climate after 2030, K increased more under both climate change scenarios because the 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% higher K under the GFDL-A1FI scenario than current climate (Figure 3b).

The impacts of changes in habitat on K 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% decreases in wood thrush abundance from the initial estimate of 794,321 adult birds under all climate scenarios by 2100 (Figure 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 thrush in these areas (Figure 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% CI's). As a result, the risk of decline for wood thrush in the Central Hardwoods was nearly identical under all three future climate scenarios (Figure 6).

Unlike wood thrush, population dynamics for prairie warblers appeared closely linked to climate driven increases in habitat over time (Figure 5b). 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. 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 (Figure 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, decreasing the risk of a 50% decline sometime during the next century by 17 points (Figure 6).

DISCUSSION

The complex and contrasting responses of prairie warbler and wood thrush populations to climate change demonstrated the importance of DLMPs as mechanistic approaches that can incorporate important processes. Climate change is predicted to have substantially less effect on the region's forests through 2100 than tree harvest and succession (Wang et al., 2015a, b). 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 the southwestern subsections resulted 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 the first 50 years 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., 2015a). 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 metapopulation processes related to other threats, prairie warblers declined from loss of habitat due to succession but began to recover due to 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 and risked misguiding conservation efforts for these species 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 omittance 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 (Millsaugh 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 3 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 reflects 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 continues to be a predominant threat to terrestrial species decline (Sala et al., 2000). None the less, 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 & 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. (2015a, b) determined the contribution of climate change to forest landscape change in the region increased substantially from 100 to 300 years in the future.

More realistic predictions, made possible by increasing the complexity and number of processes modeled, should serve as a warning in light of the many processes still not accounted for. 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. (2015a) 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 years stemmed from the longevity of its trees. Therefore, including mortality from large-scale disturbances would most likely accelerate changes to the forests, species' habitats, ultimately population dynamics. Furthermore, given the myriad of pathways climate can affect an entire species or population, our models are still far from complete. For example, our DLMPs do not currently incorporate direct effects of climate change on bird demographics, despite some knowledge of these relationships (Cox et al., 2013). 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 (This volume, chapter 3). 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). 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).

Until now it has been difficult to model both distributions and dynamics under climate change. As a result, a dichotomy has evolved where species distribution is the focus at regional and range-wide scales, while a focus on population dynamics occurs at smaller scales. Our results, however, show that this dichotomy is false. The distribution of a population or even a species is not solely determined by climatic or even habitat niches but is also the manifestation of population dynamics that occurs across all scales throughout its distribution. And, likewise, a population's dynamics are a function of life history and demography that is affected by habitat and climate variably where it is

distributed. This link explains both the shifts we observed in bird distributions and the resulting population growth, for prairie warblers. Failure to recognize this interdependency risks leaving species threatened by local processes when relying on SDMs or, in the case of population models, larger distributional shifts that could interact with the smaller population. Therefore, we suggest striving for a more comprehensive approach that can model important processes that drive population dynamics and distribution at the scales at which those processes interact.

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 & 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 (Bonnot et al., In prep; Jones-Farrand & Bonnot, 2014). 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 & Burgman, 2004; Bonnot et al., In prep; Figure 6). As DLMPs become increasingly comprehensive, their potential to provide a unifying approach to conserving species in the face of global change grows.

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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) @ HSI=1	0.50	Roth et al., 1996; Gram et al., 2003; Thompson et al., 1992; Wallendorf et al., 2007	1.00	Fink, 2003
Initial abundance (% of carrying capacity)	0.12	Gram et al., 2003; Thompson et al., 1992; Wallendorf et al., 2007	0.50	Brito-Aguilar, 2005; Fink, 2003; Thompson et al., 1992; Wallendorf et al., 2007
Maximum maternity (fem/fem/year)	1.45	Anders et al., 1997; Donovan et al., 1995; Ford et al., 2001	1.55	Fink, 2003; Nolan, 2014
Adult survival	0.61	Powell et al., 2000; Conway et al., 1995; Simons et al., 2000; Donovan et al., 1995	0.60	Lehnen & Rodewald, 2009; Nolan, 2014
Juvenile survival	0.29	Anders et al., 1997	0.32	Nolan, 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 (CV)				
Fertility	0.27	Roth et al., 1996	0.27	Roth et al., 1996
Juvenile survival	0.25	Brown & Roth, 2004; Schmidt et al., 2008	0.15	Larson et al., 2004
Adult survival	0.10	Brown & Roth, 2004	0.10	Brown & Roth, 2004
Demographic stochasticity	Yes		Yes	
Density dependence	Modified Ceiling		Modified Ceiling	
Proportion of juveniles dispersing annually	90%		90%	
Proportion of adults dispersing annually	10%		20%	

Table 2. Predicted dynamics and viability of wood thrush and prairie warbler populations in the Central Hardwoods region of the U.S. 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 climate scenario			Wood thrush climate scenario		
	Current	CGCM.T47-A2	GFDL-A1Fi	Current	CGCM.T47-A2	GFDL-A1Fi
Initial N ^a		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 (1966-2013) ^b		-2.21% (-2.78, -1.68)		-0.95% (-1.33, -0.60)		
Risk of 50% decline from initial N	65%	56%	48%	21%	23%	22%

^aN = abundance of adult females

^bSauer et al., 2014

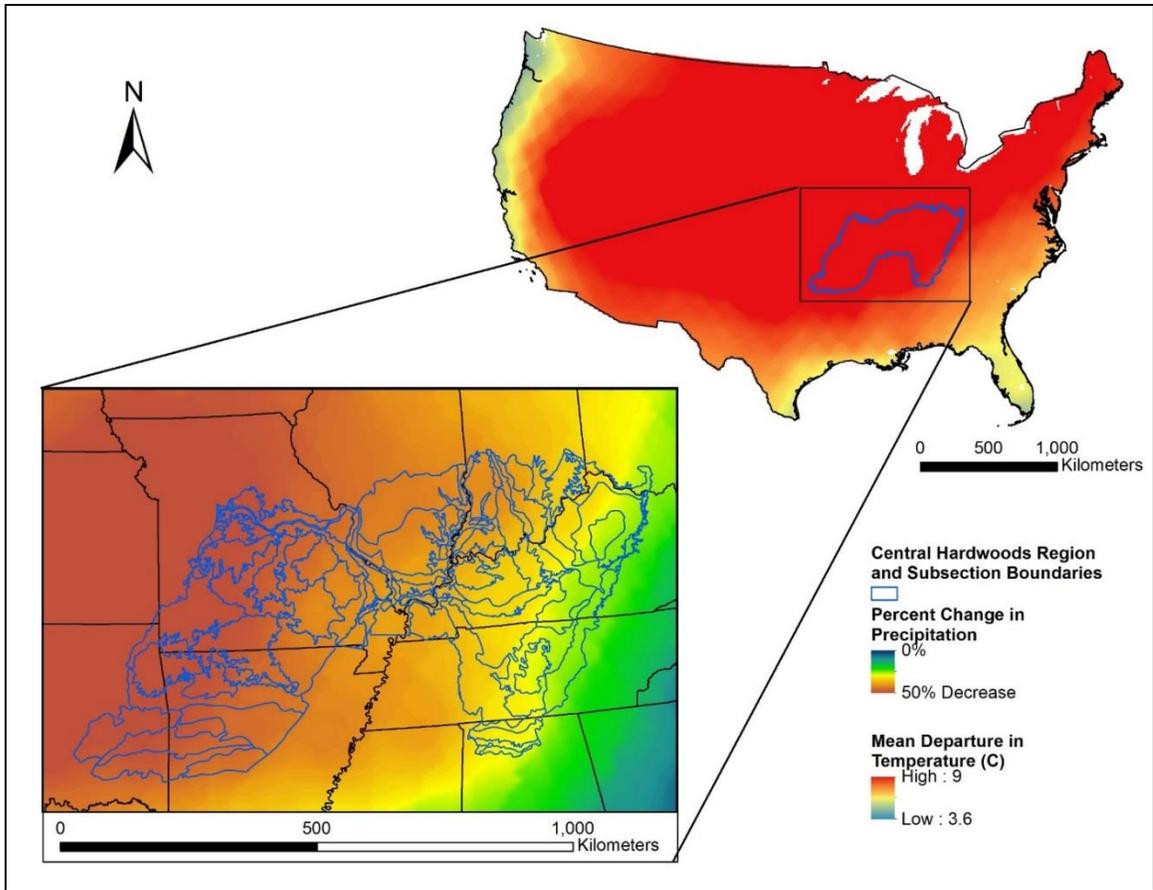


Figure 1. Dynamic-landscape metapopulation models were developed for two species of songbirds in the Central Hardwoods forested region in central U.S. The models integrate habitat with metapopulation processes to predict future changes in population dynamics and distribution throughout the region’s ecological 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 graph) and reduce summer precipitation (inset) under a GFDL-A1Fi scenario.

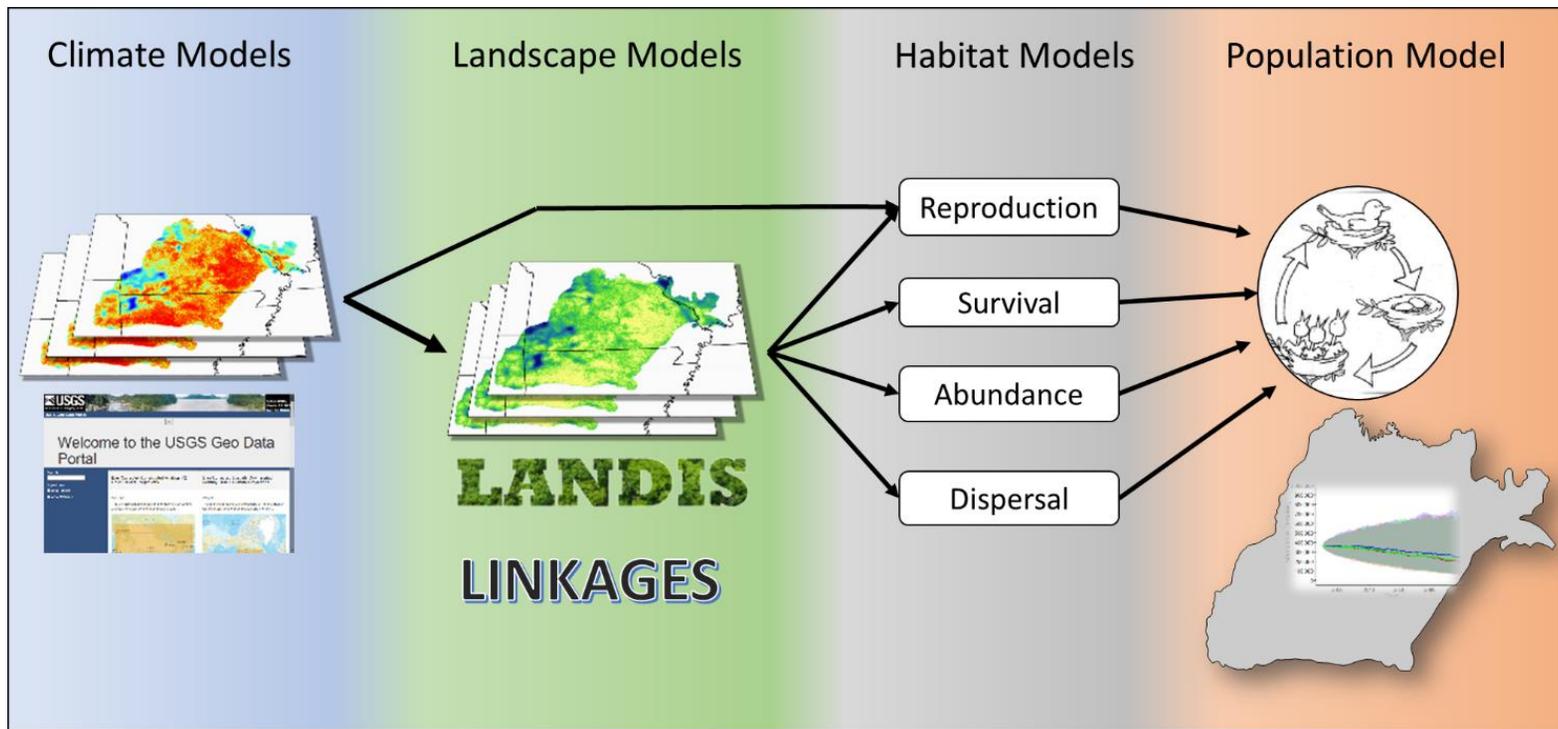
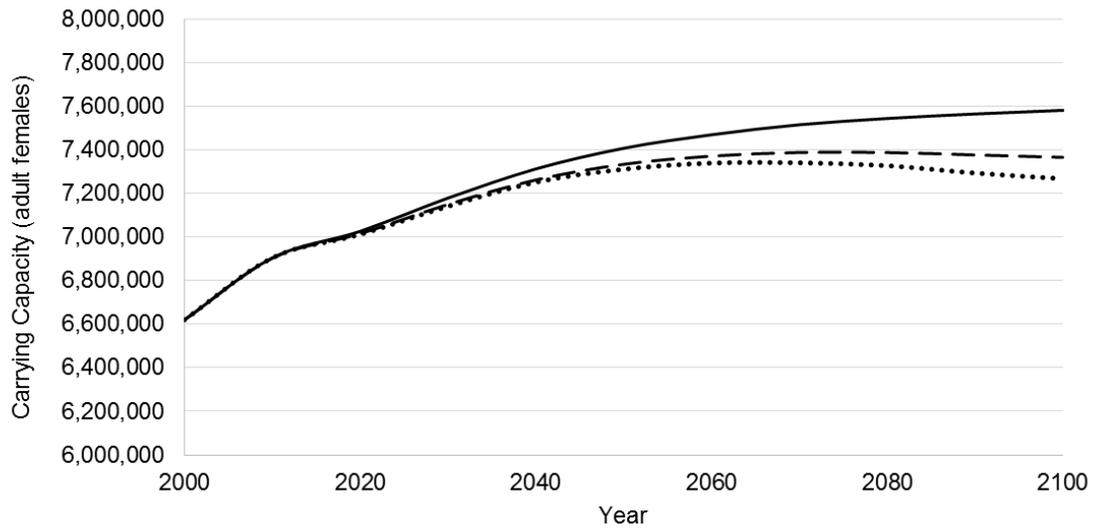
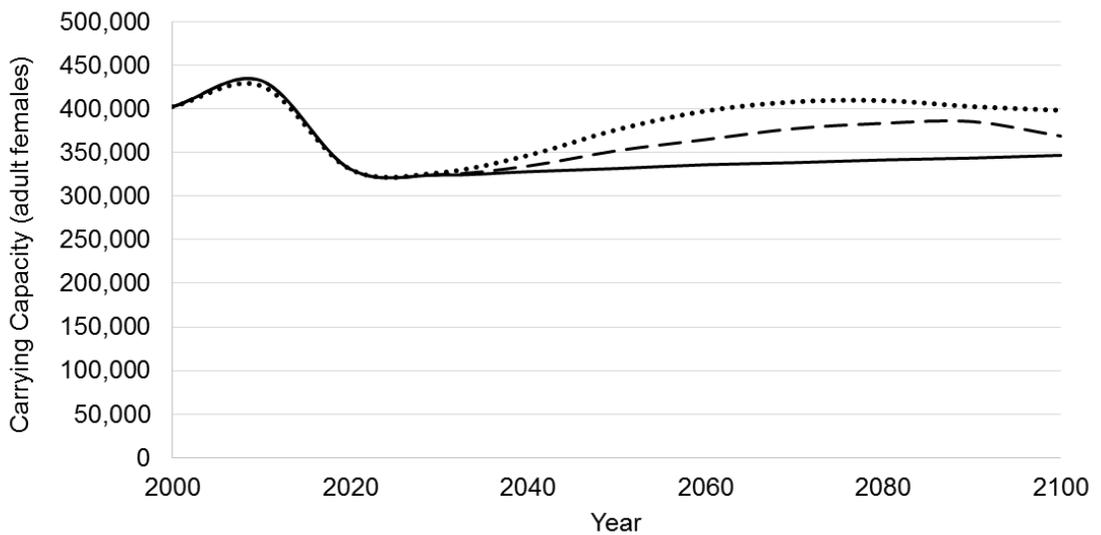


Figure 2. Dynamic-landscape metapopulation modeling approach that links local habitat to region population growth. This approach combines climate, landscape, habitat, and population models to project the responses of wildlife populations to climate and management driven changes to the landscape.

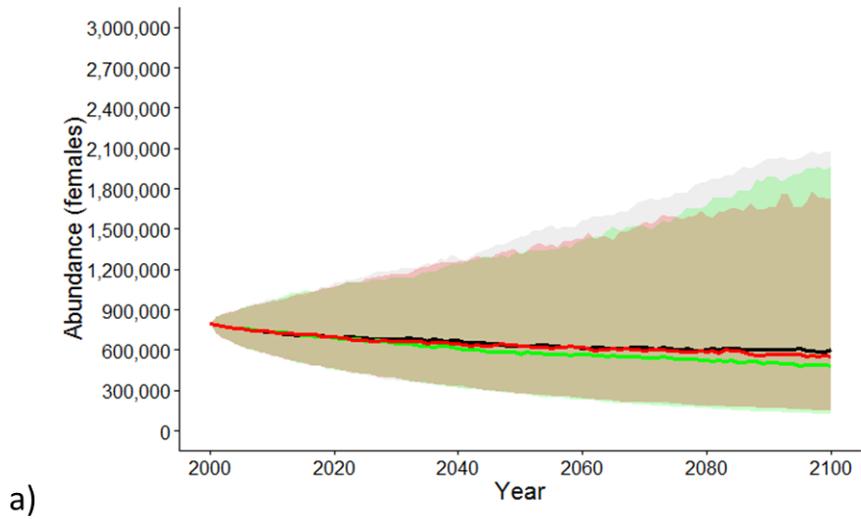


a)

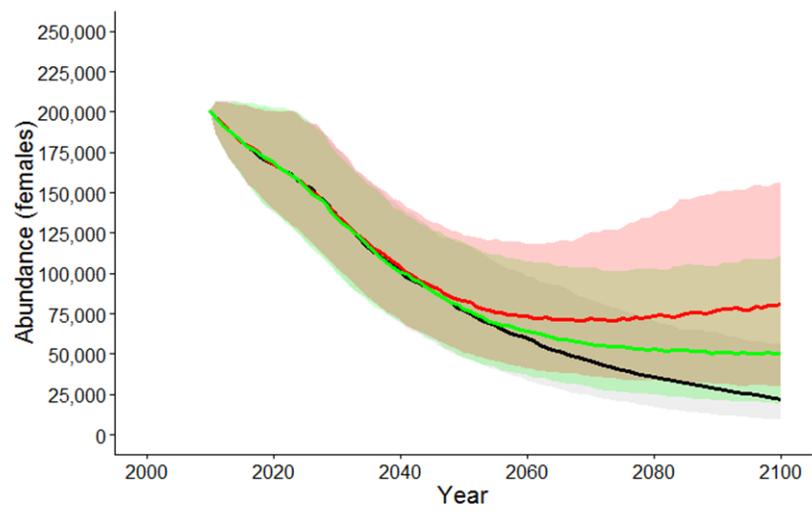


b)

Figure 3. Impacts of landscape change from climate change on a) wood thrush and b) prairie warbler habitat in the Central Hardwood's 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).



a)



b)

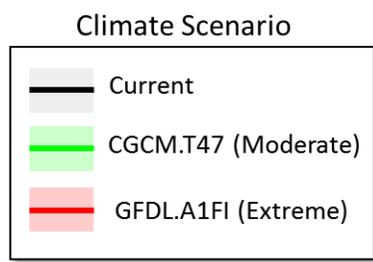


Figure 4. Projected population dynamics of a) wood thrush and b) prairie warblers in the Central Hardwoods based on landscape change under three future climate change scenarios. Shaded regions indicate 85% credible intervals.

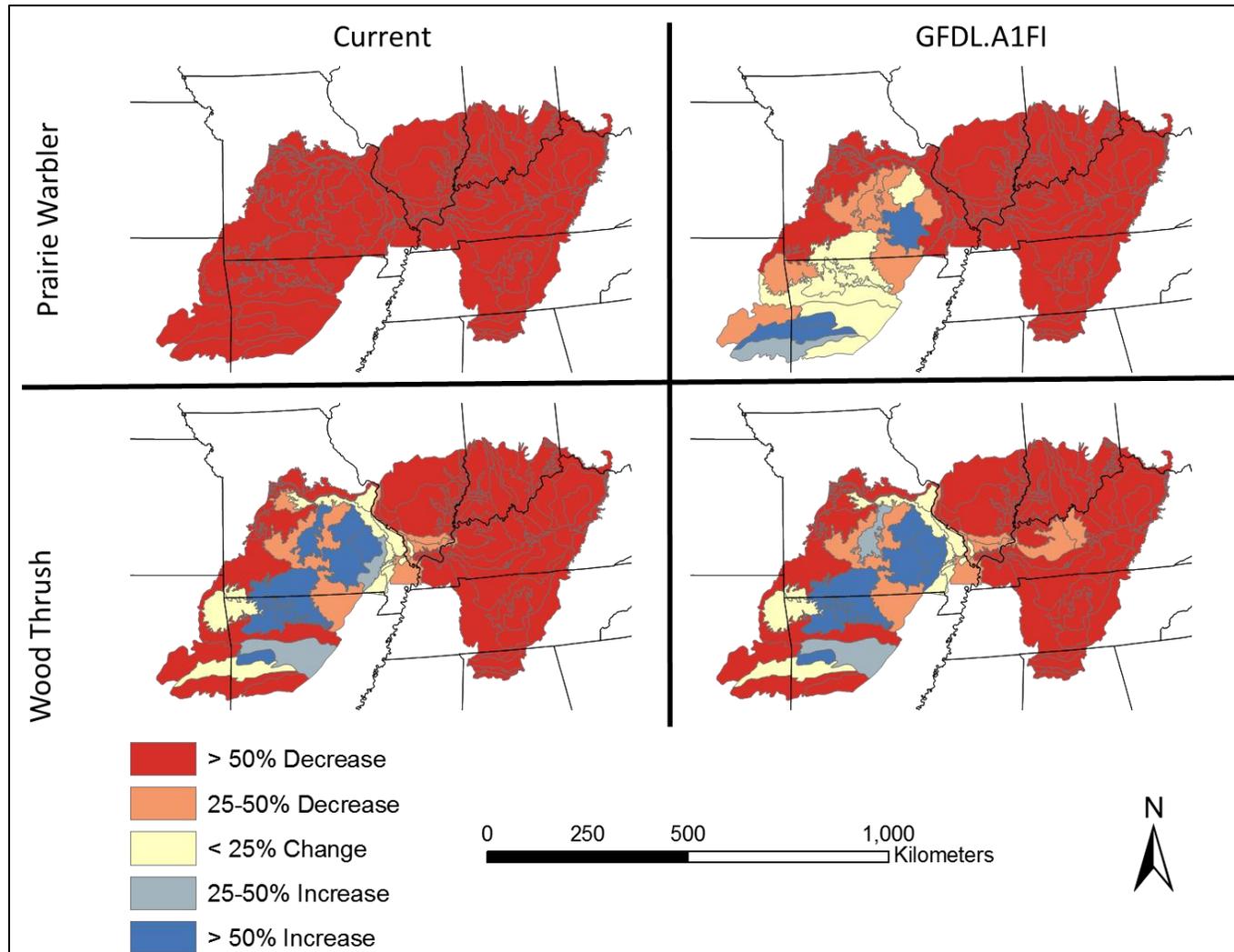


Figure 5. Predicted changes in distribution of wood thrush and prairie warbler across the Central Hardwoods under a current climate scenario and the extreme (GFDL-A1fi) climate change scenario. Shifts in distribution are apparent through the projected increases or decreases from initial bird abundances by 2100 across the region's ecological subsections.

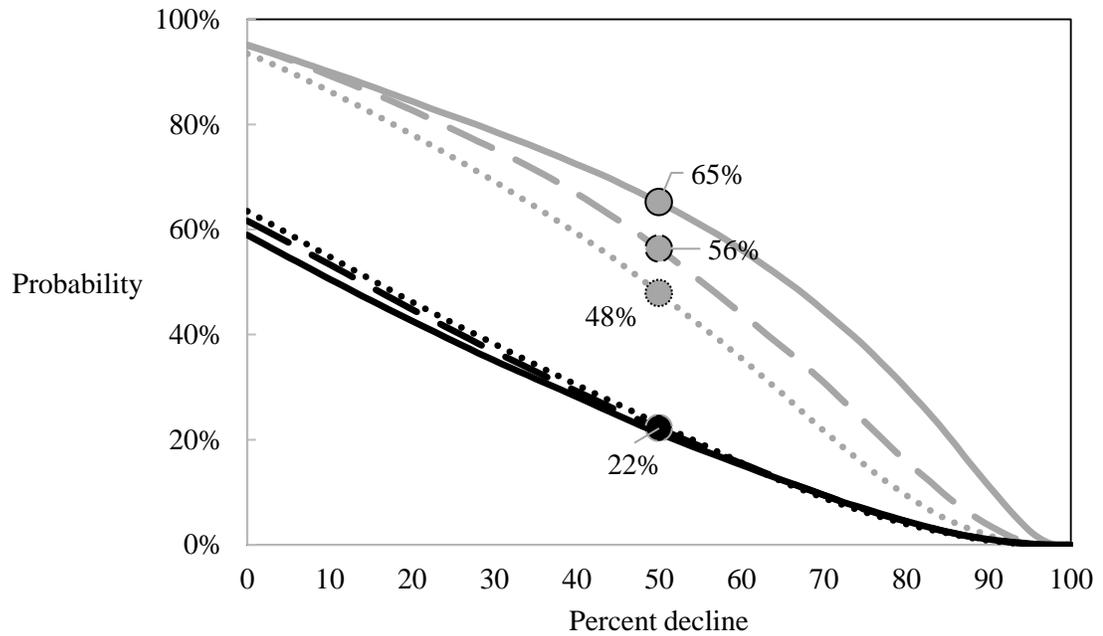


Figure 6. Projected risk to wood thrush (black lines) and prairie warbler (gray lines) populations in the Central Hardwoods from 2000-2100 based on dynamic landscape metapopulation modeling. The probabilities that a population will experience different levels of decline during the simulation are plotted for three future climate scenarios: a current climate scenario (solid), a moderate CGCM.T47-A2 climate change scenario (dashed), and an extreme climate change GFDL-A1fi scenario (dotted). 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.

CHAPTER 2
INTEGRATING DYNAMIC LANDSCAPE POPULATION VIABILITY MODELS
WITH STRUCTURED DECISION MAKING TO GUIDE CONSERVATION
PLANNING

ABSTRACT

The Gulf Coastal Plains and Ozarks Landscape Conservation Cooperative (GCPO) is a regional collaboration across agency and ownership boundaries to conserve sustainable landscapes in the face of global change. Planning for sustainable landscapes is hampered by uncertainty in how species will respond to conservation actions amidst impacts from landscape and climate change, especially when those impacts are also uncertain.

Conservation is also complicated by the complexities of the planning decisions, including tradeoffs among competing species objectives. To help guide landscape conservation design, we piloted a process that integrated dynamic-landscape metapopulation models (DLMPs) and Structured Decision Making to choose among scenarios for habitat restoration that best meet desired endpoints for focal wildlife species in the GCPO's Ozark Highlands (OZHI) region under climate change and urbanization. We coordinated with a team of planners from the OZHI throughout the decision process to determine objectives, design alternative scenarios, and use DLMPs to model the consequences of each given concurrent impacts of climate and landscape change. Overall impact of restoration on focal species was positive and presented evidence to support landscape conservation design. Despite the general effectiveness of restoration, species-specific responses to individual scenarios varied in complex ways through interactions with landscape change processes such as urbanization and climate change and the

demographic processes affecting each species. The planning team identified a scenario that targeted full acreage objectives on both private and protected lands, prioritized based on future landscapes as best reducing the average risk across species. Through this pilot project we demonstrated that planning for viable populations across large scales can be achieved under global change. The integration of DLMPs with Structured Decision Making enabled the decision to be objective and transparent, and thus defensible. Therefore, this approach has the potential to overcome the uncertainties and complexities that are inherent in the process of long-term, large-scale conservation planning.

INTRODUCTION

Global change poses serious issues for biodiversity conservation. Many species are at a far greater risk of extinction than in the recent geological past (Fischlin et al. 2007). Although landscape change and habitat loss remain the main drivers of present-day species extinction (Sodhi et al., 2009), climate change is projected to become equally or more important in the coming decades as it interacts synergistically with these threats (Brook et al. 2008). Threats to species such as climate change and habitat loss operate at regional to global scales (Fahrig and Merriam 1994, Lambeck and Hobbs 2002). Similarly, persistent populations depend on demographic processes that also occur over large scales (Pulliam et al. 1988, Faaborg et al. 2010, Bonnot et al. 2011). Thus, it is becoming increasingly clear that local or isolated efforts to conserve biodiversity in a changing environment are likely to be insufficient (Bonnot et al. 2013). Further, it is unlikely that the multiple objectives of biodiversity and ecosystem conservation can be met without managing at the scale of regional landscapes (Parrot and Meyer 2012).

With these realizations, Joint Ventures (U. S. North American Bird Conservation Initiative Committee 2000) and Landscape Conservation Cooperatives (USFWS 2010) have become important examples of collaborations across agency and ownership boundaries to conserve sustainable landscapes in the face of global change. Through Strategic Habitat Conservation and Landscape Conservation Design approaches these cooperatives (or partnerships) extend beyond the reach or resources of any one organization (Will et al. 2005, USFWS 2008, Fitzgerald et al. 2009). Strategic habitat conservation primarily focuses on management of fish and wildlife habitat and begins with assessment of landscapes to identify the best areas where current habitat can be conserved and potential habitat restored. The regional partnerships are then tasked with planning strategies that coordinate those actions across landscapes through various programs and partners that reach species population goals. But, this task can be incredibly challenging as regional planners are hindered by two major difficulties in making conservation decisions.

First, assessing the impacts of landscape change on species' populations is complicated by multiple sources of uncertainty. Climate change is expected to be a key driver of landscape change. But, the degree, rate, and nature of projected climate change is highly uncertain (IPCC 2007). So too are the diversity of habitat responses to a climate and its interactions with other stressors such as land use change (urbanization), invasive species, pathogens, pollutants (Parmesan 2006, Dawson et al. 2011, Wang et al. 2015).

Furthermore, the effects landscape changes on species also depend on metapopulation processes, species interactions and interactions between demographic and landscape dynamics (Keith et al. 2008). Because of these interactions, responses of regional

populations to landscapes affected by threats such as climate change and urbanization or the habitat conservation that addresses them are actually quite complex and sometimes counterintuitive (Brook et al. 2008, Bonnot et al. 2013). Thus, it can be difficult to predict the effectiveness of conservation plans at achieving regional population goals under Strategic Habitat Conservation.

Strategic habitat conservation has also been impeded by the complexity of the decisions planners must make. Planners can consider various management actions, such as restoring potential habitat or protecting current habitat. For some species, reintroduction, captive breeding, or efforts to reduce anthropogenic mortality (e.g., communication tower alterations) may be needed in addition to habitat conservation (Bonnot et al. 2013).

Identifying the appropriate approach is difficult given the uncertainty discussed above and it is further complicated by additional strategic considerations, including questions about the amount, configuration, and condition of habitat needed to achieve species goals. Costs, partner objectives, and private and public lands managers' interest also factor in decisions. Even when these factors are accounted for it can be difficult to identify a single best strategy when there are multiple possible future outcomes (e.g., various forest projections under different climate future (Wang et al. 2015). Finally, deciding on a conservation plan that is best for all species is complicated when different species have conflicting responses to each scenario.

