Landscape Ecol (2017) 32:1433–1446
DOI 10.1007/s10980-016-0463-x

RESEARCH ARTICLE

Bird response to future climate and forest management focused on mitigating climate change

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Received: 21 January 2016 / Accepted: 31 October 2016 / Published online: 18 November 2016

Abstract

Context Global temperatures are projected to increase and affect forests and wildlife populations. Forest management can potentially mitigate climate-induced changes through promoting carbon sequestration, forest resilience, and facilitated change.

Objectives We modeled direct and indirect effects of climate change on avian abundance through changes in forest landscapes and assessed impacts on bird abundances of forest management strategies designed to mitigate climate change effects.

Methods We coupled a Bayesian hierarchical model with a spatially explicit landscape simulation model (LANDIS PRO) to predict avian relative abundance. We considered multiple climate scenarios and forest management scenarios focused on carbon sequestration, forest resilience, and facilitated change over 100 years.

Results Management had a greater impact on avian abundance (almost 50% change under some scenarios) than climate (<3% change) and only early successional and coniferous forest showed significant change in percent cover across time. The northern bobwhite was the only species that changed in abundance due to climate-induced changes in vegetation. Northern bobwhite, prairie warbler, and blue-winged warbler generally increased in response to warming temperatures but prairie warbler exhibited a non-linear response and began to decline as summer maximum temperatures exceeded 36 °C at the end of the century.

Conclusion Linking empirical models with process-based landscape change models can be an effective way to predict climate change and management impacts on wildlife, but time frames greater than 100 years may be required to see climate related effects. We suggest that future research carefully consider species-specific effects and interactions between management and climate.

Keywords Avian abundance · Climate change · Forest management · Empirical model · Ecosystem process based model · Forest landscape change model

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Electronic supplementary material The online version of this article (doi:10.1007/s10980-016-0463-x) contains supplementary material, which is available to authorized users.

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Introduction

Climate change has the potential to alter ecosystem structure and function and have significant global and regional impacts to both vegetation and wildlife (Matthews et al. 2011; Grimm et al. 2013a, b). Wildlife populations are already experiencing pressures from human-induced changes to the landscape through habitat degradation, fragmentation, and loss (Yahner 2000; Benítez-López et al. 2010; Sih et al. 2011; Wade et al. 2013). It is likely that the direct and indirect effects of climate change will only compound these landscape-level habitat pressures (Stralberg et al. 2009; Matthews et al. 2011; Auer and Martin 2013; Ferger et al. 2014). Significant changes are expected over the next 100–300 years in tree species distributions and forest composition due to climate change and this could have cascading effects on wildlife (Iverson et al. 2008; Rodenhouse et al. 2008; Matthews et al. 2011; Wang et al. 2015).

Birds worldwide are particularly vulnerable to climate change and we may lose 100–500 species for every degree Celsius increase in temperature (Sekercioglu et al. 2008), which is alarming considering global temperatures are expected to increase by 1–6 °C by the end of the century (IPCC 2007). Langham et al. (2015) predicted just over 300 bird species in North America may lose half their ranges due to direct effects of climate change and others have predicted habitat changes for bird species across the eastern U.S. due to indirect effects from climate-induced changes to forest ecosystems (Rodenhouse et al. 2008; Matthews et al. 2011).

Scientists have suggested numerous ecosystem management strategies to adapt to or mitigate the effects of future changes to climate (Dale et al. 2000; Millar et al. 2007; Evans and Perschel 2009). The three most prevalent forest management strategies are carbon sequestration, resilience, and facilitated change (Millar et al. 2007; Lawler 2009). Managing forests to sequester carbon in either live wood or forest products can potentially mitigate carbon emissions and reduce climate change. Managing for resilience promotes a forest's ability to rebound from disturbance. Facilitated change is management actions to transition a forest to a future state, such as a change in species composition, better suited to future climate. Until recently, these strategies have been abstract ideas, but scientists are now translating these ideas into management practices (Janowiak et al. 2014) and evaluating them with landscape models (Schneiderman 2015). Furthermore, management actions are likely to have a larger impact than climate change on forest dynamics in the next 100 years (Wang et al. 2015).

Few studies have addressed both direct and indirect effects of climate change, let alone incorporating the effects of management on species distributions and abundance (Chapman et al. 2014). Potential changes in species distributions are traditionally predicted using bioclimatic envelope models (Lawler et al. 2009; Rodenhouse et al. 2009), decision trees (Iverson et al. 2005; Rodenhouse et al. 2009; Matthews et al. 2011), or population viability analysis (McRae et al. 2008). Often these species distribution models are limited to climatic variables, do not consider underlying mechanisms, or are difficult to validate (Araújo and Peterson 2012). However, recent efforts have addressed some of the limitations of niche models (Iverson et al. 2011). We suggest that linking empirical models of wildlife abundance to process-based landscape change and climate models is a more mechanistic approach to understanding wildlife responses that addresses some of the limitations associated with species distribution models.

Our objective was to couple an empirical model that predicted bird abundance with a process-based model that simulated forest landscape change to assess the direct and indirect effects of climate change and management focused on mitigating climate change on avian abundance. We predicted the response of five bird species to four climate scenarios and three forest management scenarios focused on carbon sequestration, forest resilience, and facilitated change (i.e., no harvest, uneven-aged, and even-aged management, respectively) in the Missouri Ozark Highlands 100 years into the future. We expected management to have a greater effect than climate on forest change, even-aged management would facilitate change at a greater rate than uneven-aged management, and no harvest would sequester the most carbon. We hypothesized that management plays a greater role in determining bird abundance, but that climate will affect avian species abundance through direct temperature effects as well as indirectly through climate-induced changes in vegetation. We also predicted that avian species already vulnerable to direct effects of climate are more likely to experience indirect effects associated with climate-induced vegetation changes. Our approach focused on climate and management effects on forest landscape change through impacts on tree species establishment, growth, survival, and dispersal and did not explicitly consider climate related impacts from factors such as changes in disturbance regimes or invasive species or other interspecific interactions.

