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RESEARCH ARTICLE

Scenario planning and multispecies occupancy models reveal positive avian responses to restoration of afforested woodlands

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Scenario planning is a powerful approach for assessing restoration outcomes under alternative futures. However, developing plausible scenarios remains daunting in complex systems like ecological communities. Here, we used Bayesian multispecies occupancy modeling to develop scenarios to assess woodland restoration outcomes in afforested communities in seven wildlife management areas in Arkansas, U.S.A. Our objectives were (1) to define plausible woodland restoration and afforestation scenarios by quantifying historic ranges of variation in mean tree cover and tree cover heterogeneity from 1986 to 2021 and (2) to predict changes in bird species richness and occupancy patterns for six species of greatest conservation need under two future scenarios: complete afforestation (100% tree cover) and woodland restoration (based on remotely sensed historic tree cover). Using 35 years of remotely sensed tree cover data and 6 years of bird monitoring data, we developed multispecies occupancy models to predict future bird species richness and occupancy under the complete afforestation and woodland restoration scenarios. Between 1986 and 2021, tree cover increased in all study areas—with one increasing 70%. Under the woodland restoration scenario, avian species richness increased up to 20%, and four of six species of greatest conservation need exhibited gains in occupancy probability. The complete afforestation scenario had negligible effects on richness and occupancy. Overall, we found decreasing tree cover to historic levels prior to widespread afforestation would provide community-level benefits and would do little harm even to forest-dependent species of conservation concern. Applying multispecies occupancy modeling within a scenario planning framework allows for comparing multiscale trade-offs between plausible futures.

Key words: Bayesian hierarchical models, heterogeneity, historical range of variation, trade-off, uncertainty, woody plant encroachment

> **Implications for Practice**
>
> - Combining Bayesian multispecies occupancy modeling with scenario planning shows where restoration will do the least harm and most good.
> - Multispecies occupancy modeling using next-generation remote sensing datasets as inputs can create plausible alternative futures for scenario planning.

Introduction

Scenario planning is a powerful approach for assessing potential restoration outcomes "in the face of uncontrollable, irreducible uncertainty" (Peterson et al. 2003, p. 359). Scenario planning is defined as assessing the consequences of a management decision through multiple alternative futures (i.e. scenarios; Carpenter et al. 2006). Potential scenarios should be plausible and sufficiently disparate to encompass a wide range of uncertainty relative to the restoration intervention (Peterson et al. 2003). For example, decades of research have gone into developing climate change scenarios, such as representative concentration pathways, that encompass an enormous range of possibilities while also being grounded in rigorous data and modeling (O'Neill et al. 2020; IPCC 2022). However, developing plausible scenarios for local-scale restoration outcomes remains daunting due to large data requirements for estimating community responses to changes in environmental variables (Baer et al. 2004; Manning et al. 2006; Saab et al. 2022).

Advances in community-level modeling and next-generation remote sensing technologies are poised to overcome obstacles to

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applying scenario planning to restoration outcome assessment. Multispecies occupancy modeling is a flexible approach that estimates both community- and species-level relationships to environmental variables across multiple spatial scales (Dorazio & Royle 2005; Devarajan et al. 2020). Recent extensions of multispecies occupancy models to accommodate species interactions and spatial autocorrelation may provide improved insights on occurrence patterns of diverse communities across local to continental scales (Tobler et al. 2019; Doser et al. 2023). For predictor variable inputs into these models, new remote sensing datasets such as the Rangeland Analysis Platform (RAP) can provide historical ranges of variation in environmental variables (e.g. tree cover, herbaceous biomass, etc.) at fine spatiotemporal resolutions (30×30 m) at continental extents (Allred et al. 2021; Morford et al. 2022; Roberts et al. 2022). When restoration interventions rest on manipulation of environmental variables across multiple scales (e.g. patches to landscapes, species to communities), multispecies occupancy models can be used to weigh restoration trade-offs for communities containing species with divergent habitat requirements (D'Acunto et al. 2021; Romañach et al. 2022).

Restoration of woodlands experiencing afforestation is a prime avenue for testing the use of multispecies occupancy models within a scenario planning framework. Woodland ecosystems are diverse and consist of both forest-dependent species and open habitat-dependent species (Roach et al. 2019). Afforestation, also known as "woody plant encroachment" in grassland or rangeland systems, is a global phenomenon causing declines in woodland- and open habitat-dependent species (Soulé et al. 2003; Archer et al. 2017; Gómez-González et al. 2020), and in response, land managers increasingly mount woodland restoration actions like mechanical tree removal and prescribed burning (Vander Yacht et al. 2016; Bassett et al. 2020; Roberts et al. 2022). However, woodland restoration based on habitat requirements of one or a few focal species often produces mixed results across scales or trade-offs for multiple species of greatest conservation need (Roach et al. 2019). For example, woodland restoration outcomes for vegetation communities differ strongly across soil types and ecological site potentials (Scholtz et al. 2021; Fick et al. 2022). Likewise, tree removal to improve sage-grouse (*Centrocercus urophasianus*) habitat in North America may cause corresponding decreases in imperiled Pinyon Jay (*Gymnorhinus cyanocephalus*) that require tree cover (Reinhardt et al. 2022; Tack et al. 2022). Previous applications of comparing alternative futures show promise, as demonstrated by Bonnot et al. (2013), where strategic conservation planning models resulted in larger populations and viability of both a woodland obligate and a forest obligate. Additionally, woodland and forested habitats are well-known alternative regimes (Staver et al. 2011) allowing for a robust development of plausible alternative futures. The use of multispecies occupancy models within a scenario planning framework will provide both species-level and community-level assessments of potential restoration outcomes, ultimately yielding a more holistic approach to understanding woodland restoration outcomes in afforested ecosystems.