The recent development of dynamic-landscape metapopulation (DLMP) models and the growing use of structured decision making (SDM) provide regional planners with an opportunity to overcome these difficulties. Dynamic-landscape metapopulation models link local habitat and landscape patterns to regional population growth, providing the

means to understand the impacts of landscape change on the viability of regional wildlife populations (Bonnot et al 2011). With this ability planners in the Central Hardwoods have evaluated how populations might respond to local and regional conservation actions (Bonnot et al. 2013). Recently, DLMPs have begun to incorporate the effects of climate change on future landscapes to model how regional wildlife populations might respond to these threats (Wang et al. 2015, Bonnot et al. In Review; Figure 1). With these advancements, DLMPs offer planners an important tool to predict the effectiveness of conservation strategies in sustaining wildlife amidst climate change.

Next, natural resource managers and conservation planners are increasingly employing SDM to solve complex conservation problems (Marcot et al. 2012). Structured decision making is a formal framework for analyzing complex decisions (Gregory et al. 2012). Core elements of an SDM application include defining objectives and measures of performance, identifying and evaluating alternatives, and making choices based on a clear understanding of uncertainties and tradeoffs (Gregory and Long 2009). Along this process components are addressed with an array of analytical methods, drawn from decision theory and applied ecology (Possingham et al. 2001). For example, as species have different habitat requirements, management actions detrimental to one species may enhance the chances of persistence of other, valued species (Dreschler and Burgman 2004). In SDM there are a variety of ways to resolve tradeoffs between these competing objectives. There are also approaches within SDM that directly consider uncertainty in what the outcomes of proposed alternatives are for different states of the system. This aspect is useful in the situation where multiple climate change scenarios are possible and the effectiveness of different conservation strategies depends on them. In general, SDM

has proven effective for the types of problems conservation planners face (Ralls and Starfield 1995, Drechsler 2000, McGowan 2013).

We investigated the use of DLMPs and SDM in landscape conservation design in a pilot project with the Gulf Coastal Plains and Ozarks Landscape Conservation Cooperative (GCPO). The GCPO is a federally sanctioned regional partnership charged with defining, designing, and delivering landscapes capable of sustaining natural and cultural resources now and into the future (GCPO LCC 2013a). The GCPO has been working with a team of conservationists (hereafter the “OZHI team”) to pilot a process of designing landscapes capable of sustaining healthy plant and animal communities throughout the Ozark Highlands portion of the GCPO region (Figure 1). Using Strategic Habitat Conservation the team has prioritized conservation opportunity areas across the OZHI of Arkansas, Missouri, and Oklahoma for restoration. Our objective was to demonstrate how dynamic landscape population viability models can be used to evaluate alternative restoration scenarios within a structured decision making framework to best sustain focal wildlife population in the Ozark Highlands region under climate change and urbanization. We attempted to demonstrate the importance of Strategic Habitat Conservation in reaching conservation goals and the effectiveness of the DLMP-SDM integration for informing Strategic Habitat Conservation.

STUDY AREA

The OZHI is an approximately 36 million acre (> 140 square kilometer) ecoregion within the GCPO geography that also includes the Ouachita and Boston Mountains regions (Figure 2). The landscape features rugged uplands—some peaks higher than 2,500 feet

above sea level—with exposed rock and varying soil depths and includes extensive areas of karst terrain (USGS 2009). The OZHI contains diverse topographic, geologic, soil, and hydrologic conditions that support a broad range of forest communities, including: upland oak (*Quercus* spp.)–hickory (*Carya* spp.) forests and oak-pine (*Pinus* spp.) forests, woodlands, and savannas. Although the region includes some of the most extensive forests in the middle of the continent, widespread logging in the early part of the 20th century and fire suppression in subsequent decades resulted in conversion of many glade, barren, and pine woodland communities to oak or oak-pine forests (Fitzgerald et al., 2005). The OZHI is characterized by extreme biological diversity and high endemism, having the largest extent of glade communities in North America and being home to nearly two-thirds of the 45 federally listed plants and animals in Missouri, Arkansas, and Oklahoma (USGS 2009). The OZHI is also an important center for Neotropical bird migration and breeding grounds (Fitzgerald et al., 2005).

METHODS

We led the OZHI team through an SDM process that structured the various complicating factors involved in the decisions within the “PrOACT” framework, commonly used in solving natural resource management problems (Hammond et al. 2002). PrOACT breaks complex decisions down into components, which begins with a problem (“Pr”) that is defined and clearly articulated (McGowan 2013; Figure 3). Second, the “O”bjectives were delineated with their measurable attributes (Keeney and Gregory 2005). Then a list of possible “A”lternative actions or scenarios were identified. Fourth, DLMP models were used to evaluate the “C”onsequences of those alternatives with respect to the stated

objectives. Finally, the “T” tradeoffs between competing objectives are evaluated. Because SDM is driven by the decision makers, this process was interactive.

Problem

The OZHI team comprised ecologists and conservation planners from various organizations throughout the OZHI. On the team were state wildlife habitat coordinators from Arkansas, Missouri, and Oklahoma; as well as staff from the Central Hardwoods Joint Venture (CHJV), GCPO, U. S. Geological Survey, and the U. S. Fish and Wildlife Service. The team’s vision was to achieve landscapes capable of sustaining healthy plant and animal communities throughout the OZHI through Strategic Habitat Conservation.

Beginning in 2012, the team undertook an ecosystem-based approach that prioritized conservation opportunity areas across the OZHI for seven forest communities (Table 1). These habitat types included glades, variations of oak and pine woodlands, and closed and floodplain forests and the potential distribution of these systems in OZHI was based on an ecological potential model developed by the CHJV that characterizes forested or semi-forested native communities in the larger central hardwoods region according to land-type associations, landform positions, and assumed historic disturbance regimes ((L. E. O’Brien, D. T. Jones-Farrand and J. A. Fitzgerald, unpublished data; Appendix A). Using the National Fish Habitat Partnership 1 km catchment boundaries (USGS 2010) as planning units, the team defined the relative priority of catchments for each forest community through set criteria. These criteria considered the potential to conserve the habitat within the catchment and the amount of re-purposed and developed lands it holds.

Catchments with known locations of focal species and existing conservation network lands also received priority (Figure 2).

Following the first part Strategic Habitat Conservation steps the OZHI team was at a point where they must now decide scenarios for restoring these areas that will secure wildlife species. Based on the criteria, the team identified a network of lands that have a high priority for restoration. Nearly three million hectares (6 million acres) of priority catchments were mapped for the different communities throughout OZHI (Figure 2). At this point, a multitude of plausible scenarios are possible from strategic and opportunistic standpoints. However, the OZHI team's decision is complicated by uncertainty in how wildlife populations will respond to restoration scenarios in the presence of concurrent impacts of climate change and urbanization. There is also a need to account for uncertainty associated with estimating risk to populations as well as uncertainty in exactly how the climate will change (e.g., consider projections from multiple emission scenarios and climate models). Finally, the decision of which scenarios is the best for all species when different species will likely have conflicting responses is complex.

Objectives

In April of 2015 we convened a workshop with the OZHI team to begin the SDM process. At this workshop the team identified objectives and alternatives for meeting those objectives. As indicated in their goal, the team's objectives ultimately focused on the sustainability of wildlife populations in OZHI. In restoring multiple communities, the team acknowledged that an optimal scenario needed to provide maximum benefits for a range of species associated with those habitats. Therefore, the team identified candidate

focal species representing the different communities (Table 1). We merged species for glade and open-oak woodland habitats given the similarities in these systems and the overlap in species. Species that received consideration were well-associated with the targeted communities (not habitat generalists) and had some reason for conservation concern (e.g., declining population, reduced range, threatened). The team also attempted to represent multiple taxa and species with a range of movement/dispersal abilities.

Of the list of candidate focal species, sufficient habitat and demographic data existed to model 6 species (Table 1). Songbirds comprised five of the seven species: prothonotary warblers (*Protonotaria citrea*) for bottomland forests, wood thrush (*Hylocichla mustelina*) and cerulean warblers (*Setophaga cerulean*) for closed forest, prairie warblers (*Setophaga discolor*) for glade habitat, and brown headed nuthatch (*Sitta pusilla*) in open-pine woodlands. A paucity of data prohibited modeling the team's original choice of Ozark big-eared bats (*Corynorhinus townsendii ingens*) for closed-oak woodlands. Therefore, we developed a model for *Myotis sp.* in general based on data for Indiana bats [*Myotis sodalist*] and Northern long-eared bats [*Myotis septentrionalis*]. The team also selected the eastern collared lizard (*Crotaphytus collaris*) to represent herpetofauna in glades.

For all species except eastern-collared lizards we quantified sustainability objectives in terms of viability for which we measured risk of decline for OZHI populations of each species. Risk simultaneously conveys responses of wildlife populations to conservation scenarios and the uncertainty in those responses, providing managers with a more intuitive and defensible way of comparing choices. In this way viability or risk is fundamental to making sound decisions (Millsbaugh et al. 2009). Because carrying

capacity (K) is both directly related to the amount of habitat restored and a key component in the DLMP models, we also examined K and population abundance of each species under the scenarios for added insight into the effects of conservation. However, while planners continue to focus on the amount of habitat restored and how that could increase carrying capacities of populations, evidence suggests that simple habitat-based metrics could mislead decisions when other processes are affecting populations (Bonnot et al. 2013). Similarly, projected abundances alone do not capture the sustainability of populations (Akçakaya 2000, Bonnot et al. 2013). Nevertheless, complications in the modeling of eastern-collared lizards caused us to rely only on estimates of habitat acreage available under the scenarios.

Alternatives

At the first workshop the team began developing alternative scenarios for restoring communities across priority areas to achieve wildlife objectives. In SDM, any kind of scenario can be considered, given it can be evaluated with respect to the objectives (Keeney and Gregory 2005). Therefore, we invited team members to suggest any scenario, restoring any number of areas in any arrangement, and based on any interests (e.g., agency goals, costs, or stakeholder needs). However, no alternatives were proposed by the team. Instead, the team structured alternative scenarios around key questions they face when planning conservation across large-scales over the long term. The questions related to the amount of acreage needed to benefit populations, their process for prioritization under SHC, and the relative impacts of targeting only protected lands versus restoring habitat on both private and protected lands (Figure 4). By structuring the

scenarios around these considerations, the team intended to explore the most effective vision or strategy for habitat conservation in OZHI.

Acreage. The team outlined scenarios by the amount of habitat restored. Realizing that restoring the entire network of priority areas was unrealistic, the team establish acreage goals on a biological basis. The team relied on previous work by the CHJV that estimated acreages needed for different habitats to meet population objectives of bird species associated with those habitats (CHJV 2012). They considered a full acreage scenario that targeted habitats in priority catchments at levels set by CHJV. This scenario targeted a total 1.2 million ha of restoration with individual community goals ranging from 23,059 ha of open-pine woodland to 362,232 ha of closed-oak woodland. This scenario was compared to one in which half the amount of the total acreage was targeted and a baseline scenario where no restoration occurred. By including a baseline scenario, the team could assess the general impact of habitat conservation.

Prioritization. The team also considered scenarios to evaluate the process used to prioritize the catchments. The team compared scenarios that restored habitats in catchments prioritized according to team's SHC original approach based on the current landscape with scenarios that placed restoration in random catchments, regardless of priority (Figure 5). This comparison examined the necessity of "strategic" conservation in achieving regional goals.

In a third set of scenarios the team adapted their SHC prioritization to incorporate predictions of the landscape in the future. Given that restoration scenarios would eventually be simulated on projections of future landscapes under urbanization and

climate change effects, the team chose to capitalize on those projections and reprioritize catchments based on future conditions. The following is a brief description of this reprioritization; a more thorough description of landscape projections can be found in the following paragraphs. The team's original SHC approach allotted higher scores to catchments with less developed land. Therefore, we used projected landcover data for 2100 and recalculated this score. Future landcover was derived by combining data from recent climate, landscape, and urbanization models (Terando et al. 2014, Wang et al. 2015a,b, Bonnot et al. In review). In the future-based SHC scenarios the team also incorporated projected impacts of climate change on forest conditions to prioritize areas where climate change could promote restoration efforts. Restoring woodland and glade communities across much of OZHI involves reducing the stocking to open up canopies of closed forests. However, under climate change, forests throughout parts of the region are expected to see similar shifts in their structure (Bonnot et al. In review, Wang et al. 2015a,b). Therefore, the team compared current estimates of canopy cover throughout the OZHI with estimates for forests in 2100 and increased priority for catchments, targeted for woodland and glade restoration, which predicted canopy cover decreased towards desired levels. Through this future-based prioritization the team explored the relative benefits of considering model predictions when developing conservation strategies.

Protection status. Finally, the team structured scenarios around the ownership or protection status of lands in OZHI. Although OZHI contains large amounts of publicly owned or managed land, the majority (approximately 80%) of the region's forests lie in private ownership. Federal and state sponsored programs targeting private lands have

been a growing source of conservation in the region. Despite this trend, the relative importance of private lands conservation in sustaining species is still not completely understood, leaving regional planners uncertain about their role. Therefore, the team compared scenarios that focused restoration only on public lands and lands with protected status (hereafter “protected lands”) against scenarios that targeted both protected and private forest lands (combined scenario). We identified protected lands using the Protected Area Database 1.3 (USGS 2012). Because the amount of habitat targeted under a full acreage scenario exceeded the amount of protected lands, the protected only and combined scenarios were not comparable from an acreage standpoint. However, we maintained this comparison to capture the limitation of focusing only on protected lands. We also omitted scenarios restoring half of the acreage on the protected lands given similarities in the amount of restoration.

Simulations. We simulated scenarios by selecting lands for restoration and characterizing the habitat of those lands based on the desired habitat. We designed the process of selecting lands under the scenarios to be dynamic and interactive; that it would reflect the reality of planning and carrying out restoration across the OZHI overtime. Restoration occurred at a forest patch scale which we delineated through the intersection of projected future landcover, the team’s catchment units, and the Protected Area Database. This scale was relevant to the level of forest management, while enabling distinction between catchment priorities and protected status. Because the Ecological Potential Model provided the distributions of the habitats across the region, patches could contain multiple potential habitats. Therefore, in meeting individual habitat goals we

identified patches based on the highest scoring (priority) habitat occurring within the patch.

For all scenarios, we implemented restoration goals over fifty years, selecting individual patches in each decade to fulfill the acreage goals for each habitat. Thus, we targeted approximately 244,901 ha and 122,668 ha of combined habitats each decade from 2010–2050 for the full and half-acreage scenarios, respectively (Figure 5). We considered this rate of activity reasonable given current efforts across the region. We selected patches in order of the prioritization of their catchment and its protected status as defined by individual scenarios. For example, to restore glade habitat we selected patches across OZHI with the highest priority for glades. Only when we exhausted all available patches of a given ranking did we begin restoring patches in the next highest ranking. We randomly selected patches within a priority ranking to reflect the opportunistic nature of both public and private-land restoration.

The selection process was also interactive. Landscape projections and the patches delineated from them in each decade were a function of the previous decade's landcover, the restoration simulated during the previous decade, and the urbanization projected for that decade. This combination allowed us to incorporate interactions between private and protected-lands management and projected urbanization (Figure 6). We exempted protected lands from urbanization and kept patches, restored on private lands prior to urbanization, from being developed for a period of time. We assumed a conservation lease of 20 years on private-lands restoration to reflect the nature of such agreements. Following that period, restored patches were again susceptible to development. We selected additional patches throughout the entire simulation to maintain restored acreages

targets despite losses to urbanization. All urbanization effects that removed forest were permanent and precluded restoration.

Once future habitat restoration was planned, we characterized forests on restored and unrestored lands to represent the effects of urbanization, climate change, and restoration on focal species habitat overtime under alternative scenarios. We focused on characteristics related to habitat for the focal wildlife species, including common variables such as landcover and landform. Other variables described aspects of forest structure and landscape configuration.

Translocation simulations. Concerns about dispersal limitations that could prevent brown-headed nuthatch to colonize habitat outside of its current distribution prompted the team to also consider translocation of this species in addition to habitat restoration. We simulated translocation directly in the population model by introducing 100 breeding females into the Current River Hills subsection in each of the first five years of the simulation.

Climate change and urbanization. We characterized habitat on unrestored lands by combining urbanization predictions with data on forests projected under climate change. Forest data comprised a subset of recent projections from Wang et al. (2015a, b) in the Central Hardwoods from 2000 – 2300. Wang et al. (2015a, b) 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. Tree harvest reflected current management of the regions forest based on

Forest Inventory and Analysis data from 1995–2005. Wang et al. (2015a, b) 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 II, which integrates temperature and precipitation data with nitrogen availability and soil moisture to model individual tree species growth and mortality at a site (Wullschleger et al. 2003).

We obtained estimates of urbanization from a recent GCPO study that applied the SLEUTH model to the southeastern U.S. (Belyea and Terando 2014). The SLEUTH model is the evolutionary product of the Clarke Urban Growth Model that uses cellular automata, terrain mapping and land cover change modeling to estimate the probability of urban development (Jantz et al. 2009). This approach incorporates growth rules to model the rate and pattern of outward growth of existing urban areas and growth along transportation corridors and new centers of urbanization (Belyea and Terando 2014).

We expanded on Bonnot et al.'s (In review) methods to derive habitat variables from these sources through geoprocessing in ArcGIS (ESRI 2013). We characterized NLCD landcover classes by comparing the relative importance values estimated by LANDIS PRO for deciduous versus coniferous species and incorporating probabilities of urbanization (Table 2). We grouped landcover to characterize overall forest composition and configuration across the region. We modeled additional forest characteristics from LANDIS PRO data, seral stage classifications, basal area, and stocking, from which we estimated canopy cover. We approximated densities of snags, small stems and overstory trees based on density projections for specific aged cohorts. We used a landform

classification derived from DEM (Jenness 2013) and measured distance to water based on the National Hydrography Dataset (USGS 2010)

We accounted for uncertainty in climate change projections by characterizing landscapes under three future climate scenarios. Wang et al. modeled landscapes 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-year period from 1980–2009 observed throughout the region (Wang et al. 2015a). 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. These different characterizations provided contrasting background impacts against which we could capture uncertainty in the effectiveness of conservation scenarios.

Restoration. For each decade, we characterized habitat variables on restored lands to reflect the conditions desired through restoration of the natural communities. The GCPO and CHJV have established desired endpoints for the different habitats that describe landcover and vegetation structural characteristics intended through restoration and continued management (Table 1). These values are based on ecological literature and the ecological potential model underlying the natural communities (Blaney et al. 2016, Kabrick et al. 2014, L. E. O’Brien, D. T. Jones-Farrand and J. A. Fitzgerald, unpublished data). We assigned these endpoints and any habitat variables derived from them to

restored cells. Although selection occurred at the patch level, restoration individually affected cells within a patch based on its potential community type. Thus, although a forest patch was selected for a given habitat type (e.g., open-oak woodland), any other potential forest communities within the same patch would also be restored. As a result, the amount of area restored for some communities types, which are better represented in OZHI, exceeded their targets in attempting to meet goals for less common types. We considered this a realistic assumption given management activities, such as prescribed burning, would affect entire patches.

Consequences

To predict the consequences of the alternative conservation scenarios on viability objectives, we developed DLMP models for focal species based on the landscapes simulated for each scenario. Following the approach developed by Bonnot et al. (In review), we began with landscape data projected under alternative restoration and climate change scenarios and used habitat models to translate these projections into species' habitat and demographics at each time step. Finally, we incorporated these spatially and temporally varying demographics into metapopulation models that included stochasticity and parametric uncertainty. The resulting models provided spatially and temporally explicit representations of focal species habitat and population growth throughout OZHI.

Habitat Models. We employed habitat models to link landscapes to demographic processes such as distribution, reproduction, and dispersal. We modeled distributional abundance and carrying capacity using multiscale Habitat Suitability Index (HSI) models. These models predict suitability of habitat in cells based on their attributes and the surrounding landscape (Dijak and Rittenhouse 2009). In some cases these models have

been verified and validated with empirical data (Tirpak et al. 2009). For focal bird species we relied on HSI models developed for OZHI and surrounding landscapes (Tirpak et al. 2009, Larson et al. 2003). We modeled *Myotis* habitat by combining an HSI model for Indiana bats (*Myotis sodalis*) from Rittenhouse et al. (2007) with habitat relationships for northern long-eared bats (*Myotis septentrionalis*) (Larson et al. 2003, Starbuck et al. 2014). We identified eastern collared lizard habitat as glades interconnected by adjacent woodlands. See Appendix A for more detail on the habitat models used for each species.

We followed Bonnot et al.'s (2013) approach to estimating K for cells by assuming a linear relationship between HSI and maximum densities found in the literature. We then scaled density by the area of cells and spatially filtered areas of the landscape that could not support at least one territory or colony (for *Myotis spp.*), constrained by a maximum territory or home range (for *Myotis spp.*) size found in the literature. This process more realistically captured the interaction between spatial and resource limitations inherent in estimating K. Shifts in distribution over time due to the climate's effect on habitat were captured by subsequent changes in K.

We used a Relative Productivity Index (RPI; Bonnot et al. 2011) model to link breeding productivity of birds affected by parasitism to habitat fragmentation. The RPI index (0–1) modifies reproductive success of birds breeding in fragmented landscapes and proximate to edge based on the amount of forest cover in a 10-km radius and edge within a 200-m radius.

Finally, we applied dispersal models to estimate cell-based movements of dispersing individuals to the surrounding landscape based on species specific functions of distance

between cells, weighted by K of the destination cell (Bonnot et al. 2011). Thus, changes in future dispersal movements reflected shifts in the distribution of focal species in the region.

Population Modeling. We linked the regional populations of focal species to landscapes by treating ecological subsections as subpopulations and summarizing their demographics for each subsection. The region contained 32 subsections which we delineated into 45 unique subpopulations (Cleland et al. 2007). For each subpopulation we summarized results of the habitat models to obtain estimates of initial abundance (year 2010) and K at each decade. We averaged cell RPI's in each subpopulation, weighted by their K in each decade, so that productivity estimates reflected any changes in distribution of birds over time. For each decade dispersal movements were summarized by subpopulation and standardized to obtain relative rates of dispersal from each subpopulation to surrounding ones (Bonnot et al. 2011). Because we ultimately modeled population dynamics annually, we calculated yearly values of spatial demographics by linearly interpolating between decadal estimates and stored them in spatio-temporal arrays.

We programmed the population models in Program R (R Core Team 2013). We used female only, Lefkovitch matrix models comprising various stages, dependent on species life history. We specified stage-specific survival and maternity rates from the literature and assumed a post-breeding census (Table 3). For species affected by parasitism, we multiplied RPI's with published estimates of maternity to obtain population-specific fertility estimates in each decade. We specified breeding and natal dispersal rates for relevant stages that determined the proportion dispersing each year and

redistributed them among the subpopulations according to multinomial distributions with probabilities equal to the relative dispersal rates for that year. We used a Ricker contest and modified ceiling density dependence model to incorporate density dependence. The modification to the commonly referred to ceiling density dependence (Akçakaya and Brook 2009) prohibits individuals over K in a population from breeding but allows them to remain in the population or disperse. See Appendix A for detailed discussion of the parameters used in population models for focal species.

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 1,000 iterations from beta and gamma distributions, respectively, with means equal to their overall estimates and corresponding error, derived from the literature (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. 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.

Tradeoffs

We relied on decision theory methods to process the uncertainties inherent in DLMP projections and multiple climate futures, and resolve the tradeoffs between competing

objectives (i.e., disparate species responses). We pooled projections across climate models and estimated median projections with 85% credible intervals for each scenario. We translated error into risk by quantifying the proportion of the 1,000 iterations for which the each focal population declined below different sizes (Akçakaya 2000). This metric estimated the risk of populations declining by various percentages from the initial size through 2100, under each restoration scenario. We further identified a 25% decline as the threshold which to compare risk because it provided greater contrasts across scenarios and species.

We considered various approaches to summarizing risk from scenarios across species and selecting scenarios based on the summaries. These included choosing the scenario that presented the lowest average risk of a 25% decline across focal species. We discussed with the team the possibility of a weighted average based on species conservation status or the responsibility of the OZHI in conserving each species relative to other regions. We also considered a mini-max strategy that minimized the maximum risk across species and a maxi-min strategy that maximized the minimum gains in viability across scenarios (Drechsler and Burgman 2004, Polasky et al. 2011).

RESULTS

Overall impact of restoration on focal species was positive and presented evidence to support landscape conservation design. Restoration scenarios increased habitat for most species relative to the base scenario. Growth of focal populations either responded favorably to restoration scenarios or were unaffected. As a result, restoration scenarios generally reduced risk of declines for focal wildlife under climate change and

urbanization, compared to baseline projections. Despite the general effectiveness of the restoration, species-specific responses to individual scenarios varied in complex ways through interactions with landscape change processes such as urbanization and climate change and the demographic processes affecting each species. Detailed descriptions of individual species projections are provided in Appendix A.

Base Projections

In the absence of restoration scenarios, landscape changes due to climate, forest succession, and forest management processes produced substantial changes in habitat of the focal species. For example, habitat for species such as prairie warbler, cerulean warbler, and brown-headed nuthatch involves particular aspects of forest structure such as open canopies, increased small stems, or mid-range stocking rates. Following historic losses in these habitats, our initial carrying capacity estimates indicated that OZHI could support >96,000 breeding individuals for each of these species (Table 4). However, with an inability of current forest management to maintain that structure, natural forest succession forests under the current climate resulted in dense, mature, closed forests, causing 34%, 85%, and 71% decreases in carrying capacities of these birds by 2100 in the base scenarios. The base scenario for these species under the two climate change models projected similar habitat losses early on. But, by the latter half of the century, reduced precipitation and elevated temperatures began to alter forest structure, reducing tree stocking and resulting in lower canopy cover and more open forest structure that allowed prairie and cerulean warbler habitat to rebound (Appendix A). It is also possible that slight shifts in forest composition to pine species may have played a role in the positive effects of climate change on brown-headed nuthatch carrying capacity (Table 4).

In contrast, base scenario projections for wood thrush, prothonotary warbler, and *Myotis spp.* (species associated with characteristics of mature forests) identified increases in habitat through the first half of the century driven by forest succession. Under the current climate model, these increases plateaued later in the century as more forests reached climax stages. However, we projected decreases in wood thrush carrying capacity under the GFDL-A1Fi model; a negative response to the same processes benefiting prairie warblers.

How species responded to the baseline changes in habitat further depended on varied demographic processes affecting population growth. Except for brown-headed nuthatch, all focal populations declined $\geq 19\%$ through 2100 in the base scenario (Table 5). Driven by early habitat losses, prairie warblers and cerulean warblers declined early in the simulations. By midcentury prairie warbler began responding to the increased habitat created under the GFDL-A1Fi model, eventually reaching abundances twice that under the current climate model (Figure 6). Cerulean warblers also saw increased habitat later in the century from climate change but, the population had little time to react. As such their declines were similar for the base scenario under all climate models (Figure 5).

Despite increases in habitat, we projected declines in wood thrush, prothonotary warblers, and *Myotis spp.* for the base scenario under all climate models. Declines in wood thrush and prothonotary warblers likely stemmed from the impacts of fragmentation on reproduction. *Myotis spp.* were unaffected by changes in habitat. Projections for brown-headed nuthatch suggested they were most limited by habitat. Their population growth closely tracked changes in carrying capacity, resulting in projections of a declining,

stable, and growing population under the current, CGCM.T47-A2, and GFDL-A1Fi climates, respectively (Table 5).

Ultimately, under the base scenario, we projected moderate to high risk of decline for focal species across all climate models, without restoration. With a 7% chance of a 25% decline by 2100, brown-headed nuthatch is the only population with risk of 25% decline < 30% (Table 6). Stemming from early declines due to habitat loss, prairie warblers and cerulean warblers are most at risk of losing a quarter of their populations at 59% and 53%, respectively. Despite available habitat, risk for wood thrush, prothonotary warblers, and *Myotis spp.* ranged from 34-39% for the base scenario.

Species Responses to Restoration Scenarios

Restoration scenarios interacted with climate-driven baseline changes in the landscape to variably affect species habitat overtime. Scenarios that focused only on protected lands failed to reach acreage targets given limited extents of these lands. Only scenarios that combined private with protected lands achieved acreage goals. General in its use of mature, closed forest, wood thrush habitat was abundant in the OZHI and projected to increase in the absence of restoration. Therefore, much of the restoration geared towards woodlands and glades opened forest structure, decreasing wood thrush K 2-10% below baseline projections (Table 4). Except for *Myotis spp.*, habitat for the other focal species increased under restoration scenarios. Restoration provided increases in K over the base scenario most for cerulean warblers. Under the current climate model, restoration was projected to support 335-602% more cerulean warblers than in the base scenario (Table 4). These increases were less substantial under the climate change models given K was

already elevated due to climate effects. Prairie warbler, brown-headed nuthatch and prothonotary warbler K's also increased under most restoration scenarios however, prairie warbler habitat declined under the random scenario. In contrast to the climate driven, habitat increases for these species, K increased immediately under restoration scenarios. *Myotis spp.* habitat was relatively unaffected by climate change or restoration (K changed < 2%).

We projected complex responses of focal populations to the changes in their habitat from restoration. In addition to their positive responses to climate change, prairie warblers and cerulean warblers showed the greatest responses to conservation as their abundances under some scenarios doubled that projected with no restoration (Table 5; Figure 7). Although prairie warbler carrying capacity increased <10% under the scenarios, the population responded greatly, in some cases reversing declines and cutting the risk of significant decline by half (Table 6; Figure 8). In contrast to the late habitat increases cerulean warblers experienced under the GFDL-A1Fi model, the population had the time to respond to habitat provided by restoration earlier in the simulations (Figure 8). Wood thrush, prothonotary warbler, and *Myotis spp.* population growth was largely unaffected by restoration. Because the wood thrush population is primarily influenced by fragmentation and not habitat availability, their population growth was largely unaffected by restoration, although scenarios decreased wood thrush habitat, Projected wood thrush abundance under different restoration scenarios ranged from 14% below to 27% above base projections. However, the substantial uncertainty surrounding these projections suggests a lack of an overall response. Indeed, risk of declining 25% varied < 2 points

across scenarios when pooling climate models (Table 6). Risk for prothonotary warblers and *Myotis spp.* also remained relative unchanged (Figure 8).

Despite being habitat limited with restoration increasing their habitat region wide, brown-headed nuthatch populations declined with restoration alone. Restoration of open-pine forests mainly took place in the Current River Hills and Black River Border subsections, outside of this bird's current distribution (brown-headed nuthatch are currently limited to the Boston Hills and adjacent sections). The majority of restoration occurring where the current population is actually decreased K causing population declines. Scenarios that incorporated translocation of brown-headed nuthatch to the Current River Hills subsection in addition to restoration overcame the dispersal limitations and allowed these birds to utilize the new habitat, leading to population growth (Figure 7). With added translocation, risk of decline for brown-headed nuthatch under restoration scenarios fell below 5% (Table 6). The various complex processes that affected how each species responded to restoration ultimately resulted in a different ideal scenario for each species.

Although the effectiveness of scenarios varied across species, general patterns were evident among comparison of scenarios. Base scenarios with no restoration or randomly placed restoration presented the most risk to species (Table 6). Scenarios that targeted full acreage objectives best reduced risk for the most threatened species (prairie warbler and cerulean warbler), while avoiding added risk to other species. When controlling for the amount of land restored, management of protected lands was more effective at reducing risk of decline than distributing restoration across private and protected lands. Prioritizing restoration based on estimates of future landscapes conditions only slightly improved responses of focal populations. Based on averages across focal species, the

scenario that targeted the full acreage objectives on both private and protected lands, prioritized based on future landscapes best reduced risk for species (Figure 9). This scenario also provided the most habitat for eastern collared lizards.

