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RESEARCH ARTICLE

Demonstrating a decision support process for landscape conservation design

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Abstract

Despite the recent increase in landscape conservation and the design processes agencies are undertaking, there remains an implementation gap due to an inability to evaluate general strategies and account for uncertainties faced by managers. We demonstrated how a decision support process (DSP), recently developed to inform landscape conservation design, can address uncertainties and complexities inherent in landscape conservation to facilitate long-term, large-scale conservation planning. We applied the DSP to landscape conservation efforts within conservation opportunity areas (COA) of states in the Gulf Coastal Plains and Ozarks region. We engaged state planners within the region to identify important landscape conservation uncertainties they face in planning. We developed, simulated, and modeled the impacts of conservation addressing 3 uncertainties identified by state wildlife managers and evaluated the impacts by examining the responses of state and local populations of 2 bird species of conservation concern, prairie warbler (*Setophaga discolor*) and wood thrush (*Hylocichla mustelina*). The responses of prairie warbler populations to conservation strategies indicated that both approaches of protecting quality habitat from land-use change and restoring and enhancing lower quality and non-habitat improved their viability at regional, statewide, and COA scales. However, we noted that the relative effectiveness of strategies varied among states in ways that suggest a state's process for delineating COAs and what threats they face could influence which conservation approach to consider. Our findings highlight the need for regional coordination and the use of decision-support processes to guide effective conservation at landscape scales.

KEYWORDS

Conservation Opportunity Area, habitat model, population model, prairie warbler, restoration, State Wildlife Action Plan, wood thrush

Public agencies in the U.S. are increasingly focused on long-term, landscape-scale approaches to conservation to address global change and that emphasize coordination among partners (Baldwin et al. 2018). Partnerships across state, federal, and other jurisdictional boundaries can extend the reach and resources of any 1 agency, organization, or landowner (Ostrom 2010, Johnson et al. 2021, Lubell and Morrison 2021). Partnership programs, often organized around ecoregions, capitalize on the ability of governmental agencies and other organizations to establish and manage conservation reserves and protected areas (Chape et al. 2005, Turner and Pressey 2009) and access programs that support habitat conservation on private lands (Rey Benayas et al. 2009, Gordon et al. 2011, Graves et al. 2019).

However, a partnership's ability to coordinate landscape-scale conservation strategies can be limited by conflicting priorities, uncertainty in the condition of the landscape, or a lack of data on biodiversity, habitats, and ecological processes that might be vulnerable under future threats such as urbanization or climate change (Groves and Game 2016, Ledee et al. 2020). Therefore, partnerships often rely on a process formalized by the U.S. Fish and Wildlife Service known as landscape conservation design (LCD) to help guide partners in their planning. Landscape conservation design is an iterative, collaborative, and holistic process that produces information, analytical tools, maps, and strategies to achieve landscape goals collectively held among partners (U.S. Fish and Wildlife Service 2017, Campellone et al. 2018, Rittenhouse et al. 2023). Landscape conservation design begins with convening partners to set clear values and objectives, compiling data to assess current and projected future conditions of the landscapes (e.g., species' populations and habitats, natural communities, or ecosystem processes), and integrating data to assess vulnerabilities and conservation opportunities that can be prioritized. The latter stages of LCD relate to the development of spatial designs or strategies for conservation that can be considered and evaluated for their implementation (Campellone et al. 2018, Schwartz et al. 2018).

Despite substantial development in the initial stages of LCD, designing and deciding strategies for landscape conservation remains challenging for multiple reasons. The Southeast Conservation Adaptation Strategy, the Midwest Landscape Initiative, and the North Atlantic Landscape Conservation Cooperative are all examples of regional partnerships that are developing or have developed spatial blueprints that compile and integrate landscape data in LCD to highlight where the threats and opportunities exist across landscapes to guide conservation decisions (Knight et al. 2011, North Atlantic Landscape Conservation Cooperative 2017, Southeast Conservation Adaptation Strategy 2022, Midwest Landscape Initiative 2023). Many states have also used similar aspects of LCD to prioritize specific landscapes in which to focus conservation efforts. For example, State Wildlife Action Plans are developed by U.S. states and territories for conserving wildlife and habitat before they become too rare or costly to restore. Each plan addresses specific required elements including the identification of Species of Greatest Conservation Need, descriptions and locations of key habitats and communities essential for them, and plans for conservation actions proposed to conserve those species and habitats. In 2015, the Association of Fish and Wildlife Agencies recommended that, in their action plans, states spatially depict areas that offer the best opportunities for conservation by engaging partners and focusing resources, referring to each as a Conservation Opportunity Area (COA). However, despite an increasing number of blueprints and prioritizations and specification of COAs, there still remains an implementation gap for landscape conservation as efforts often stop short of the final stages of the LCD process (Campellone et al. 2018).

Failure to carry out strategic planning and action in LCD can be attributed to nontrivial barriers. First, choosing the best strategy requires an estimate of the effectiveness of competing strategies in reaching goals. However, evaluating strategy effectiveness is difficult when goals are oriented around species or population objectives, landscape or habitat quality, or ecosystem health that require advanced and integrated modeling or are dependent on the impacts of large-scale evolving and future threats such as climate and land-use change. Furthermore, the complex interactions of anthropogenic and natural processes suggest that impacts of strategies may not be straightforward (e.g., Bonnot et al. 2011). There are many examples where population viability analyses or systematic conservation planning models have facilitated decisions, but instances where these approaches comprehensively and simultaneously address multiple goals and landscape processes at large scales are limited. As such there have been calls for increased development of decision support tools based on modeling that allows impact evaluation or counterfactual analysis to address this need (Adams et al. 2019, Bonnot et al. 2019, Grace et al. 2021, Pressey et al. 2021). Secondly, deciding landscape conservation strategies is impeded by the complexity of the decisions that planners must make (Wright et al. 2020). Partners can consider various management actions, such as restoring degraded habitat or protecting current habitat, and may have to fulfill multiple objectives. Costs, partner needs, public policy, and private and public lands managers' interest all factor into landscape decisions. Even within environmental considerations, planners may need to balance objectives related to biodiversity, ecological processes, and ecosystem services (Groves and Game 2016). For example, deciding on a conservation plan that is best for a suite of focal species is complicated when different species have conflicting responses to each scenario. Therefore, evaluating strategies within structured decision frameworks that can reduce complexity and promote learning and decisions is also crucial (Bonnot et al. 2019).

