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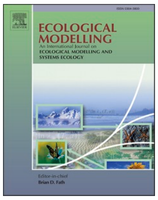

Integrating multiple data sources with species distribution models to estimate the distribution and abundance of northern bobwhite (*Colinus virginianus*) in the United States

William B. Lewis [a,*], Sprih Harsh [a], Patrick Freeman [b], Victoria Nolan [a], Justin Suraci [b], Bridgett E. Costanzo [c], James A. Martin [a]

[a] *Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA, USA*
[b] *Conservation Science Partners, Inc., Truckee, CA, USA*
[c] *Landscape Conservation Initiatives, Natural Resources Conservation Service, Washington DC, USA*

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ABSTRACT

Species distribution models (SDMs) have traditionally focused on occupancy despite abundance potentially being a more useful metric for informing conservation initiatives. Integrating m*ultiple species* abundance datasets could retain the strengths of each data type and, at least partially, offset their weaknesses, potentially improving the performance of abundance-based SDMs. We developed spatially-non-stationary, abundance-based SDMs to assess the environmental drivers of spatial variation in abundance and to predict the abundance and distribution of northern bobwhite (*Colinus virginianus*) across the United States. We fitted Bayesian SDMs with regionally-partitioned coefficients by integrating structured North American Breeding Bird Survey (BBS) and semi-structured eBird count data. We found that bobwhite abundance was concentrated in three main regions: southern Texas, the Great/Midwestern Plains, and the southeastern coastal plain. Total abundance across the range was estimated at 8,577,291 (8,292,554 - 8,933,202). While the spatial extent of the predicted bobwhite range was generally similar across models, models fit with single data sources appeared to vastly underestimate (eBird) or overestimate (BBS) abundance, though abundance estimation was improved through data integration. Most covariate effects exhibited non-stationarity across the range, potentially leading to inappropriate inferences or management decisions from a spatially-stationary model. Our study provides an important example of how datasets collected at different spatial scales under different observation protocols can be integrated via SDMs to improve abundance-based modeling and correct for weaknesses of individual datasets. Our modeling framework provides regional estimates of the drivers of bobwhite abundance and range-wide estimates of abundance for guiding both local and range-wide bobwhite conservation.

1. Introduction

Land-use change is one of the most significant factors behind declining biodiversity, primarily via habitat loss and habitat fragmentation (Semper-Pascual et al., 2021). When habitat is lost, landscapes become more fragmented, containing smaller and more isolated patches separated by a matrix of human-altered land cover (Haddad et al., 2015). Understanding how species will respond to dynamic landscapes is one of the current key challenges in ecology and biodiversity conservation (Piirainen et al., 2023). Species distribution models (SDMs) are one of the most important tools currently available to assess the potential impacts of land-use change on spatial variation in the abundance and occupancy of species (Franklin, 2023). These models are widely used for modeling and forecasting species' spatial distributions in response to global landscape and climate change (Renner et al., 2019). SDMs can, therefore, help to identify conservation needs, define alternative conservation actions, evaluate the effects of such actions, and prioritize biodiversity conservation efforts.

Due to the widespread availability of presence and presence/absence data, SDMs are frequently used to relate occupancy to environmental characteristics for predicting species distributions (Hill et al., 2017; Jiménez-Valverde et al., 2021). Despite the utility of occurrence-based

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* Corresponding author.
E-mail address: william.lewis27@uga.edu (W.B. Lewis).

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SDMs, predicting spatiotemporal variation in abundance may be a more useful metric for assessing population status and risks. Abundance can vary greatly over space and time with only minimal changes in occupancy, such that occupancy analyses may underestimate rates of population change or range shifts (Ashcroft et al., 2017; Maxwell et al., 2019; Strebel et al., 2022). Furthermore, management and conservation actions are frequently based on estimates of abundance rather than occupancy, such as identifying priority conservation areas and assessing local extinction risk (Johnston et al., 2015; Waldock et al., 2022). Predicted habitat suitability from occupancy-based SDMs is often poorly correlated with abundance and is more reflective of maximum possible abundance in an area (Dallas and Hastings, 2018; Jiménez-Valverde et al., 2021; VanDerWal et al., 2009), necessitating direct modeling of abundance with SDMs.