DISCUSSION

We have provided an important confirmation that planning for viable populations can be achieved under global change. Because the largest impacts of climate change are still decades in the future, a new level of proactive management is required (Lawler 2010). At the same time it is becoming increasingly clear that local or isolated efforts to conserve biodiversity in a changing environment are likely to be insufficient (Bonnot et al. 2013). Ultimately, the OZHI team identified an alternative for habitat conservation that most reduced the average risk to focal populations across a large region throughout a century of climate change and urbanization (Figure 9). Because of the approach used, that decision was objective and transparent, and thus defensible. The decision accounted for numerous sources of uncertainty, from error in demographic rates to uncertainty among emissions scenarios. And it was actionable, comprising detailed guidance on specific conservation activities that managers can take to the ground. Therefore, this approach has the potential to overcome the uncertainties and complexities that are inherent in the process of long-term, large-scale conservation planning.

The effectiveness of this pilot approach stems from the integration of the two methods and how they complement one another. Although DLMPs provide information of the effects of climate change on populations or the responses of populations to conservation actions, this information alone does not make the decision (Beisinger and McCullough

2002). Rather decisions, are still plagued by complexity of competing objectives and the uncertainty stemming from model error and uncertain climate futures (Naujokaitis-Lewis et al. 2008, Iverson et al. 2016). To the contrary, structured decision making enables decisions by simplifying their inherent complexity and uncertainty. But, the degree to which they are good decisions is dictated by how well the effects of climate change and conservation activities on populations are represented in the process (Marcot et al. 2012). Integrating the two methods resolved these issues and provided planners a structured way to compare the effectiveness of alternative conservation scenarios on multiple species under various climate change possibilities while being confident that important ecological and population processes were captured in each outcome. Estimating risk is fundamental to population modeling but, it is also fundamental to decision making as it more intuitively conveys the severity and uncertainty of potential impacts to planners and policy-makers (Millspaugh et al. 2009). Thus, a key advantage of this integration lies in the ability of DLMPs to estimate risk and the ability of decision makers to structure their decisions around it.

Use of decision analysis theory allowed the team to address key uncertainties and complexities that plague largescale, long-term planning. Managers must continually account for multiple objectives (e.g., biological benefits, cost, public interest) in conservation planning (Lambeck and Hobbs 2002, Noon et al. 2009). Such considerations create potential for conflicts. Rather than avoid these conflicts, decision theory provides methods to address competing objectives, such as multicriteria decision and tradeoff analyses (Schwenk et al. 2012, Thompson et al. 2013). In this way, the OZHI team viewed the needs of multiple species as competing objectives and adapted a

multicriteria decision analysis to objectively resolve tradeoffs among them. The largest source of climate-related uncertainty for the future is not model error but, rather the path of emissions scenarios taken by society (IPCC 2013). We accounted this uncertainty by pooling risk across possible climate change scenarios. However, by relying on the average risk across climate scenario and species, we implicitly assumed equal probabilities for each future. Given the current lack of probabilities of climate change outcomes (Kujala et al. 2013), this assumption may or may not be valid. In such cases, other summaries of risk, such as maxi-min or mini-max regret, are preferred because the optimal choice does not depend on knowing probabilities of future outcomes (Polasky et al. 2011, Thompson et al. 2013).

The results indicate that habitat restoration, implemented strategically through a landscape conservation design process, can effectively conserve multiple species in the face of climate and landscape change. Species, such as prairie warblers and brown headed nuthatch that associated with woodland and glade communities, dramatically benefited from restoration. The loss and alteration of these communities over the last century were responsible for the concern and risk surrounding prairie warblers. We expected restoration scenarios to reduce habitat for wood thrush but, its population was unaffected by these changes, with the impacts of fragmentation instead driving declines. Similar patterns were projected for other species. Therefore, restoration scenarios balanced competing habitat needs. Results also indicated how climate change could alter forest structure later in the century, essentially opening forests and creating woodland habitat. While prairie warblers did respond to these changes, the ability of restoration to provide habitat earlier prevented larger declines in their population and reversed declines

of cerulean warblers. Given that adaptation of forest communities to climate change is a current focus in management, the notion that current efforts could restore important habitats for these species, while at the same time adapting landscape for climate change is an encouraging finding.

More generally, this project illustrated how targeting ecosystem-based management within the DLMP-SDM framework reflects a blend of climate adaptation approaches. An important approach to climate adaptation has been resiliency, focusing on the capacity to adapt to changing conditions and thereby conserve certain key processes, and the capacity to transform to a completely new mode of operation if the old mode becomes untenable (Polasky et al. 2011). Often general and inclusive in the processes addressed, resilience can require targeting threats originally affecting populations, which is an important aspect of DLMPs (Harwood 2000). For example, our restoration scenarios, while targeting the effects of habitat loss and fragmentation responsible for wood thrush and prairie warbler declines, also helped to build resiliency of the populations under climate change. While the tradeoff with a resiliency approach is that it can be too general to develop specific plans (Polasky et al. 2011), the alternatives used in our example not only increased resiliency but, are themselves specific plans which can be implemented.

Our approach also closely resembles the use of scenario planning in climate adaptation. In scenario planning, contingency plans are developed for a range of future impacts (Polasky et al. 2011, Amer et al. 2013). Important assumptions of this approach are that potential impacts are foreseen and that plans will be effective at addressing them. Our approach helps uphold this assumption. The OZHI team originally did not expect the positive impact of severe climate change on prairie warbler habitat. Nor did it foresee the

negative impact of habitat restoration without translocation on brown-headed nuthatch. But, outputs from the population models provided important insights into what could happen and the potential limitations of our approaches. These instances informed planners of important processes, that were impacting species, allowing them to better develop multi-faceted plans to conserve populations under multiple threats (Bonnot et al. 2013).

Although we demonstrated the capability of the DLMP-SDM process to guide conservation decisions, the effectiveness of this framework to provide robust decisions across applications will depend greatly on the rigor of the science and the capacities of the decision teams. Optimal decisions require an accurate representation of species responses to conservation amidst any threats (Beisinger and Westphal 1998). However, one of the weaknesses in our pilot was that habitat models for some species likely did not thoroughly capture the effects of climate change and restoration activities on their habitat and demographics. Such incomplete models might explain why projections of *Myotis spp.* remained unchanged across scenarios. Furthermore, the DLMP models in our pilot did not incorporate recent evidence of the threat that climate warming poses for songbird reproductions (Cox et al. 2012, This volume, chapter 3). Significant declines projected by such processes could render habitat restoration ineffective and thus, irrelevant in the decision. Therefore, identifying quality plans will require that decisions are based on the most thorough and accurate information available.

The utility of this approach will also be determined largely by the ability of the decision teams to correctly frame their problems, agree on their objectives, and design alternatives. Decision environments can range from long-term visions for agency wide

programs to time-sensitive and dynamic scenarios that allow day to day responses to changing conditions (Thompson et al. 2013). Having a clear idea of the planning context for a decision and being able to match objectives and alternatives to that situation is important (Drechsler and Burgman 2004). For our example, considering millions of hectares of habitat restoration to target population viability objectives over the next century made sense from long-term planning perspective of the GCPO. However, team members, such as state habitat coordinators, that are restricted to planning management over smaller extents with shorter time frames and smaller budgets, saw less utility of this approach in their daily decisions. Additionally, this pilot project constrained planning to the biological objectives despite a full awareness that stakeholder and partner interest, cost, and other factors will need to be weighed in any decision (Keeney 2007, Powledge 2012). Finally, the OZHI team's structuring of alternatives resulted in very similar restoration plans. As a result, population responses were at times similar and the overall decision among risks, close. To avoid these potential difficulties, it will be crucial that decision makers balance creativity and experience to entertain a wide range of alternatives (Gregory et al. 2012). The range of alternatives is only limited by the ability to model their consequences in terms of the objectives. Recruiting diverse interdisciplinary teams that have experience with the system of interest and expertise in different fields can help greatly in such cases (Polasky et al. 2011).

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Table 1. Forest vegetation communities targeted for restoration in the Ozark Highlands. Dynamic-landscape metapopulation models were used to predict responses of focal wildlife species (bold), selected from lists of candidate species representing each community, to alternative scenarios for restoring communities. Acreage objectives for restoration were derived from the Central Hardwoods Joint Venture bird population objectives. Restoration of forest communities was simulated in scenarios with desired forest characteristics, reflective of each community.

Forest vegetation community	Candidate species ^a	Targeted acreage		Simulated forest characteristics				
		Hectares	Acres	Canopy cover	Small-stem density ^b	NLCD class	Stocking	Hardwood basal area ^c
Glade	Prairie warbler, Eastern collared lizard , Diana fritillary, Wood rat	77,938	192,589	5%	8,000	41	10%	5
Open-oak woodland		479,193	1,184,110	40%	10,000	41	30%	8
Closed-oak woodland	Ozark big-eared bat, Myotis sp	895,095	2,211,824	70%	4,000	41	50%	13
Open-pine woodland	Brown-headed Nuthatch , Eastern tiger salamander	56,979	140,798	40%	6,000	42	30%	3
Pine-oak woodland	Chuck-will's-widow, Whip-por-will, Ringed Salamander	471,530	1,165,174	70%	4,000	43	50%	8
Mesic forest	Wood thrush , Wood frog, Ozark Salamander, Cerulean warbler	654,451	1,617,181	90%	2,000	41	70%	16
Riparian/bottomland forest	Prothonotary warbler , Oklahoma Salamander, Rafineque's Big-eared Bat	363,363	897,888	90%	2,000	90	70%	19

^a Scientific names: prairie warbler (*Setophaga discolor*), eastern collared lizard (*Crotaphytus collaris*), Diana fritillary (*Speyeria diana*), wood rat (*Neotoma floridana*), Ozark big-eared bat (*Corynorhinus townsendii ingens*), brown-headed nuthatch (*Sitta pusilla*), eastern tiger salamander (*Ambystoma tigrinum*), Chuck-wills-widow (*Antrostomus carolinensis*), whip-por-will (*Caprimulgus vociferus*), ringed salamander (*Ambystoma annulatum*), wood thrush (*Hylocichla mustelina*), wood frog (*Lithobates sylvaticus*), Ozark salamander (*Plethodon angusticlavius*), cerulean warbler (*Setophaga cerulea*), prothonotary warbler (*Protonotaria citrea*), Oklahoma salamander (*Eurycea tynnerensis*), Rafinesque's big-eared bat (*Corynorhinus rafinesquii*)

^b Stems/ha

^c m²/ha

Table 2. Description of processes for deriving variables used to model habitat of focal wildlife species in the OZHI. Raw output from SLUETH and LANDIS PRO sources was transformed to estimate habitat variables based on ecological relationships provided in literature.

Model Source	Source output	Habitat Variable	Processing
SLUETH ^a	Probability of development	Landcover	Classified cells as deciduous forest if the combined importance of deciduous species > 65% and coniferous forest if such species comprised > 47% of the cell's importance. Forested cells not classified as either deciduous or coniferous were assigned to the mixed forest type. Further classified deciduous forest cells as woody wetlands for any cells with this original NLCD class. Incorporated changes from urbanization by assigning cells with > 50% probability of being urbanized as developed lands.
	Importance value		
	Tree age	Snag index	Used maximum tree age of cell to approximate the density of snags (Larson et al. 2003).
		Large snag index	Applied relationship with maximum tree age derived by Rittenhouse et al. 2007. The function is based on the estimates of snag density by stand rotation age, weighted for larger snags.
LANDIS PRO ^b	Tree density	Small stem density	Approximated density of stems (< 2.54 cm DBH) by the density of all tree species in the 0–10 age cohort. Based on assumption that most hardwood species take approximately 10 year to reach 2.54 cm DBH (Johnson et al. 2009).
		Overstory stem density	Approximated by the density of potential overstory tree species in the 70--300 age cohort.
	Basal area and tree density	Seral stage	Calculated QMD from cell basal area and tree density. Classified QMD into 5 seral stages: grass-forb (< 2.5 cm dbh), shrub-seedling (2.5 to 7.5 cm), sapling (7.5 to 12.5 cm), pole (12.5 to 37.5 cm), and sawtimber (> 37.5 cm) (Tirpak et al. 2009).
		Stocking	Calculated total stocking from QMD and tree density using allometric equations for coniferous and deciduous species.
		Canopy cover	Estimated based on empirical relationship with stocking identified for hardwood forests in the region [Canopy Cover = (41.83 * Log ₁₀ (1.21 + STOCKING))] (Blizzard et al. 2013).
	Basal area	Hardwood basal area	Extracted basal area for hardwood species.

^a Belyea and Terando 2014

^b Wang et al. 2015a

Table 3. Species specific demographic parameters used in dynamic-landscape metapopulation models of focal wildlife species in the Ozark Highlands. The models were stage-based models that incorporated published estimates of survival and fertility rates. Carrying capacity and initial abundance were estimated by modeling empirical densities. Processes such as density dependence, parasitism, and dispersal varied across species.

		Species					
		Brown-headed Nuthatch	Prairie Warbler	Wood Thrush	Prothonotary Warbler	Cerulean Warbler	Myotis sp.
Survival	Adult	0.67	0.6	0.61	0.675	0.6	0.9
	Juvenile	0.3	0.32	0.29	0.18	0.28	0.57
	Pup						0.898
Fertility (females/females/year)	Adult	1.3	1.55	1.45	1.95	1.5	0.42
	Juvenile						0.279
Density (females/ha)	Carrying Capacity	0.225	1	0.5	0.6	2	0.1
	Initial	0.169 (75%) ^a	0.5 (50%)	0.06 (12%)	0.03 (5%)	0.14 (7%)	0.025 (25%)
Density Dependence		Modified Ceiling	Modified Ceiling	Modified Ceiling	Modified Ceiling	Modified Ceiling	Ricker (Contest)
Parasitism		None	RPI ^b	RPI	RPI	RPI	None
Dispersal Distance ^c (km)		1.27	70	70	70	70	None

^a Percentage of carrying capacity

^b Relative productivity index is applied to fertility rate to account for parasitism processes in reproduction of open-nesting birds.

^c Percentage of carrying capacity

Table 4. Effects of restoration scenarios and climate change on the habitat of focal wildlife species in the Ozark Highlands by 2100. Final carrying capacities for the base scenario under models of the current climate, moderate (CGCM.T47-A2) and extreme (GFDL.A1Fi) climate change are listed. The relative impacts of each restoration scenario on final carrying capacity relative to the baseline are presented as the percent difference. Scenarios that resulted in less capacity compared to the base scenario are highlighted in red.

	Base	<u>Prioritized for Current Landscape</u>			<u>Prioritized for Future Landscape</u>			<u>Random</u>
		<u>Combined lands^a</u>		<u>Protected</u>	<u>Combined lands</u>		<u>Protected</u>	<u>Combined lands</u>
		Full	Half	Full	Full	Half	Full	Full acreage
		acreage	acreage	acreage	acreage	acreage	acreage	
<u>Prairie Warbler (96,008)^b</u>								
Current	63,603	4%	4%	4%	14%	6%	6%	-15%
CGCM.T47-A2	69,185	-22%	-17%	9%	11%	6%	7%	-15%
GFDL-A1Fi	82,841	-3%	-1%	1%	1%	1%	4%	-16%
<u>Wood Thrush (3,046,160)</u>								

	Current	3,450,832	-4%	-2%	-2%	-8%	-6%	-7%	-7%
	CGCM.T47-A2	3,395,167	-10%	-9%	-3%	-8%	-6%	-7%	-7%
	GFDL-A1Fi	3,345,546	-4%	-2%	-2%	-8%	-6%	-6%	-7%
	Prothonotary Warbler (255,200)								
	Current	394,119	11%	5%	4%	10%	5%	4%	10%
	CGCM.T47-A2	396,326	31%	27%	4%	10%	5%	4%	10%
	GFDL-A1Fi	398,656	11%	5%	4%	10%	5%	4%	10%
	Cerulean Warbler (120,870)								
	Current	238,021	602%	335%	370%	771%	385%	427%	496%
	CGCM.T47-A2	622,367	257%	144%	141%	287%	144%	159%	186%
	GFDL-A1Fi	2,505,305	44%	25%	25%	57%	29%	30%	34%
	Brown-headed Nuthatch (106,191)								
	Current	31,008	33%	16%	18%	45%	20%	30%	10%
	CGCM.T47-A2	38,105	-18%	-9%	5%	31%	14%	17%	6%
	GFDL-A1Fi	47,410	14%	8%	5%	24%	10%	10%	-2%
	Myotis sp. (597,608)								

Current	666,782	0%	0%	0%	0%	0%	0%	0%	0%
CGCM.T47-A2	667,744	2%	2%	0%	0%	0%	0%	0%	0%
GFDL-A1Fi	678,216	0%	0%	0%	-1%	-1%	-1%	-1%	-1%

^a Combined lands comprise both privately-owned and protected lands.

^b Initial carrying capacities (breeding individuals) in year 2010.

Table 5. Projected sizes of focal wildlife populations in the Ozark Highlands by 2100 under restoration scenarios amidst landscape change from urbanization and climate change. Abundance of breeding birds and bats is given for each alternative scenario under models of the current climate, moderate (CGCM.T47-A2) and extreme (GFDL.A1Fi) climate change. The impact of each scenarios on populations relative to the base scenario with no restoration is indicated by the percent difference value (italics and underlined).

	<u>Prioritized for Current Landscape</u>				<u>Prioritized for Future Landscape</u>				<u>Random</u>						
	Base	<u>Combined lands^a</u>		<u>Protected</u>	<u>Combined lands</u>		<u>Protected</u>	<u>Random</u>							
		Full acreage	Half acreage	Full acreage	Full acreage	Half acreage	Full acreage	Full acreage							
<u>Prairie Warbler</u>															
(48,284) ^b		% ^c	%	%	%	%	%	%	%						
Current	12,700	41,351	<u>226</u>	31,420	<u>147</u>	23,447	<u>85</u>	42,834	<u>237</u>	28,402	<u>124</u>	33,300	<u>162</u>	22,195	<u>75</u>
CGCM.T47-A2	14,263	34,386	<u>141</u>	33,484	<u>135</u>	43,507	<u>205</u>	44,617	<u>213</u>	25,592	<u>79</u>	37,160	<u>161</u>	27,665	<u>94</u>
GFDL-A1Fi	27,763	57,227	<u>106</u>	49,696	<u>79</u>	45,142	<u>63</u>	55,633	<u>100</u>	41,112	<u>48</u>	52,099	<u>88</u>	45,165	<u>63</u>
<u>Wood Thrush</u>															
(363,946)															
Current	238,677	246,051	<u>3</u>	216,293	<u>-9</u>	205,302	<u>-14</u>	233,926	<u>-2</u>	254,564	<u>7</u>	248,158	<u>4</u>	222,855	<u>-7</u>
CGCM.T47-A2	201,696	191,735	<u>-5</u>	244,467	<u>21</u>	204,123	<u>1</u>	191,048	<u>-5</u>	231,364	<u>15</u>	250,522	<u>24</u>	256,087	<u>27</u>
GFDL-A1Fi	207,960	219,760	<u>6</u>	204,340	<u>-2</u>	217,254	<u>4</u>	199,564	<u>-4</u>	224,334	<u>8</u>	234,948	<u>13</u>	240,218	<u>16</u>
<u>Prothonotary Warbler</u>															
(12,533)															
Current	10,126	10,516	<u>4</u>	10,690	<u>6</u>	9,393	<u>-7</u>	10,061	<u>-1</u>	9,764	<u>-4</u>	9,790	<u>-3</u>	7,598	<u>-25</u>
CGCM.T47-A2	9,158	9,123	<u>0</u>	10,252	<u>12</u>	9,099	<u>-1</u>	8,958	<u>-2</u>	9,063	<u>-1</u>	8,920	<u>-3</u>	8,726	<u>-5</u>

GFDL-A1Fi	9,497	11,949	<u>26</u>	10,986	<u>16</u>	9,388	<u>-1</u>	9,440	<u>-1</u>	9,462	<u>0</u>	9,783	<u>3</u>	8,530	<u>-10</u>
Cerulean Warbler															
(120,870)															
Current	32,661	138,023	<u>323</u>	125,135	<u>283</u>	161,945	<u>396</u>	134,234	<u>311</u>	151,750	<u>365</u>	205,055	<u>528</u>	56,573	<u>73</u>
CGCM.T47-A2	45,227	121,658	<u>169</u>	158,989	<u>252</u>	142,828	<u>216</u>	139,422	<u>208</u>	127,985	<u>-100</u>	166,779	<u>269</u>	56,325	<u>25</u>
GFDL-A1Fi	40,784	161,390	<u>296</u>	118,445	<u>190</u>	162,003	<u>297</u>	149,483	<u>267</u>	123,344	<u>202</u>	136,227	<u>234</u>	57,406	<u>41</u>
Brown-headed															
Nuthatch ^c (19,428)															
Current	15,672	29,053	<u>85</u>	25,550	<u>63</u>	26,420	<u>69</u>	32,255	<u>106</u>	27,293	<u>74</u>	28,677	<u>83</u>	28,891	<u>84</u>
CGCM.T47-A2	19,584	22,213	<u>13</u>	26,421	<u>35</u>	26,466	<u>35</u>	34,666	<u>77</u>	30,202	<u>54</u>	30,238	<u>54</u>	32,017	<u>63</u>
GFDL-A1Fi	22,600	37,109	<u>64</u>	35,178	<u>56</u>	32,584	<u>44</u>	39,297	<u>74</u>	34,722	<u>54</u>	33,575	<u>49</u>	33,438	<u>48</u>
Myotis sp. (307,237)															
Current	237,475	242,973	<u>2</u>	255,057	<u>7</u>	242,241	<u>2</u>	251,085	<u>6</u>	248,363	<u>5</u>	244,575	<u>3</u>	251,458	<u>6</u>
CGCM.T47-A2	245,671	254,538	<u>4</u>	252,205	<u>3</u>	250,324	<u>2</u>	243,760	<u>-1</u>	248,128	<u>1</u>	247,914	<u>1</u>	246,443	<u>0</u>
GFDL-A1Fi	244,397	250,901	<u>3</u>	247,283	<u>1</u>	246,959	<u>1</u>	244,590	<u>0</u>	248,751	<u>2</u>	246,533	<u>1</u>	244,231	<u>0</u>

^a Combined lands comprise both privately-owned and protected lands.

^b Initial estimate of abundance (breeding individuals) in year 2010.

^c Percent difference.

^d Results for brown-headed nuthatch assume added translocation efforts.

Table 6. Estimated risk of decline for focal wildlife populations in the Ozark Highlands under proposed restoration scenarios amidst landscape change from urbanization and climate change. Values represent the probability of the population declining by 25% from its initial abundance through 2100. Estimates are pooled across future climates modeled under the current climate, moderate (CGCM.T47-A2) and extreme (GFDL.A1Fi) climate change.

Species	Base	<u>Prioritized for Current Landscape</u>			<u>Prioritized for Future Landscape</u>			<u>Random</u>
		<u>Combined Lands^a</u>		<u>Protected</u>	<u>Combined Lands</u>		<u>Protected</u>	<u>Combined Lands</u>
		Full	Half	Full	Full	Half	Full	Full
		acreage	acreage	acreage	acreage	acreage	acreage	acreage
Prairie Warbler	59%	26%	45%	32%	28%	40%	37%	50%
Wood Thrush	39%	39%	37%	37%	39%	38%	40%	37%
Prothonotary Warbler	34%	34%	35%	33%	31%	32%	34%	37%
Cerulean Warbler	53%	30%	33%	28%	29%	32%	28%	46%
Brown-headed Nuthatch ^b	7%	5%	3%	5%	13%	4%	7%	3%
Myotis sp.	36%	35%	35%	36%	35%	34%	36%	35%
Average	38%	28%	31%	28%	29%	30%	30%	35%

^a Combined lands comprise both privately-owned and protected lands.

^b Results for brown-headed nuthatch assume added translocation efforts.

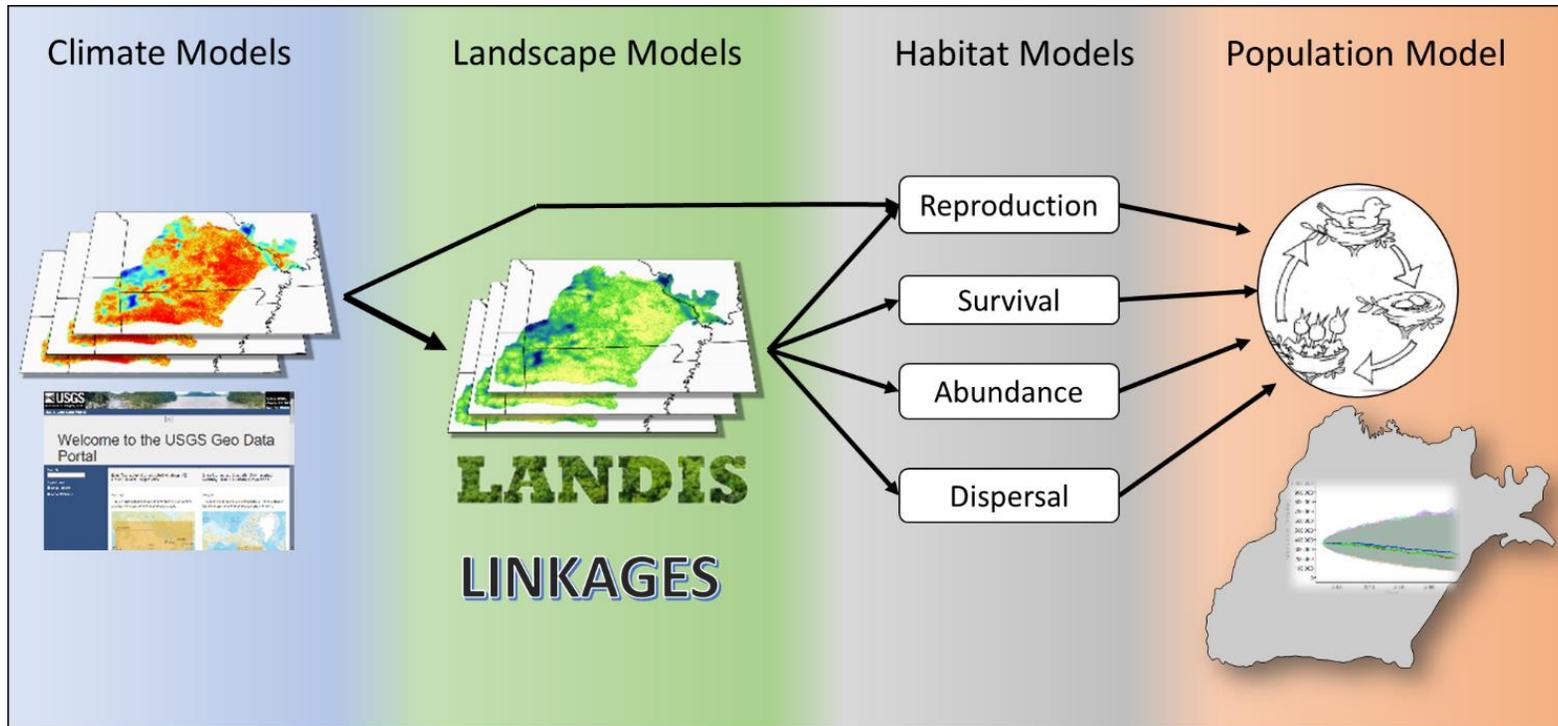


Figure 1. Dynamic-landscape metapopulation modeling approach that links local habitat to region population growth. This approach combines climate, landscape, habitat, and population models to project the responses of wildlife populations to climate and management driven changes to the landscape.

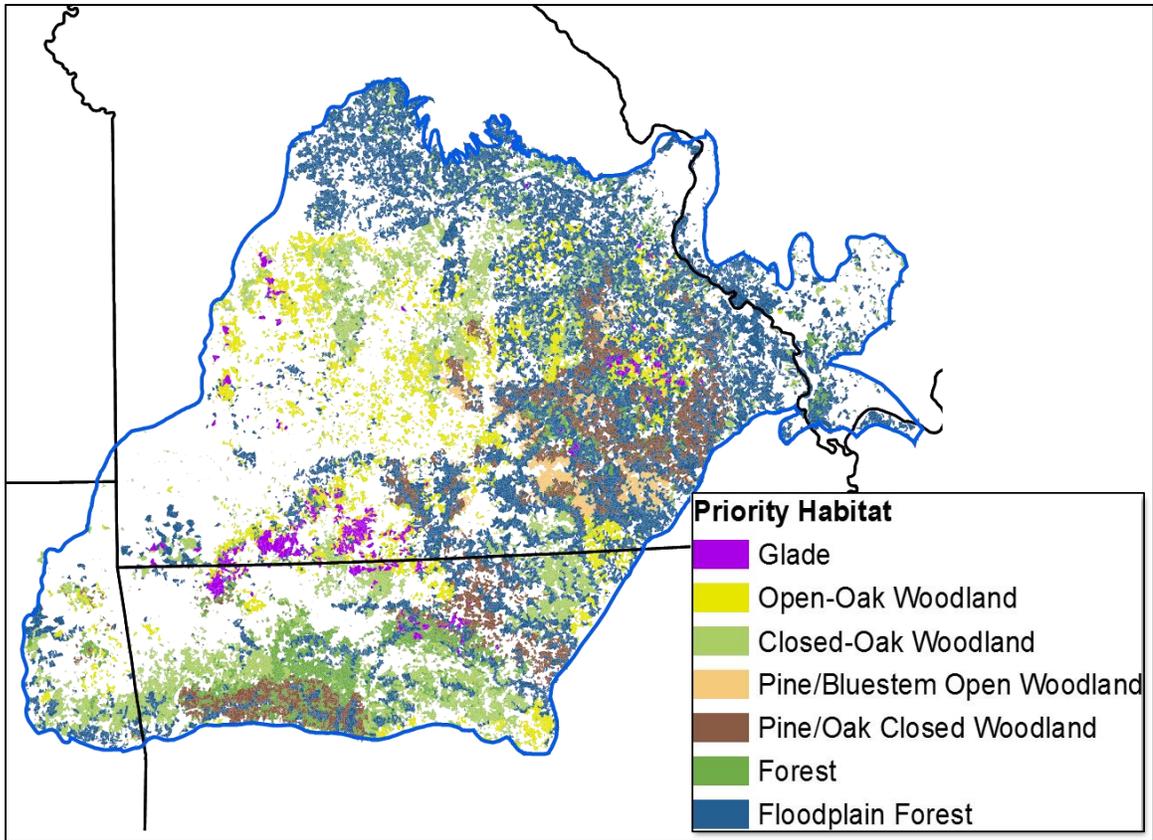


Figure 2. Priority areas identified through a Landscape Conservation Design processes conducted by the Ozark Highlands planning team. An ecosystem-based approach, priority areas relate to different focal vegetation communities.