Previously, we developed a decision-support process (DSP) that integrates dynamic-landscape metapopulation models (Bonnot et al. 2017) within a structured decision making approach (Figure 1) to evaluate impacts of strategies and thus help guide landscape conservation design. Structured decision-making is a formal decision analysis framework for addressing complex decisions (Gregory et al. 2012). In our initial pilot of the DSP, a team of partners was able to choose among scenarios for habitat restoration that best met desired endpoints for focal wildlife species in the Ozark Highlands region under climate change and urbanization (Bonnot et al. 2019). In that pilot, we identified focal species to represent priority ecosystems, designed and simulated alternative scenarios, and modeled the consequences of each relative to a baseline, given concurrent impacts of climate and landscape change. We demonstrated that the decision support process has the potential to address many of the uncertainties and complexities that are inherent in the process of LCD and ultimately support decisions about long-term, large-scale conservation. However, the pilot also highlighted an impracticality of LCD–most states and agencies, which must implement landscape conservation over smaller areas and shorter time frames with smaller budgets, are not set up to decide, commit, and carry out long-term, large-scale plans and thus saw less utility of this approach in their daily decisions (Bonnot et al. 2019, Ledee et al. 2020). Despite this realization, there was unanimous agreement that a DSP could still be useful for increasing our understanding of learning the tradeoffs of strategies.

Our objective was to demonstrate how the DSP can be used to evaluate landscape conservation strategies within COAs across the states in the Gulf Coast Plains and Ozarks Landscape Conservation Cooperative (GCPO). We engaged state planners within the GCPO to identify important uncertainties they have about landscape conservation strategies. We then used the DSP to develop, simulate, and model the impacts of conservation scenarios addressing those uncertainties. We evaluated the impacts by examining the responses of regional populations of 2 bird species of conservation concern: prairie warbler (*Setophaga discolor*) and wood thrush (*Hylocichla mustelina*). By comparing and contrasting how modeled populations of each species responded to the conservation

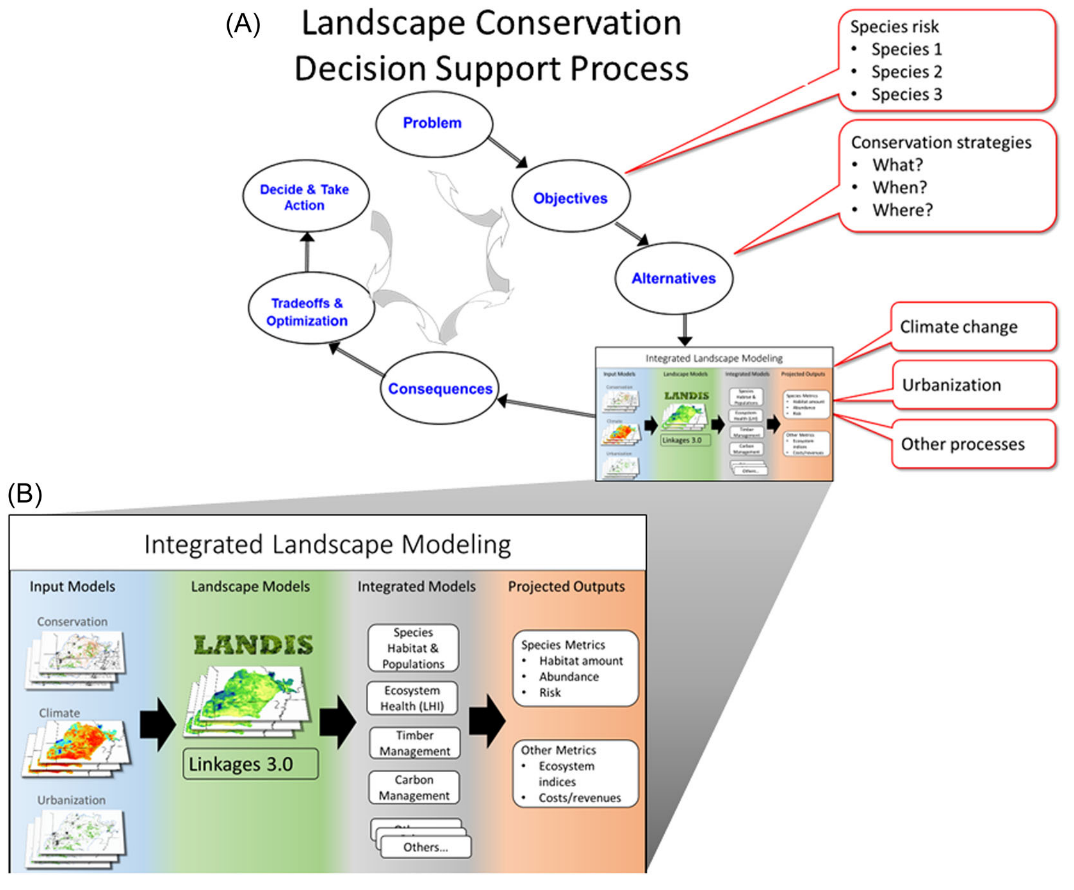

FIGURE 1 Illustration of the decision support process (A) developed by Bonnot et al. (2019) for landscape conservation design. The process combines integrated landscape models that are spatial and temporal in nature (B) into a structured decision making to informing specific decisions and examine overarching questions about strategies and assumptions in landscape conservation that landscape planners commonly face.

strategies across the states in the GCPO, we can begin to inform long-term planning and help guide landscape conservation design.

STUDY AREA

We simulated conservation strategies across a landscape conservation partnership region. The GCPO region spans >70 million ha and includes all of Arkansas and Mississippi and parts of 11 additional states (Figure 2). Priority ecological communities such as upland hardwoods, open pine, grasslands, and tidal marsh are the focus of conservation assessments and planning by the partnership and state partners. Our focus was on actions in COAs that have been outlined by the states as part of their State Wildlife Action Plans. At the time of this study, 8 of the states in the GCPO region delineated COAs (Figure 2). However, the processes by which they selected these areas varied. For example, in Missouri, Alabama, and Illinois, COAs are based on natural communities and ecosystems. In contrast, plans from Louisiana, Mississippi, Kentucky and Tennessee focused on species distribution and overlap when selecting COAs. Certain states explicitly considered surrounding land use patterns or risks of development, such as