Here, we assess the application of multispecies occupancy models within a scenario planning framework for comparing potential restoration outcomes, using woodland restoration in afforested systems as a model situation. Our objectives are twofold: (1) to define plausible woodland restoration and afforestation scenarios by quantifying historic ranges of variation in mean tree cover and tree cover heterogeneity from 1986 to 2021, and (2) to predict changes in (i) occupancy patterns for species of greatest conservation need and (ii) bird species richness under complete afforestation (i.e. 100% tree coverage) and woodland restoration scenarios (i.e. historic conditions). We set our study in a context that is generalizable for woodland restoration efforts in temperate ecoregions: we used data from seven wildlife management areas distributed across multiple ecoregions in Arkansas, U.S.A., where natural resource agencies are currently conducting woodland restoration work and interested in prioritizing conservation efforts and assessing potential consequences of woodland restoration for forest-dependent species.

Methods

Study Area

The seven wildlife management areas (Table S1) in this study are distributed across five ecoregions derived from the U.S. Environmental Protection Agency Level III Ecoregions: the Ozark Highlands, the Arkansas Valley, the Boston Mountains, the South Central Plains, and the Mississippi Alluvial Plains (Omernik & Griffith 2014). The Ozark Highlands Ecoregion is dominated by woodland and forest. Primary land uses are logging, housing, recreation, poultry, and livestock farming. The Arkansas Valley Ecoregion lies between the Ozark and Ouachita Mountains regions and is largely characterized by plains, hills, floodplains, terraces, and scattered mountains, on top of sandstone, shale, and siltstone bedrock. While originally a mix of forest, woodland, deciduous forest, and floodplains, many of the areas have since been cleared for pastureland, hayland, poultry, and livestock farming. The Boston Mountain Ecoregion of northwest Arkansas consists of oak–hickory and oak–hickory–pine forests. The South Central Plains Ecoregion is comprised of oak–hickory–pine forests and bottomland hardwood forests. The Mississippi Alluvial Plains Ecoregion runs north–south across almost the entire length of eastern Arkansas. The region contains emergent wetlands, swamps, and other poorly drained woodlands.

Data Collection

Environmental Variables. To quantify historic ranges of tree cover and derive predictor variables for multispecies occupancy models, we used the RAP dataset version 3.0 (Allred et al. 2021). RAP estimates subpixel (30×30 m or 900 m^2) percent cover of multiple vegetation functional groups on a yearly basis starting in 1986 and is updated annually (Jones et al. 2018). We reemphasize that we define "historic ranges of tree cover" as tree cover between 1986 and 2021 and that these

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data do not reflect "optimal" or "natural" states of our study areas (e.g. pre-European colonizer disturbance). Because tree cover and herbaceous cover are the key state variables for woodland versus forest alternative states (Staver et al. 2011), we used the RAP's tree cover and perennial forb and grass cover (hereafter "perennial herbaceous cover") data (Allred et al. 2021). We calculated mean percent tree and perennial herbaceous cover and tree and perennial herbaceous cover heterogeneity (standard deviation) at local (50×50 m or $2{,}500$ m^2) and broad (500×500 m or $250{,}000$ m^2) scales.

To account for patch-scale variation in avian species-specific occupancy probabilities, we used elevation and aspect derived from the U.S. Geological Survey's national elevation data layer (Gesch et al. 2002). We checked for correlations (Pearson coefficient $\geq |0.7|$) between all predictor variables prior to modeling. All environmental data extractions and calculations were performed on Google Earth Engine (Gorelick et al. 2017).

Bird Data. *Bird Community Data.* In each wildlife management area (Table S1), Arkansas Game & Fish Commission selected two sites for woodland restoration based on perceived restoration need and logistical constraints (e.g. accessibility for timber harvest, fire risk), and the Commission selected an untreated "control" site. Bird surveys were then conducted within each site: six survey points were distributed in a grid, at a minimum of 250 m apart. Therefore, each wildlife management area had 18 bird survey points (1 wildlife management area $\times$ 3 sites $\times$ 6 survey points $=$ 18). Forest treatments, which all had the goal of restoring woodland-like habitat, began in 2011 and continued throughout the study. Data on exact dates and types of treatments was incomplete and therefore not used in this analysis, but treatment types included prescribed fire, tree thinning via mechanical removal, and chemical injection of trees.