Methods

Study area

The study region covered the southern two-thirds of the State of Missouri including the Ozark Highlands (Fig. 1). The region ranged in elevation from 100 to 600 m and mean annual temperatures ranged between 10–17 °C and average annual precipitation ranged from 760 to 1220 mm (McNab and Avers 1994). The area was approximately 11 million ha and included ten ecological subsections and a gradient of land cover from agriculture to mature forest. Landform based on topography and soil composition included bottomlands, north and east slopes, south and west slopes, upland drainages and ridge tops. Forest covered approximately five million ha and was dominated by oaks (*Quercus* spp.), shortleaf pine (*Pinus echinata*), and hickories (*Carya* spp.) (Shifley and Brookshire 2000; McNab et al. 2007). Tallgrass prairie originally dominated non-forested land which now is primarily agriculture and concentrated urban areas in the east (St. Louis) and west (Kansas City; U.S. NABCI Committee 2000).

Avian abundance models

We used empirical avian abundance models developed (LeBrun et al. 2016) to predict effects of changes in temperature, precipitation, and landscape-scale habitat attributes on abundances of five bird species with various migration patterns and habitat preferences. The worm-eating warbler (*Helmitheros vermivorum*) is a Neotropical migrant dependent on large tracts of forests with a dense understory. The pine warbler (*Setophaga pinus*) is a resident/short-distance migrant associated with large tracts of pine forests. The northern bobwhite (*Colinus virginianus*) is a non-migratory resident dependent on patches of agriculture interspersed amongst early successional habitat. The prairie warbler (*Setophaga discolor*) and blue-winged warbler (*Vermivora cyanoptera*) are Neotropical migrants associated with open early successional habitats. LeBrun et al. (2016) used Bayesian

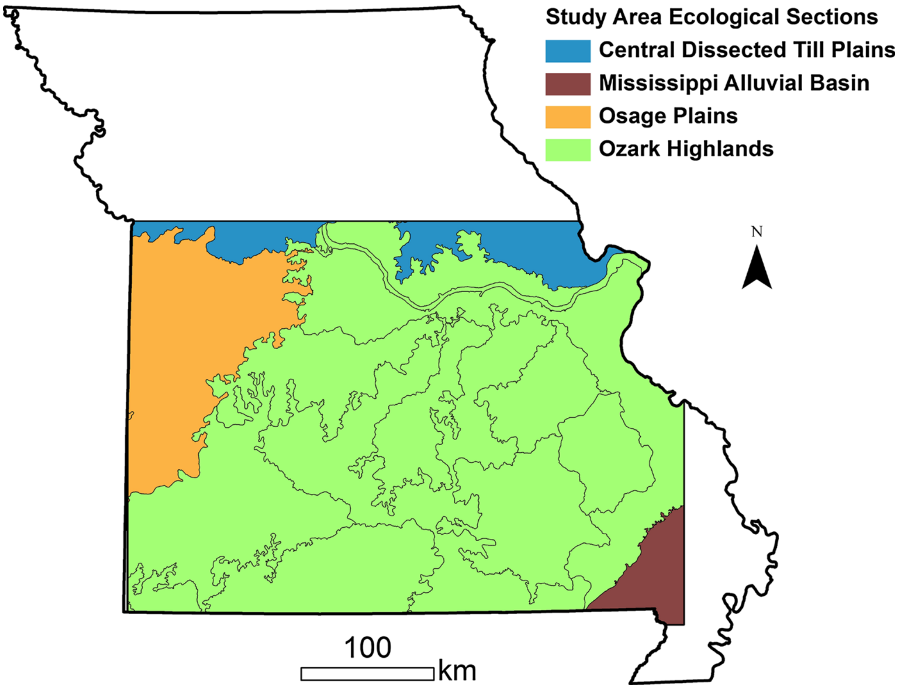


Fig. 1 Study area in Missouri for which we simulated forest landscape change in response to climate change and forest management and predicted resulting changes in abundances of five bird species

hierarchical models and Markov chain Monte Carlo (MCMC) simulation in WinBUGS to fit models for each species that related total bird abundance per route to landscape attributes and climate. They used 2140 North American Breeding Bird Survey (NABBS) route counts from 410 routes surveyed from 1997 to 2003 and landscape attributes derived from 2001 National Land Cover Data (NLCD) and 1996 to 2002 PRISM Climate Data within 1 km buffers around each route. They relied on measures of percent cover of forest types, forest age classes, and land covers that represented potentially important habitat attributes and that were determined from remote sensing (Table 1).

Climate scenarios

We investigated a current climate scenario based on temperature and precipitation from 1980 to 2003 and three climate change scenarios consisting of downscaled climate projections that were based on general circulation models (GCMs) coupled with emission scenarios (Stoner et al. 2011; Schneiderman 2015). We created climate scenarios that represented the low and high extremes of projected climate (IPCC 2007; Schneiderman et al. 2015). We coupled the Parallel Climate Model with the low (B1) emission scenario, the Geophysical Fluid Dynamics Laboratory Coupled Model version 2.1 with the high (A1fi) emission scenario, and the Hadley Centre Coupled Model version 3 with A1fi emission scenario to create our PCM, GFDL, and Hadley climate change scenarios, respectively (IPCC 2007).