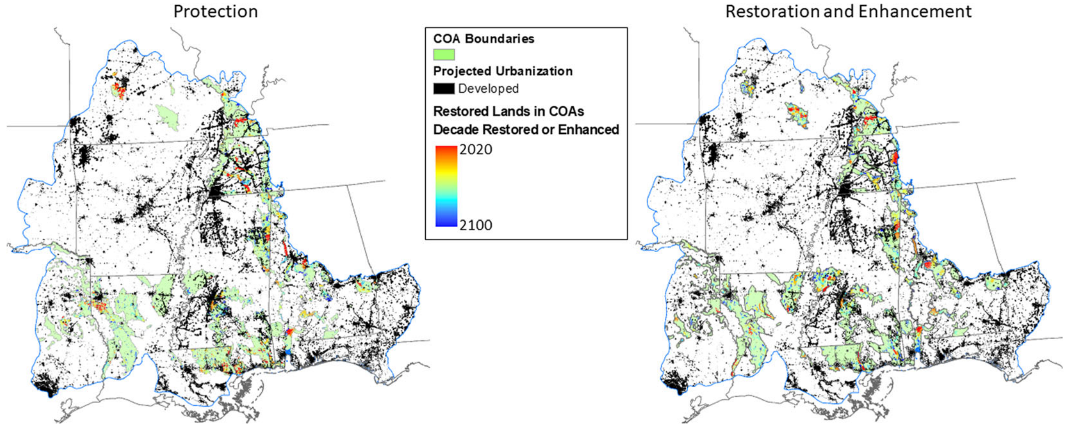

FIGURE 2 Placement of simulated conservation activities within Conservation Opportunity Areas (COAs) by states within the Gulf Coastal Plains and Ozarks region. At the time of this study, 8 states in the region had outlined COAs in which to focus landscape conservation to address threats such as projected urbanization over time (areas projected to be developed by 2100 shown). Under the protection and restoration and enhancement strategies, patch units were selected and management was simulated over time within conservation opportunity areas. Selection of patches was dynamic and interactive with model projections of urbanization.

Louisiana, Alabama and Missouri. Some states even incorporated partner opportunities when identifying COAs. The differences in approaches resulted in the range of COA characteristics and contexts (e.g., the number, size, and shape of COAs and their proximity to threats such urbanization; Figure 2).

METHODS

The overall approach in the DSP is the use of structured decision making that combines engagement with partners to identify and develop simulations with integrated modeling of landscapes, habitat, and populations to evaluate impacts of scenarios and strategies on species viability. Therefore, the methods below detail the identification and simulation of strategies across landscapes. Landscapes are projected into the future under those simulations using forest and ecosystem models. Habitat models are used to estimate the amount of habitat for carrying capacity and initial abundance and predict demographics such as productivity for wildlife species based on the landscape projections. Then, the results are integrated into population models that project their population growth into the future and assess for risk impact.

SWAP coordinator engagement and scenario identification

We engaged State Wildlife Action Plan coordinators within the GCPO region to provide guidance on landscape conservation design strategies within COAs geared to states' needs. We began by holding a scoping meeting where we introduced the DSP and discussed the planning processes used by states in developing their COAs. Three states participated in the meeting. During the meeting we noted any uncertainties coordinators expressed regarding conservation strategies in their COAs. These uncertainties ranged from which overall management approach is best to where to work at within COAs.

Following the meeting, we polled SWAP coordinators in the region as well as conservation planners in the region to objectively identify the most important information needs for landscape planning. We expanded on the uncertainties noted in the meeting and asked respondents to rate on a Likert scale the importance of specific information needs to their state or agency (see Supporting Information).

We also explored concerns regarding conservation efforts on private lands such as the longevity of habitat maintenance and the lack of verification of habitat management. Finally, to help simulate strategies that were relevant to planners, we asked respondents about what constraints should be incorporated into simulated actions. For example, we asked planners their estimates for the ideal, minimum, and expected proportions of a COA that could be affected by conservation activities. We also polled respondents as to whether scenarios should control for costs or acreage as a means of comparison.

Based on the questionnaire results, we developed simulations around 3 uncertainties about conservation strategies: 1) the relative impact of protection versus restoration approaches; 2) the importance of connectivity within a COA; and 3) the effects of prolonged management on private lands (Table 1). First, planners indicated the need to understand the relative effectiveness of 2 fundamental strategies to landscape conservation; should they approach conservation in COAs by protecting high quality habitats from land-use change (i.e. protection strategy) or by restoring and enhancing low and moderate quality habitats (i.e. restoration and enhancement strategy)? Due to the size of many COAs, the second set of simulations focused on whether placement of conservation actions within them should prioritize landscapes with increased connectivity. Specifically, is it beneficial to prioritize actions on lands within a COA that have higher occurrence of habitat in the surrounding landscape? Finally, planners were concerned about the potential lack of private lands maintenance for the habitat restoration and enhancement strategy. Thus, what would be the impacts if habitat maintenance on 50% of these lands discontinued and the habitat transitioned out of the desired state? We structured 6 conservation simulations around these strategies in a way that would allow us to examine their interactions and identify their relative impact to landscape conservation design in COAs (Table 1). All simulations included effects of climate change and land-use change on habitats. We also included a baseline simulation that only considered the effects of climate change and land-use change without any conservation strategy as a control.

Strategy simulation and landscape modeling

The process for simulating conservation strategies involved selecting lands over time, characterizing the habitat and the protected status of those lands based on the strategy and desired or expected conditions, and then modeling any changes in that habitat to reflect scenarios about habitat maintenance. Strategies were simulated spatially and dynamically, in that we selected and characterized specific cells in maps and interactively selected lands and characterized management amidst concurrent real-time impacts of urbanization and forest changes from projected climate change. In this way, the simulations reflected the reality of planning and carrying out management among threats over time.

To incorporate urbanization and climate-driven forest change into our simulations we used habitat and land-use data provided by the GCPO blueprint (GCPO 2016). Data on forest composition and structure under climate change were available from Wang et al. (2019), who combined LANDIS PRO with the ecosystem model LINKAGES 3.0 (Dijak et al. 2017) to model forest changes due to succession, harvest, and climate change. LINKAGES integrates temperature and precipitation data with nitrogen availability and soil moisture to model individual tree species growth and mortality at a site. LINKAGES provided estimates of the early growth and establishment of different tree species and the maximum allowable tree biomass over time under climate change, which were then used in LANDIS PRO to simulate tree growth across the landscape given the impacts of climate in addition to the other forest and landscape processes (Wang et al. 2019). They validated their models using long-term forest monitoring data from the U.S. Department of Agriculture-Forest Service as well as other concurrent modeling efforts.

Projections of urbanization were available from Terando et al. (2014) based on the SLEUTH model for the Southeastern United States. The SLEUTH model is an adaptation of the Clarke Urban Growth Model that uses cellular automata, terrain mapping, and land cover change modeling to estimate the probability of urban development

TABLE 1 Scenarios considered in the application of a decision-support process to guide landscape conservation design in state Conservation Opportunity Areas (COAs) across the Gulf Coastal Plains and Ozarks Region. Scenarios were structured around 3 overarching strategies identified by State Wildlife Action Plan coordinators and regional planners regarding the approach to conservation, the location of conservation activities, and assumptions of the maintenance of management on private lands. Simulations of habitat management were run under each of the 7 scenarios and occurred against baseline changes from climate and land-use change based on published projections.