Bird surveys were conducted during the breeding season between 15 May and 30 July from 2016 to 2021. Surveys began 15 minutes after sunrise and concluded for the day by 4.5 hours after sunrise (Robbins 1981). Upon arriving at each point, the surveyor waited 2 minutes and then recorded all birds seen or heard up to a distance of 100 m for 10 minutes. To account for variation in detection probability, observer name, wind speed, sky cover, precipitation, temperature, date, and start times were recorded for each point. Within each year a given wildlife management area was surveyed, all 18 points were surveyed twice.

To identify "species of greatest conservation need," we used the two most recent (2011 and 2020) species of greatest conservation concern lists from the Arkansas State Wildlife Action Plan (Arkansas Game & Fish Commission 2020; Table S2).

Quantify Trends in Tree Cover in Wildlife Management Areas

Using the RAP's cover data, we used Google Earth Engine's reducer algorithms to calculate mean tree cover and tree cover heterogeneity (standard deviation of tree cover) across all 900 m^2 (30×30 m) pixels within each conservation area for each year from 1986 to 2021. We then developed separate generalized additive models (Wood 2006) for each conservation area to quantify trends in tree cover. For the generalized additive models, we set mean tree cover and standard deviation in tree cover as response variables, and we set time (year) as a thin-plate spline smoothed predictor variable (Wood & Wood 2015).

Predict Changes in Bird Communities Under Complete Afforestation and Woodland Restoration Scenarios

Estimate Bird Community Occupancy and Richness. We used a multispecies occupancy model to determine species-specific relationships between landscape and vegetation covariates for predicting richness and occupancy under future scenarios. Multispecies occupancy models estimate species-specific occupancy probabilities while accounting for imperfect detection of species (Dorazio & Royle 2005). Species-specific effects are treated as random effects arising from a common community-level distribution, which allows for inference of management effects on both individual species and overall communities (Zipkin et al. 2010). This hierarchical approach has been shown to provide more precise occupancy estimates of rare species as well as more precise estimates of species richness that explicitly account for imperfect detection (Zipkin et al. 2010). To avoid model convergence issues, we only used species that were observed in ≥2.5% of the surveys. Across all wildlife management areas combined, we recorded 89 species; per our ≥2.5% cut-off, we included 47 species in our models. We fit Bayesian multispecies occupancy models using Markov chain Monte Carlo via the spOccupancy package in R (Doser et al. 2022; R Core Team 2022). Because our goal was to make plausible and generalizable scenarios, we included data from all wildlife management areas in a single model.

We used the widely applicable information criterion (Watanabe 2010) to determine the most supported landscape and vegetation cover predictors of bird occupancy patterns among a set of fixed effect candidate models (Table S3). The variables we considered in the candidate model set were elevation, aspect, mean perennial herbaceous cover at 250,000 m^2, standard deviation of tree cover at 250,000 m^2, mean tree cover at 2,500 m^2, and mean tree cover at 250,000 m^2. We explored linear and quadratic effects of all variables except aspect, which we only allowed to have a linear effect.

To account for temporal and spatial autocorrelation in the ecological process, we created a nested random effect, with "site" nested in wildlife management area, nested in year. These random effects also accounted for differences in treatment histories across sites despite the lack of treatment history information. To account for variation in detection probability across space and surveys, we used wind speed code (Beaufort scale), date, and temperature as fixed-effect predictors, and we allowed intercept to vary by observer identity. We used vague priors (normal distribution, mean $=$ 0, variance $=$ 2.72) for all parameters following standard recommendations (Broms et al. 2016; Doser et al. 2022). For each candidate model, we ran three chains with 200,000 iterations, allowing 100,000 burn-in iterations with a thinning rate of 10, resulting in a total of 10,000 posterior samples. After we determined the top model, we conducted a

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posterior predictive check to assess model fit, and we summarized results of the check using Bayesian *p*-values (Hobbs & Hooten 2015).

Using the top model, we predicted total bird species richness and occupancy patterns for species of greatest conservation need for each conservation area. Although all observed species' ranges included all wildlife management areas, not all species were observed in all wildlife management areas. Therefore, we took a conservative approach and did not include species in richness or occupancy predictions for a given conservation area if they had not been observed there at least once. We set all random effects to their average value (zero) and predicted richness and occupancy across 250,000 m^2 (500 × 500 m) grid cells in our study area using the full posterior distributions from the Bayesian model. We qualitatively compared landscape (wildlife management area) versus patch (pixels) scales by mapping the predicted richness for two example wildlife management areas.