Mean winter and summer temperatures varied 3.5–4.6 and 7–9 °C, respectively, among climate scenarios over time (Online Appendix A). The lowest mean winter temperature was under GFDL in year 50 and the highest was under Hadley in year 100, whereas

Table 1 Explanatory variables and posterior distribution means for the best competing models used for predicting abundance of prairie warbler, blue-winged warbler, northern bobwhite, pine warbler and worm-eating warbler in the Missouri study region

Ecological covariates	Prairie Warbler	Blue-winged Warbler	Northern Bobwhite	Pine Warbler	Worm-eating Warbler
Conif	−0.05	**−1.65**		**1.09**	
Early	**0.28**	**−0.44**	**−0.29**		
Mature				0.24	
Canopy				**2.45**	**2.67**
Contag			**−0.72**		
SumPrecip	0.07				
SumTemp	**0.27**	−0.30			
SumTempSq	−0.03	**0.32**			
WinPrecip			**−0.02**		
WinTemp			**0.22**		
For[a]	**1.90**	**2.35**	**0.93**		
Grass[a]	−0.34	−0.92			
Shrub[a]	0.15		**−0.46**		**−0.88**
Crop[a]			**1.05**		
FoPA[a]				**−0.29**	−0.14

Values in bold typeface indicate variables with significant relationships (credible intervals that did not overlap zero)

Conif percentage of coniferous forest in the landscape, *Early* percentage of the forest <20 years old, *Mature* percentage of the forest >20 years old, *Canopy* percentage of canopy cover in the landscape, *Contag* percentage of contagion in the landscape (when contag = 100 then the landscape consists of a single patch), *SumPrecip* summer average (average June, July and Aug) precipitation from the previous year, *SumTemp* summer average maximum (average June, July and Aug) temperature from the previous year, *SumTemp* summer average maximum (average June, July and Aug) temperature squared from the previous year, *WinPrecip* winter average (average Dec, Jan and Feb) precipitation from the previous year, *WinTemp* winter average minimum (average Dec, Jan and Feb) temperature from the previous year, *For* percentage of forest in the landscape, *Grass* percentage of grass in the landscape, *Shrub* percentage of shrub in the landscape, *Crop* percentage of crop in the landscape, *FoPa* mean patch size of forest cover

[a] Indicates a variable held constant over time and space

the lowest summer temperature was under PCM in year 50 and the highest was under GFDL in year 100. Winter and summer temperatures increased by ~2 and 9 °C respectively, by the end of the century under Hadley and decreased <0.5 °C for winter and increased <2 °C for summer under PCM. Winter precipitation decreased across all scenarios from current conditions, while summer precipitation varied greatly from 135 mm under PCM in year 50 to 10 mm under GFDL in year 100.

Land management scenarios

We designed management scenarios based on the status quo and on the goal of mitigating climate effects through managing forests for carbon sequestration (i.e., the storing of carbon through increased stocking), resilience (i.e., the ability of an ecosystem to rebound from a disturbance), and facilitated change (i.e., facilitate an ecosystem to change from one state to another) (Millar et al. 2007; Evans and Perschel 2009; Galatowitsch et al. 2009). Our four management scenarios were (1) current management, (2) no-harvest to promote carbon sequestration, (3) uneven-aged management to promote resilience, and (4) even-aged management with pine conversion to facilitate change (for details see Online Appendix B). We thought the no harvest scenario would maximize the amount of carbon in the landscape by resulting in older forests with greater biomass. We reasoned uneven-aged management would promote forest resilience by increasing species and age diversity at the stand level and even-aged management would facilitate change through tree species turnover accelerated by harvest and planting pine species better suited to future climates.

Landscape simulation data

We used simulated forest landscape change data (Schneiderman 2015) to calculate habitat covariates for use in our bird abundance models. Schneiderman (2015) coupled an ecosystem process-based model (LINKAGES 2.2) with a spatially explicit forest landscape model (LANDIS PRO; Fig. 2). LINKAGES integrates climate, soil, and tree species information to produce tree species establishment probabilities (SEP) for LANDIS PRO parameterization (He et al. 1999; He 2008; Wang et al. 2015). LANDIS PRO then incorporated SEPs with both spatial (i.e. species composition, land types, management units, fire regimes, wind regimes, and insect/disease regimes) and non-spatial information (i.e. species attributes, prescribed burn, fuel removal, and timber harvest prescriptions) to create simulated landscape maps through time (Wang et al. 2014, 2015). Schneiderman et al. (2015) selected tree species to model based on their abundance, economic value, range, or likelihood of range expansion into the region due to climate change and included: a white oak group (*Quercus alba, Q. stellata, Q. bicolor, Q. macrocarpa*), red/black oak group (*Quercus rubra, Q. velutina, Q. falcate, Q. palustris, Q. shumardii, Q. coccinea, Q. marilandica*), shortleaf pine (*Pinus echinata*), loblolly pine (*Pinus taeda*), eastern red cedar (*Juniperus virginiana*), sugar maple (*Acer saccharum*), other eastern soft hardwoods group (*Ulmus* spp., *Salix* spp., *Aesculus* spp., *Alnus* spp., *Betula* spp.), and an understory group (*Cornus florida, Carpinus caroliniana, Nyssa sylvatica, Ostrya virginiana*). The LANDIS PRO parameterization was calibrated and validated based on FIA data as described by Wang et al. (2013).

LANDIS PRO simulations were run for 100 years at 10 years time steps for the four management scenarios under each of the four climate scenarios. SEPs were held constant under current climate, but for the three climate change scenarios, they were interpolated between current climate and future climate projections at 10 years intervals. Initial base maps for LANDIS PRO were created using Landscape Builder (Dijak 2013) with 2001 NLCD and 2004–2008 Forest Inventory Data (FIA) (Schneiderman 2015). Final simulated output from LANDIS PRO included rasters representing the number of trees by species-age cohort, species basal area, and species importance values (Wang et al. 2014).