Approach	Connectivity	Private lands maintenance
Baseline		
Protect patches with high quality habitat	Patches surrounded by connected landscapes are prioritized within COAs	
	Patches are randomly selected within COAs	
Restore and enhance patches with low quality and moderate quality habitat	Patches surrounded by connected landscapes are prioritized within COAs	Habitat quality is maintained on restored patches assuming management is continued
		50% of patches revert to mature forest assuming discontinuation of management
	Patches are randomly selected within COAs	Habitat quality is maintained on restored patches assuming management is continued
		50% of patches revert to mature forest assuming discontinuation of management

(Jantz et al. 2010). It 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 (Terando et al. 2014).

We simulated conservation strategies over 90 years (2010–2100) in decadal increments. To obtain a realistic estimate of the rate of habitat conservation across the region over time, we pooled data from the Conservation Almanac that track the amount of land acquired for conservation in each state (Trust for Public Land 2019). We found an average of 50,000 ha of conservation per decade across the states in the GCPO (1998–2015) and adjusted it for the proportion of the state in the GCPO region (Table 2). The adjustment assumed that states would use resources evenly across their footprint and ensured representativeness of state contributions to conservation in the GCPO. As a result, conservation acreage targets within the GCPO ranged from <3,000 ha/decade for Kentucky to >49,000 ha/decade for Mississippi, with a combined total of approximately 170,000 ha/decade (Figure S1, available in Supporting Information). We simulated all conservation activities within COAs and assumed no more than 50% of a COA could be affected, based on responses from planners. The lack of COAs for Arkansas, Kansas, Oklahoma, Florida, and Georgia precluded simulation of conservation in these states, however, we still simulated the baseline scenario of landscape and climate change and modeled wildlife populations across them.

Patch selection

We selected patches for management and characterized habitat on those patches using algorithms based on prioritizations and data from the GCPO Blueprint. The GCPO created the Blueprint to provide a common

TABLE 2 Summary of areas within states and Conservation Opportunity Areas (COAs) that were targeted for protection and restoration and enhancement strategies across 13 states within the Gulf Coastal Plains and Ozarks (GCPO) region. Total amount of area simulated under conservation was based on an average of 50,000 ha of conservation per decade observed across states for the period 1998–2015 and adjusted for the proportion of each state in the GCPO region. Although equal amounts of land were targeted across scenarios, the composition and context of COAs within some states constrained overall totals. For example, by locating COAs in landscapes with larger proportions of protected lands, Missouri's ability to protect additional acreage was limited by model constraints.

State	Area within GCPO	Total area of state	Percent of state in GCPO	Projected decadal conservation	Area within COA	Cumulative area of restoration and enhancement	Cumulative area of protection
Alabama	8,229,088	13,367,923	62%	30,779	1,724,374	1,697,268	1,717,279
Arkansas	13,769,090	13,769,090	100%	50,000	0	0	
Florida	2,156,227	14,637,237	15%	7,366	0	0	
Georgia	2,176,020	15,223,239	14%	7,147	0	0	
Illinois	818,163	15,008,469	5%	2,726	387,761	266,356	211,003
Kansas	11,605	21,312,339	0%	27	0	0	
Kentucky	529,916	10,452,509	5%	2,535	522,708	475,847	446,808
Louisiana	9,572,075	12,149,518	79%	39,393	3,016,393	1,846,010	1,855,583
Mississippi	12,344,325	12,357,940	100%	49,945	2,864,973	2,381,886	2,404,770
Missouri	9,754,416	18,057,471	54%	27,009	489,099	1,258,483	574,677
Oklahoma	3,738,307	18,103,984	21%	10,325	0	0	
Tennessee	2,732,588	10,918,152	25%	12,514	1,053,672	903,917	808,085
Texas	7,121,329	68,673,829	10%	5,185	899,383	304,784	338,240

framework for describing habitats and landscapes in the GCPO region to help answer the perennial conservation questions of how much is available, where can more be accessed, and what needs to be done? The Blueprint comprises a linked set of geospatial data products designed to provide a scientific approach to identifying the next best places for collaborative conservation effort. The Blueprint entails: 1) ecological assessments to rank current habitat condition across the region; 2) layers that identify the potential ecological conditions that would be desired and general actions needed to achieve those conditions; and 3) ranking of landscapes across the region based on the relative proportions of their current and potential habitat. Although the GCPO LCC is no longer active, previously developed products have been integrated into and can be found at the Southeast Conservation Adaptation Strategy.

Selection of lands within COAs occurred at a patch unit scale that we delineated through the intersection of landcover, COA, and protected area data layers. The scale we chose was relevant to the level of land management, while enabling distinction between COA lands and protected status. We only selected patch units within COAs, that were in an undeveloped land use, and >10 ha in size.

Selection of patch units differed between protection and restoration and enhancement strategies. In its ranking of lands for conservation, the GCPO Blueprint spatially maps opportunities for management across the region into 3 broad categories: maintenance of good condition sites, enhancement of out-of-condition sites, and restoration of sites with potential for the habitat system but are currently under an alternative land cover or land use class

(GCPO 2016). We used these rankings to select patch units appropriate under each strategy. Protection strategies selected patch units which were predominantly suitable for maintenance of good condition habitat and permanently protected them from a change in land use. The restoration and enhancement strategies selected patch units predominantly comprised of the latter 2 categories and restored the habitat to desired conditions. For each simulation, we prioritized selection of units with higher total area and relative proportion of that ranking.

We also used the Blueprint rankings to address the connectivity strategies. Within each of the 3 broader categories, the Blueprint also considers landscape configuration surrounding a site. Sites nested within large contiguous patches of habitat and in a landscape that is extensively forested receive sub-rankings that are higher than when in large patches in fragmented landscapes, followed by sites in small patches in fragmented landscapes (GCPO 2016). Therefore, because habitat connectivity is a function of landscape configuration, we prioritized these sub-rankings for patch units in simulations that targeted connectivity. The contrasting strategies disregarded the sub-rankings and selected suitable patch units at random within COAs.

We simulated selection in an interactive manner, such that 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. By interactively combining the three processes, we could compare divergent effects of urbanization on private and protected lands among the conservation strategies (Figure 2). We exempted targeted lands from urbanization. All urbanization effects that removed lands from potential selection were permanent and precluded protection or restoration. In each decade of the simulation, we selected patches within COAs across states according to the strategies until we met the constraints for 50% of a COA or the maximum acreage for the state.