Predict Bird Community Responses Under Future Scenarios. We created two future scenarios to assess bird community responses. The first was a heterogeneous woodland restoration scenario based on historic tree cover data, and the second was a complete afforestation scenario. For the heterogeneous woodland restoration scenario, we used the tree and perennial herbaceous cover that occurred in 1986 (prior to afforestation; Turner et al. 2003). For the complete afforestation scenario, we increased tree cover across all wildlife management areas at all scales to 100% and decreased perennial herbaceous cover at all scales to 0%. Because we observed tree cover up to 100% in many locations across wildlife management areas, this is a plausible scenario, albeit unlikely given random disturbances such as wind falls, fire, etc. would probably make tree cover less than 100% at any given time. However, this complete afforestation scenario aligns with the purpose of scenario planning by providing an extreme, but plausible, future (Peterson et al. 2003).

Results

Quantify Trends in Tree Cover in Wildlife Management Areas

Tree cover increased across all wildlife management areas from 1986 to 2021 (Fig. 1). In 1986, mean tree cover ranged from 36 to 71%. Tree cover increased rapidly from 1986 to 2000 and slowed around 2000 for most wildlife management areas. By 2021, mean tree cover ranged from 62 to 91%. Cut-Off Creek and Harold E Alexander wildlife management areas showed initial dips in mean tree cover in the early 1990s but increased similarly to other wildlife management areas by 2021 above their initial start in 1986.

Variation in tree cover, as measured by the standard deviation of tree cover across all 900 m^2 pixels, decreased in six out of the seven wildlife management areas. Cut-off Creek, Gulf Mountain, and Gene Rush wildlife management areas shared similar rates of gradual and consistent decline. St. Francis Sunken Lands does not follow the declining trend but appears to increase with oscillating peaks and valleys. Harold E Alexander, Wattensaw, and Petit Jean showed a similar trend dip in 2008 followed by a rebound to values slightly less than the original standard deviation in 1986.

Predict Changes in Bird Communities Under Complete Afforestation and Woodland Restoration Scenarios

Model selection revealed that mean tree cover at 2,500 m^2 and mean tree cover at 250,000 m^2 best explained bird community occurrence patterns among our candidate models (Table S4). The Bayesian *p*-value for the overall model was 0.498, indicating a good model fit (Table S5).

Species of Greatest Conservation Need. Our six species of greatest conservation need exhibited idiosyncratic responses to complete afforestation and woodland restoration scenarios (Table S2; Fig. 2). Overall, we detected little change in occupancy probability under the complete afforestation scenario, although Eastern Towhee (*Pipilo erythrophthalmus*) and Hooded Warbler (*Setophaga citrina*) appeared to benefit slightly. In contrast, the woodland restoration scenario produced responses in four out of our six species of greatest conservation need. Under woodland restoration, Hooded Warbler occupancy declined slightly in some wildlife management areas (as much as −12% in St. Francis Sunken Lands), while Kentucky Warbler (*Geothlypis formosa*), Prairie Warbler (*Setophaga discolor*), and Prothonotary Warbler (*Protonotaria citrea*) occupancy probability increased up to +73% (Gulf Mountain), +147% (Gulf Mountain), and +17% (Cut Off Creek), respectively (Fig. 2).

Richness. Wildlife mean species richness responses to complete afforestation and woodland restoration scenarios were less idiosyncratic than individual species' responses, but differences still emerged (Fig. 3). Compared to current conditions, mean species richness changed little under the complete afforestation scenario, ranging from a −0.54 decline in richness to a +0.48 increase in richness. But notably, under the complete afforestation scenario, variation in species richness denoted by the width of 50 and 95% quantiles decreased in all wildlife management areas. In contrast, under the woodland restoration scenario, mean species richness increased in six out of the seven wildlife management areas, with three wildlife management areas gaining more than two species on average and one wildlife management area gaining more than five species. Variation in richness also declined under the woodland restoration scenario but less than in the afforestation scenario.

Locations that could most benefit under woodland restoration scenarios emerged when we mapped predicted richness across two wildlife management areas with divergent responses to conservation scenarios (Fig. 4). In the Gene Rush wildlife management area, portions in the north-central and east-central of the conservation area had higher richness than under woodland restoration relative to current conditions and the complete afforestation scenario, whereas the western and southeastern portions had similar richness regardless of conservation scenario. In the