Data processing and analysis

We derived habitat covariates for predicting bird abundance from LANDIS PRO outputs. We processed the number of individual trees by species, total basal area, total number of trees, and individual tree species importance values predicted by LANDIS PRO in Python 2.6.9 (Python Software Foundation 2013) using the ArcPy package. We converted LANDIS PRO outputs for individual tree abundance to land

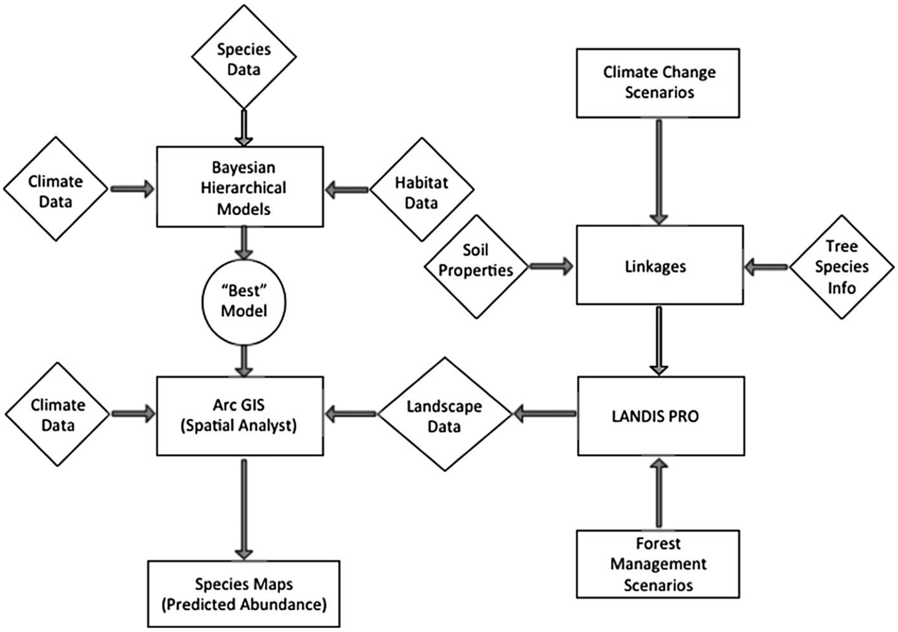


Fig. 2 The general modeling approach used to link empirical Bayesian Hierarchical Models of bird abundance with process-based models (i.e., Linkages and LANDIS PRO) of landscape change resulting from management and climate change

cover classes for use as covariates in our avian abundance models. We calculated the percent cover of water, grass, shrub, row crop, urban, herbaceous wetland, deciduous forest, coniferous forest, and mixed forest land cover classes at a 9030 m resolution across the study area. We summarized the original NLCD and LANDIS PRO outputs at a 9030 m resolution (8154 ha) from their original 30 m resolution because we wanted to make predictions of bird abundance for cells of comparable area to the 1 km buffered BBS routes that the bird models were based on. LANDIS PRO only simulated the forested areas so water, urban, shrubland, grassland, row crop, and herbaceous wetland were constant and calculated from 2001 NLCD. We classified a pixel as deciduous, mixed, or coniferous land cover if $\geq$0.47, $\geq$0.33 and <0.47, or <0.33 of the total of species importance values were deciduous (versus coniferous) species, respectively. These cutoff values were consistent with the original 2001 NLCD values for this region (LeBrun 2015). We calculated percent canopy cover, early successional forest, and mature forest for use in our bird models from basal area and trees per acre outputs from LANDIS PRO. We first calculated percent stocking from trees per acre and basal area and converted stocking to canopy cover (Gingrich 1967; Johnson et al. 2009; Blizzard et al. 2013; LeBrun 2015). We then calculated early-successional and mature forest using a function we created to predict quadratic mean diameter from trees/acre and basal area based on the Gingrich (1967) stocking diagram. The function transitioned between low-density stands <25.4 cm to high-density small diameter stands for early- successional habitat. We acknowledge that the original avian abundance variables were based on predictor variables available from GIS products that could be applied regionally and that we had to derive comparable values from LANDIS PRO outputs. Nevertheless, these predictors performed well in their original validation and application (Lebrun et al. 2016) and we believe they were relevant at the scale we applied them. We calculated zonal statistics for each 9030 m pixel for all habitat covariates, temperature, and precipitation.

Lastly, we combined the original bird models with environmental covariates derived from the simulated landscapes produced by LANDIS PRO and the four climate scenarios to predict bird abundance (Fig. 2). We conducted simulations using WinBUGS MCMC generated output to randomly draw from the posterior distributions for each environmental covariate. We ran simulations in RStudio Version 0.98.1091 (RStudio Team 2014) for a total of 500 iterations for each of the five species for a combination of four management, four climate scenarios, and three time steps (0, 50, and 100 years). The final output included the mean regional relative abundance and confidence interval and relative abundance maps for each species for the sixteen combined management and climate scenarios. The confidence intervals captured the uncertainty or error in the parameters in the bird abundance models as applied to the simulated landscapes in this study; they did not represent potential uncertainty in the simulated landscapes.