Characterization

Once patch units were selected for protection or restoration and enhancement, we characterized habitat attributes to represent the effects of urbanization, climate change, and restoration on species habitat over time under each simulation. We focused on characteristics related to habitat for 2 focal species, prairie warbler and wood thrush. The characteristics we considered were determined *a priori* based on published, species-specific habitat models and included variables such as landcover and landform, as well as aspects of forest structure and landscape configuration. Depending on the strategy, our characterization of these habitat attributes across the region over time incorporated impacts from restoration and protection against a backdrop of urbanization and forest changes from climate change. We expanded on the methods by Bonnot et al. (2017) to characterize habitat from the output of the SLEUTH and LANDIS PRO models. We derived NLCD land cover classes by comparing the relative importance values estimated by LANDIS PRO for deciduous versus coniferous species and incorporating probabilities of urbanization. We grouped land cover to characterize overall forest composition and configuration across the region. We derived additional forest characteristics from LANDIS PRO data: seral stage classifications, basal area, and stocking, from which we estimated canopy cover. We approximated densities of small stems based on LANDIS density projections for specific aged cohorts. We used a landform classification derived from DEM (Theobald et al. 2015). All landscapes were processed with a cell size of 30 m.

For the strategies that protected quality habitat, we protected selected patch units from development from the decade of initial selection for the remaining years of the simulation. However, because we assumed resources were devoted to land acquisition, we did not simulate further restoration of the habitat. Rather, habitat characteristics only reflected the background changes from climate change and natural succession.

For restoration and enhancement simulations, we characterized habitat data on restored patch units to reflect a transition to the conditions desired through restoration of the natural communities. The GCPO established desired endpoints for the different habitats that describe landcover and vegetation structural characteristics intended through restoration and continued management (Table 3). The values are based on expert judgement, ecological

TABLE 3 Desired levels of habitat characteristics for variables in prairie warbler and wood thrush habitat models. As a way to simulate management geared to each habitat type, patch units selected for restoration and enhancement were given these levels based on their ecological site potential. Levels were derived from literature and expert opinion.

Potential habitat	Canopy cover (%)	Small-stem density (stems/ha)	NLCD class	Stocking (%)
Beaches and Dunes	0	0	31	0
Freshwater Marsh	0	0	95	0
Glades	5	8,000	41	10
Grass Prairie	0	0	71	0
Tidal Marsh	0	0	95	0
Forested Wetlands	70	2,000	90	70
Longleaf Pine Flatwoods	45	4,000	42	40
Longleaf Pine Woodland	45	4,000	42	30
Mixed Forest	80	2,000	43	70
Shortleaf/Loblolly Pine Woodland	50	4,000	42	30
Upland Hardwood Woodland	50	5,000	41	40
Upland Hardwood Forest	90	2,000	41	70

literature and an ecological potential model underlying the Blueprint (Kabrick et al. 2014, Blaney et al. 2016, GCPO 2016). We assigned endpoints and any habitat variables derived from them to restored cells. Although selection occurred at the patch level, restoration of individual cells within a patch was based on its potential community type. Thus, when a forest patch was selected for a given habitat, all potential forested cells within that patch would be restored to their potential forest type. To account for a realistic transition from current land condition to the desired conditions we staged the various habitat characteristics over time to reflect the direction of any changes (e.g., ag field to forest or forest to woodland).

In scenarios that addressed the potential discontinuation of habitat management on restored and enhanced lands, we randomly selected a proportion of patch units for which the desired habitat would no longer be maintained and that would transition to unmanaged forest. We identified these units by randomly selecting 50% of the patches in each decade following the decade of their initial restoration and enhancement. For all discontinued patches we set habitat characteristics equal to that of closed mature forests (reflecting observed succession patterns).

Habitat modeling

We used integrated landscape modeling within the decision-support process to model the impacts of each scenario on prairie warbler and wood thrush populations. Following the approach developed by Bonnot et al. (2017), we began with landscape data simulated under each strategy and used habitat models to translate these projections into species' habitat and demographics in each decade. Then, we incorporated the spatially and temporally varying demographics into population models that included stochasticity and parametric uncertainty. The resulting models provided spatially and temporally explicit representations of focal species habitat and population growth throughout the region (see Figure S3 in Supporting Information). Although conservation was simulated across some states, we still modeled habitat and populations within these states both as a form of control, as well as to gain a more realistic complete assessment of the populations across the region.

Habitat models linked landscapes to demographic processes such as distribution, reproduction, and dispersal. We modeled distributional abundance and carrying capacity using multiscale Habitat Suitability Index (HSI) models. The models predict suitability of habitat in cells based on their attributes and the surrounding landscape and have been verified and validated with empirical data (Dijak and Rittenhouse 2009, Tirpak et al. 2009).

The prairie warbler breeds throughout most of the Eastern United States and Southern Ontario in shrubby old fields, early-stage regenerating forests, and 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 (Woodward et al. 2001, Nolan et al. 2014). We used the HSI model by Tirpak et al. (2009) to model prairie warbler habitat. 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 adjacency to mature forest stands.

The wood thrush inhabits a wide variety of deciduous and mixed forests. Key habitat features are a sub canopy layer of shrubs, shade, moist soil, and leaf litter, which enhance feeding and nesting (Evans et al. 2011). Each feature is reflected in the species' use of mature hardwood and mixed forests with relatively closed canopies (Bell and Whitmore 2000, Evans et al. 2011). 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 modeling

We modeled the regional populations of each species as a spatially-structured population model by intersecting a grid of 10,000-km^2 hexagons with the state and COA boundaries to create 464 subpopulations (Figure S2, available in Supporting Information). Subpopulations ranged in size from 518–1,000,000 ha. 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 reproductive indices in each subpopulation, weighted by K in each decade, so that productivity estimates reflected any changes in distribution of birds over time. Because we modeled population dynamics annually, we calculated yearly values of spatial demographics by linearly interpolating between decadal estimates. We programmed the population models in Program R version 3.1.2 (R Core Team 2014). We used female only, Lefkovitch matrix models comprising adult and juvenile life stages based on species life history. We specified stage-specific survival and fertility rates from the literature and assumed a post-breeding census.

For prairie warbler 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. 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. 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.

For wood thrush we used demographic parameters from Bonnot et al. (2011). 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 percent 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 females/female/year, derived from 3 estimates from contiguous forests within the Central Hardwoods (1.21 – Anders et al. 1997; 1.86 – Donovan et al. 1995; and 1.40 – Ford et al. 2001).

We used a relative productivity index (Bonnot et al. 2011) model to link breeding productivity of these birds affected by parasitism to habitat fragmentation. The 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 (Bonnot et al. 2011). We multiplied relative productivity indices by estimates of maternity to obtain population-specific fertility estimates in each decade. We used a modified ceiling density dependence model to incorporate density dependence. The modification prohibited individuals over K in a population from breeding but allowed them to remain in the subpopulation or disperse.