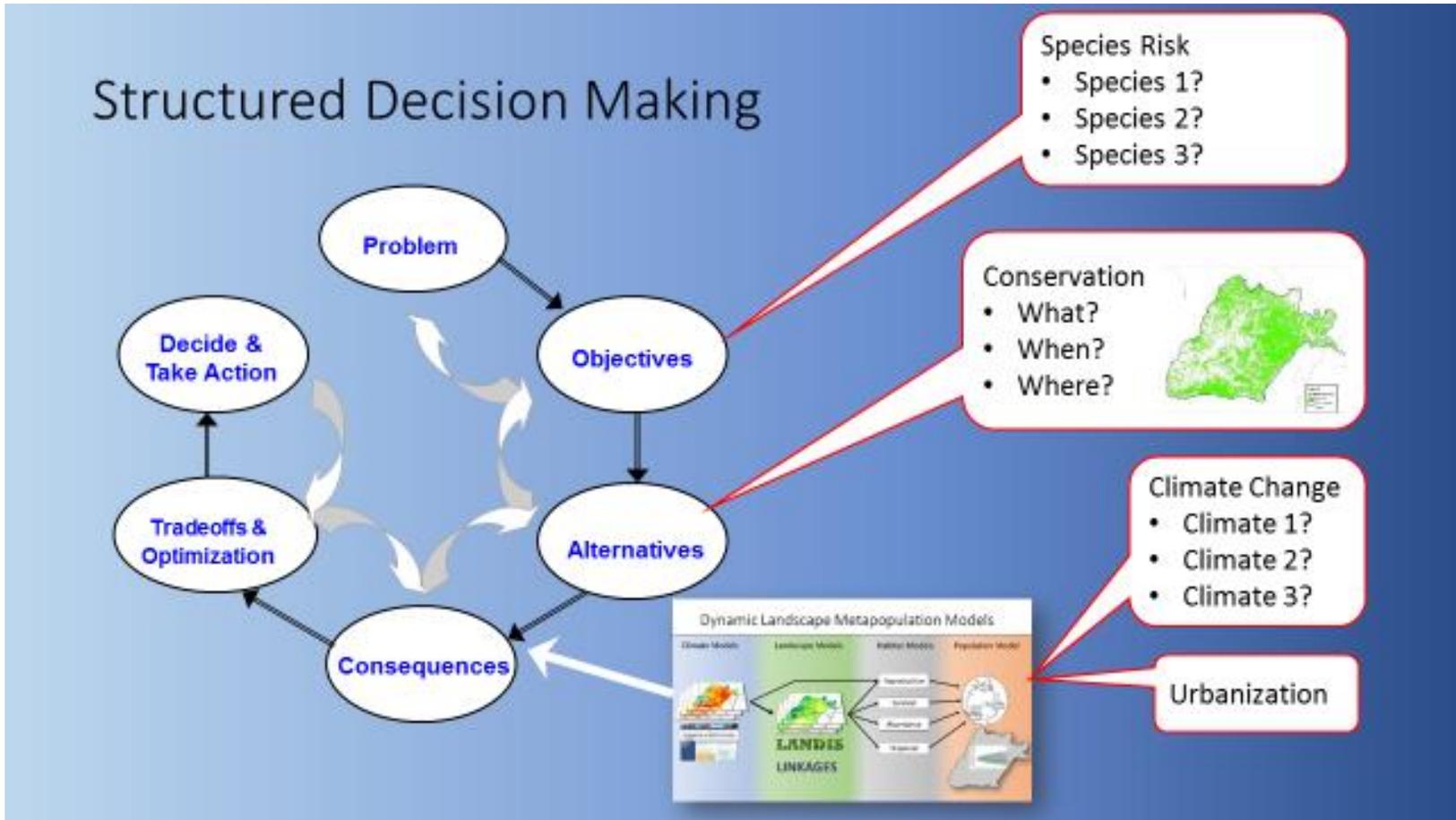


Figure 3. Overview of the pilot process for integrating dynamic-landscape metapopulation models and structured decision making to decide conservation plans amidst uncertainty and complexities. The ProACT process is used to structure components of the decision.

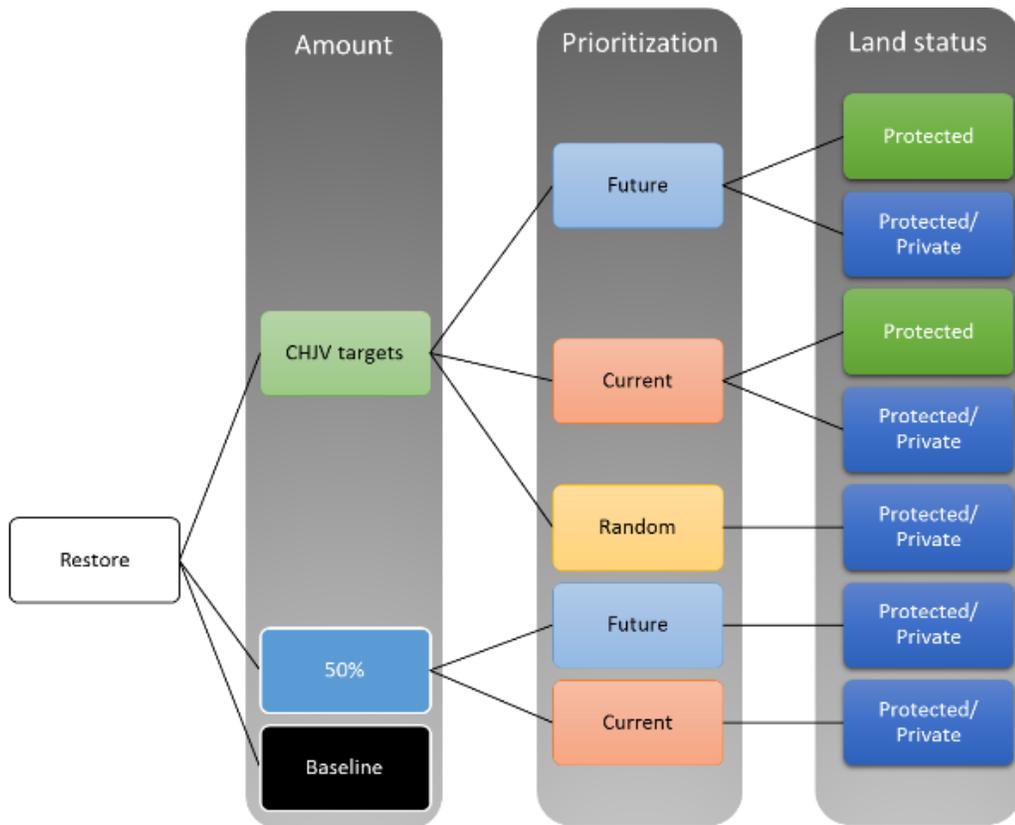


Figure 4. The planning team structured alternative restoration scenarios around three considerations: the amount of habitat to be restored, the basis for prioritizing areas to restore, and the protection status of lands to be restored.

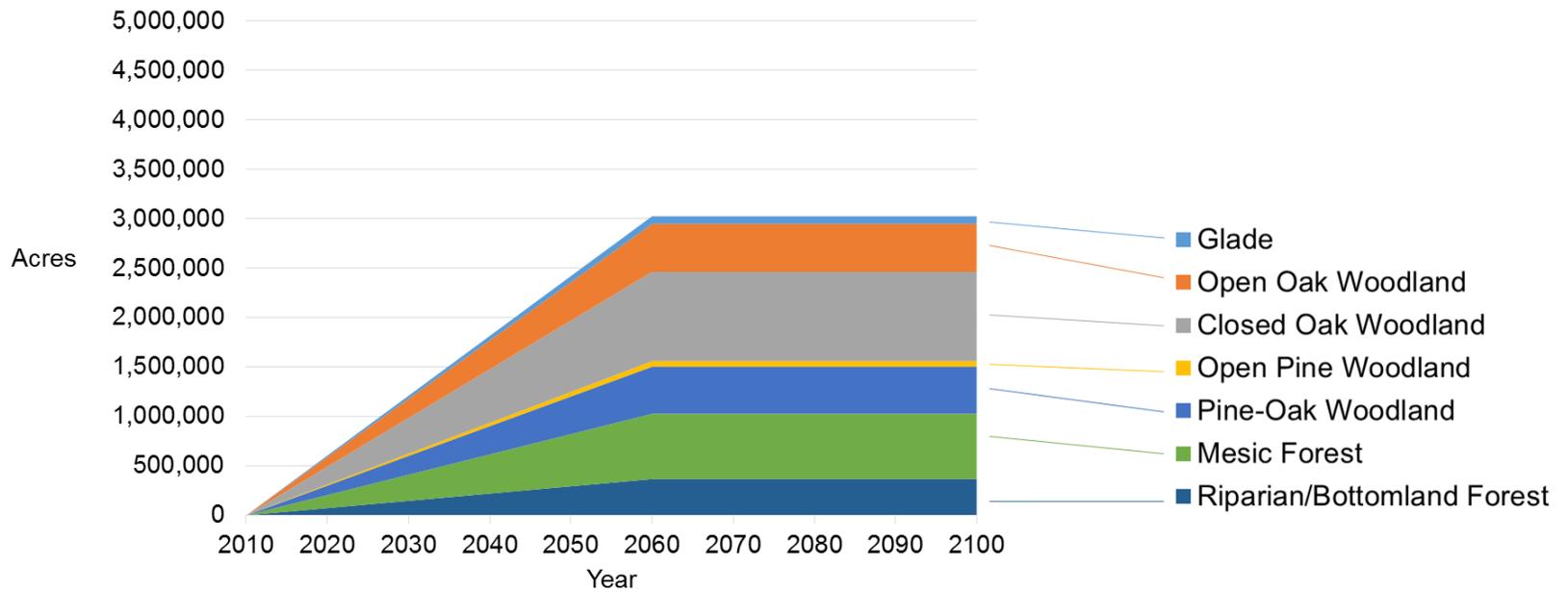


Figure 5. Simulations implemented restoration acreage targets over a fifty-year period (2010–2060). Under the full habitat acreage scenarios (shown), approximately 3,000,000 acres of combined habitats were targeted for restoration in the Ozark Highlands.

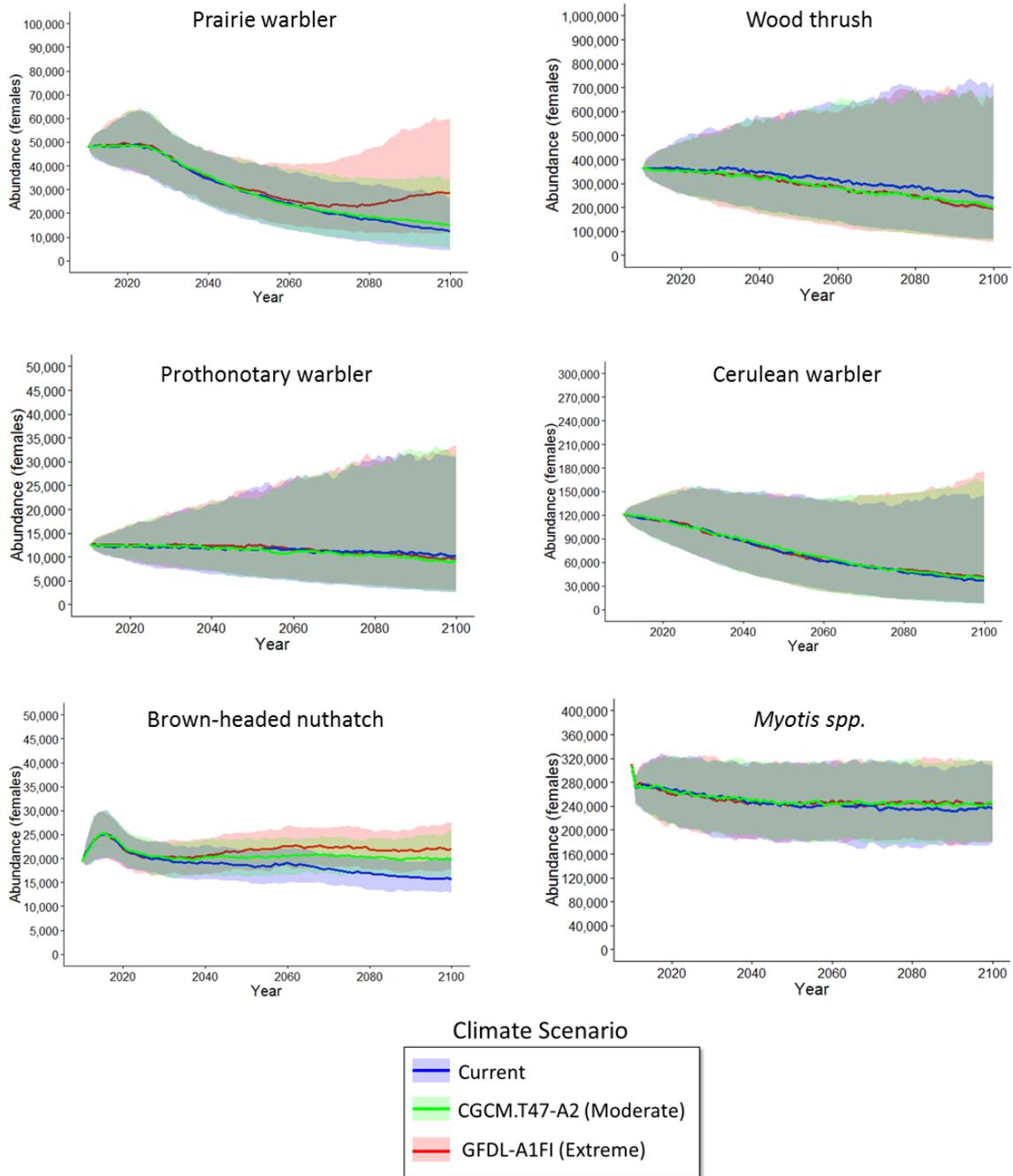
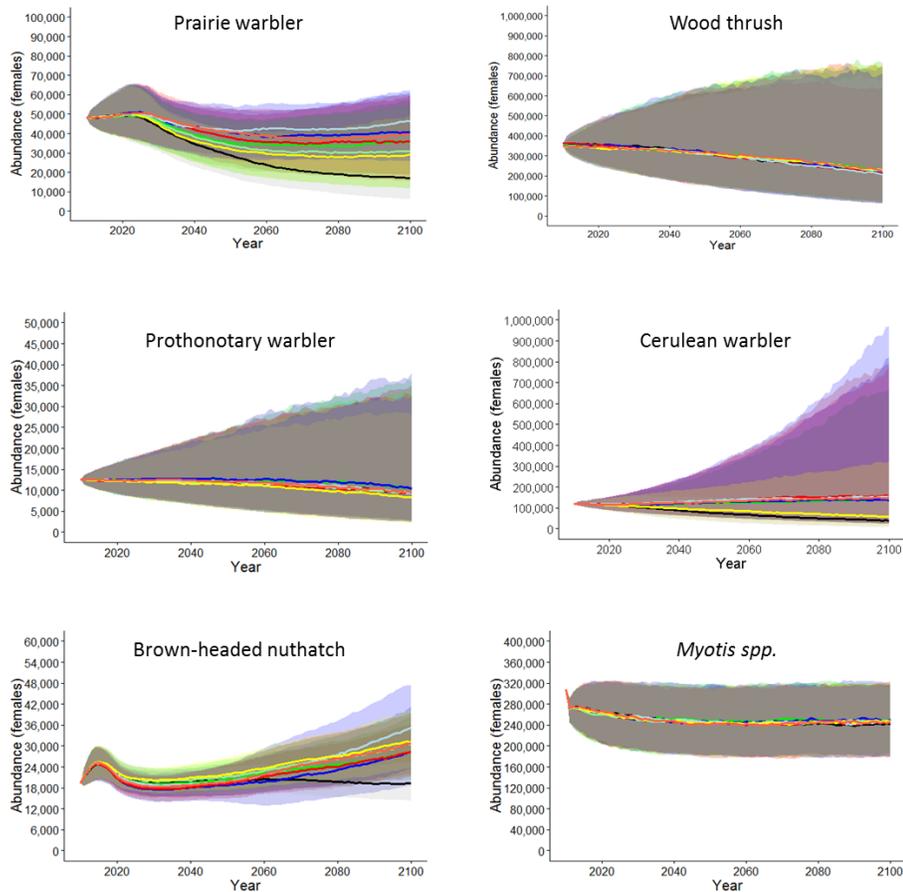


Figure 6. Projected population growth of focal wildlife species in the Ozark Highlands for the base scenario of no forest restoration. Predictions are based on dynamic-landscape metapopulation models applied to landscapes projected under urbanization and models of a current climate, moderate (CGCM.T47-A2) and extreme (GFDL.A1Fi) climate change. Shaded regions indicate 85% Credible Intervals



Restoration Scenarios

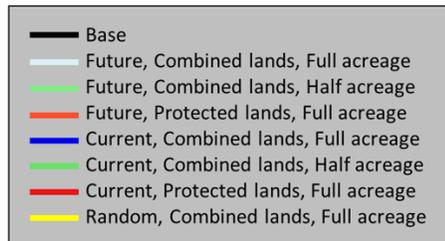


Figure 7. Projected population growth of focal wildlife species in the Ozark Highlands under alternative habitat restoration scenarios, proposed by a team of planners. Predictions are based on dynamic-landscape metapopulation models applied to landscapes projected under climate change and urbanization. Projections are pooled across model of a current climate, moderate (CGCM.T47-A2) and extreme (GFDL.A1Fi) climate change. Shaded regions indicate 85% Credible Intervals. Results for brown-headed nuthatch assume added translocation efforts.

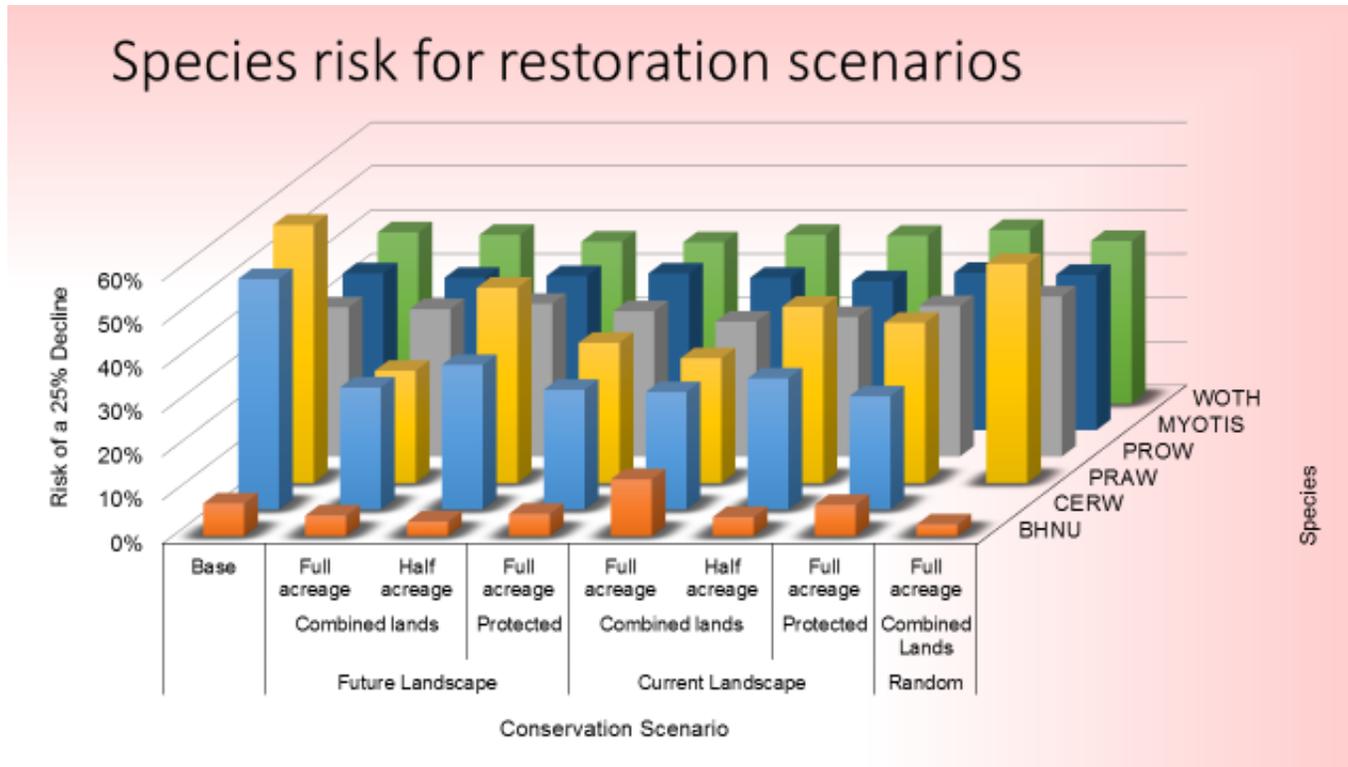


Figure 8. Estimated risk of populations declining by 25% under alternative habitat restoration scenarios, proposed by the Ozark Highlands team. Risk is pooled across projections under urbanization and three future climate models that range from continuation of the current climate, moderate climate change, and extreme climate change. Focal species include (brown-headed nuthatch-BHNU, cerulean warblers-CERW, prairie warblers-PRAW, prothonotary warblers-PROW, *Myotis spp.* Bats, and wood thrush-WOTH). Results for brown-headed nuthatch assume added translocation efforts.

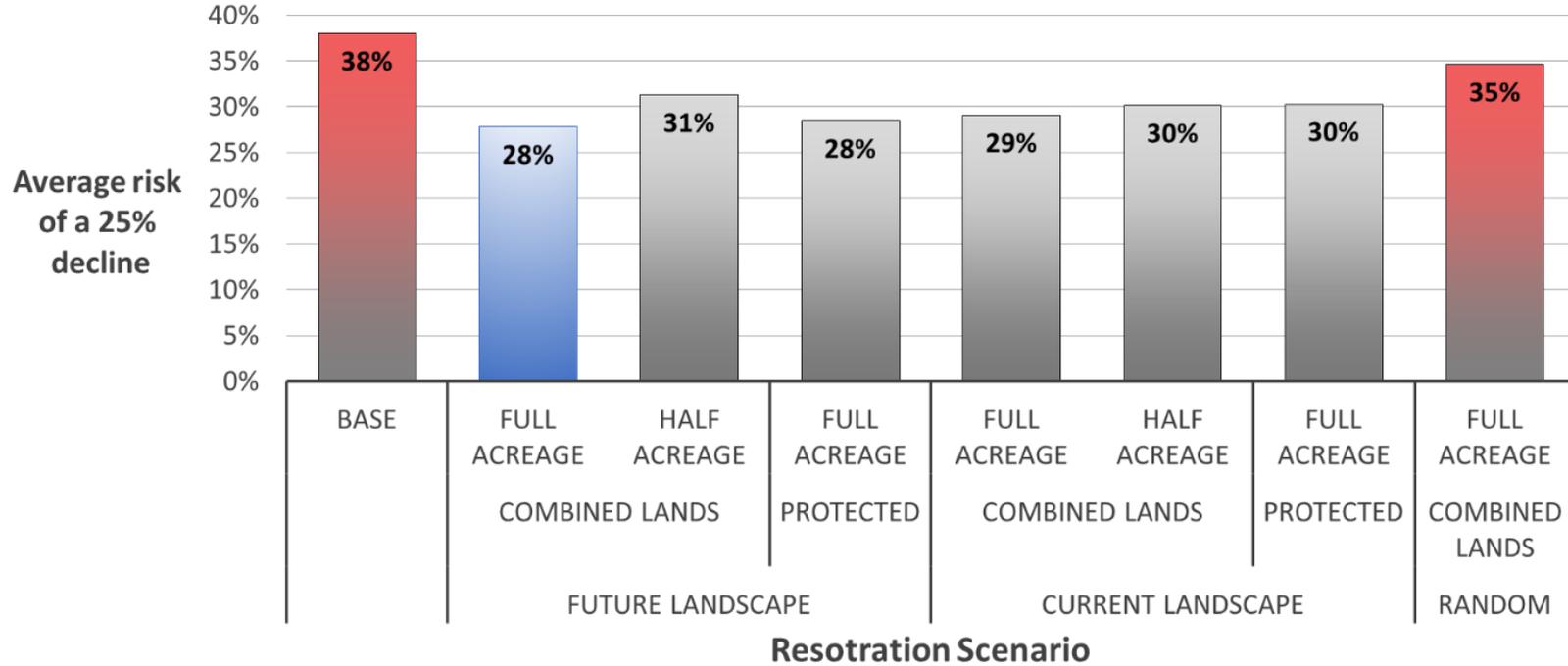


Figure 9. Average risk of a 25% decline for all focal species in the Ozark Highlands under alternative habitat restoration scenarios, proposed by the planning team. Risk is pooled across projections under three future climate models that range from continuation of the current climate, moderate climate change, and extreme climate change. The alternative that restored full acreage targets on both private and protected lands based, prioritized by future landscape conditions resulted in the lowest risk across species.

CHAPTER 3

COMBINING INDIVIDUAL-BASED MODELING WITH DYNAMIC- LANDSCAPE METAPOPULATION MODELS TO PREDICT THE DIRECT EFFECTS OF CLIMATE CHANGE ON BIRD PRODUCTIVITY AND POPULATION VIABILITY

ABSTRACT

Predicting the impacts of global change on populations of species for conservation planning requires approaches that are comprehensive enough to model important biological processes at the scales at which they interact with climate. We combined individual-based and metapopulation models to estimate direct effects of climate change on daily nest survival, annual productivity, and ultimately population viability of Acadian flycatchers (*Empidonax virescens*) across the Central Hardwoods region of the U.S through 2099. The individual-based model estimated productivity based on daily nest survival that considered landscape and climatic factors such as daily temperature and precipitation. We integrated future productivity estimates into dynamic landscape metapopulation models that projected growth of the regional populations overtime. Models projected increasing declines in annual productivity and lower nest survival from increasing levels of warming under three scenarios for future climate change. Average annual productivity across the region declined an average of 6%, 15%, and 27% to 1.8, 1.7, and 1.5 females/female/year by the end of the century under mild (PCM-B1), moderate (CGCM.T47-A2), and severe (GFDL-A1Fi) climate change scenarios, respectively. Reduced productivity drove significant population declines across a range of adult and juveniles rates indicating that climate change poses a substantial risk to

ACFLs in the Central Hardwoods. These results highlight the importance of considering direct effects of climate change on demographics when assessing vulnerability of species and planning conservation.

INTRODUCTION

Biodiversity and ecosystems are more stressed than at any time in human history. There is increasing evidence of population declines and localized extinctions that can be directly attributed to climate change (Monzón et al. 2011, Staudinger et al. 2013).

Climate change is also causing shifts in species' distributions and phenologies, which could substantially alter ecosystem structure and function (Schneider and Root 2002, LaSorte and Thompson 2007). Moreover, global threats to biodiversity such as habitat loss and fragmentation from land-use change, invasive species, and disease will likely be exacerbated by climate change (Fischlin et al. 2007, Brook et al. 2008). Therefore, understanding global change processes that could ultimately threaten species is critical for deciding on the most appropriate actions for conservation (Cushman 2006, Selwood et al. 2015).

Efforts to identify how climate change will affect species occur across a range of ecological and empirical scales. At a large scale, there is an emphasis on developing approaches that can assess vulnerability by predicting how populations will respond to climate change and what those impacts ultimately mean for the species viability (e.g., Lawler et al. 2010, Dawson et al. 2011). Approaches at this scale often take the form of species distribution (or niche models) and population models. These models predict shifts in distribution or changes in population dynamics across large-scales based on changes in climate and vegetation (Elith & Leathwick, 2009; Iversen et al. 2016). These

approaches have been criticized for the lack of processes they consider (Fischlin et al. 2007, Swab et al. 2015). For example, distribution models are often based only on climate, questionably assuming that species and their habitat/niche closely track climate (but see Fordham et al. 2013, Wang et al. 2015, Ralston et al. 2016). Bonnot et al. (In review) developed a dynamic landscape metapopulation model (DLMP) that mechanistically and more comprehensively modeled both population dynamics and distribution based on changes in habitat under climate change. Yet, they acknowledged that their predictions failed to consider potentially significant direct impacts of climate on demographic processes.

At the other end of the scale there is an attempt to understand how the ecological processes that underlie population growth will be affected by climate change. These are functional processes that have long been considered the basic mechanisms of ecology, contributing to demographics and population growth (Levin 2009). While we may understand these processes, it is seldom that we know how climate influences them (Dawson et al. 2011). Examples include how vulnerability of species traits to climate or climate-driven offsets in phenology affect survival (Griffiths et al. 2010, Miller-Rushing et al. 2010). Hunter et al. (2010) estimated declines in polar bear (*Ursus maritimus*) survival with declining sea ice. In birds, nest survival is a reproductive process that is critical to population persistence (Donovan and Thompson 2001, Faaborg et al. 2010). However, evidence is beginning to suggest that this process is related to climate. For example, Cox et al. (2013) identified a negative effect of maximum temperature on daily nest survival and ultimately productivity of Acadian flycatchers (*Empidonax vireescens*; ACFL) in Missouri. Related studies have suggested that this effect is based on higher

levels of predation, due to increased snake activity with warmer temperatures (Weatherhead et al. 2012, Cox et al. 2013, George et al. 2016). Given that these processes are likely to be equally affected by climate change as they are by current threats, they provide a critical understanding of how climate can affect species at an individual level and ultimately population growth (Fordham et al. 2013, Selwood et al. 2015). However, identifying what affected demographics mean for the fates of entire populations or species in the future requires integration into the larger approaches (Tavecchia et al. 2016).

Translating individual-level climate effects into overall populations impacts can be difficult. First, these processes often occur in the form of empirical findings or statistical models that relate to local temporal and spatial scales (Evans et al. 2016). Cox et al. (2013) modeled the effects of climate on nest survival on a daily timescale based on local and landscape-level habitat and daily temperature and precipitation. However, generating realistic predictions of how ACFL productivity will change under future climates requires estimates of climate data at scales congruent with nest survival process (i.e., daily predictions). Many processes are also subject to variation in individual traits, behaviors or adaptations that can mitigate impacts (Beever et al. 2015). In the ACFL example, breeding pairs can choose to reneest following failure, potentially offsetting climate's impacts on nest survival on eventual productivity (Powell et al. 1999). The stochastic nature of individual behavior in these contexts can complicate predictions and prevent generalizations. Therefore, accurately predicting the impacts of climate change on the ACFL productivity and population growth will require methods that can model nest

survival under future climates and in a way that accounts for individual behavior which then can be integrated into population models.

Individual-based models (IBMs) provide the framework for estimating population-level changes stemming from individual-level ecological processes. Conceptually, IBMs model the interrelationships between individual traits and behaviors (e.g., nesting) and the emergent properties of system dynamics (e.g., annual productivity; Grimm and Railsback 2005). These approaches have been used to model nesting in songbirds (Powell et al. 1999, Mattsson and Cooper 2007, Hirsch-Jacobson 2011). These examples account for variability between individuals in nesting behavior to achieve unbiased estimates of productivity.

We used an individual-based approach to estimate direct effects of climate change on reproduction and ultimately population viability of ACFL across the Central Hardwoods region of the U.S. We applied Cox et al.'s empirical nest success models to spatio-temporal data on habitat and climate under future emissions scenarios to derive realistic estimates of nesting survival and brood size overtime throughout the region. We integrated these estimates within an IBM that simulated behavioral adaptations of ACFL, such as renesting and double brooding, that could mitigate impacts to overall productivity. Finally, we incorporated the productivity projections into a DLMP model that enabled us to predict the risk climate change poses to the ACFL population based on its observed effects on nesting. While climate may affect other aspects of ACFL demography or habitat, we focused on its effects on productivity because of known relationships between climate and nesting success.