Results

Habitat covariates varied more among management scenarios than among climate scenarios at year 50 and 100 (Online Appendix C). Habitat covariates changed by 1–24% from year 0 to 50, depending on management scenario: however, they changed <3% across all climate scenarios for any given management scenario. Only early successional forest and coniferous forest changed significantly over time (95% confidence intervals not overlapping). Early successional forest declined 9–11% between year 0 and 50 under all management scenarios. Coniferous forest increased under even-aged management 24 and 23% from year 0–50 and 50–100, respectively.

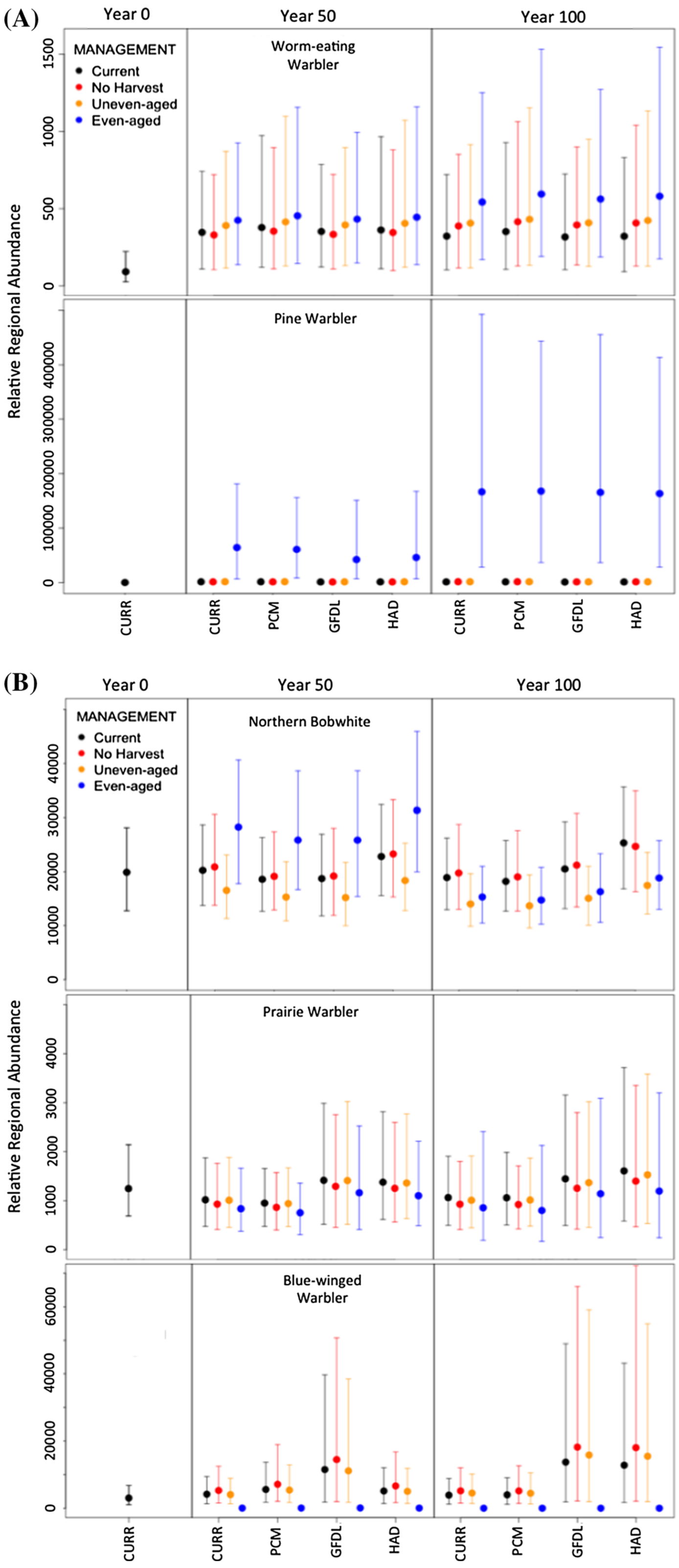
Differences in habitat covariates among management scenarios were primarily the result of difference in percent coniferous forest, contagion, and canopy cover under even-aged management compared to the remaining three scenarios (Online Appendix C). Percent coniferous forest cover changed from 1% in year 0 to ~48% in year 100 under even-aged management, but to less than 1% under current, no-harvest, and uneven-aged management. Contagion decreased 4% by year 50 but increased 11% by year 100 under even-aged management; however, it decreased 18 and 5% by years 50 and 100, respectively, under uneven-aged management. Canopy cover was consistently greatest under even-aged management followed by uneven-aged management and no harvest, due to tree planting and high stocking in resulting pine forests.

Management effects on avian abundance were species specific and varied greatly across scenarios (Fig. 3). The worm-eating warbler and pine warbler increased under even-aged management, but for different reasons. The worm-eating warbler increased in response to increasing canopy cover, whereas pine warblers increased in response to increasing canopy cover and coniferous forest (Fig. 3A; Online Appendix C). No single management scenario benefitted all three early successional species. The northern bobwhite was most abundant under even-aged management at year-50 but abundance dropped by ~45% by year 100 (Fig. 3B). Northern bobwhite steadily decreased in abundance over time under uneven-aged management (~16% drop for both 50 and 100 year time steps), which coincided with an increase in contagion (Online Appendix C). Prairie warbler abundance was similar across management scenarios, but greatest under current management followed by uneven-aged (<5% drop from current management), no-harvest (12% drop from current management) and even-aged management (18% drop from current management; Fig. 3B). Blue-winged warbler was more abundant under no-harvest than current and uneven-aged management, and almost disappeared from the landscape under even-aged management (Fig. 3B). The decreases in abundance of prairie warbler and blue-winged warbler under even-aged management resulted from greater stocking and canopy cover compared to current and uneven-aged management. Even-aged-management with conversion to pine by planting resulted in greater stocking, and hence canopy cover, than natural regeneration of deciduous forests under current and uneven-aged management.