We specified breeding and natal dispersal rates for each stage that determined the proportion dispersing each year and redistributed them among the subpopulations according to multinomial distributions with probabilities equal to the relative movements of those dispersers to the surrounding subpopulations based on distance and the quality of their habitat (Bonnot et al. 2011). We modeled the rate of movement among subpopulations as decreasing with distance according to a negative exponential function:

$$m_{c,c'} = \begin{cases} e^{-\frac{d(c',c)}{b}} & \text{if } \; d(c',c) > D_{\max} \\ 0 & \text{if } \; d(c',c) \le D_{\max} \end{cases}$$

where $d(c', c)$ is the distance between the starting and destination subpopulations, which we calculated as the distance between centroids. b is a constant representing the average dispersal range observed for the species and $D_{\max}$ is the maximum dispersal distance allowed. The average dispersal range is set at 70 km (Tittler et al. 2006), with $D_{\max}$ twice that of b to permit some larger dispersal movements that seemed reasonable for a migratory songbird. We standardized and weighted dispersal rates by K to add a density dependent component to dispersal. We assumed no dispersal mortality aside from that incorporated into the stage survival rates.

We used Monte Carlo iterations to induce parameter uncertainty and stochasticity in our population dynamics. We accounted for 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). Patterns in annual survival rates were correlated among subpopulations based on a negative exponential relationship with the distances among them (Bonnot et al. 2017). We based variances for these distributions on the amount of temporal variation empirically observed for survival or reproduction in the literature. 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.

We summarized the population responses of each species at multiple scales to understand the relative impacts of conservation strategies in each state given their circumstances and their approaches to defining COAs and how that contributed to species conservation across the region. We also compared populations on COAs to the rest of the state lands to assess the importance of COAs in state planning. For each simulation, we calculate changes in each population's habitat, size, and viability/risk across the entire region, in each state, and specifically on COAs. We quantified risk as the expected maximum decline that a population could expect to experience any time through 2100. It is calculated as the mean of the minimum population sizes from each of the 1,000 iterations. Therefore, it simultaneously conveys both our projections for population growth and our uncertainty in them.

RESULTS

Baseline scenario

Baseline projections of prairie warbler and wood thrush populations both showed overall declines in the regional population but varied in the nature and timing of those declines (Figure 3). We estimated an initial abundance of 1,526,758 adult female prairie warblers with a K of >1.7 million adults across the region. Based on K, habitat

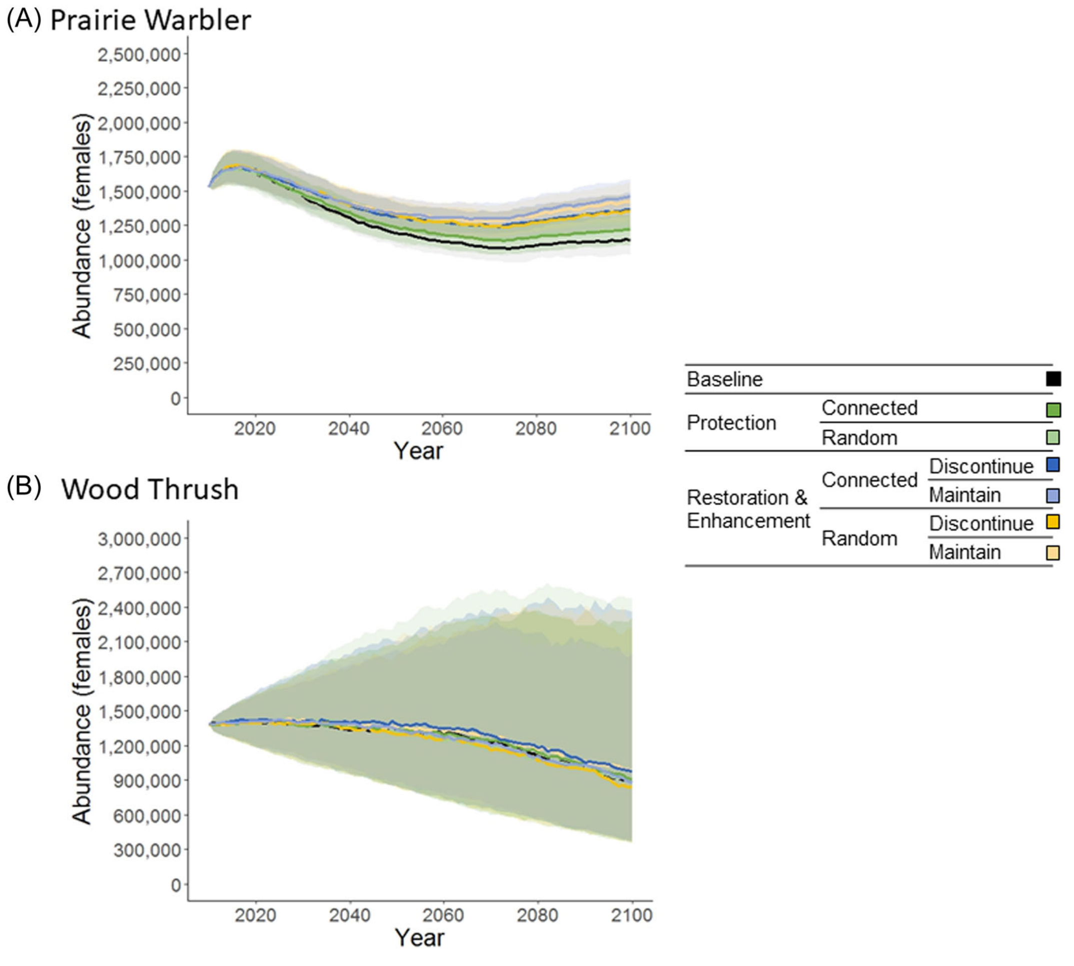

FIGURE 3 Projections of A) prairie warbler and B) wood thrush population growth 7 conservation simulations within Conservation Opportunity Areas (COAs) across the Gulf Coastal Plains and Ozarks region. A baseline simulation that considers climate and land-use change impacts on habitat is compared with simulations of conservation strategies. Conservation strategies reflected 2 different approaches: protection of high quality habitats from development or restoration and enhancement of low and moderate quality habitats. Conservation simulations also compared prioritization of connected patches within the landscapes or a random selection. Finally, restoration and enhancement simulations compared scenarios that maintained habitat management throughout the entire time period versus scenarios where habitat management on 50% of patches is discontinued.

declined across all states (see Figures S4 and S5 in Supporting Information). As a result, the regional population declined between 1% and 2% annually through midcentury. It reached its lowest predicted abundance of just over 1,000,000 females by 2075. However, after that point the prairie warbler population reversed those declines with marginal growth to finish at 1,143,600 females by 2100, a 25% decrease in the population. Following losses of prairie warbler habitat through the first half of the century, the reversal stemmed from climate-driven changes to the forest that began to increase habitat beyond 2075.