STUDY AREA

We focused on the population of ACFL in a 39.5 million ha (395,519 km²) portion of the Central Hardwoods forest in the center of the U.S. (Figure 1). The area encompasses portion of 10 states and a variety of vegetation, terrains, soils, and climates (Cleland et al. 2007). The topography varied from relatively flat Central Till Plains to open hills and irregular plains (e.g., Interior Low Plateau), to highly dissected Ozark Highlands. The region supports a diversity of forest ecosystems, including upland oak (*Quercus spp.*)–hickory (*Carya spp.*) forests and oak-pine (*Pinus spp.*) forests, with less common woodlands, glades, and savannas. The area is in the Central Interior Broadleaf Forest Province of the Hot Continental Division and the climate is continental with long, hot summers and cool winters. Mean annual temperatures range from 12-16 °C with the warmer temperatures in the south. Annual precipitation range from 115 cm in the northwest to 165 cm in the southeast, occurring mostly in spring and fall (Livneh et al. 2013).

Acadian flycatchers are long-distance migrants that breed in mature deciduous forests in the forested landscape of the eastern United States (Whitehead and Taylor 2002). The species is area-dependent and sensitive to forest fragmentation. It experiences high rates of parasitism by brown-headed cowbirds and nest predation in small forest fragments. Breeding Bird Survey data suggest that populations of ACFLs are relatively stable over their range, following declines through the early 20th century (Sauer et al. 2014). Current estimates indicate that the Central Hardwoods population is currently growing 1% annually over the last decade.

METHODS

Individual-based model of productivity

We modeled productivity from 2010 to 2099 using an individual-based approach that simulated nesting activity across the Central Hardwoods during each breeding season. This approach followed individual ACFL territories throughout each season on a daily basis as they attempted to successfully nest and produce offspring. We defined productivity as the number of female offspring produced per breeding female per season. Productivity depended on multiple processes, including: 1) the survival of nests for the duration required for broods to fledge, 2) the size of broods in nests, and 3) species behavioral patterns that dictate nesting activity throughout the season (e.g., length of nesting cycles and seasonal variation in probability of renesting or attempting second broods). We simulated these processes using empirical models of daily nest survival and brood size for this species.

We modeled nesting activity in cells across the Central Hardwoods region during annual breeding seasons. We set the length of breeding season at 93 days (May 15–August 15) based on observations for ACFL (Whitehead and Taylor 2002). We simulated territories using a cell size of 120 m (1.4 ha) to reflect estimates of territory size for the species (Whitehead and Taylor 2002). Thus, each cell in the landscape comprised an individual territory. We assumed that all territories began constructing nests on May 15 and allowed 5 days before egg laying (Walkinshaw 1966, Whitehead and Taylor 2002). Thus, all nests were initiated on day 5 of the simulation. We allotted 5 days for egg laying, 8 days for incubation, and 15 days for nestling care. Overall we assumed nests successfully fledged young on day 28. Renesting attempts began 4 days following a failed nest. We allowed unlimited number of renesting attempts prior until July 19 (< 28

days prior to end of season) but none after because a bird could not complete a nest cycle before the end of the nesting season.

Upon successful completion of a nest we required 7 days for the dependent post-fledging period before a second brood attempt was considered. Initiation of a second brood was modeled as a Bernoulli process with a probability based on the day of year. We estimated this probability by fitting a logistic model between observations of whether or not ACFL pairs attempted second broods and the day of completion of their first nest using data from Hirsch-Jacobson (2011). The estimated model demonstrated declines in the propensity to attempt a second brood after June (Figure 2).

We simulated the fates of nests each day based on the probability of nest survival estimated using a model developed by Cox et al. (2013). Cox et al. (2013) used 20 years of nest-monitoring data on > 1,000 nests from study sites across a gradient of habitat fragmentation in Missouri, USA, to investigate the relative influence of weather variables and landscape factors on nest survival and brood size. In addition to precipitation, temporal, and stage-dependent factors, their most supported model indicated a strong forest cover \times temperature interaction driving ACFL daily nest survival. While only extreme precipitation events were associated with lower nest survival, increased daily maximum temperature substantially reduced nest survival as part of a 3-way interaction with edge density within 500 m and the percent of forest within 10 km . Nest survival was also lower for ACFLs in areas surrounded by more edge and in landscapes composed of less forest (Cox et al. 2013). In addition to spatial variation, nest survival varied throughout the season, where survival probabilities decreased during the nestling stage but, increased in general as the season progressed.

We estimated daily nest survival throughout each season across the Central Hardwoods using spatially-explicit, down-scaled climate predictions, based on three CMIP3 general circulation models with two different CO₂ emission scenarios (PCM-B1, CGCM.T47-A2, and GFDL-A1fi; IPCC 2007). The climate models PCM, CGCM.T47, and GFDL represented a gradient from the lowest to highest predicted increases in summer temperatures in the region, respectively; and B1, A2, and A1fi represented a gradient from the least to most fossil fuel intensive emission scenarios (IPCC 2007). 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 in the region (Figure 1; Girvetz et al. 2009). We obtained the daily climate data, down-scaled to 1/12th km resolution for the Central Hardwoods region for the period 2010–2099 from the U. S. Geological Survey Center for Integrated Data Analysis (USGS CIDA) Geo Data Portal (Stoner et al. 2011). For each year, we extracted precipitation and daily maximum temperature predictions for the days corresponding to the breeding season and stored them in multi-dimensional arrays. We modeled forest cover variables based on National Land Cover Data (NLCD; Fry et al. 2011). We estimated the percent of forest within 10 km and the density of forest/nonforest edge within 500 m through focal analyses in ArcGIS 10.3 (ESRI 2012). We assumed NLCD classes 41, 42, 43, 50, and 95 as forest cover. We maintained a constant landscape based on 2011 NLCD for all future projections.

We derived stochastic estimates of daily nest survival on each territory by using the model and its associated variance-covariance matrix to obtain the mean predictions and error on the linear scale. Mean predictions and standard deviations were based on the forest cover and edge density values for each territory, the current stage of nesting, and

the day of year. We included maximum temperature and precipitation predictions for each territory on each day. We constrained projected daily maximum temperatures to $< 38.9^{\circ}\text{C}$ (102°F); the maximum temperature observed by Cox et al. (2013). We sampled point estimates from normal distributions with the estimated means and variances and then transformed them into probabilities of survival using the logit link. We simulated the fate of the nests as a Bernoulli trials with their respective survival probabilities.

We estimated brood sizes for completed nests using additional models developed by Cox et al. (2013). They associated the number of young produced in a successful nest on with the surrounding landcover and cowbird parasitism status (whether the nest was parasitized) using a generalized linear model with a normal distribution. Cox et al. (2013) found that parasitism status had a pronounced influence on fledging brood size; ACFL fledged 36% fewer young in parasitized vs. unparasitized nests. Fledging brood size was also lower in less forested landscapes independent of parasitism.

For completed nests we sampled brood sizes from Poisson distributions with a means estimated by the brood size model. Because these estimates require specification of parasitism status of nests, we simulated parasitism across nests as a Bernoulli process with probabilities based on a logistic function fit by Cox et al. (2013) that demonstrated increased risk of parasitism with increasing edge density and decreasing forest cover in the surrounding landscape. We constrained Poisson samples to a maximum of 4 young per nest to reflect biological limitations of this species (Whitehead and Taylor 2002).

We conducted 10 independent replicates of the IBM in each year. In each replicate, we summed brood sizes across completed nests in each territory (i.e., cell) and calculated means and variances across replicates. We repeated this for the all three climate change

scenarios to predict mean annual productivity and its error throughout the Central Hardwoods from 2010–2099 under varying levels of climate change.

Metapopulation model

To understand the impacts of future productivity under climate change on ACFL population viability, we integrated productivity projections into a DLMP model developed for ACFL in the Central Hardwoods. This approach links local climate, habitat and landscape patterns overtime to regional population dynamics, providing the means to understand the impacts of climate and landscape change on the viability of wildlife populations (Bonnot et al. In Review). The process centers on the use of habitat models to translate climate and landscape data into projections of species' habitat and demographics overtime. These spatially and temporally varying demographics are summarized within ecological subsections (that serve as subpopulations) to parameterize a metapopulation model that includes stochasticity and uncertainty (Bonnot et al. 2011).

We estimated distributional abundance and carrying capacity (K) of ACFL using a multiscale Habitat Suitability Index (HSI) model (Tirpak et al. 2009). Habitat suitability models use a conceptual, meta-analytic approach that incorporates published findings across a range of studies to predict the suitability of cells based on important habitat and landscape characteristics (Dijak and Rittenhouse 2009). Tirpak et al.'s (2009) HSI model for ACFL has been verified and validated with empirical data and includes seven variables: landform, landcover type, successional age class, distance to water, canopy cover, forest patch size, and percent forest within 1-km. We derived land- and forest cover data from the 2011 NLCD. We used 2011 canopy cover estimates from the Multi-Resolution Land Characteristics Consortium (Homer et al. 2011). We classified

successional age using data on DBH, derived from imputation techniques on Forest Inventory and Analysis data and MODIS imagery (Wilson, B. unpublished data; see also Wilson et al. 2012). We used a landform classification derived from DEM (Jenness 2013) and measured distance to water based on the National Hydrography Dataset (USGS 2010).

We followed Bonnot et al.'s (2013) approach to estimating K for cells by assuming a linear relationship between HSI and maximum density found in the literature (1.89 breeding females/ha; Johnston and Odom 1956). We then scaled density by the area of cells and spatially filtered areas of the landscape that could not support at least one territory, constrained by a maximum territory size (2.84 ha; Whitehead and Taylor 2002). This process more realistically captured the interaction between spatial and resource limitations inherent in estimating K. We set initial abundances at 50% of K based on current densities (Reidy et al. 2011). We used the dispersal model of Bonnot et al. (2011) to estimate cell-based movements of dispersing individuals to the surrounding landscape based on a negative exponential function of distance between cells, weighted by K of the destination cell.

We parameterized the metapopulation model by summarizing ACFL demographics for each subsection. The region contained 71 subsections which we delineated into 87 unique subpopulations (Figure 1; Cleland et al. 2007). For each subpopulation we summarized results of the habitat models to obtain estimates of initial abundance and K. Dispersal movements were summarized by subpopulation and standardized to obtain relative rates of dispersal from each subpopulation to surrounding ones (Bonnot et al. 2011). We averaged annual productivity predictions in each subpopulation, weighted by

K, so that subpopulation reproduction reflected the distribution of breeding activity. To isolate the effects of changes in productivity from climate change we assumed a constant landscape, holding K and dispersal constant each year while allowing productivity to vary based on climate projections.

We programmed the population model in R v3.0.1 (R Core Team, 2015) because of its efficient vector-based computation and widely available statistical functions. We used a female only, Lefkovich matrix model comprising adult and juvenile stages (Caswell, 2001). We set reproductive rates equal to subpopulation specific mean productivities. Survival estimates for ACFL are sparse and incomplete. Therefore, we conducted 121 simulations that estimated population viability under a range of adult and juvenile survival rates. We varied adult survival from 50–70% and juvenile survival from 30–50%. Based on the range of published estimates for migratory songbirds, we felt these ranges adequately spanned likely ACFL survival (Jenkins et al 2016). We set adult and juvenile breeding and natal dispersal at 10% and 90%, respectively, that determined the proportion dispersing each year and redistributed them among the subpopulations according to multinomial distributions with probabilities equal to the relative dispersal rates for that year (Bonnot et al. 2011). We used a modification to the commonly referred to ceiling density dependence (Akçakaya 2002) such that individuals over K in a population were prohibited from breeding but could remain in the population or disperse (Bonnot et al. In review).

We quantified viability or risk by using Monte Carlo simulations to induce parameter uncertainty and stochasticity in our population dynamics (McGowan et al. 2011). We simulated parameter uncertainty by sampling a different survival rate in each of the 1,000

iterations from a beta distribution with mean set as the overall estimate and corresponding variance derived from the literature. In each iteration the rate drawn were used to construct another beta distribution, from which annual survival could be drawn. We based variances for these distributions on the amount of temporal variation empirically observed in survival. 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 also drew annual productivity rates from a lognormal distribution with mean and variances corresponding to the subpopulation predictions. 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.

RESULTS

Temperature increased on average during the next century (Figure 1). Mean daily maximum temperature during the breeding season averaged 31°C for 2010-2020.

Temperatures increased an average of 4%, 9%, and 15% by the last decade of the century under the PCM-B1, CGCM.T47-A2, and GFDL-A1Fi scenarios, respectively. However, annual projections were highly variable, with mean temperatures fluctuating > 5°C between years. Some of the greatest warming was projected for the southwest portion of the region, in the Ozark and Ouachita mountains. Precipitation also varied considerable through 2099. Total projected precipitation increased on average 8% under the PCM-B1 and CGCM.T47-A2 scenarios but, decreased 36% under the GFDL-A1Fi scenario.

Daily nest survival ranged from >96% to <90% depending on temperature and landscape factors. Interaction between temperature and forest composition meant that more

forested areas of the region experienced both high and low nest survival. Nest survival rates were consistently low in fragmented landscapes regardless of climate. The greatest impacts of temperature occurred under the GFDL-A1Fi scenario where the probability that a nest could successfully survive to fledge young decreased by 50% (0.30 to 0.11), on average, by the end of the century (Figure 2).

We projected diverging patterns in future productivity for ACFL among the climate change scenarios. In all scenarios annual estimates varied substantially, changing by as much as 30% between years (Figure 3). Despite this variability, average productivity for the first 3 decades generally remained consistent and similar across climate scenarios with values ranging between 1.5 – 2.1 females/female/year. Following 2040, we estimated only slight decreasing pattern in productivity under the PCM-B1 scenario, where projections averaged 1.9 and 1.8 females/female/year over the first and last decades, respectively. However, we projected subsequent declines under the two more severe scenarios. By the last decade productivity throughout the Central Hardwoods under the CGCM.T47-A2 scenario averaged 1.7 females/female/year, a 15% decrease. Predicted changes in climate under the GFDL-A1Fi scenario drove a 27% decline in average productivity across the region by the last decade. With this scenario, some estimates indicated that ACFLs breeding in the Ozarks subsections, while experiencing some of the highest levels of productivity early on, could produce < 1 female/female/year by 2100.

The effects of climate warming on productivity greatly affected the projected viability of the ACFL population in the Central Hardwoods. We estimated an initial abundance of 7,129,030 breeding females in the population in 2010. For the majority of adult and

juvenile survival rate combinations we projected regional population declines over the next century. Only with the upper 10% of survival rates (e.g., adult > 0.64; juvenile > 0.44) did we project population increases. The effects of climate on ACFL population growth became most apparent when assuming likely, midrange combinations of survival rates. For example, based on models assuming an adult survival of 67% and juvenile survival of 36%, we projected a median abundance in 2099 of 4,878,029 females, 1,766,197 females, and 344,530 females for the PCM-B1, CGCM.T47-A2, and GFDL-A1Fi scenarios, respectively (Figure 5). These equate to 32%, 75%, and 95% declines in the regional population under climate change. Based on these projections, we estimated greater risk of declines for increasingly more severe climate change scenarios. Risks of a 50% decline in the population ranged between 0–96% across climate scenarios depending on the combination of adult and juvenile survival rates (Figure 6). However, increasing severity of climate change posed greater overall risk to ACFLs in the Central Hardwoods. The proportion of survival rate combinations for which there existed a 50% risk of such a decline increased from 74% under the PCM-B1 scenario to 87% under the GFDL-A1Fi scenario (Figure 6).

DISCUSSION

A major source of concern in conservation has been our inability to understand how climate change will affect basic ecological processes and what that means for entire populations and species. Here we used an IBM that estimated significant impacts of climate change on productivity and explored the implications of those impacts in a metapopulation model that ultimately projected substantial declines in the ACFL population under climate change. Although productivity was negatively affected by both

forest fragmentation and climate factors in the underlying model, holding the current landscape constant allowed us to isolate the role of climate change in threatening this species. Despite uncertainty in survival that forced us to consider a wide range of projections, increasing levels of climate warming posed increasingly greater risk of significant declines, in some cases by as much as 95%.

These results are ominous for multiple reasons. First, ACFLs could be considered a common species that draws less concern than other, more threatened species. They have are relatively more abundant in the Central Hardwoods with stable and even slightly increasing trends as of late (Sauer et al. 2014). Yet, by the end of the century we could expect a population at < 10% of its current estimated size, driven by declines in reproduction in what are considered valuable source landscapes in the region. If ACFLs face such declines, then what is the risk facing birds with already suppressed populations, given that many species are affected by nest predation (Haché et al. 2016). Second, under climate change we predicted the potential loss of > 6,000,000 female ACFLs from the Central Hardwoods within less than a century. Therefore, it is possible that ACFLs as well as other wildlife species could face significant impacts before predicted changes in climate are averted or management is identified and undertaken that can conserve populations.

These results provide a powerful warning as to the relative role that direct effects of climate change on demographics play in threatening wildlife populations. Considerable effort has been given to identifying how climate change will impact species from the standpoint of habitat (Moritz and Agudo 2012). Many have explored impacts through projections of range loss and shifts in distribution based on patterns in habitat and climate

(Matthews et al. 2011, Langham et al. 2015, Lawler et al. 2010a). Realizing the importance of metapopulation processes has led others to consider how population dynamics are impacted by habitat (Fordham et al. 2012, Swab et al. 2012). Bonnot et al. (In review) even observed habitat driven benefits of climate change on prairie warbler viability for the Central Hardwoods. However, our results add to the increasing evidence of large impact climate change can have on a species when directly acting on their demographics (Jenouvrier et al. 2009, Hunter et al. 2010, Fordham et al. 2012). Even with adequate habitat, we projected ACFL declines, implying that assessing vulnerability through only through the lens of habitat could leave wildlife populations at risk (Akçakaya et al. 2014). For example, although they have not been studied, prairie warbler productivity is subject to the same nest survival and parasitism pressures as ACFLs. Thus, if Bonnot et al. (In review) were able to include these processes, the effects of climate change on productivity might have overwhelmed any benefit of climate change or conservation to the prairie warbler population. We suggest more attention should be given to climate's effects on demographics, interspecific interactions, and other basic ecological processes if we are to have a realistic understanding of the threats facing species.

The use of an IBM to simulate nesting processes revealed both the nature of how climate change impacted productivity and the adaptive capacity of ACFLs to mitigate those impacts. Changes in temperature from climate warming could affect species in a variety of manners (e.g., average degree of warming, more extreme temperature, or changes in variability; Fischlin et al. 2007). Our IBM used daily maximum temperature, among other factors, to model the survival of nests each day. Therefore, because nest survival

occurs on a daily scale, it wasn't simply increased in maximum temperatures, but rather the frequency of days with increased temperatures that drove declines in productivity (Figure 7). This is particularly true given that we constrained future temperature data to within the range of values used to develop the original model. The IBM also incorporated the well-known propensity of songbirds to renest following a failed attempt. This behavior, combined with increased nest survival later in the season, enabled pairs of ACFLs to successfully produce young even after previous failures. As a result, we projected relatively smaller declines in productivity, compared to nest survival (Figure 8). These mechanisms reduced the loss in productivity due to warming and provides an overlooked example of phenotypic plasticity that gives ACFLs an inherent capacity to adapt to climate change (Beever et al. 2015). Nevertheless, it highlights the importance of considering important processes at the scales which they interact with climate.

Our projected outcomes are based on past relationships that we applied to future conditions and it is appropriate to question the stationarity of the processes on which the predictions are based. Revisiting the mechanisms by which temperature might be influencing nest survival, Cox et al. (2013) suggested that the effect of temperature could be due to its influence on nest predation by snakes. A frequent predator in the Central Hardwoods, snakes predation rates increase with increasing ambient temperatures due to increased metabolic rates and mobility (Weatherhead 2012, Cox et al. 2013). However, snakes reduce activity during periods of extremely warm temperatures ($> 35^{\circ}\text{C}$; Lillywhite 1987, Weatherhead 2012, George et al. 2016). Given that a large proportion of the daily maximum temperatures projected under the severe climate change scenario exceed this threshold, we might expect snake predation to plateau, lessening estimated

declines in nest survival. However, Cox et al. (2013) point out that metabolic requirements also increase for endothermic predators such as small mammals. Thus, the observed patterns may continue. It is also unlikely that we would see a traditional predator/prey numerical response given most predator prey upon nests opportunistically (Weatherhead 2003). Though we did not focus on it, we incorporated cowbird parasitism-based reductions in estimated productivity. However, studies have indicated that cowbird populations and associated rates of parasitism in the Central Hardwoods have declined in recent decades, allowing modest increases songbird productivity in fragmented landscapes (Cox et al. 2012). Thus, decreased parasitism could provide a reprieve for ACFL facing increased nest predation. These uncertainties can be best addressed by directly incorporating predation and parasitism mechanism in future productivity models.

Predicting the impacts of global change on populations of species for conservation planning is going to require approaches that are comprehensive enough to model important biological processes at the scales at which they interact with climate. We demonstrated how nest survival, an important process that determines productivity, can be modeled at fine spatial and temporal scales under future climates can be integrated into larger DLMPs to ultimately predict the growth and viability of regional populations. An additional benefit of DLMP framework is that it can also be used to simulate conservation activities that might address or offset productivity declines. For example, although we indicated that habitat restoration for the sake of more habitat may not be effective, restoration that reduces forest fragmentation and decrease edge could reduce predation and parasitism rates and improve productivity (e.g., Bonnot et al. 2013).

Survival is another key demographic underlying population growth (Morris and Doak 2000, Bonnot et al. 2011). And simulations have demonstrated the power of reducing mortality can have on songbird populations in this region (Bonnot et al. 2013).

Therefore, as we better understand the mechanism through which climate change will threaten populations, we increase our ability to plan conservation to address those threats.

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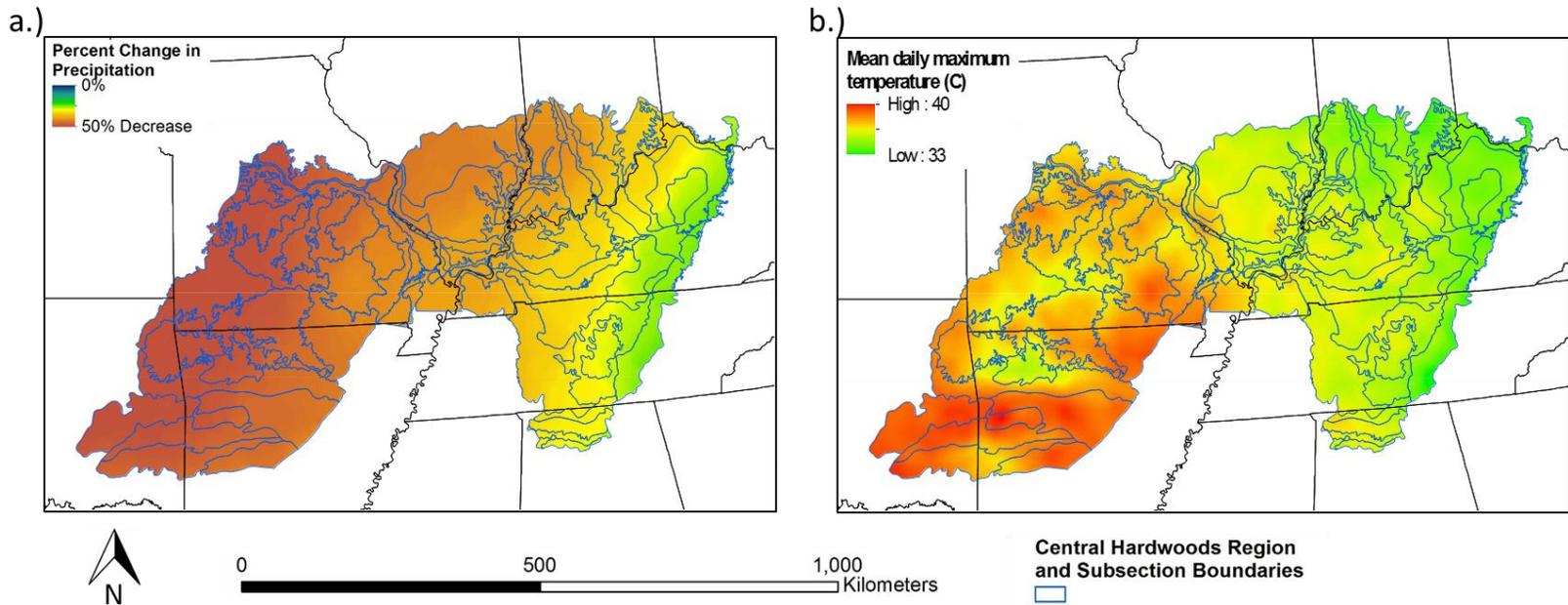


Figure 1. Downscaled projections of daily precipitation (a) and maximum temperature (b) during the breeding season from 2010–2099 under various climate change scenarios (GFDL-A1Fi shown) was integrated with landcover to estimate productivity of Acadian flycatchers across the Central Hardwoods region.

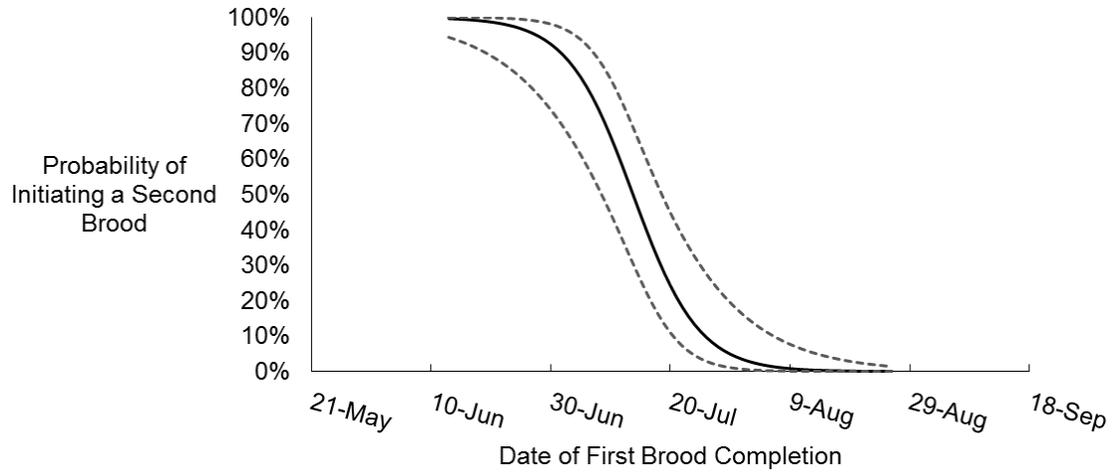


Figure 2. Logistic model estimating the probability of Acadian flycatchers initiating second brood based on the date upon which they completed their first brood. The model was estimated using season-long data on nesting pairs from Hirsch-Jacobson (2012). Estimates were incorporated into an individual based model of flycatcher nesting to project annual productivity under future climate change.

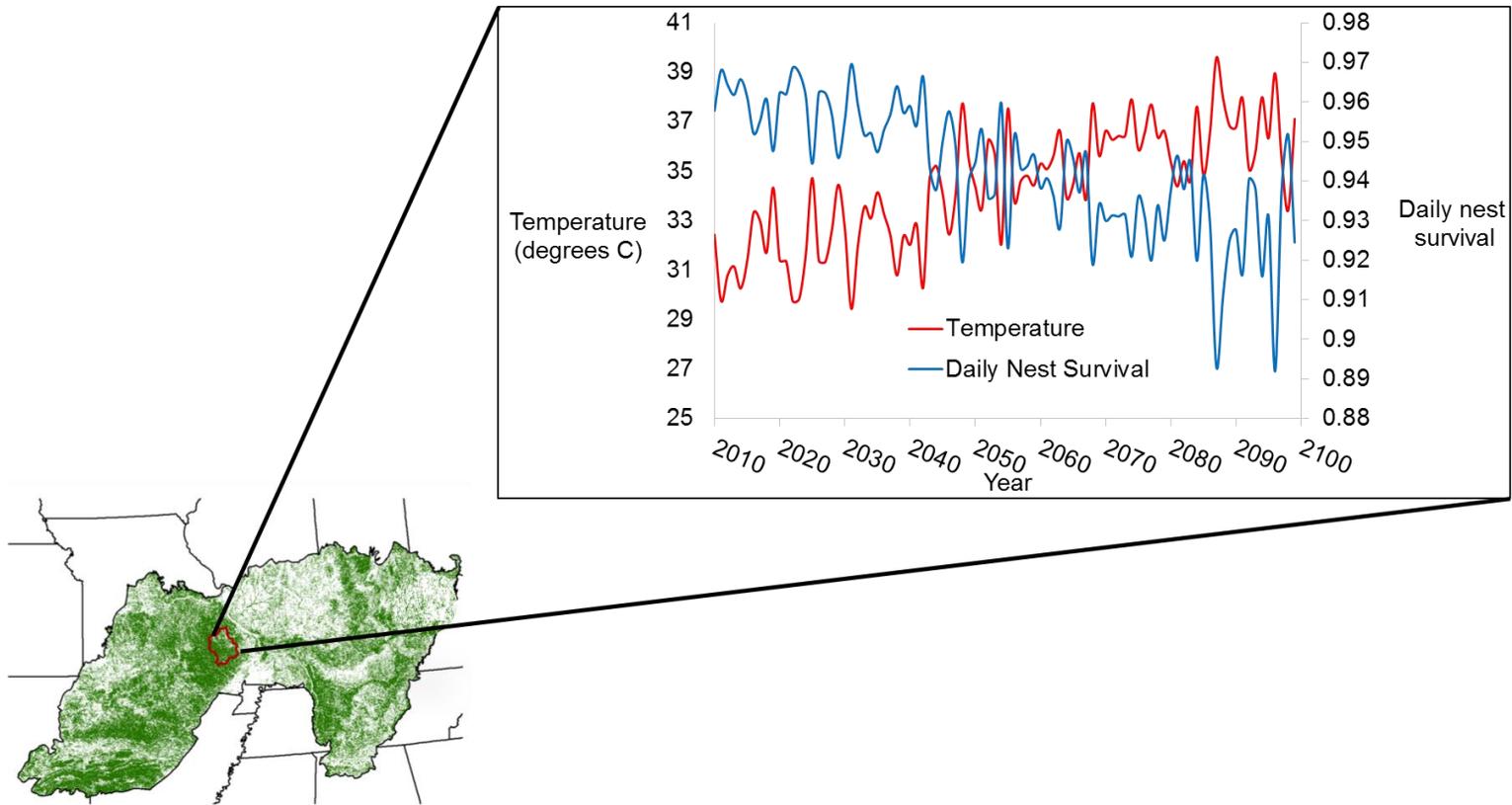


Figure 3. Mean daily nest survival of Acadian flycatchers in relation to mean daily maximum temperature predictions during the breeding under future climate change. Nest survival estimates were generated by applying the model by Cox et al. (2013) to downscaled climate data from different climate change scenarios (GFDL-A1Fi shown). The original model associated decreased nest survival with increased temperature especially in highly forest landscapes such as the Current River Hills subsection in the Ozarks (inset).