Models for Northern bobwhite, prairie warbler, and the blue-winged warbler included temperature and precipitation, but only temperature had any significant effect under our scenarios (Fig. 3B). Northern bobwhite total mean abundance increased 14–15% by year 50 and 26–37% by year 100 for all management scenarios under the Hadley climate scenario (Fig. 3B). This change in abundance corresponded with an increase in mean average winter temperature 3.5 and 4.5 °C for years 50 and 100, respectively (Figs. 3B, 4). Prairie warbler abundance increased with increased summer temperature at year 50, but at year 100 it hit a threshold (36.5 °C) that resulted in a 7% decrease under GFDL (Figs. 3B, 4). In contrast, to the prairie warbler, blue-winged warbler abundance increased linearly with temperature resulting in a 2% increase at year 100 under the same scenario (Figs. 3B, 4).

Only the northern bobwhite was affected by climate-induced changes to forest vegetation (Fig. 5). Under current management, Northern bobwhite abundance was 10% greater at year 100 under the Hadley scenario than under current climate, which coincided with a 2% decrease in mean contagion. Other species exhibited

Fig. 3 Simulated direct (temperature and precipitation) and indirect effects of climate (climate-induced changes to vegetation) on mean relative abundance and 95% confidence intervals. **A** Mature forest species (i.e., worm-eating warbler and pine warbler). **B** Early successional species (i.e., northern bobwhite, prairie warbler, and blue-winged warbler) at years 0, 50, and 100 under current climate (CURR), PCM-B1 (PCM), GFDL-A1FI (GFDL), and Hadley-A1FI (HAD) climate scenarios and current, no harvest, and even-aged management scenarios



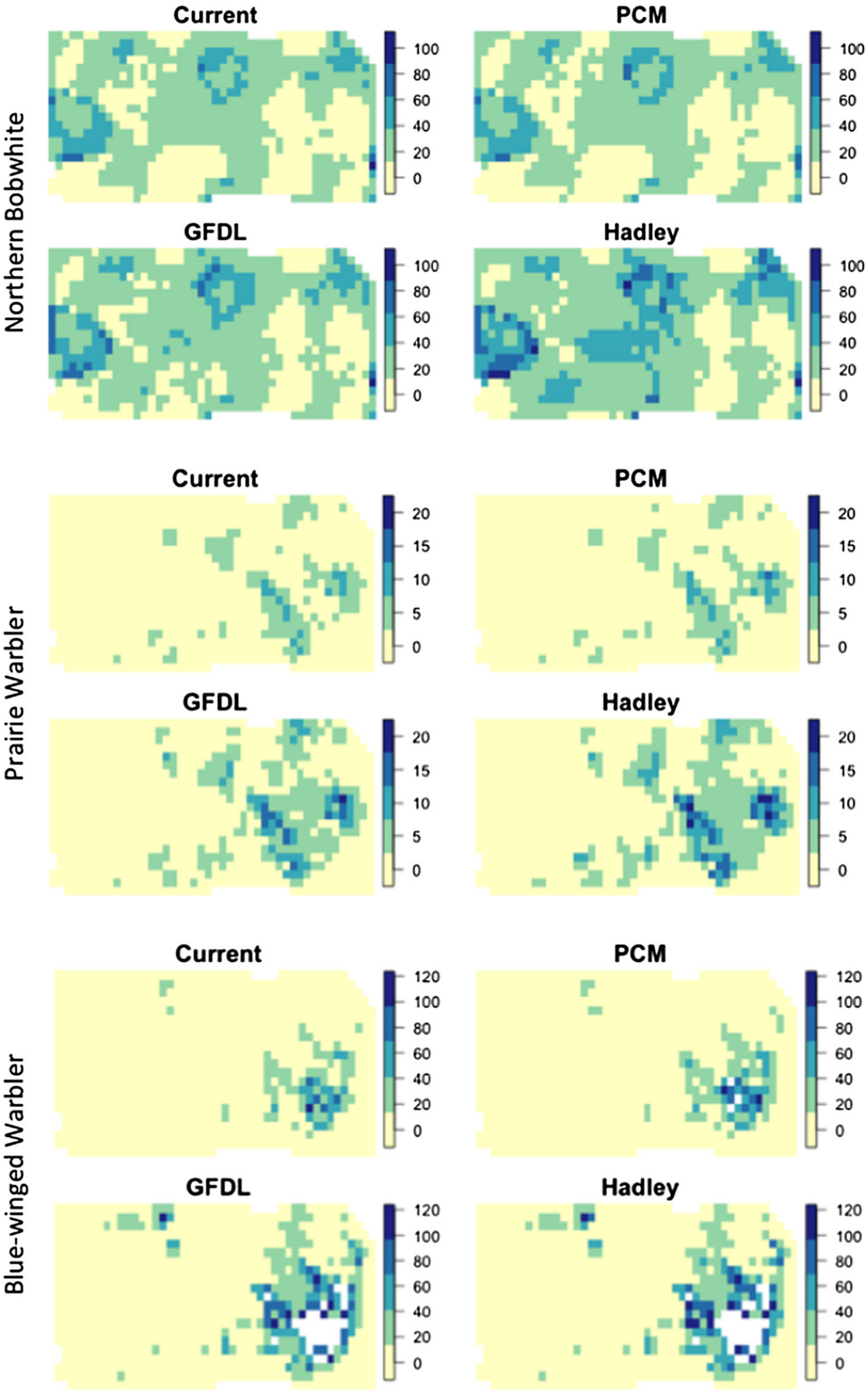


Fig. 4 Predicted abundance of northern bobwhite, prairie warbler, and blue-winged warbler under current climate, PCM-B1, GFDL-A1FI, and Hadley-A1FI climate scenarios at year 100 under current management on 8154 ha pixels across our southern Missouri landscape

differences that were not large enough to be attributed to more than just model uncertainty. For example, pine warbler had lower abundance under PCM than current climate under even-aged management.