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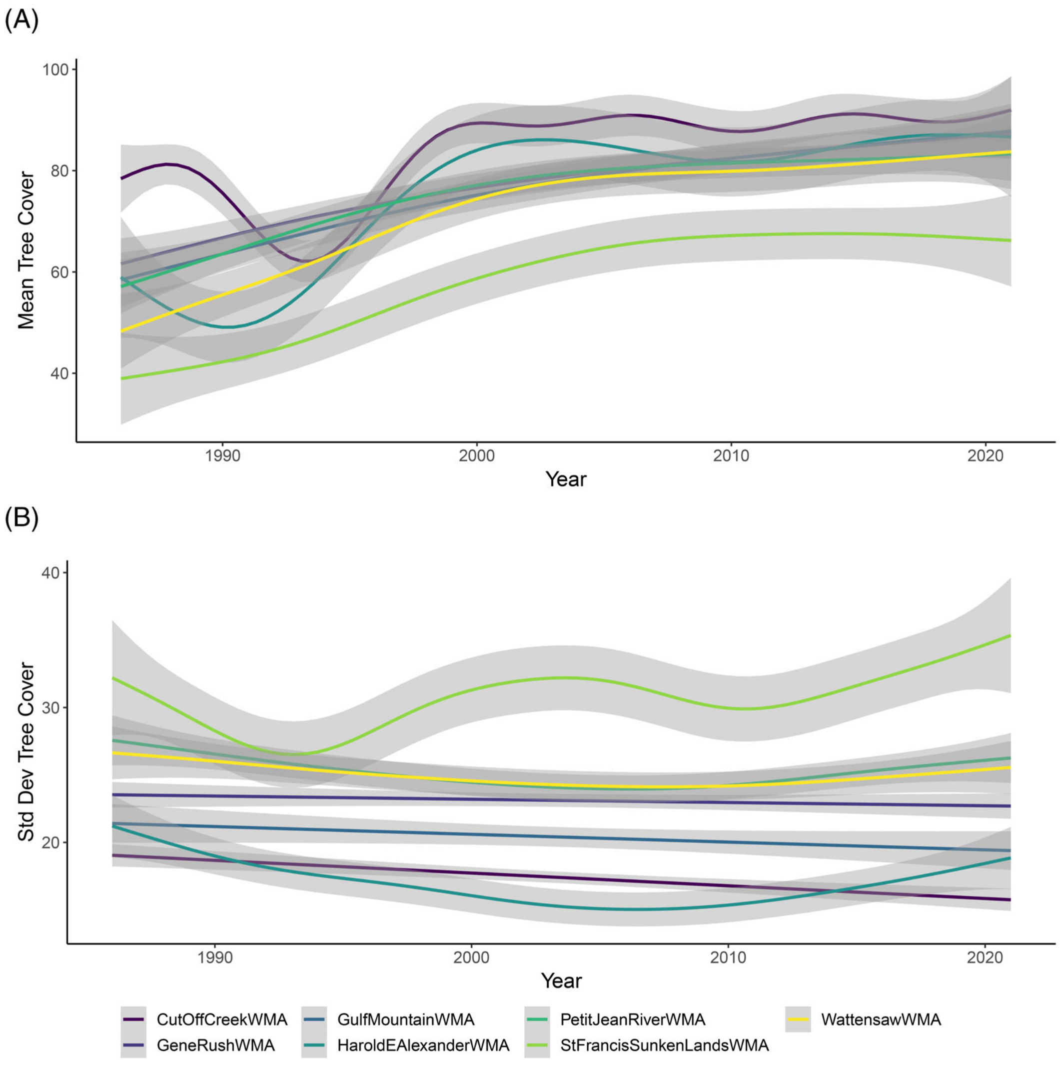

Figure 1. Mean (A) and standard deviation (B) of tree cover from 1986 to 2021 in seven wildlife management areas in Arkansas, U.S.A. Colored lines indicate predicted trends from generalized additive models in different wildlife management areas, and gray ribbons indicate 95% CI.

Mike Freeze Wattensaw wildlife management area, richness under the woodland restoration scenario was similar to current conditions, and complete afforestation had minor—but uniform—increases in richness across the conservation area.

Discussion

Decreasing overall tree cover and increasing tree cover heterogeneity to simulate historic woodland-like conditions provided community-level benefits and predicted little harm even to forest-dependent species of conservation concern. Our results revealed positive community-level responses to the woodland restoration scenario in six out of seven wildlife management areas, with avian species richness predicted to increase up to 20%. Additionally, although three out of our six species of conservation concern are forest-dependent species (Hooded Warbler, Kentucky Warbler, and Prothonotary Warbler), none of them demonstrated significant negative responses to woodland restoration. Given that local (2,500 m^2) tree cover was important in our model, our findings suggest relatively small-scale woodland restoration will have some positive effects on woodland-dependent species' presence and community-level richness. This is all the more striking given that wildlife management areas varied in elevation and precipitation, were distributed across five ecoregions, and had widely different historical tree cover ranges. Our findings are in line with past research that heterogeneity increases avian diversity in both open habitat and forest communities (Fuhlendorf et al. 2006; Mabry et al. 2010; Vander Yacht et al. 2016).

Basing management decisions on individual species' needs is inconsistent with best practices for managing systems with low certainty and low controllability (Peterson et al. 2003), such as ecosystems experiencing woody plant encroachment (Archer et al. 2017). As an example from our study, topographic factors complicated individual species' responses to both woodland restoration and complete afforestation. More narrowly, even our