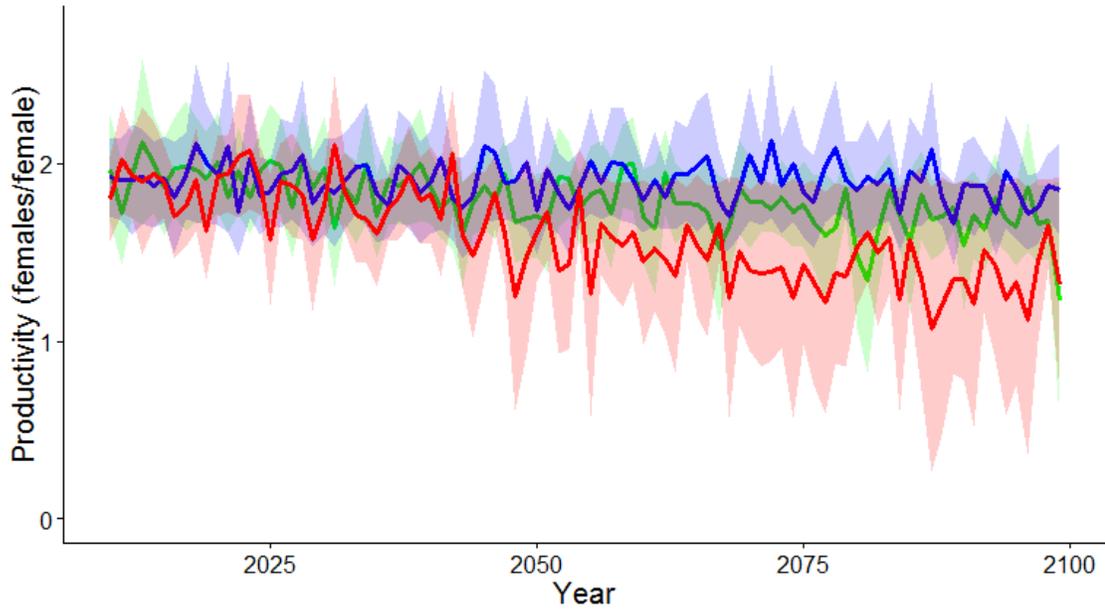


Figure 4. Estimated mean annual productivity of Acadian flycatchers across the Central Hardwoods from 2010–2099 under three scenarios for future climate change. Projections were derived from an individual-based model that simulated the effects of future temperature and precipitation on daily nest survival of flycatchers. Declines in productivity increased with increasing levels of climate warming under the PCM-B1 (blue), CGCM.T47-A2 (green), and GFDL-A1Fi (red) climate scenarios.

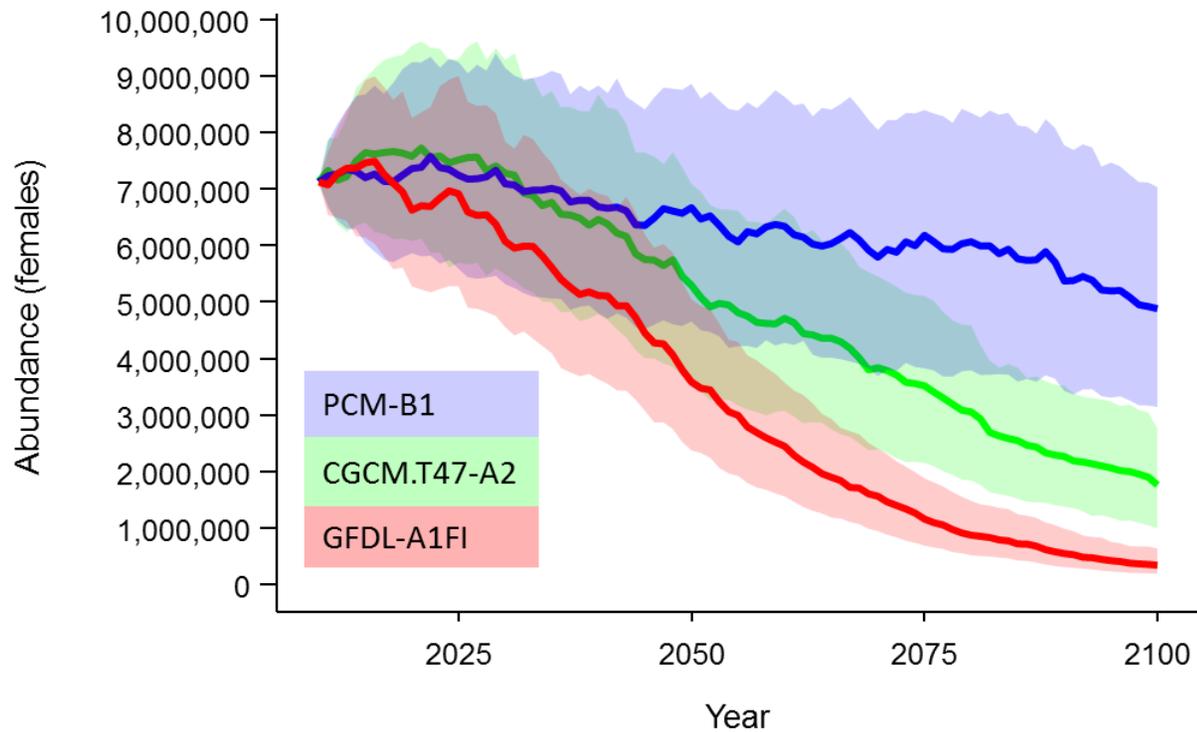


Figure 5. Projected declines of the Central Hardwoods population of Acadian flycatchers under future climate change. A dynamic-landscape population model was used to examine the impacts of decreased productivity under mild (PCM-B1), moderate (CGCM.T47-A2), and severe (GFDL-A1Fi) climate warming. After estimating carrying capacity and initial distribution across the region, the landscape and habitat were held constant to isolate climate's effects on reproduction in driving population declines. The projections shown assume an 67% adult annual survival and 36% juvenile survival.

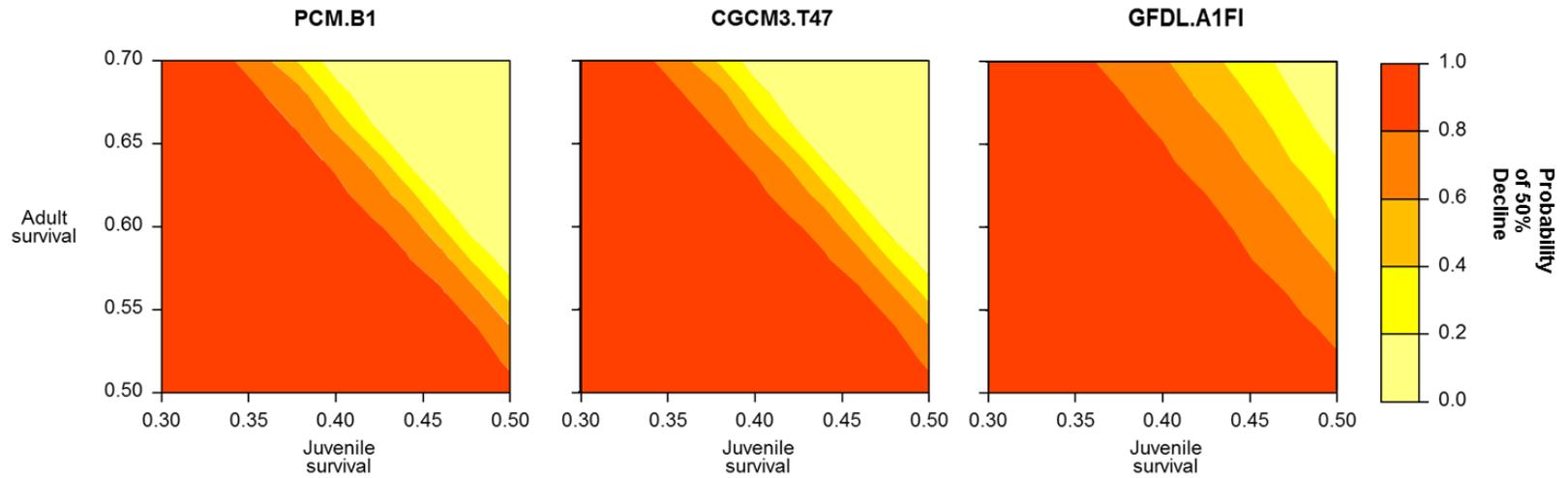


Figure 6. Risk of decline of the Central Hardwoods population of Acadian flycatchers under mild (PCM-B1), moderate (CGCM.T47-A2), and severe (GFDL-A1Fi) scenarios of climate warming. Estimates of risk are based on population projections from a dynamic-landscape metapopulation model that incorporated annual predictions of productivity.

Productivity predictions capture published effects of increased temperatures decreasing flycatcher nest survival. Due to a lack of knowledge on survival in this species, populations were modeled under a range of annual adult and juvenile survival rates.

Overall this species is most at risk of severe declines under severe climate change.

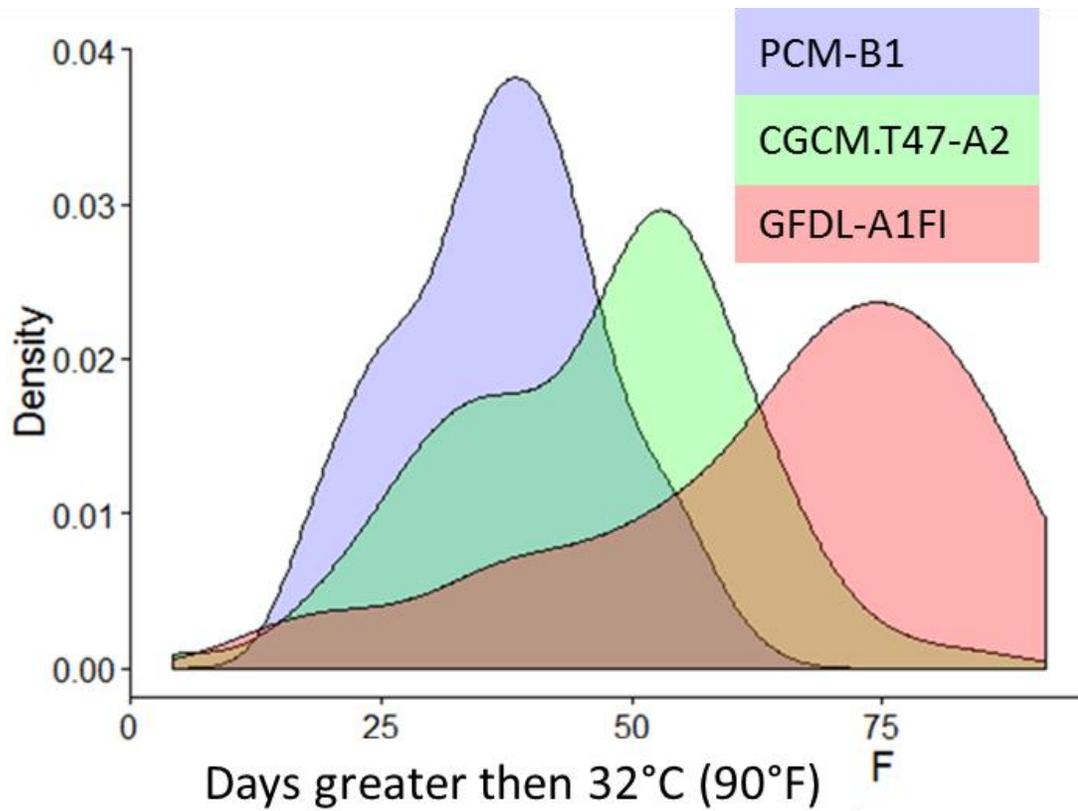


Figure 7. Distribution of the frequency of hot days (>32°C) during Acadian flycatcher breeding seasons under three scenarios for future climate warming. Based on published relationships demonstrating decreased flycatcher nest survival with increased daily maximum temperature, higher frequencies of hot days during the breeding season were responsible for declines in annual productivity under scenarios of mild (PCM-B1), moderate (CGCM.T47-A2), and severe (GFDL-A1Fi) future climate warming.

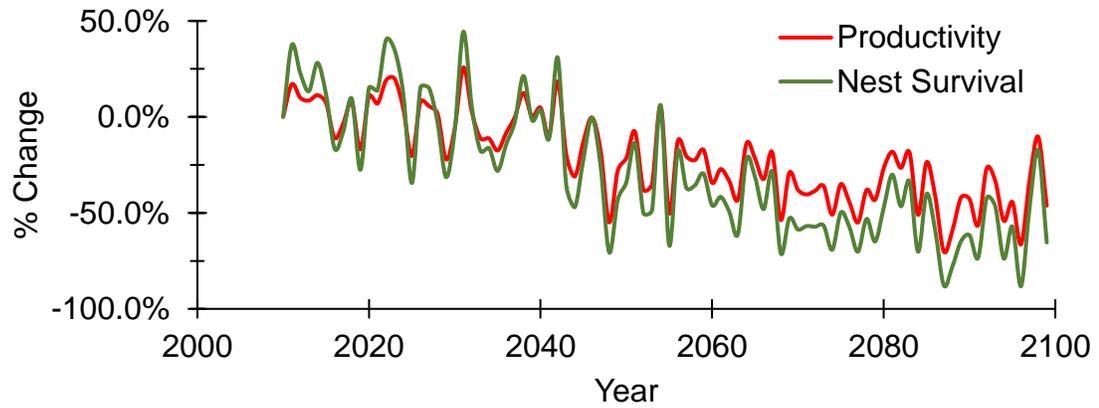


Figure 8. Relative changes in nest survival and productivity of Acadian flycatchers in the Central Hardwoods from 2010–2099 under the GFDL-A1Fi climate change scenario. Productivity declined comparatively less than nest survival when using an individual-based model to simulate daily nesting. The ability of birds to renest, should previous attempts fail, appears to be an example of adaptive capacity, effectively mitigating the negative effects of temperature and precipitation on daily nest survival and allowed pairs to still produce young.

APPENDIX 1

Habitat and demographic details and projected results from dynamic-landscape metapopulation models used to project effects of climate change and forest restoration scenarios on the habitat availability and population growth of focal wildlife species in the Ozark Highlands. Habitat availability is described by the carrying capacity (K) of each species. Projections for base scenarios with no conservation are discussed prior to results for restoration scenarios to better understand their impact. Population responses to restoration scenarios are presented both for individual climate models and pooled across climate models.

Prairie Warbler

Habitat Model

Throughout most of the eastern United States and in southern Ontario, the Prairie Warbler breeds in shrubby old fields, early-stage regenerating forests as well as glades and woodlands (Nolan et al 2014). Open canopy and shrubby understory are important structural components in addition to patch size and the predominance of forest in the surrounding landscape (Tirpak et al., 2009). The prairie warbler nests in shrubs and small trees away from forest edge (Nolan et al., 2014, Woodward et al., 2001).

We used the Habitat Suitability Index (HSI) model by Tirpak et al. 2009 to model prairie warbler habitat in OZHI. Components in the model include a suitability index assigned to combinations of landform, landcover, and successional age class on the basis of habitat associations. In other variables, prairie warbler's association with larger forest patches and shrubby understory is incorporated through logistic functions of patch size and increased small-stem densities. Suitability also declines with increasing canopy cover and adjacent to mature forest stands.

Population Model

We based K on the maximum observed density in the region (0.99, Fink, 2003) and set $K = 1.0$ pairs/ha when a cell's HSI = 1.0 (Table 1). We set initial abundances of prairie warblers at 50% of K, which is similar to the average density (0.52 pairs/ha) observed in Missouri (Brito-Aguilar, 2005; Fink, 2003; Thompson et al., 1992; Wallendorf et al., 2007).

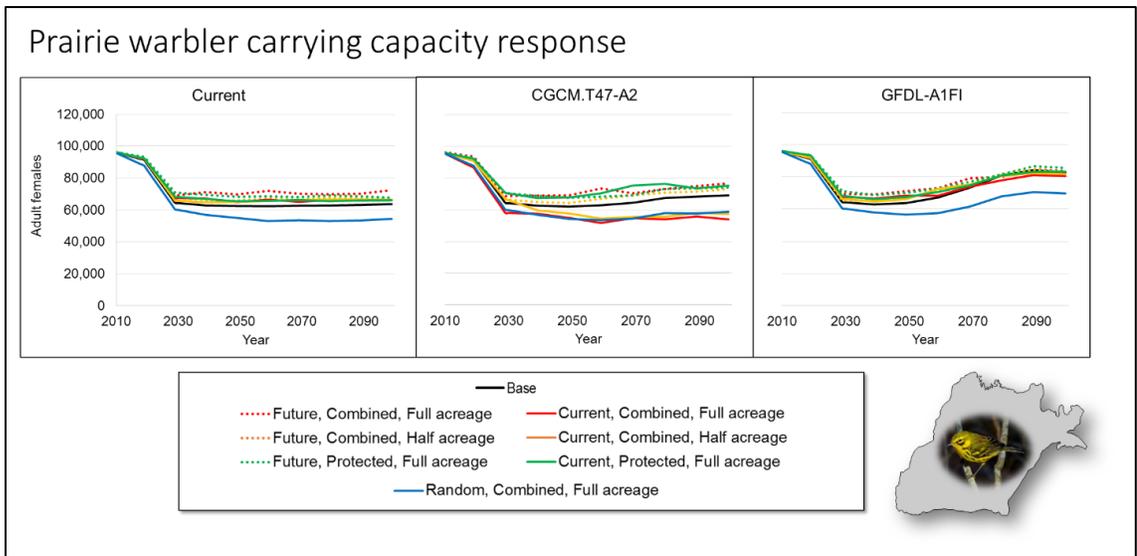
We set adult survival of prairie warblers at 0.60, which we obtained by averaging rates presented by Nolan et al. (2014) with 0.65 and Lehnen and Rodewald (2009) at 0.55. For juvenile survival of prairie warblers we used 0.32 based on Nolan et al. (2014) estimates of post-fledging and overwinter survival.

Results

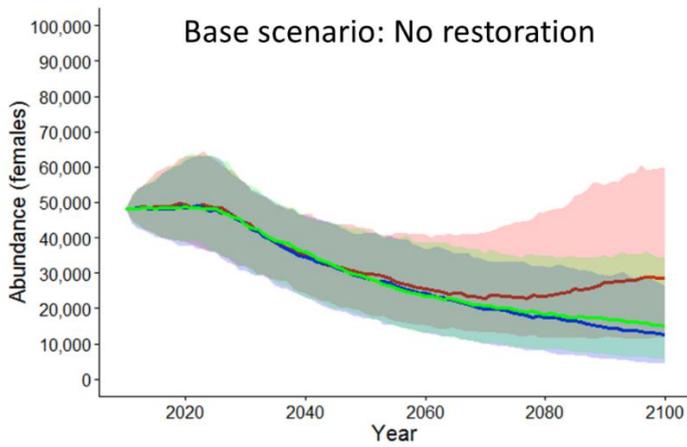
Prairie warbler habitat declined in the first two decades, driven by interactions between succession and management. Hit equilibrium beyond 2030. Under current climate model that amount of habitat continued. Under climate change models habitat for PRAW

increased as patterns in temperature and precipitation began opening forests. These patterns are reflected in the population projections where under the current climate and moderate climate change (CGCM.T47-A2) PRAW continued declining. Projections under extreme climate change (GFDL-A1fi) showed declines stopping by 2070, after which the population began growing again.

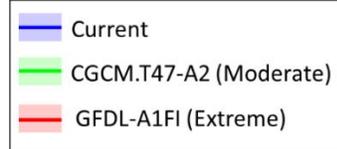
Although restoration scenarios only moderately affected habitat, these activities generally benefited PRAW. All scenarios, except for those with a random prioritization and two under the CGCM.T47-A2 climate model, increased habitat marginally (<10%). These changes, however, effectively slowed and, for scenarios restoring full acreage objectives, reversed PRAW declines. Under the GFDL-A1Fi climate model, scenarios that targeted full acreages even resulted in greater abundances in 2100 than initial estimates. Projections pooled across climate models identified that restoring full acreage, on both private and protected lands, prioritized by future conditions posed the greatest benefit to PRAW. This scenario resulted in abundances twice that of the base scenario with no conservation and reduced the risk of losing a quarter of the population by half (base – 59%, future, combined, full – 26%).



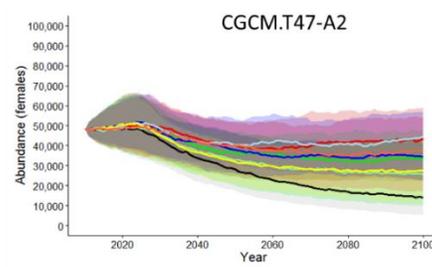
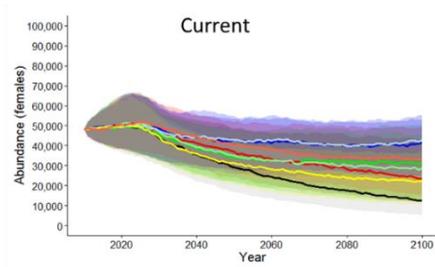
Prairie warbler population response



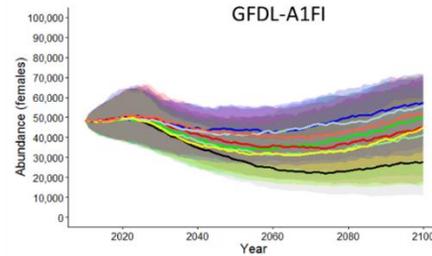
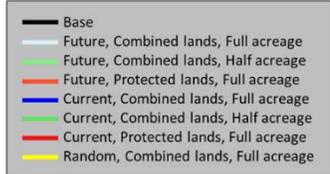
Climate Scenario

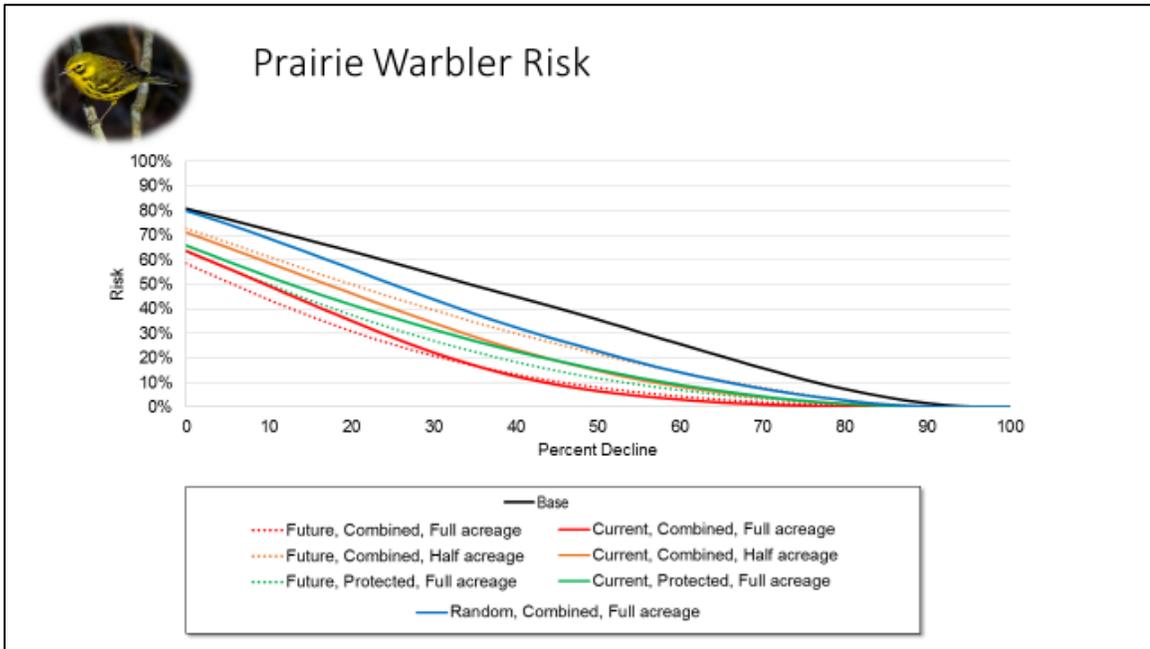
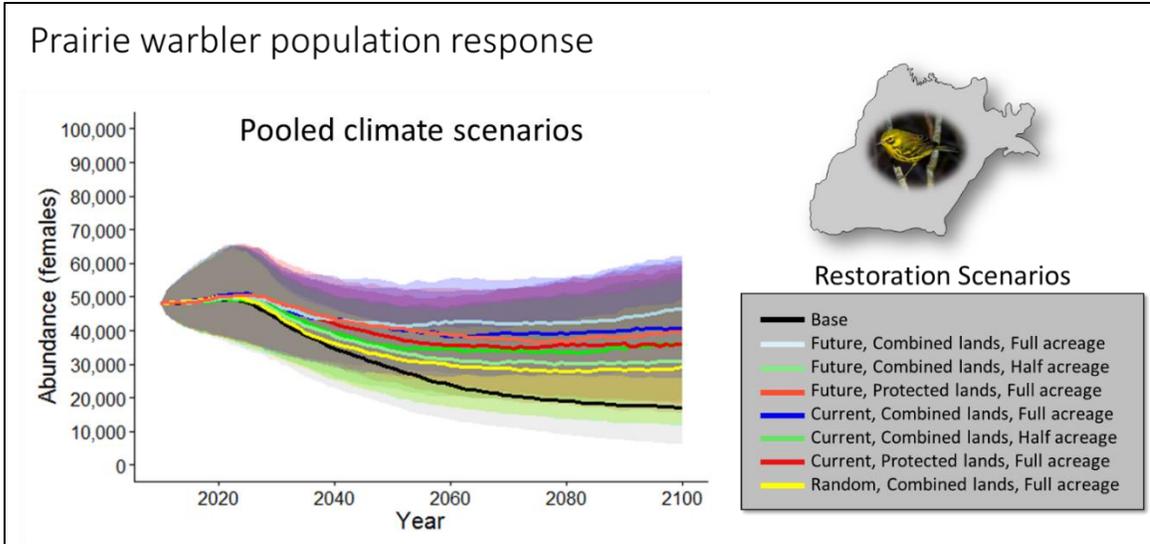


Prairie warbler population responses under climate models



Restoration Scenarios





Wood Thrush

Habitat Model

This thrush inhabits a wide variety of deciduous and mixed forests. Key primary habitat features are a sub canopy layer of shrubs, shade, moist soil, and leaf litter, which enhance feeding and nesting (Evans et al. 2011). These features are reflected in the species' use of mature hardwood and mixed forests with relatively closed canopies (Evans et al. 2011, Bell and Whitmore 2000). Wood thrush display area sensitivity in productivity but not in occupancy of habitats (Tirpak et al. 2009).

We used the Tirpak et al. (2009) wood thrush HSI model. In the model, suitability of forests varied by landform, landcover, and seral stage. Higher suitability is found in

forest patches > 1 ha and in landscapes predominantly forested. Other variables in the model included logistic and inverse logistic relationships with canopy cover and small stem density, respectively.

Population Model

We used demographic parameters from Bonnot et al. (2011) in the wood thrush DLMP model. We set $K = 0.5$ pairs/ha when $HSI = 1.0$. We based initial abundances of wood thrush breeding pairs on the 0.06 pairs/ha average, thus the initial abundance of wood thrush in each cell was 12% of K .

We specified adult wood thrush survival at 0.61, based on the average of the 3 estimates used in Bonnot et al. (2011). We set juvenile survival at a rate of 0.29 reported by Anders et al. (1997). We incorporated parasitism by applying mean RPI values to a maximum wood thrush maternity of 1.45 fem/fem/year, derived from three estimates from contiguous forests within the CHBCR (1.21–Anders et al., 1997, 1.86–Donovan et al., 1995, and 1.40–Ford et al., 2001 – interior study site only) and Evans et al (2011).

The model assumed that 90% of juveniles and 10% of adults dispersed annually. Dispersal distance was modeled as a negative exponential function with a mean distance of 70 km (Tittler et al. 2006). We accounted for density dependence using a modified ceiling model.

Results

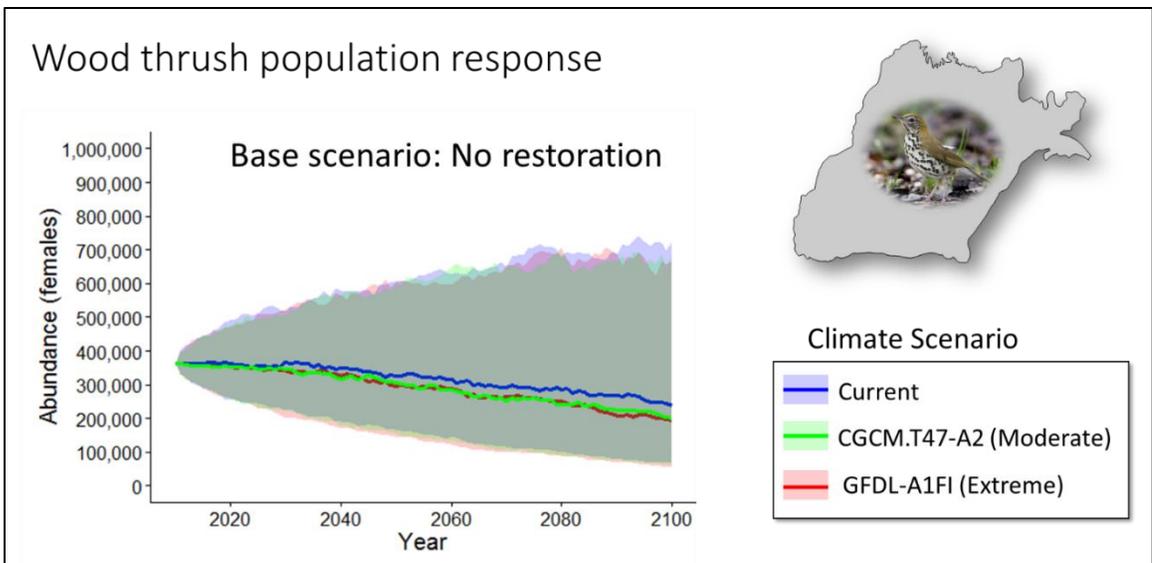
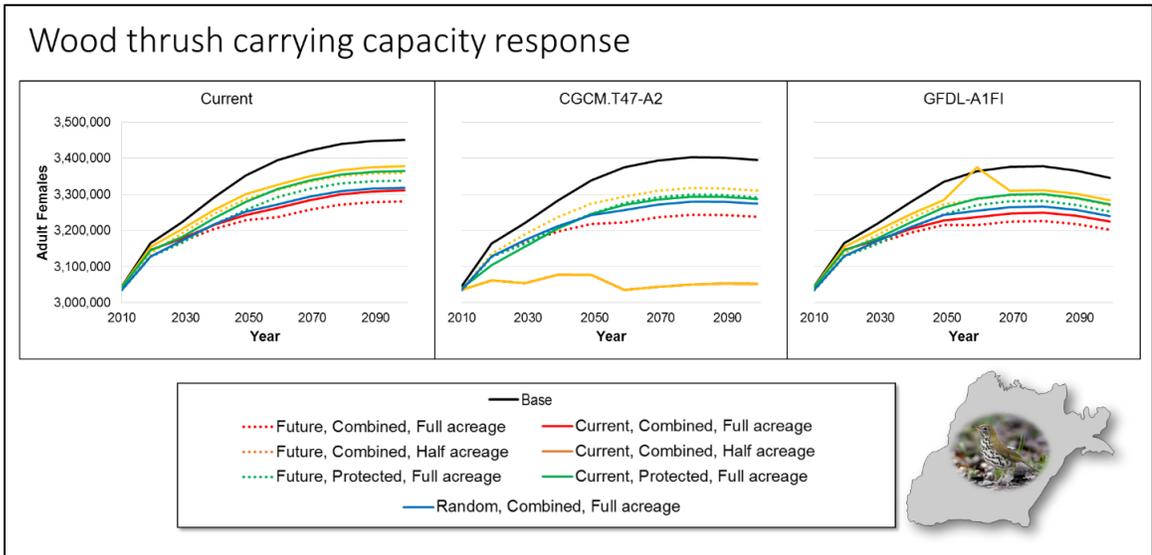
Baseline scenarios projected increases in wood thrush habitat through 2070 due to natural forest succession. Gains in K were less substantial under climate change and by 2090 wood thrush K began declining under both climate change models. Despite these baseline increases in habitat, we projected steady declines in wood thrush through 2100, with slightly greater losses under climate change models (>40% decline through 2100) compared to the current climate (34% loss).