Discussion

Management had a greater effect on forest change than did climate change. We found <3% difference among

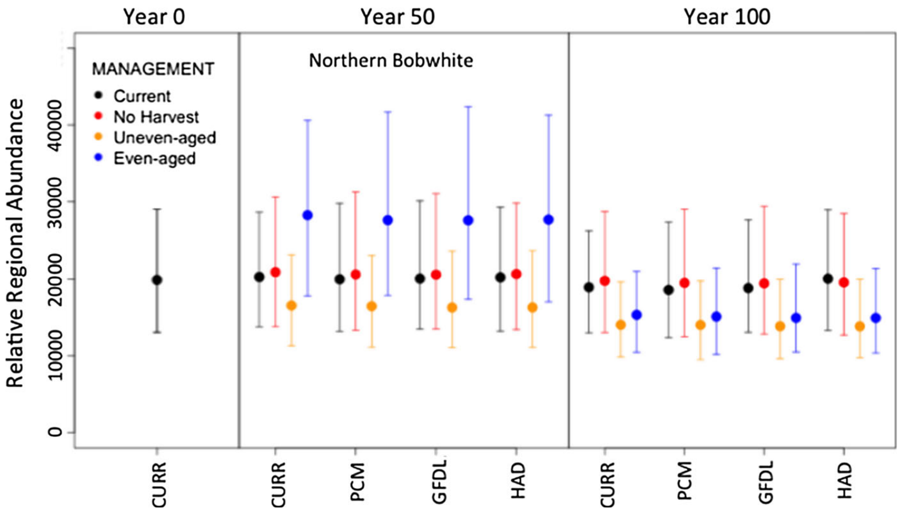


Fig. 5 Simulated effects of climate-induced changes to vegetation on mean relative abundance and 95% confidence intervals for northern bobwhite at years 0, 50, and 100 under current climate (CURR), PCM-B1 (PCM), GFDL-A1FI (GFDL), and Hadley-A1FI (HAD) climate scenarios and current, no harvest, and even-aged management scenarios in southern Missouri

habitat covariate values across climate scenarios at year 100, whereas there was up to a 50% difference among habitat covariate values among management scenarios at year 100. Our results are consistent with other modeling studies that predict climate change will cause minimal changes to central hardwood forests in the next 100 years (Brandt et al. 2014; Wang et al. 2015). However, it is likely that the effect of climate will become greater over longer time frames (e.g. 300 years; Wang et al. 2015). Climate induced change can take a long time in the absence of disturbance because trees have long life expectancies and they have limited dispersal abilities in the absence of planting. Climate change is expected to cause decreases in sugar maple and increases in shortleaf pine and some oaks in the region over the next 100-300 years (Schneiderman et al. 2015; Wang et al. 2015); however, changes in our forest land cover classes were minimal because we pooled species. Nevertheless, even a <2% change in a habitat attribute resulted in a 10% increase in mean abundance of northern bobwhite under the Hadley climate scenario.

Even-aged management with planting facilitated change in forest composition to include a much greater percentage of coniferous forest (i.e. shortleaf and loblolly pine) as hypothesized. Even-aged management also likely sequestered the most carbon. We expected the no-harvest scenario to sequester the most carbon in live trees. However, even-aged harvest and subsequent planting to loblolly and shortleaf pine resulted in greater canopy cover and stocking levels, which is likely indicative of greater carbon stores (D'Amato et al. 2011). Timber removals under even-aged and uneven-aged management would also sequester carbon in some wood products, but we did not account for this in our study. Tree planting also facilitated the turnover of deciduous species to coniferous forest across our landscape under even-aged management. Southern pines are predicted to fare better under future climates in our region (Iverson et al. 2008; Brandt et al. 2014; Wang et al. 2015), however, unless there is active management promoting pine species there will likely be little turnover in the next 100 years.

Management was a greater driver of future avian abundance than direct (i.e., temperature or precipitation) or indirect (i.e., climate-induced changes to vegetation) effects of climate for most of our species. As predicted, no single management strategy increased or decreased abundance for all species due to their varied habitat requirements. Prairie warbler was an exception and experienced a stronger response to climate than management. The amount of forest cover was the primary driver of prairie warbler abundance, and since the amount of total forest cover did not change over time, climate related drivers had a greater effect on abundance. In addition, current harvest and uneven-aged management had modest and similar levels of harvest and resulted in similar amounts of early-successional forest and as a result, similar prairie warbler abundance. Finer scale changes to tree stocking and canopy cover are known to affect prairie warbler abundance, but these were not accounted for in our bird models (Reidy et al. 2014).

Our forest landscape simulations allowed forest composition and structure to change, but the total amount of forest and its location on the landscape was held constant. We held the total amount of forest on the landscape constant for simplicity and because we were not focused on land-use conversion, but in reality this assumption is not likely. The Ozark Highlands historically experienced extensive losses in forest cover. However, in the last 50 years forest cover only decreased <3% (Karstensen 2010). This decline in net forest loss will likely not continue and is heavily dependent on regional economics associated with wood products, agriculture, tourism, and urbanization (Lubowski et al. 2008; Karstensen 2010; Hamilton et al. 2013). There is evidence, however, that even small conversions can result in significant declines in species abundance when the conversions occur around protected areas or in population source areas (Bonnot et al. 2013; Wood et al. 2015).