The pattern of loss for the regional wood thrush population contrasted that of prairie warblers. Beginning with an estimated initial population of 1,382,832 adult female wood thrush across the GCPO, we projected initially slight declines for the population. However, following midcentury the decline worsened resulting in a predicted abundance of 899,124 females by 2100, a 35% overall decline. For wood thrush, this decline was less related to habitat or K; we projected an increase in K from 11.4 million birds to >13 million over that time across all states. Rather, the negative growth was caused by declining productivity in these birds as urbanization, and as a result, fragmentation increased throughout the century (see Figure S6 in Supporting Information).

Conservation strategies

Prairie warbler

Conservation scenarios resulted in carrying capacities above the baseline scenario for all states except Texas (Supporting Information). Restoration and enhancement scenarios managed to increase habitat in Louisiana, Tennessee, Illinois, and Kentucky. Other states such as Alabama, Mississippi, and Missouri benefited from conservation scenarios but only to reduce declines in habitat. Restoration and enhancement strategies produced larger Ks than Protection strategies. Within restoration and enhancement, scenarios with discontinuation of habitat maintenance allowed for 5,000–20,000 less females across states than scenarios that maintained habitat. All increases in habitat above the baseline scenario were due to activities on COA lands as no conservation took place elsewhere in the states. Across approaches, scenarios that evaluated the prioritization of connectivity were similar and showed little difference in habitat.

When modeling population growth based on the changes in habitat, all states except for Florida, Louisiana, and Texas experienced population declines in the baseline scenario without conservation (Supplemental Information). The exceptions benefited from climate change impacts on habitat and relatively fewer impacts from projected urbanization. Except for Texas, all states with simulated conservation in COAs saw final population sizes above the baseline projections (Figure 4). The patterns in population growth and final abundance among scenarios followed those for habitat. Restoration and enhancement resulted in the highest final abundances across states. Under these scenarios we projected net growth on all state COAs, except Texas. Protection scenarios also reduced declines, but to a lesser degree. Maintaining restored and enhanced habitat also allowed more prairie warblers over time than if management discontinued. Finally, prioritizing connectivity did not have a noticeable effect.

In most cases the improved growth from conservation scenarios translated into improved viability of prairie warblers across the GCPO. Under the baseline scenario the expected maximum declines ranged from 10–90% across states (Figure 5). States where no conservation occurred, in addition to Texas, expected little change in risk of prairie warbler declines from the baseline. For most states we projected smaller expected maximum declines when restoring and enhancing habitat than when protecting habitat (Figure 5). Maintaining habitat also reduced expected declines of prairie warblers compared to discontinuing management. We did observe some contrary but explainable results that differed from these general patterns. For example, prairie warblers in Louisiana benefited the least from conservation scenarios in terms of viability, likely because of its low risk initially. Also, for prairie warbler populations in COAs in Tennessee, Mississippi, and Kentucky, expected maximum declines for protection scenarios were more similar to restoration and enhancement scenarios (Figure 5). Finally, patterns of risk for populations in Kentucky and Illinois were primarily driven by the actions in COAs, given the predominance of COA lands in those states' footprints.

Wood thrush

In general, we observed little impact of the different conservation strategies on wood thrush in the GCPO. Habitat for wood thrush increased under all conservation scenarios in a manner similar to the baseline (Supporting Information). Despite increasing K, we projected declining wood thrush abundances on all COA and state lands (Figure 3). The declines were only slightly smaller for the conservation scenarios and no patterns emerged among the scenarios. Ultimately, we estimated only small effects of scenarios on the wood thrush viability, providing slight

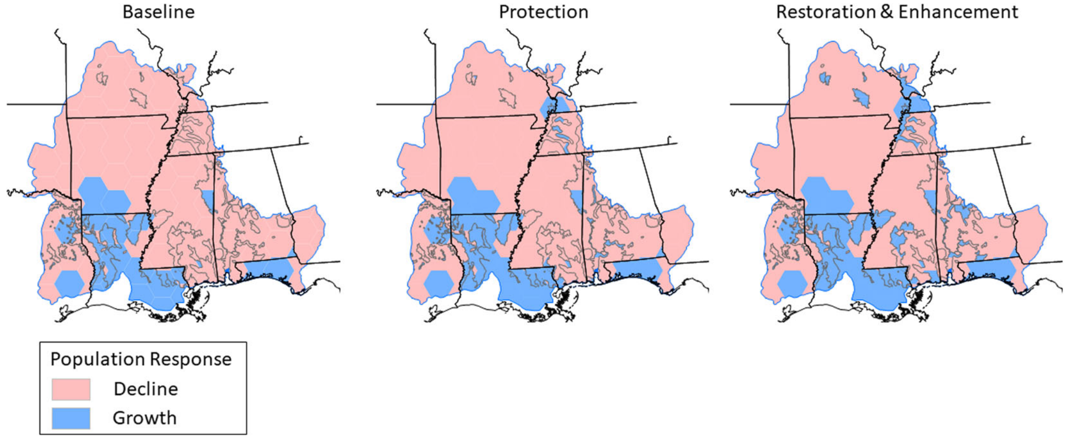

FIGURE 4 Spatial projections of population growth or decline from 2010—2100 by prairie warblers across the Gulf Coastal Plains and Ozarks region in response to landscape conservation strategies. A baseline simulation that considers climate and land-use change impacts on habitat is compared with simulations of conservation strategies across Conservation Opportunity Areas (COAs) by states across the region. Conservation strategies reflected protection of high quality habitats from development or restoration and enhancement of low and moderate quality habitats. The specific conservation simulations shown here also focused on connectivity within the landscapes and assumed habitat management is maintained throughout the entire time period.