Of all focal species, wood thrush habitat was most affected by restoration activities. All restoration scenarios reduced K between 2-10% below the base scenarios. These reductions translated to as many as 330,000 fewer females supported under scenarios that targeted full acreage objectives.

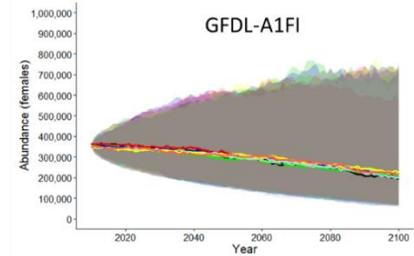
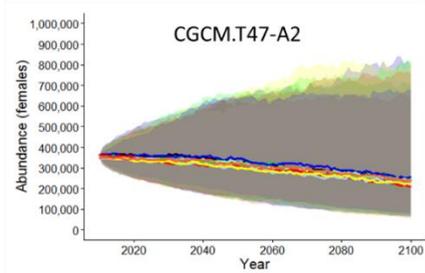
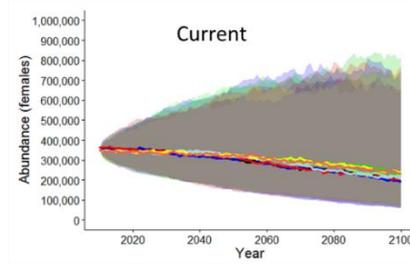
Wood thrush population growth, however, responded little to loss of habitat from restoration scenarios. Rather, all scenarios, regardless of climate model, showed declines similar to baseline projections. Considerable uncertainty surrounded wood thrush projections. Based on 80% credible intervals (shaded portions of population graphs), projected final wood thrush abundances for most scenarios ranged between 100,000 – 800,000 females.

Similar responses by wood thrush to restoration scenarios combined with high uncertainty resulted marginal differences in risk to this population across scenarios. Thus, no one scenario was overwhelmingly better for wood thrush. Instead, we projected

37-40% risk that wood thrush numbers would decline by 25% by 2100, with scenarios that restored less acreage presenting slightly lower risk.



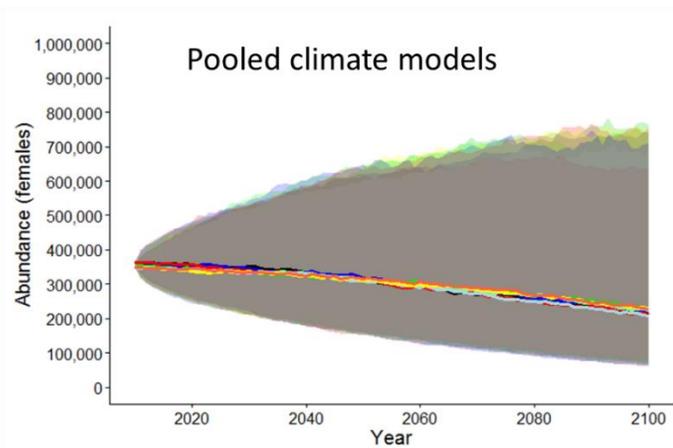
Wood thrush population responses under climate models



Restoration Scenarios

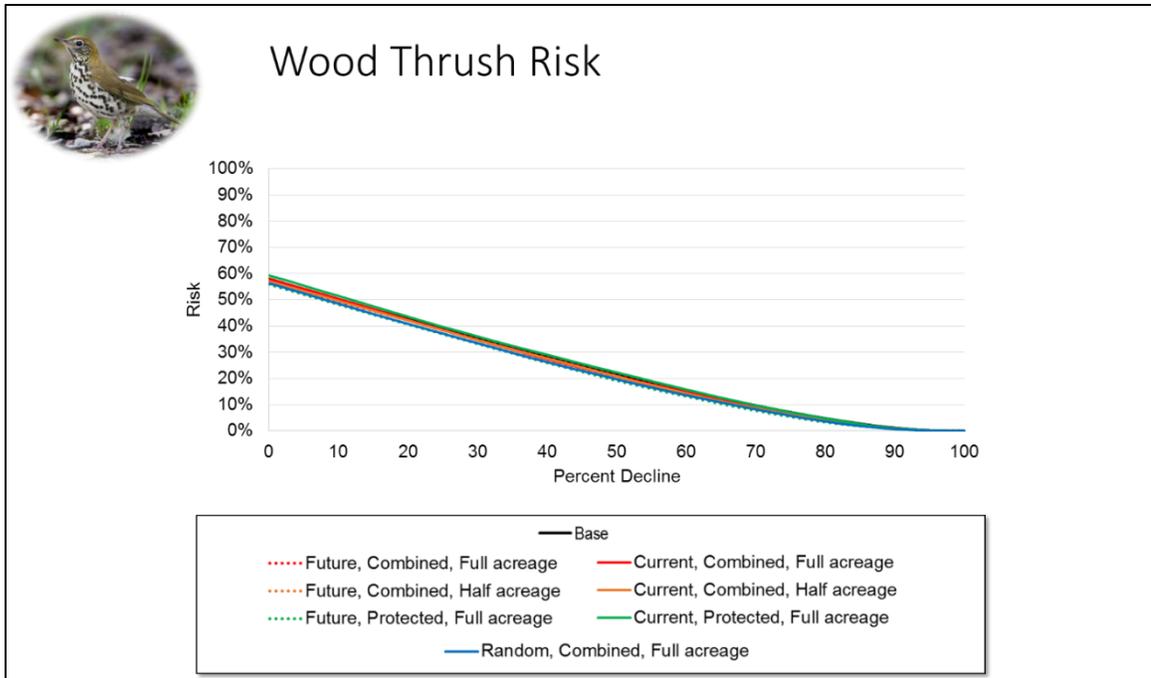
- Base
- Future, Combined lands, Full acreage
- Future, Combined lands, Half acreage
- Future, Protected lands, Full acreage
- Current, Combined lands, Full acreage
- Current, Combined lands, Half acreage
- Current, Protected lands, Full acreage
- Random, Combined lands, Full acreage

Wood thrush population response



Restoration Scenarios

- Base
- Future, Combined lands, Full acreage
- Future, Combined lands, Half acreage
- Future, Protected lands, Full acreage
- Current, Combined lands, Full acreage
- Current, Combined lands, Half acreage
- Current, Protected lands, Full acreage
- Random, Combined lands, Full acreage



Prothonotary Warbler

Habitat Model

The prothonotary warbler is a bird of bottomland hardwood forests and other forested wetlands (Petit 1999). Key habitat features are presence of water near wooded area with suitable cavity nest sites. Other important habitat correlates include low elevation, flat terrain, and shaded forest habitats with sparse understory (Petit 1999).

We approximated the HSI model for prothonotary warbler from Tirpak et al. (2009). In the model, suitability of forests varied by landform, landcover, and seral stage. Suitability is also based on the presence of water (identified by NLCD and national hydrology datasets) within 270 m. Two variables accounted for the interaction between forest patch size and the amount of forest within 1 km size in the area sensitivity in this species (Kahl et al. 1985). Finally, Tirpak et al. related suitability to snag density for nesting. Because LANDIS does not model snags, we approximated snag densities using the age of oldest trees projected on a site based on Rittenhouse et al. (2007).

Population Model

We estimated K and initial abundances from HSI model assuming density at $K = 0.6$ pairs/ha when $HSI = 1.0$ (Kleen 1973, Graber et al. 1983). We assumed a maximum territory size of 4 ha when using a moving window to identify habitat supporting territories (Reynolds 1997). We based initial abundances of prothonotary warblers on the 0.03 pairs/ha average or 5% of K (Twedt 2015).

We specified adult prothonotary warbler survival at 0.675 (Cooch et al. 1997, Hoover and Reetz 2006). We set juvenile survival at a rate of 0.18 (McKim-Louder et al. 2013). We

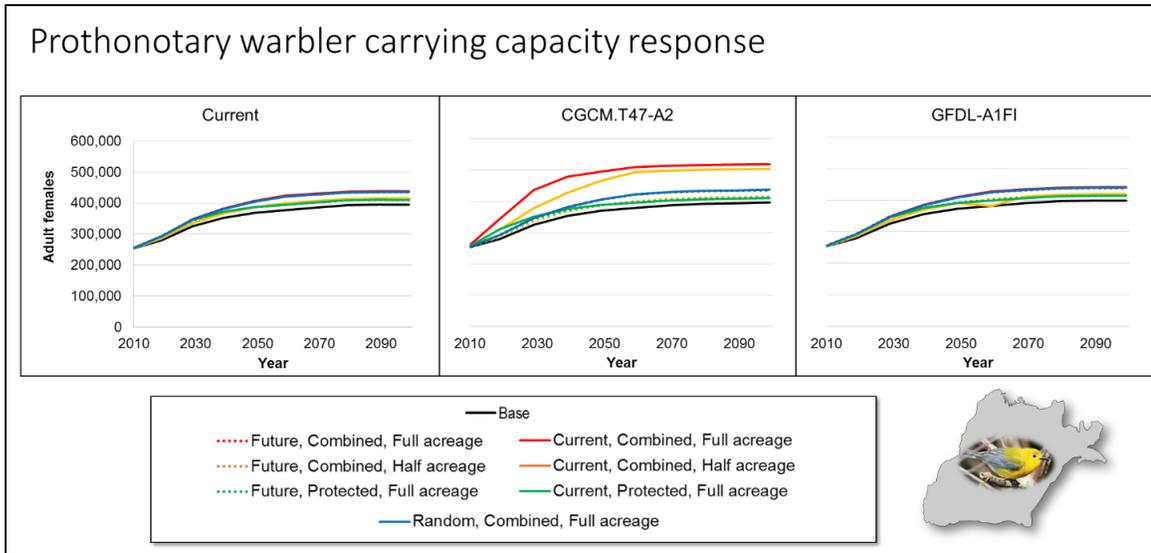
incorporated parasitism by applying mean RPI values to a maximum maternity of 1.95 fem/fem/year (Petit and Petit 1996).

The model assumed that 90% of juveniles and 10% of adults dispersed annually. Dispersal distance was modeled as a negative exponential function with a mean distance of 70 km (Bonnot et al. 2011). We accounted for density dependence using a modified ceiling model.

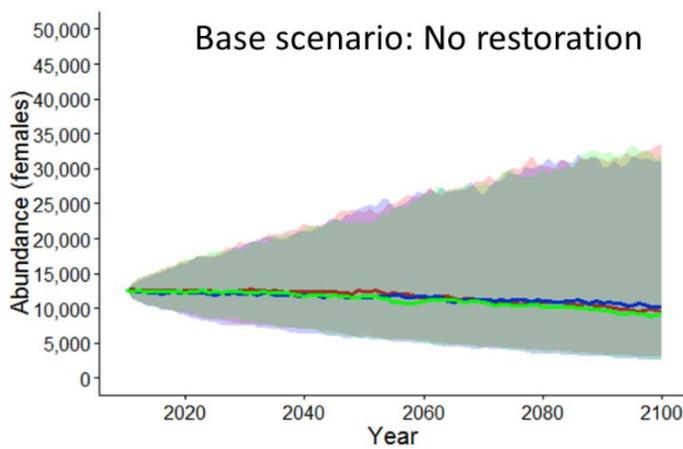
Results

Similar to wood thrush, aging forests increased habitat for prothonotary warblers in baseline scenarios to support >100,000 additional birds by 2070. However, increases in K tapered off by 2100. These patterns in habitat were similar across climate models. Despite increased K, we projected >20% declines in the prothonotary warbler population due to forest fragmentation.

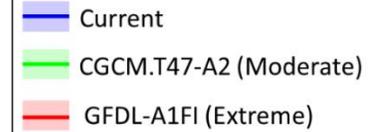
Restoration scenarios provided additional habitat, increasing K between 4-37% across scenarios and climate models. Alternatives that targeted full acreage objectives increased K the most. The added habitat, however, resulted in slightly larger declines. Only scenarios restoring habitat on combined lands, prioritized for the current landscape, resulted in greater population sizes compared to base scenarios. These were also the only scenarios that substantially reduced the risk of declines. Random restoration actually increased risk to prothonotary warblers in OZHI.



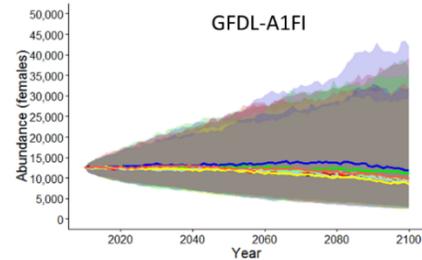
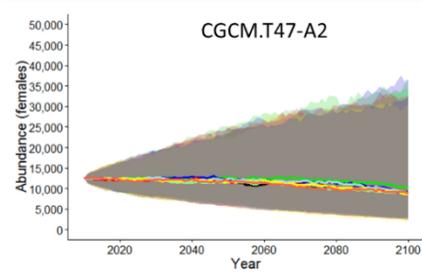
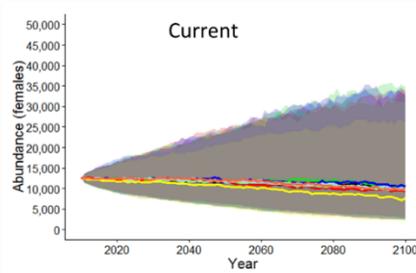
Prothonotary warbler population response



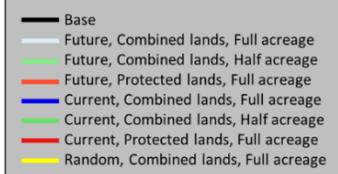
Climate Scenario

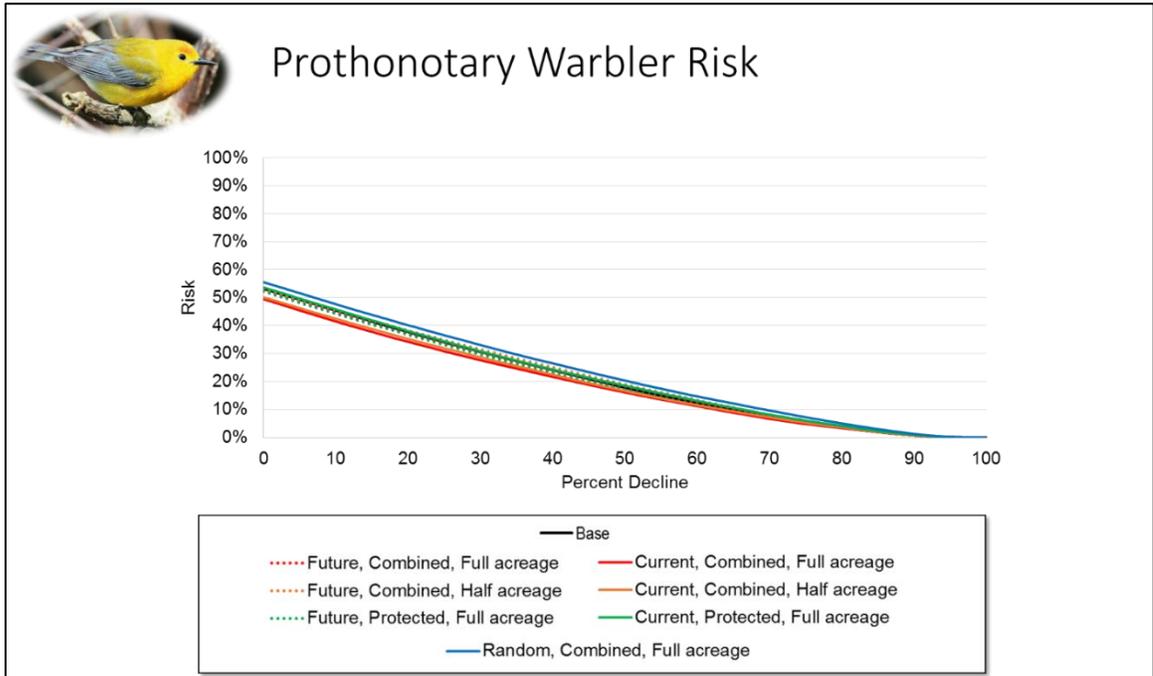
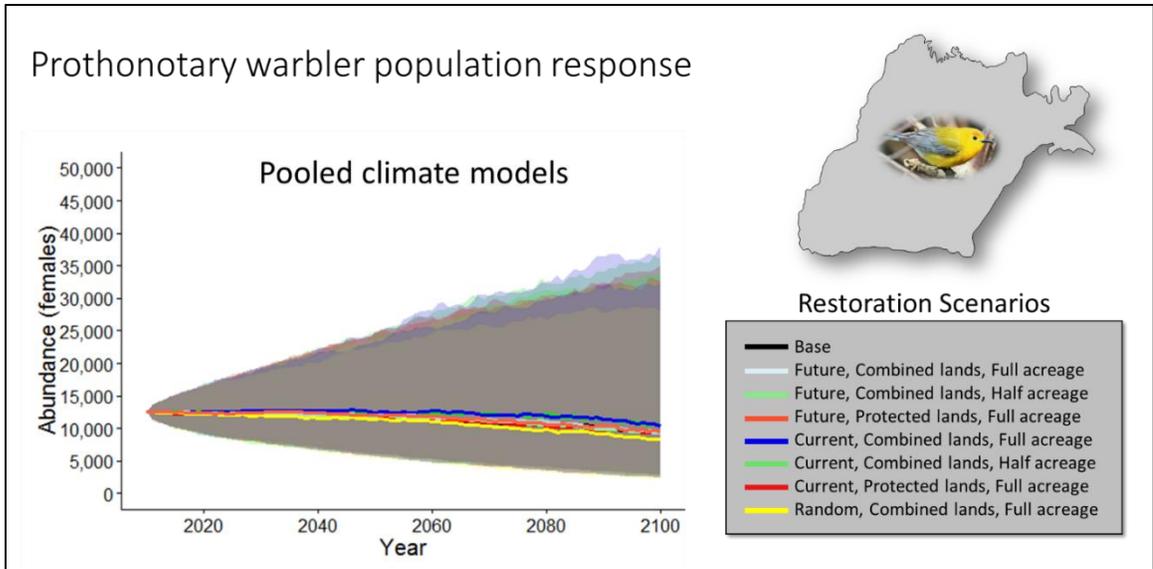


Prothonotary warbler population responses under climate models



Restoration Scenarios





Cerulean Warbler

Habitat Model

This small, canopy-foraging insectivore breeds locally in mature and older deciduous forests with broken canopies across much of the eastern United States (Buehler et al. 2013). Although it requires large forest tracts, the cerulean warbler establishes territories near interior forest gaps (Tirpak et al. 2009).

We adapted the HSI model for cerulean warbler from Tirpak et al. (2009). The first component combines landform, landcover, and successional age class and assigns

suitability scores to these combinations on the basis of habitat associations of the cerulean warbler outlined in Hamel (1992). A logistic function is used to address this species' area sensitivity to patches of forest < 1,000 ha. Other variables incorporated selection for canopy cover between 75-100% and predominantly forested landscapes. Tirpak et al. (2009) used dominant tree density to address the vertical and horizontal canopy structure used by cerulean warblers. However, we added a component to this index that required overstory density and stocking values between 50-80%.

Population Model

We estimated K and initial abundances from HSI model assuming density at K = 2 pairs/ha when HSI = 1.0 (Boves 2013, Buehler et al. 2013, Jones-Farrand and Bonnot 2014). We used the average of maximum territory sizes (2 ha) in Buehler et al. (2013) when using a moving window to identify habitat supporting. We based initial abundances of cerulean warblers on the 0.14 pairs/ha (7% of K; Reidy et al. 2011).

We specified adult survival for cerulean warblers at 0.6 through a combination of rates reported in Buehler et al. (2013): Apparent annual – 0.49 (Jones et al. 2004), monthly breeding – 0.98 (Jones et al. 2004), monthly wintering – 0.97 (Bakermans et al. 2009). We set juvenile survival at a rate of 0.28 (Jones-Farrand and Bonnot 2014). We incorporated parasitism by applying mean RPI values to a maximum cerulean warbler maternity of 1.5 fem/fem/year (Boves et al. 2015).

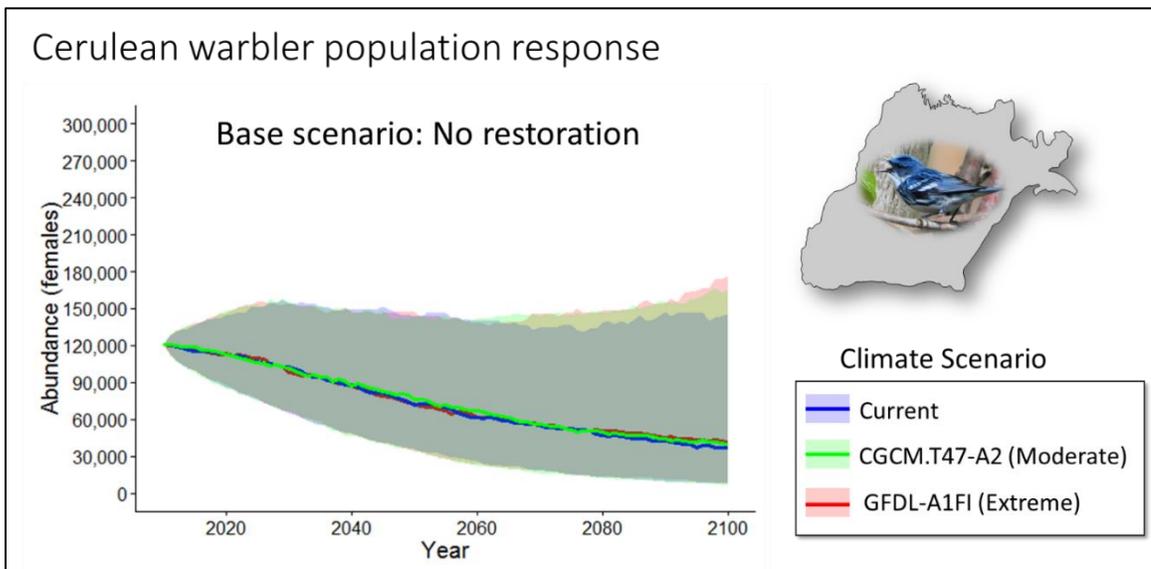
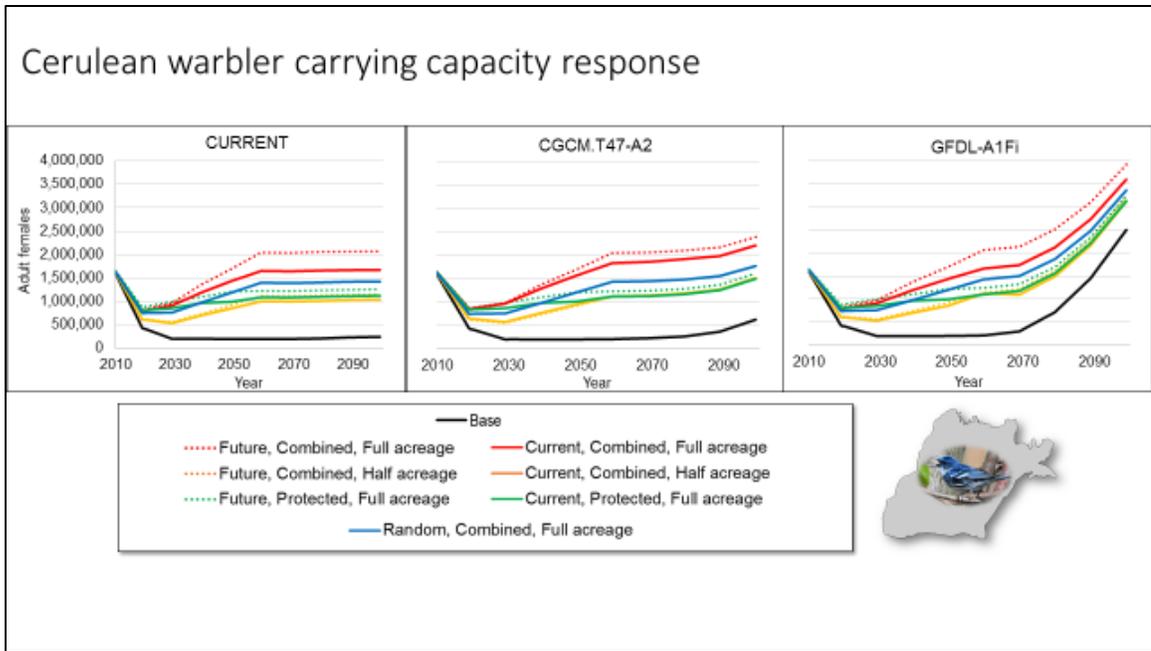
The model assumed that 90% of juveniles and 10% of adults dispersed annually. Dispersal distance was modeled as a negative exponential function with a mean distance of 70 km (Bonnot et al. 2011). We accounted for density dependence using a modified ceiling model.

Results

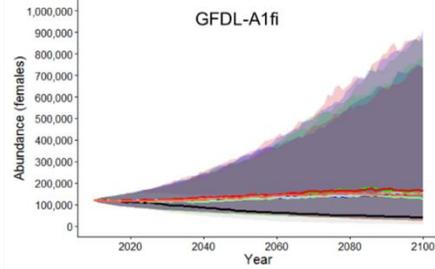
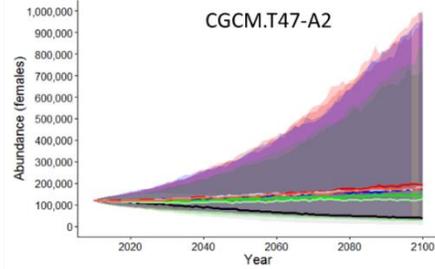
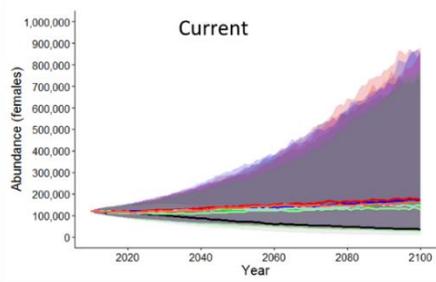
Similar to prairie warblers, the importance of forest structure characteristics to cerulean warblers resulted in substantial declines (86%) in K due to interactions between forest succession and management the first two decades. Base projections indicated K decreased >1,000,000 females during this period. Under climate change models, this loss of habitat eventually began recovering by the end of the century as those structural characteristics shifted more in line with cerulean warbler habitat. The baseline scenario under the GFDL-A1Fi model projected K by 2100 to be an order of magnitude than that for the current climate. The population responses to these changes were far less significant. Under all climate models cerulean warblers experienced >1% annual declines throughout most of this century. As a result, we estimated the probability that the population would decline by 25% at 0.53.

Model projections demonstrated dramatic responses of cerulean warblers to restoration scenarios. By 2030, habitat restored under the alternative scenarios stemmed declines in K by half. By 2050, we projected K for restoration scenarios at 4-7 times that for the base scenario under all climate models. The additive effects of restoring full acreage

objectives in addition to increased habitat under the GFDL-A1Fi scenario allowed K in 2100 to quadruple the initial estimate (initial abundance = 821,049 females; final abundance = 3,357,109 females). In contrast to climate change alone, cerulean warbler population responded positively to restoration scenarios. Regardless of climate model, all scenarios, except for those with random prioritization, prevented any significant declines. Although we projected similar responses across most alternatives, scenarios that focused on protected lands presented the lowest risk for cerulean warblers through 2100.



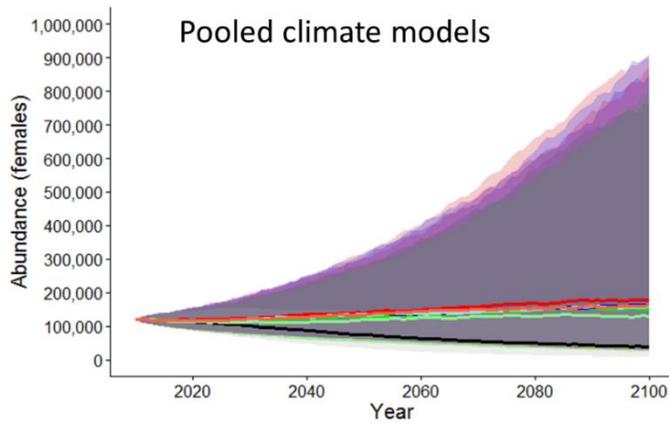
Cerulean warbler population responses under climate models



Restoration Scenarios

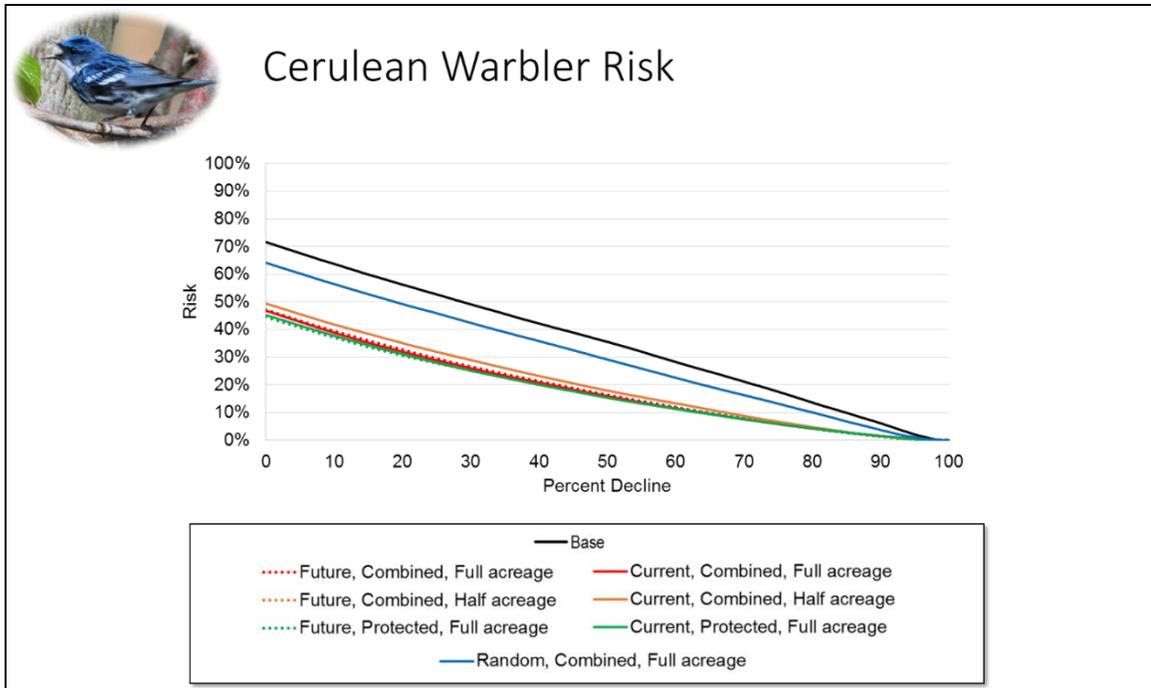
- Base
- Future, Combined lands, Full acreage
- Future, Combined lands, Half acreage
- Future, Protected lands, Full acreage
- Current, Combined lands, Full acreage
- Current, Combined lands, Half acreage
- Current, Protected lands, Full acreage
- Random, Combined lands, Full acreage

Cerulean warbler population response



Restoration Scenarios

- Base
- Future, Combined lands, Full acreage
- Future, Combined lands, Half acreage
- Future, Protected lands, Full acreage
- Current, Combined lands, Full acreage
- Current, Combined lands, Half acreage
- Current, Protected lands, Full acreage
- Random, Combined lands, Full acreage



Brown-headed Nuthatch

Habitat Model

Brown-headed nuthatch are endemic to pine forests of the southeastern United States, and rarely seen far from pine-dominated areas (Slater et al. 2013). The habitat of this species is defined by two habitat elements: mature pines for foraging and cavities for nesting (Wilson and Watts 1999, Dornak et al. 2004).