The direct effects of climate change both positively and negatively affected bird abundances. The northern bobwhite was positively affected by warming temperatures under the Hadley climate scenario, while the blue-winged and prairie warblers experience both positive and negative effects under the same scenario. The prairie warbler showed evidence of a threshold effect where at the highest temperatures, abundance began to decline. The ranges of prairie warblers and blue-winged warblers are shifting northward in latitude (Hitch and Leberg 2007). Our results provide a mechanism behind this shift northward and suggest this trend may continue if temperatures increase.

Only the northern bobwhite showed any indirect effect of climate through climate-induced vegetation changes. Other species only exhibited small differences in abundance among climate scenarios, which was contrary to what we expected. It is well established that bird abundance can be related to landscape attributes such as those measured here (Thogmartin and Knutson 2007; LeBrun et al. 2012; Reidy et al. 2016). The main reason we did not observe changes in abundance due to climate-induced changes in vegetation was that climate change had minimal effects on some of the important habitat covariates in our bird abundance models. For example, the amount of forest cover was an important predictor of abundance for prairie warbler and blue-wing warbler, but forest cover was held constant in our landscape modeling approach. In contrast, contagion was affected by climate and management and resulted in changes in abundance of northern bobwhite. Another reason why we did not detect greater response in abundance to some climate or management scenarios was because our abundance models were originally developed using remotely sensed landscape variables and did not consider finer scale changes in vegetation species and structure. Most of these species respond to changes in forest structure and composition, which would be affected by management and climate change. So, even though the GFDL climate scenario is predicted to result in lower tree stocking on some land types in the Ozark highlands (Schneiderman 2015; Wang et al. 2015), which should benefit prairie warblers (Reidy et al. 2014), our model could not predict this.

Some predictions were contrary to our expectations. Blue-winged warblers declined in abundance under warming temperatures, which is consistent with studies showing populations shifting northward (Hitch and Leberg 2007; Matthews et al. 2011). Blue-winged warblers significantly increased in mean abundance at temperatures >34 °C, which may be unrealistic. This may have resulted from sampling only a portion of the species breeding range, not considering the variation in temperature extremes across the breeding season, and sparse data in this temperature range (Bolger et al. 2005; Albright et al. 2010, 2011; LeBrun et al. 2016). We also expected blue-winged warblers to have higher abundance under even-aged management because of their affinity for early successional forest (Gill et al. 2001; Reidy et al. 2014); however, our initial abundance models showed a negative relationship to early successional habitat. This is likely because our definition of early successional habitat was broad (forests <20 years old) when they actually prefer younger forests (<7 years old) and shrubland (Gill et al. 2001), or because at this scale (8154 ha) forest cover was more important (LeBrun et al. 2012). Even though some aspects of the model were contrary to expectations, the model should produce credible estimates at this scale and for this region based on LeBrun et al.'s (2016) model validation. Lastly, worm-eating warblers increased in mean abundance under even-aged management that planted pine trees when worm-eating warblers are known to favor deciduous and mixed forests (Vitz et al. 2013). This was likely because our worm-eating warbler model did not include forest type (coniferous, mixed, deciduous) and high abundances were a function of increased canopy cover provided by even-aged management and planting. These conflicting results emphasize the importance of taking into account the original scope of the models when applying them in a different study.

Linking empirical wildlife models with process-based landscape change models can be an effective way to predict changes in abundance due to future climate and management. However, there are still some challenges with implementing these techniques. LANDIS PRO has the ability to simulate landscape structure as well as individual tree species at a relatively fine resolution over broad geographic regions (Wang et al. 2014). Developing empirical models to match this resolution and scale can be difficult and more work bridging this gap could be helpful. For instance, integrating LIDAR imagery (Goetz et al. 2010) and FIA plot data (Wang et al. 2013) could help develop finer scale measures of habitat structure across larger spatial extents. Development of hierarchical models that include both regional drivers of bird abundance (e.g. forest cover) from large scale surveys like BBS and local surveys linking bird density to habitat structure (e.g. canopy cover, tree density) might better capture effects of changes in forest structure. Bayesian modeling techniques have the ability to account for uncertainty associated with predictions from processed-based models (Radtke and Robinson 2006; Wilson and Silander 2014). As technology improves and run times decrease for LANDIS PRO additional model replicates can be run and integrated into a Bayesian framework to propagate uncertainties across the empirical and process-based model predictions (Radtke and Robinson 2006).

Using a combination of processed-based landscape change models and empirical wildlife models can help managers prioritize areas for conservation and evaluate strategies for managing for climate change. Succession and management were the primary drivers of the changes we predicted, but even small changes in key habitat features resulting from climate change can still significantly alter avian populations. We looked at a small number of bird species and management alternatives, but believe these examples show the utility of these approaches for evaluating climate and management impacts on wildlife abundance at a regional scale. Given the potential importance of management and climate, we suggest that approaches such as those used here are valuable for evaluating conservation alternatives and landscape conservation design within the context of climate change. Furthermore, these approaches are spatially explicit and can potentially be used to identify priority areas for conservation and habitat refugia.

Acknowledgements We thank the many volunteers collecting North American Breeding Bird Survey counts, without whose efforts this study would not have been possible. This project was funded by the USDA Forest Service Northern Research Station, Department of Interior USGS Northeast Climate Science Center graduate fellowships, and the University of Missouri-Columbia. Its contents are solely the responsibility of the authors and do not necessarily represent views of the Northeast Climate Science Center or the USGS. This manuscript is submitted for publication with the understanding that the United States Government is authorized to reproduce and distribute reprints for Governmental purposes.

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