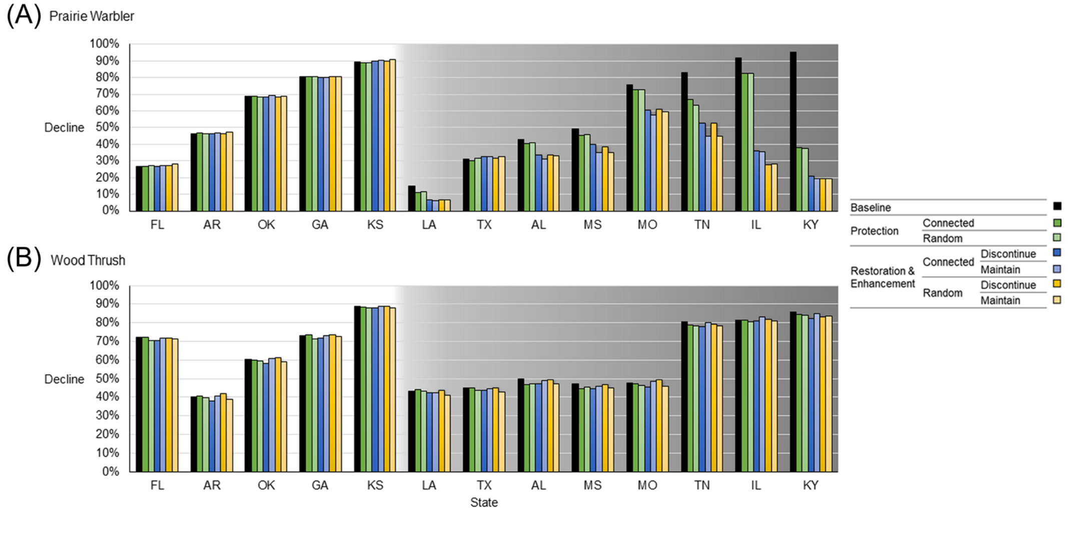

FIGURE 5 Estimated risk to state A) prairie warbler and B) wood thrush populations within the Gulf Coastal Plains and Ozarks region under baseline and conservation strategies. Habitat conservation was simulated within the Conservation Opportunity Areas (COAs) in 8 states (grouped with the gray background). Risk is quantified as expected (mean) maximum decline in each state for each species and reflects the most likely maximum decline each population could face through 2100. At the time of this study, 5 states had not designated COAs. Conservation strategies reflected 2 different approaches: protection of high quality habitats from development or restoration and enhancement of low and moderate quality habitats. Conservation simulations also compared prioritization of connected patches within the landscapes or a random selection. Finally, restoration and enhancement strategies also compared scenarios that maintained habitat management throughout the entire time period versus scenarios where habitat management on 50% of patches is discontinued.

reduction in the expected maximum declines that were consistent across the different scenarios (Figure 5). These small changes in risk were likely a result of protection and restoration efforts slowing the rate of fragmentation and productivity declines. Although conservation efforts in some Missouri and Kentucky COAs did reverse productivity declines, the remaining COAs experienced up to 12% reduction in relative productivity over time (Supporting Information).

DISCUSSION

Our application demonstrates the utility of decision support tools for designing and deciding strategies in LCD, which might address the research-implementation gap commonly noted in conservation planning (Adams et al. 2019, Coetzee and Gaston 2021). In our correspondence, SWAP coordinators were unsure of specific strategies or portfolios (combinations) of strategies for implementing conservation within COAs. However, they readily identified key questions they viewed as important to consider in their planning. Designing scenarios that address those questions and evaluating species' responses to them allowed us to assess the relative importance of those strategies and help formulate general principles that can guide planning. For example, scenarios to address connectivity among conservation lands as a strategy within COAs led to the realization that its importance is dependent on factors such as scale of planning and species of interest. We found little benefit to focusing on connectivity within COAs for migratory birds, but we realize this could be important for species with limited dispersal or when delineating COAs at a larger scale (e.g., regional or state level). Therefore, balancing connectivity with other conservation strategies, depending on species and contexts, may be wise (Hodgson et al. 2009). Additionally, scenarios related to private lands management reinforced support for restoration and active management on working lands even if those activities are only partially maintained across participants. Learning from these results could enable planners to begin developing informed visions for scenario development.

Our results also highlight the insight that can be obtained from impact evaluations at regional scales when attempting to coordinate the efforts of partners. States used a range of processes for defining COAs within their SWAPs which resulted in a range of sizes, shapes, and arrangements of COAs among states; from Missouri's smaller and targeted COAs to Louisiana's expansive and comprehensive approach. Whether these variations arose due to differences in goals or planning processes, the resulting suite of COAs provided an opportunistic evaluation of their impacts given background threats such as land use and climate change. For example, the relative effectiveness of restoration and enhancement versus protection approaches varied among states in a way that suggests the interaction between a state's process for deciding COAs and what urbanization threats they face could influence which conservation approach to consider. States that targeted landscapes with lower urbanization risk realized greater benefits from restoring and enhancing land versus protection. In contrast, states in which COAs were more at risk from urbanization saw benefits of protecting land that were similar to restoration. Graves et al. (2019) also suggested the importance of location when protecting public and working lands, such as through easements. We treated these strategies as mutually exclusive for learning purposes but, it is important to note that ultimately, plans that strategically combine both actions may be preferred, especially when also considering other factors such as cost (Van der Burg et al. 2018). Impact evaluation is increasingly viewed as critical to successful landscape conservation planning under future threats (Pressey et al. 2021). Our results demonstrate how decision and modeling tools that can represent important processes and their interactions will be key to understanding scenarios where no analogs are available.

The contrasts in scenario effectiveness among states sheds light on both the necessity and struggle facing regional efforts to understand and coordinate effective conservation across large scales (Baldwin et al. 2018). States have the freedom to carry out conservation within their means and objectives and in a way that accounts for financial resources and nonmonetary factors, such as stakeholder interests, system uncertainty, and complex governance structures (Wright et al. 2020). While independent and isolated efforts by states could limit the overall effectiveness at a regional scale for goals such as conserving a wildlife species of regional concern, it could be counterintuitively unifying to learn how each state can contribute to the overall regional success given their landscapes and programs. Every partner can have a role even if it is not the same role; they just need to be coordinated. It is, therefore, the challenge of regional partnerships to coordinate those roles, and DSPs like this one can help.

The scalability of this decision support process can be helpful for translating plans between regional and local scales. Within the same modeling framework, we were able to evaluate species and population responses regionally, by state, and even individual COA. This provided a measurable link between the specific population changes in managed landscapes and the regional viability of a species. Thus, we are able to see how the activities in a COA actively contribute to the larger regional population goals. We feel this scalability is beneficial for 2 reasons. First, it can help generate support among and for partners to identify how their actions can directly contribute to conservation goals. Second, it can help address the knowledge-implementation gap as the process and the scenarios it considers are spatially and temporally specific and mechanistic in nature, forcing specification of detailed activities over time that can then be rolled directly into planning. The ability to step large-scale strategies down to local scales has been identified as one of the main limitations in climate adaptation efforts (Ledee et al. 2020). To that end this process can also be used to understand how local adaptation actions can manifest at larger scales and longer time periods.

MANAGEMENT IMPLICATIONS

The responses of prairie warbler populations to conservation scenarios indicated that both approaches of protecting quality habitat from land-use change and restoring and enhancing lower quality and nonhabitat improved their viability at regional, statewide, and COA scales. However, we noted that the relative effectiveness of these 2 approaches varied among states in a way that suggests a state's process for deciding COA and what urbanization threats they face could influence which conservation approach to consider. We found that prioritizing connectivity when locating conservation within a COA was relatively unimportant for these 2 migratory birds. Also, our projections indicated that while prairie warbler populations responded best when restored habitat was maintained on restored private lands over the long term, even restoration without the guarantee of long-term management was beneficial. Finally, the lack of response by wood thrush populations to conservation scenarios indicated that projected declines would not be reversed unless efforts to reduce forest fragmentation within a landscape were focused and substantial.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

This study adhered to all relevant regulations. No animals were handled or affected in this study. No personal identifying information was collected in the questionnaire.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

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