We used the brown-headed nuthatch model, developed by Tirpak et al. (2009). In the model, suitability of forests varied by landform, landcover, and seral stage with later stages of mixed and evergreen forests being most suitable. Because LANDIS does not model snags, we relied on projected stand ages as a proxy for the original snag density variable that increased suitability with snag density (Rittenhouse et al. 2007, Tirpak et al. 2009). The model also considered small stem density to account for the preference of the brown-headed nuthatch for open understories. Finally, suitability indices declines with increasing hardwood basal area as birds are less abundant in habitats with a greater hardwood component (Wilson et al. 1995, Wilson and Watts 1999, Slater et al. 2013).

Population Model

Carrying capacity and initial abundances of brown-headed nuthatch were estimated from HSI model assuming density at $K = 0.5$ pairs/ha when $HSI = 1.0$ (Wilson et al. 1995). We assumed a maximum territory size of 3.2 ha when filtering habitat not supporting territories (Slater et al. 2013). Because brown-headed nuthatch are likely habitat limited we set initial abundance 75% of K .

We assumed an adult survival rate of 0.67 based on the average of female rates in two Florida populations (Cox and Slater 2007). No estimates of juvenile survival exist, therefore we used convention estimates of 0.3 (Bonnot et al. 2011). We set maternity at 1.3 females/females/year based and did not model parasitism in this population (Cox and Slater 2007).

The model assumed that 90% of juveniles and 10% of adults dispersed annually. Dispersal distance was modeled as a negative exponential function with a mean distance of 1.27 km, based on models for another short-distance dispersing resident, golden-cheeked warblers (Connette et al. In Prep). We accounted for density dependence using a modified ceiling model.

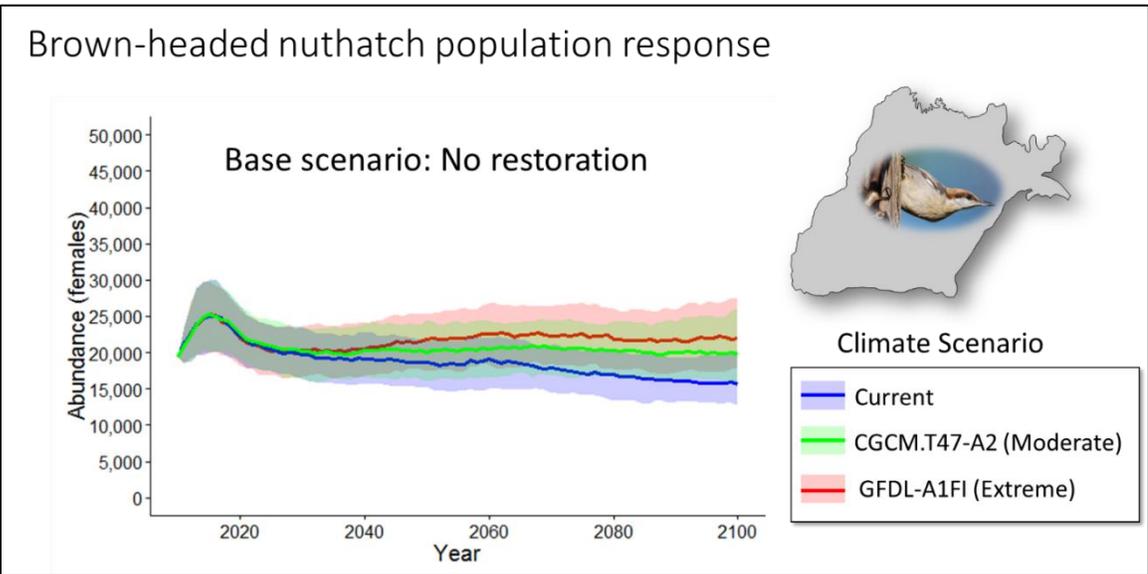
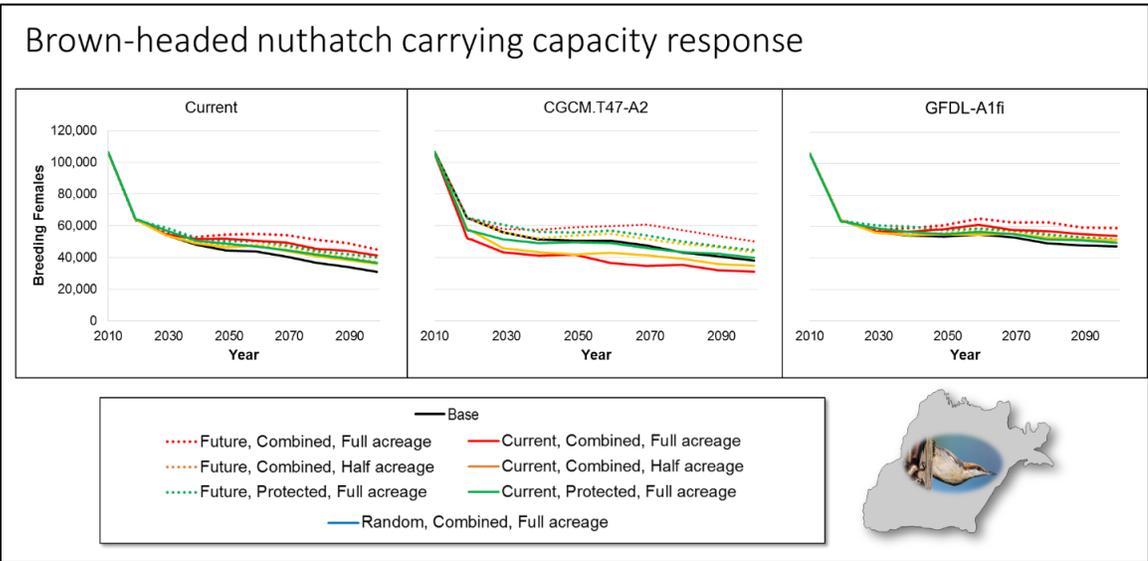
Results

Under base scenarios with no conservation we projected reductions in brown-headed nuthatch habitat over the next century. As an open-pine specialist, K for this species decreased from succession and dominance of hardwoods. Carrying capacities under the two climate change scenarios finished higher than the current climate, probably due to the effects of climate that opened forest structure and favored pine species. These differences in habitat availability were apparent in their base population projections. Brown-headed nuthatch declined 19% through 2100 under the current climate model, whereas the population was stable and grew 16% under the CGCM.T47-A2 and GFDL-A1Fi models, respectively.

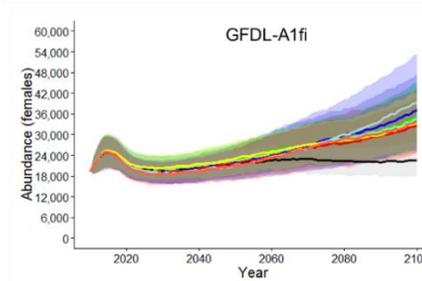
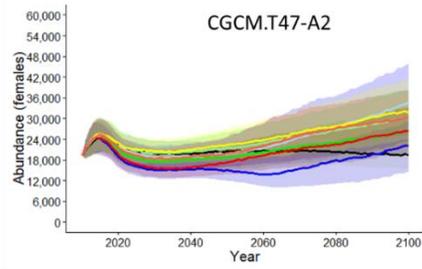
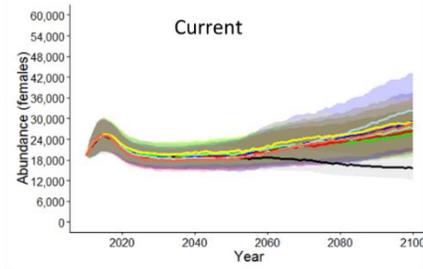
In general, restoration moderately offset habitat loss. For most scenarios, we projected final K 's 5-45% above base scenarios. Under the CGCM.T47-A2 model, the two scenarios that restored habitat on combined private and protected lands, prioritized by future landscapes resulted in lower K compared to the base scenario.

Despite scenarios providing habitat, we projected major differences between brown-headed nuthatch responses for restoration efforts alone and when restoration scenarios were simulated with translocation. Without translocation, all restoration scenarios, regardless of climate model, negatively affected population growth. These scenarios reduced the population 15% below baseline projections when averaged across climate models. This species is currently limited to the southern portion of the OZHI in the Boston and White River Hills subsections. Most open-pine restoration occurred outside of its current distribution in the Current River Hills and Black River Ozark Border subsections. Therefore, not only did the limited dispersal of brown-headed nuthatch prevent it from utilizing the newly restored habitat, the restoration where they were distributed targeted oak woodlands which removed habitat and caused population declines. This realization was the motivation for the team's decision to combine translocation efforts with restoration scenarios, giving the species a chance to colonize newly created habitat. When paired with translocation, all restoration scenarios reversed population declines. The new populations of birds grew substantially and drove abundances 30-102% greater than initial estimates of 19,428 brown-headed nuthatch

females. Likely limited most by habitat, this population was relatively stable, with only a 7% chance of a 25% decline, most restoration scenarios reduced this risk 2-4 points. The random restoration scenario presented the lowest risk for this species (3%).

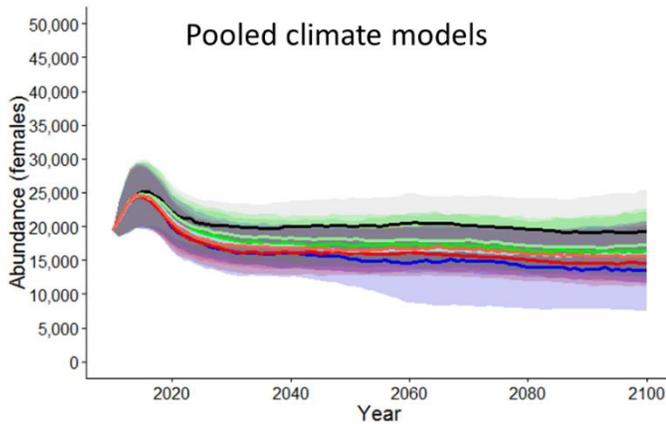


Brown-headed nuthatch population responses under climate models

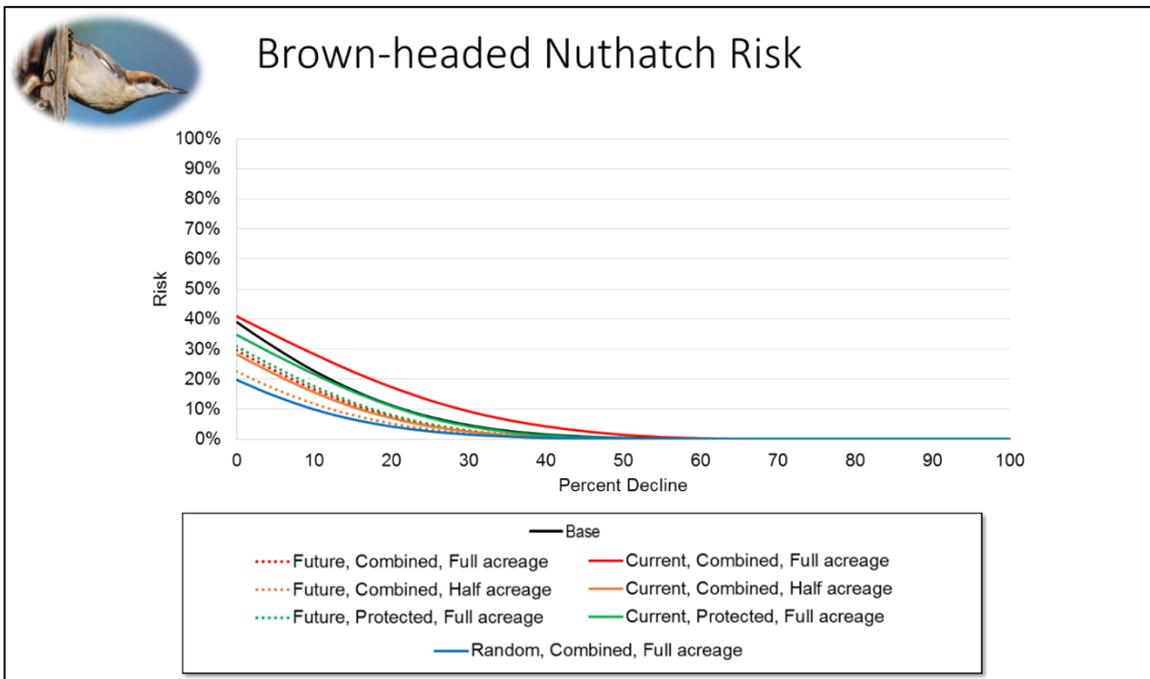
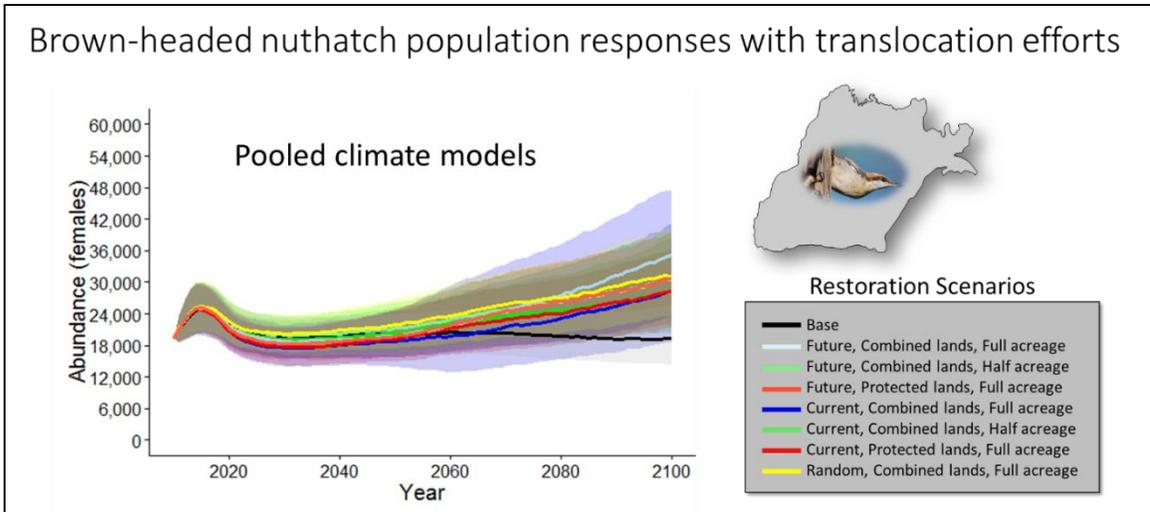


- Restoration Scenarios**
- Base
 - Future, Combined lands, Full acreage
 - Future, Combined lands, Half acreage
 - Future, Protected lands, Full acreage
 - Current, Combined lands, Full acreage
 - Current, Combined lands, Half acreage
 - Current, Protected lands, Full acreage
 - Random, Combined lands, Full acreage

Brown-headed nuthatch population responses without translocation



- Restoration Scenarios**
- Base
 - Future, Combined lands, Full acreage
 - Future, Combined lands, Half acreage
 - Future, Protected lands, Full acreage
 - Current, Combined lands, Full acreage
 - Current, Combined lands, Half acreage
 - Current, Protected lands, Full acreage
 - Random, Combined lands, Full acreage



Myotis spp.

Habitat Model

Our *Myotis spp.* model reflected habitats for Indiana and Northern long-eared bats. Both of these species breed in mature forests and hibernate in caves during winter. Primary non-winter habitat components are roosting sites, foraging areas, and water (Kurta 2002, Larson et al. 2003).

To develop the *Myotis* HSI model we combined components from models for Northern long-eared bats and Indiana bats. The first component identified pole and saw seral stages of various forest cover type as suitable habitat. Roost sites are predominantly in large dead trees, under exfoliating bark or inside hollows or crevices. (Foster and Kurta

1999). Therefore, we used the quadratic function by Rittenhouse et al. (2007) that identified roost tree availability for Indiana bats. This function estimates snag density by tree age class. We also varied suitability with distance to nearest water source, where sites < 1 km from water were most suitable (Rittenhouse et al. 2007). We adapted a variable from Larson et al. (2003) that reduces suitability by half for sites > 120 m from a forest edge, given northern bats forage in mature deciduous forest with small gaps. Finally, recent work has shown the importance of the surrounding landscape for occurrence of northern long-eared bats. We varied suitability with the percent of forest within 10 km (Starbuck et al. 2015). We also reduced suitability for sites with increased small stem densities (Starbuck et al. 2015).

Population Model

Carrying capacity and initial abundances of *Myotis* spp. were estimated from HSI model assuming density at $K = 0.1$ pairs/ha when $HSI = 1.0$ (K Womack, pers. comm.). Because these species breed in colonies, we assumed a maximum home range size of 1500 ha and removed any habitat which K supported < 60 breeding females over the area (K. Womack, pers. comm.). We assumed initial abundances occurred at 25% of K .

We used demographic rates from a stage structured model of Indiana bats with 3 stages (Thogmartin et al. 2013). We set survival rates for adults, juveniles, and pups (fall and winter survival only) at 0.9, 0.57, and 0.898, respectively. We assumed fertility for adults is 0.42 fem/fem/year and for juveniles, 0.279 fem/fem/year (Thogmartin et al. 2013).

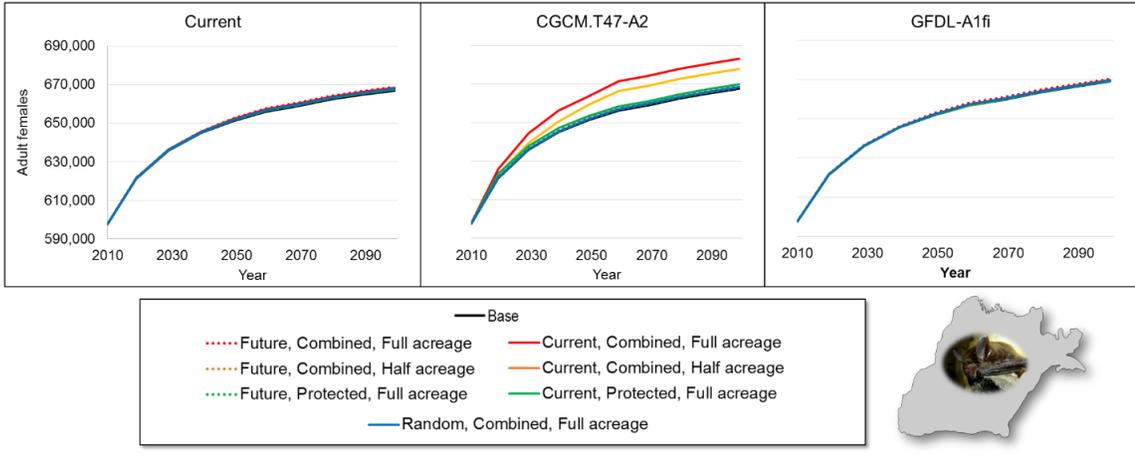
Because of the limited dispersal in these species we did not model dispersal between populations. We modeled density dependence using a Ricker contest model where survival decreased with increasing abundance of bats (Erickson et al. 2015)

Results

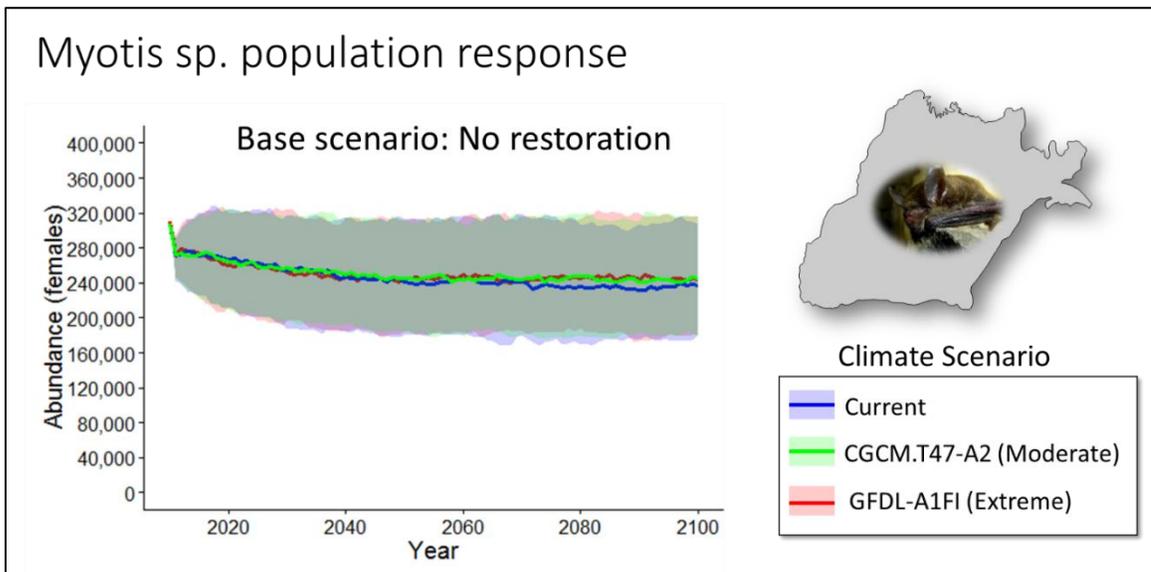
Habitat increased for *Myotis* in the base simulations such that K for bats grew from its initial estimate of 597,608 females by >70,000 under all climate models. However, we projected 20% declines in the simulated population under the 3 future climates by 2100.

Restoration scenarios did little to affect habitat for *Myotis* and only slightly lowered risk. Except for scenarios under the CGCM.T47-A2 model, restoration did not alter K . For this climate model restoration prioritized by the current landscape did result in K above the base scenario. Our models did not project any response by *Myotis* population to climate change or restoration. In all scenarios we estimated a 34-36% risk of a 25% decline through 2100. Restoring half of the acreage on private and protected lands based on the current prioritization presented the lowest risk of decline (34%).

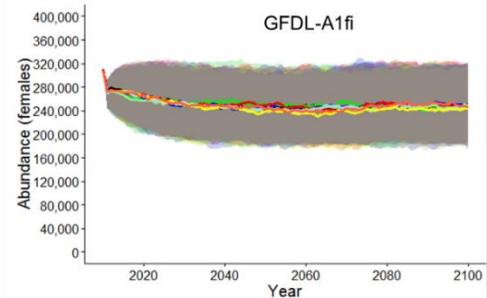
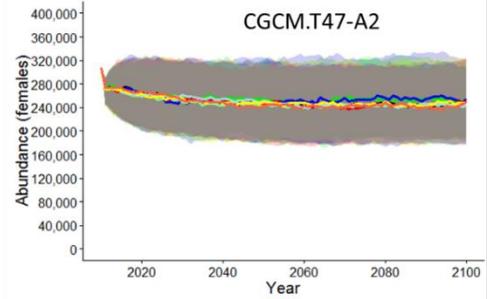
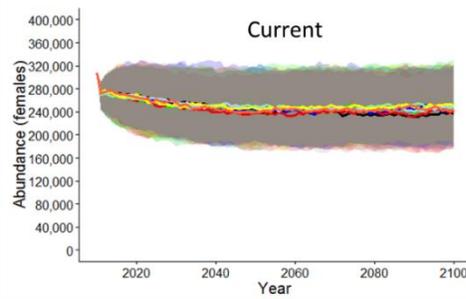
Myotis sp. carrying capacity response



Myotis sp. population response



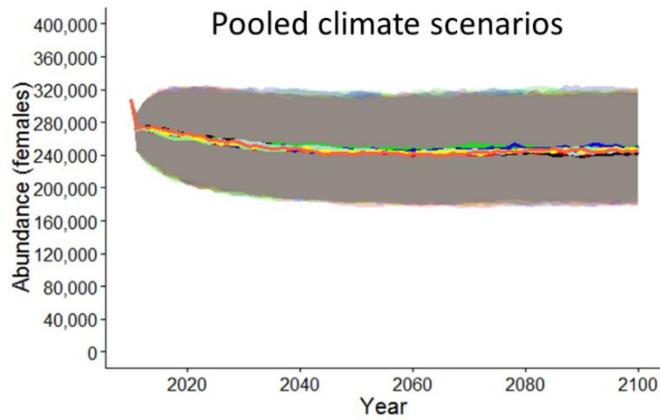
Myotis sp. population responses under climate models



Restoration Scenarios

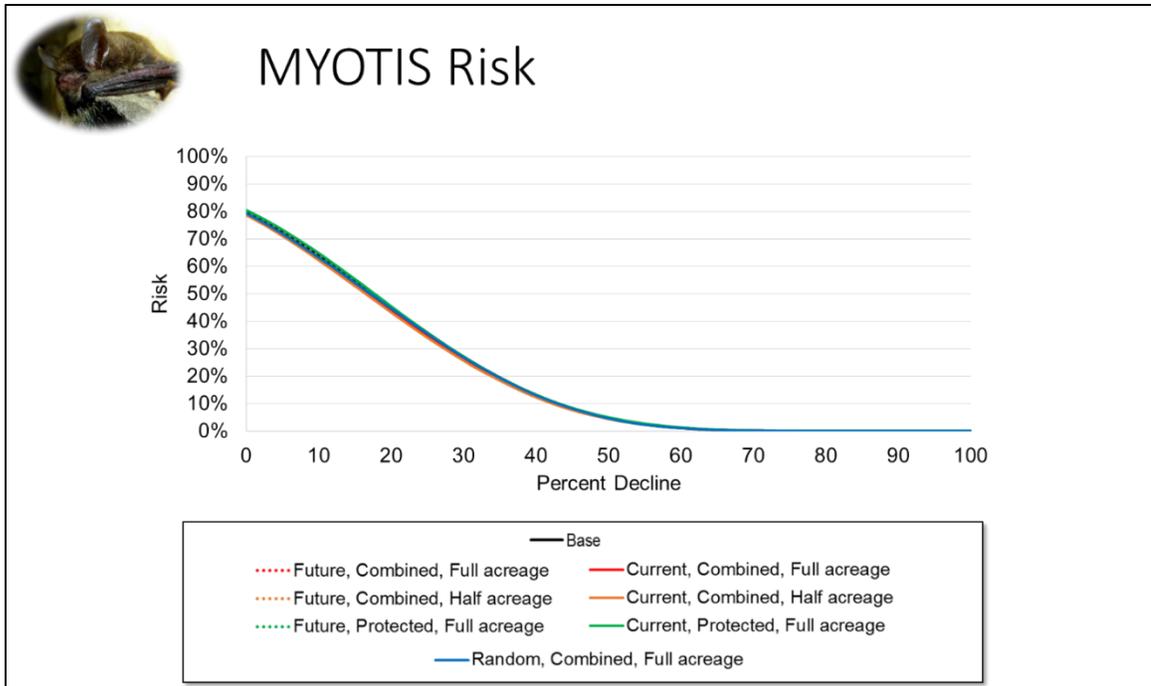
- Base
- Future, Combined lands, Full acreage
- Future, Combined lands, Half acreage
- Future, Protected lands, Full acreage
- Current, Combined lands, Full acreage
- Current, Combined lands, Half acreage
- Current, Protected lands, Full acreage
- Random, Combined lands, Full acreage

Myotis sp. population response



Restoration Scenarios

- Base
- Future, Combined lands, Full acreage
- Future, Combined lands, Half acreage
- Future, Protected lands, Full acreage
- Current, Combined lands, Full acreage
- Current, Combined lands, Half acreage
- Current, Protected lands, Full acreage
- Random, Combined lands, Full acreage



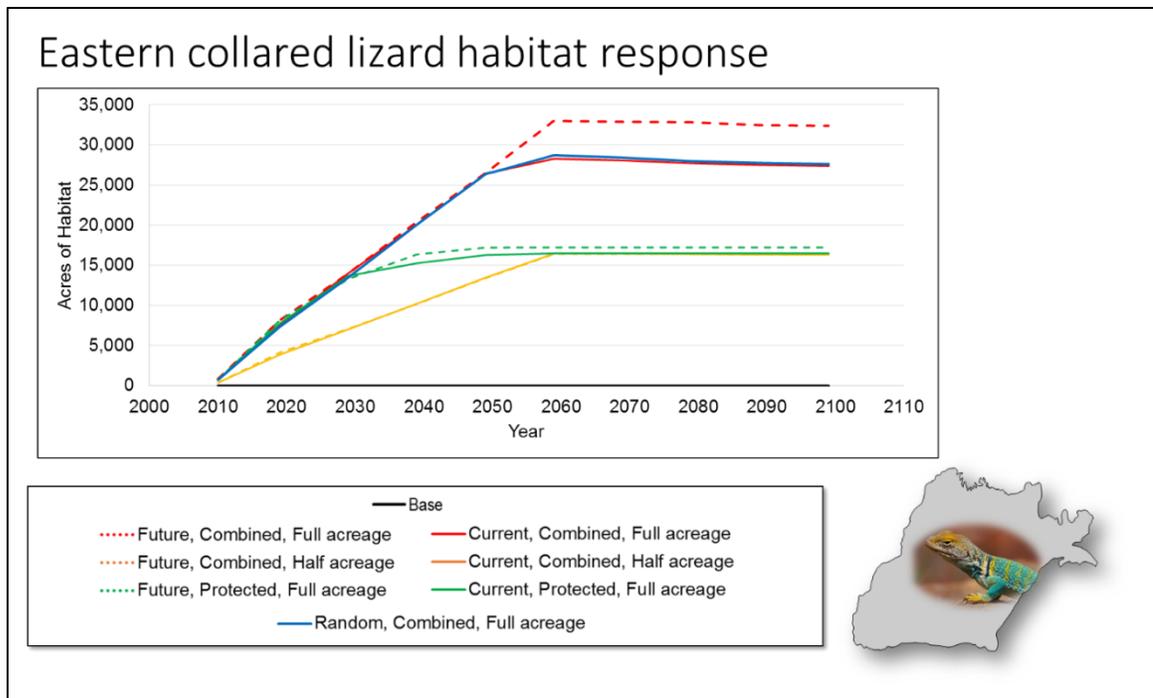
Eastern Collared Lizard

Habitat model

Given the lack of data on habitat for eastern collared lizards. We considered the general use of glades as habitat. However, because colonization of glades by this species, in a metapopulation context, depends on their connectedness by woodlands (forests with open canopies and understory vegetation) (Brisson et al. 2003). We considered glades as habitat only if they were connected to ≥ 1 other glade by woodland forests. We evaluated the effects of restoration scenarios by summing the acreage of habitat provided under each scenario.

Results

All restoration scenarios increased habitat for eastern collared lizards. The number of acres of lizard habitat was proportional to the total acreage restored across scenarios. Scenarios targeting full acreage objectives on private and protected lands provided the most habitat. Random restoration scenarios also provided substantial habitat.



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VITA

Thomas Bonnot was born and raised in central Missouri. After graduating from Fatima high school in 1998, Thomas attended the University of Missouri from 1999–2002, where he studied fisheries and wildlife sciences. Upon completion of his B.S. degree, he worked as a resource science technician for the Missouri Department of Conservation. There he conducted field and laboratory research on river otters and mourning doves. In 2003 Thomas returned to the University of Missouri as a graduate research assistant in Fisheries and Wildlife Sciences. His master's research examined the nesting ecology of black-backed woodpeckers in the Black Hills of South Dakota. During his master's work, Thomas became interested in habitat use and population dynamics of wildlife populations. He completed his master degree in 2006 and continued to study these topics for 6 years as a research associate until initiating his last degree in 2012 in the School of Natural Resources at the University of Missouri. During this time he began to combine his interests in landscape, habitat, and population ecology to develop approaches that could help assess the impacts of global change threats on wildlife populations and guide conservation to address them.