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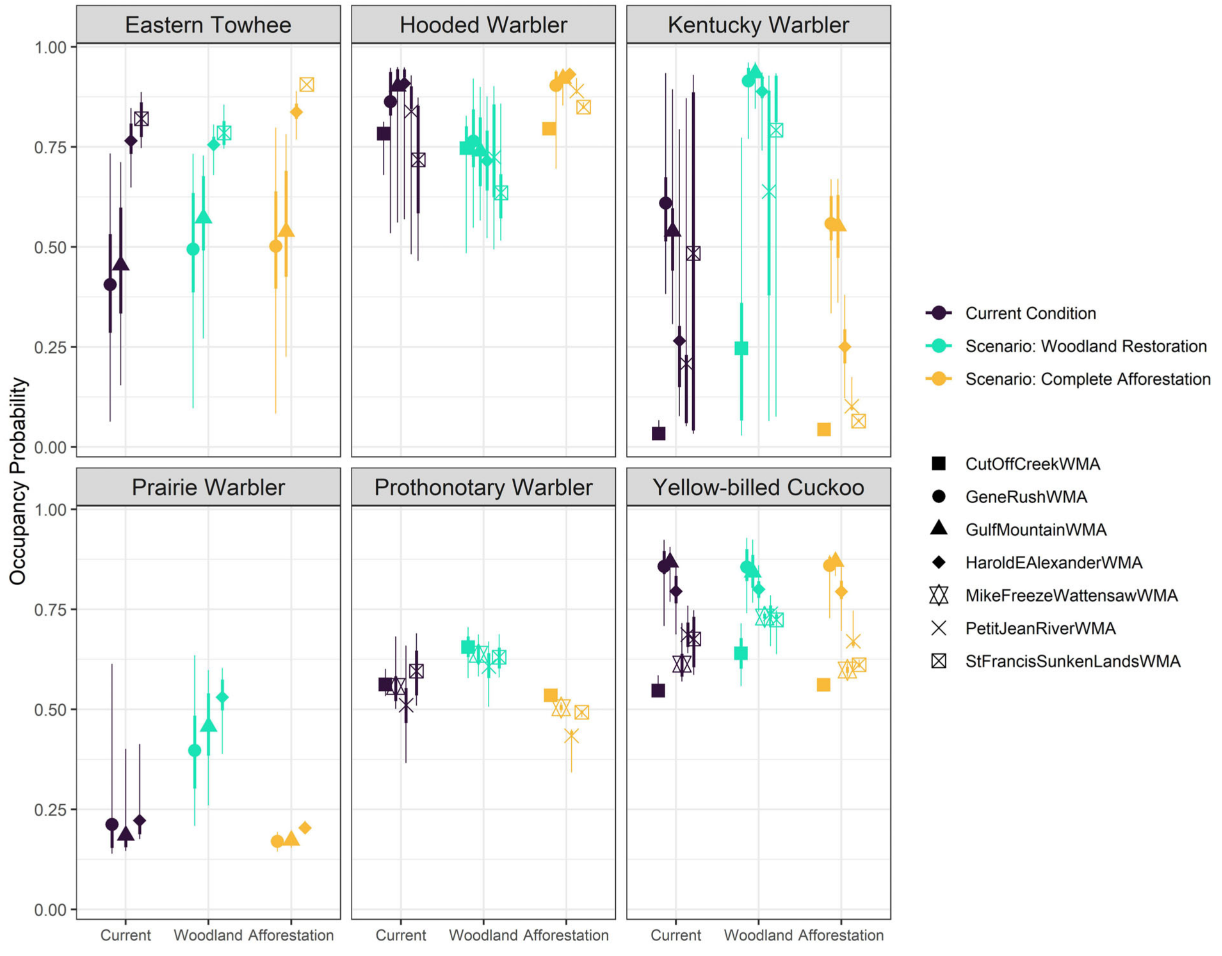

Figure 2. Probability of occupancy for six species of greatest conservation concern under current conditions and two different conservation scenarios across seven wildlife management areas in Arkansas, U.S.A. Shapes indicate mean occupancy probability across all 500 × 500 m pixels in different wildlife management areas. Vertical lines represent variation in occupancy probability across all 500 × 500 m pixels within each conservation area: thick vertical lines indicate 50% quantiles and thin vertical lines indicate 95% quantiles. Colors indicate scenario identity.

six species of greatest conservation need require four different nesting substrates: two are ground nesters (Eastern Towhee and Kentucky Warbler), two are shrub nesters (Hooded Warbler and Prairie Warbler), one is a cavity nester (Prothonotary Warbler), and the last is a tree nester (Yellow-billed Cuckoo). This means management that optimizes habitat for any one species—or any one functional group—will likely have unexpected impacts on the others (Catford et al. 2021). As with any disturbance, woodland restoration can favor some species and not others in terms of species' abundances (Roach et al. 2019). These complexities can overcomplicate decision-making and lead to management paralysis (Keith et al. 2011). Despite this, current laws, policies, and management frameworks tend to encourage species-specific strategies and research while providing few or no incentives for community-level management (Simberloff 1998; Hiers et al. 2016; Angeler et al. 2020).

We showcase how applying multispecies occupancy modeling can help overcome species-centric decision-making by modeling wildlife–environmental relationships at multiple ecological scales (species and communities) and multiple spatial scales (e.g. patches and landscapes) simultaneously. An example of this in our results is the variation in magnitude of the changes in richness within and between landscape and patch scales under the woodland restoration scenario. For example, in one of our wildlife management areas, changes in patch-scale richness between the current and woodland restoration scenario are predicted to range between 10 species gained and 1 species lost. Similarly, patch-scale responses to the afforestation scenario varied from two species gained to seven species lost. Comparing which patches are predicted to gain the most species from woodland restoration and which will lose the least (or gain the most) from afforestation is a strong potential strategy for netting gains in species richness across landscapes. This ability of multispecies modeling represents an advancement over individually modeling species responses to potential conservation scenarios, especially when a limited number of state variables (e.g. tree cover, water depth, management techniques) drive community-wide responses (Zipkin et al. 2010).

Our results echo afforestation and tree invasion literature that hypothesize a threshold for tree cover impacts on avian

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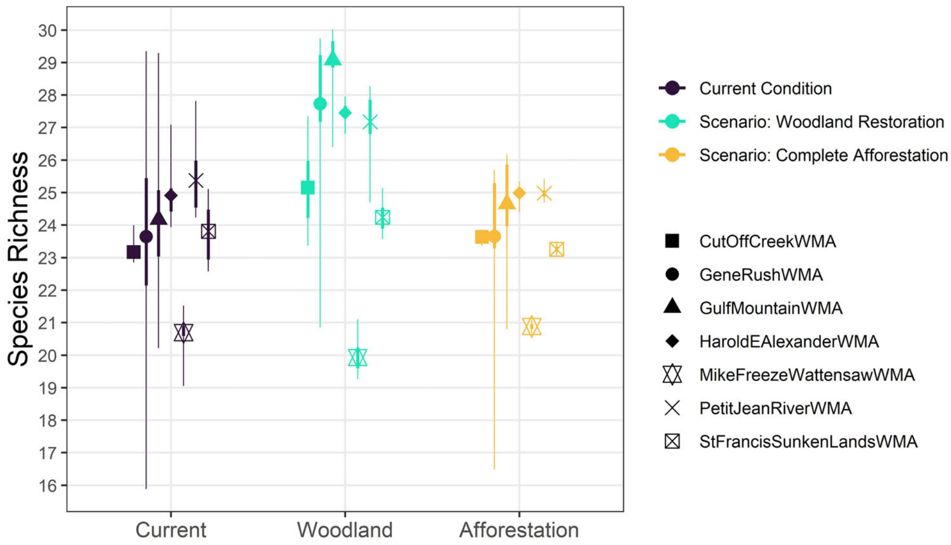

Figure 3. Predicted species richness under current conditions and two different conservation scenarios across seven wildlife management areas in Arkansas, U.S.A. Shapes indicate mean species richness across all 500 × 500 m pixels in different wildlife management areas. Vertical lines represent variation in richness across all 500 × 500 m pixels within each conservation area: thick vertical lines indicate 50% quantiles and thin vertical lines indicate 95% quantiles. Colors indicate scenario identity.

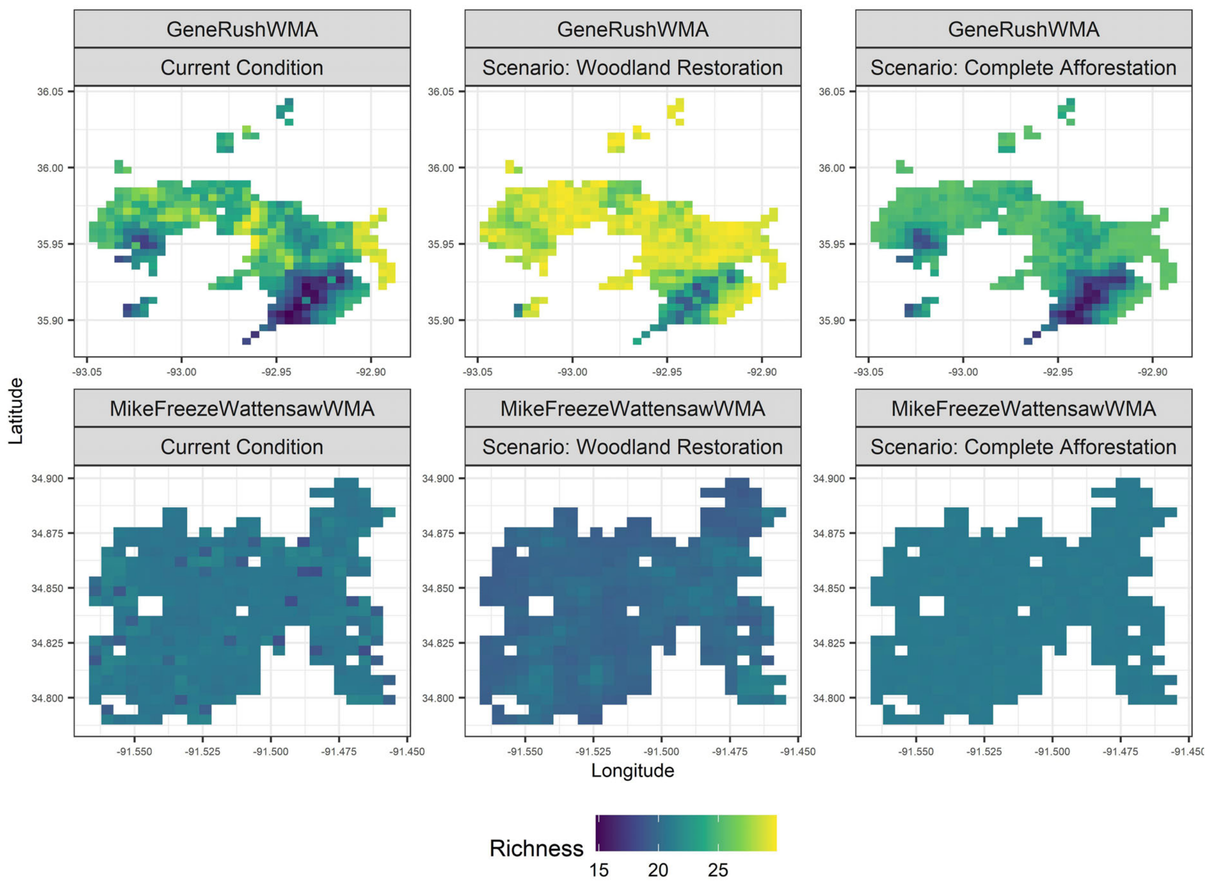

Figure 4. Maps of predicted species richness in two wildlife management areas under current conditions and two different conservation scenarios in Arkansas, U.S.A. These two example wildlife management areas demonstrate divergent biodiversity outcomes of conservation scenarios. Pixels are 500 × 500 m.

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communities. Grant et al. (2004) found as little as 25% tree cover can deter avian grassland species. Across multiple spatial scales, grassland species are strongly averse to afforestation and respond positively to tree removal (Cunningham & Johnson 2006; Thompson et al. 2014). In our study, this tree cover threshold appears to already have been surpassed. Both individual species' occupancies and community richness exhibited negligible changes between the current levels of afforestation (ranging from 62 to 91% mean tree cover in 2021) and the complete afforestation scenario (100% mean tree cover). This means management actions ranging from maintaining current levels of tree cover to permitting complete afforestation will likely retain species occupancy and richness at current levels. Forest-dependent species will continue to dominate, and woodland-dependent species will remain rare.

Importantly, our models and scenarios do not account for lagged or very broad-scale effects that could lead to significant changes in avian communities. For instance, our scenarios cannot predict lagged extinction debt that complete afforestation could lead to, particularly in woodland-dependent species whose habitat would disappear under complete afforestation (Mabry et al. 2010). Conversely, species that require large, unbroken tracts of tree cover could experience population gains or newly colonize completely afforested areas (Bonnot et al. 2013). And clearly, our scenarios do not consider global-scale change drivers such as climate change that could create synergisms or antagonisms with afforestation or woodland restoration (Archer et al. 2017; García Criado et al. 2020). However, because land managers tend to make decisions at the scale of the lands they manage (e.g. wildlife management areas; Arkansas Game & Fish Commission 2020), our results are relevant and applicable at local to landscape spatial scales.

Applying multispecies occupancy modeling within a scenario planning framework allowed us to compare trade-offs between two extreme (but plausible) futures—landscape-scale restoration of a historically derived woodland ecosystem or complete afforestation. For avian communities in afforested eastern North American systems, we show the trade-offs are minimal. Gains in woodland-dependent species will likely have a broader-scale benefit that outweighs potential losses in forest-dependent species (Davis et al. 2000; Vander Yacht et al. 2016; Roberts et al. 2022). This is further supported by the fact that, globally, losses in woodland- and open habitat-dependent species dwarf losses in forest-dependent species (Newbold et al. 2016), particularly in North America (Rosenberg et al. 2019).

But in thornier situations where trade-offs are more complicated, scenario planning supported by rigorous multispecies modeling will serve all the better. Examples of such situations range from when managers juggle multiple imperiled species with disparate habitat requirements (Tack et al. 2022) to where managers must weigh competing needs of stakeholders versus species (Romañach et al. 2022). By examining multiple potential futures resulting from divergent choices, scenario planning via multispecies modeling can provide essential information for decision-makers on where interventions can do the most good and least harm (Bonnot et al. 2013). This approach will be increasingly useful as more species become imperiled and as human demands on natural resources climb.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. The seven conservation priority areas sampled, their respective locations, and their area in hectares.

Table S2. The common name, scientific name, four-letter species code, major habitat association, nesting substrate category, and species of greatest conservation need (SGCN) status of each bird included in the model.

Table S3. Candidate model table showing the model name, and the variables included of models we used to explain the relationships between avian communities in the restored WMAs.

Table S4. Model rankings from model selection based on widely applicable information criterion.

Table S5. Bayesian *p*-values for species- and community-levels from the multispecies occupancy model using a chi-squared fit statistic.

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