Several factors have historically impeded abundance modeling with SDMs. In contrast to occupancy datasets, broad-scale abundance data are lacking for many species. Abundance is also a more complex process than occupancy but contains more information about state processes and extinction risk. Local abundance may be affected by non-equilibrium dynamics or biotic conditions, such as competition or predation, thereby weaking the link between abundance and the environmental or climatic gradients used for prediction (Laundré et al., 2014; Levine and Rees, 2002; Pulliam, 2000; Rodenhouse et al., 1997). Studies have found conflicting results on the effectiveness of modeling abundance with SDMs. Some have successfully developed abundance-based SDMs for a variety of species (e.g., Potts and Elith, 2006; Schindler et al., 2022; Strebel et al., 2022) while others have found generally poor predictive performance (e.g., Johnston et al., 2013; Waldock et al., 2022). These varying conclusions may be attributable to differences in study systems, statistical algorithms employed (e.g., generalized linear models vs. machine-learning methods), model formulation (e.g., predictor variables, accounting for imperfect detection), or the quality and types of abundance data available for inclusion in the models.

Data integration is a promising avenue for alleviating some of the issues associated with abundance-based SDMs and improving model performance. While structured abundance surveys are often geographically restricted (Boersch-Supan and Robinson, 2021; Zipkin et al., 2021), the rise of citizen-science initiatives means that broad-scale abundance data may be available for many species. These semi-structured citizen-science data are generally opportunistically collected and associated with numerous forms of bias (Jiménez et al., 2019; Johnston et al., 2021); however, they are still potentially informative concerning species abundance and the processes that drive dynamics in space and time (Isaac et al., 2020). Data integration may therefore help to improve spatial coverage of abundance data and can, at least partially, compensate for weaknesses in individual datasets while retaining their strengths (Saunders et al., 2019). Integrating structured and semi-structured data can be performed in a Bayesian joint-likelihood framework (Miller et al., 2019), in which all datasets jointly estimate state parameters but each dataset is modeled as arising from a separate observation process. Performing data integration in such a manner allows for direct modeling of imperfect detection, which is often not incorporated into SDMs despite having the potential to substantially bias results (Guillera-Arroita et al., 2015; Kéry et al., 2010). Integrating multiple datasets that vary in spatial coverage and data quality has been shown to improve precision, convergence rates, and predictive accuracy of SDMs (Hill et al., 2017; Koshkina et al., 2017; Miller et al., 2019), including for abundance-based SDMs (Strebel et al., 2022).

SDMs have also frequently assumed a stationary (i.e., not varying spatially or temporally) relationship between environmental predictors and occupancy or abundance; however, species' responses to the environment may vary across the range (Osborne et al., 2007; Thorson et al., 2023). For example, populations near range edges are likely to be near the climatic tolerances of the of the species (Brown, 1984; Holt et al., 2005) and so may be more sensitive to changes in climate compared to populations within the range core (Amburgey et al., 2018; MacArthur, 1972). Similarly, widespread species may be locally-adapted to differing environmental conditions found throughout the range (Hällfors et al., 2016; Valladares et al., 2014). Several methods have been developed for accounting for non-stationarity in environmental responses, such as geographically-weighted regression, spatially-varying coefficients, and regional portioning of data (Doser et al., 2024; Osborne et al., 2007). In cases when non-stationarity may be expected, such as when modeling range-wide abundance for a widespread species, stationary models can bias results and lead to incorrect inferences (Osborne and Suárez-Seoane, 2002; Thorson et al., 2023). Besides improving model performance, non-stationary SDMs can also infer spatial variation in the drivers of population states to better inform local management efforts (Doser et al., 2024).

Here, we develop an integrated, spatially-non-stationary SDM incorporating structured and semi-structured data to estimate the abundance of northern bobwhite (*Colinus virginianus*, hereafter, bobwhite) across their geographic range in the United States. Bobwhite are an ideal target for abundance-based species distribution modeling, as broad-scale abundance data are available from across the range via both structured breeding abundance surveys and citizen-science datasets. Bobwhite detections during the breeding season primarily consist of males giving a distinctive "bob-white" call, so the effects of misidentifications in the datasets should be relatively minimal. Long-term data from the North American Breeding Bird Survey (BBS) and Christmas Bird Count indicate a widespread decline of bobwhite populations across the range (Hernández et al., 2013; Sauer et al., 2020). Habitat loss and fragmentation are considered the primary causes of the range-wide decline in bobwhite populations (Brennan, 1991; Hernández et al., 2013). The widespread downward population trajectories of this commercially-and-culturally-important species have led to the formation of initiatives aimed at reversing population declines, such as the Northern Bobwhite, Grasslands, and Savannas Framework for Conservation Action implemented by the U.S. Department of Agriculture Natural Resources Conservation Service's (NRCS) Working Lands for Wildlife (WLFW) program (NRCS, 2022). This range-wide initiative requires accurate and fine-scale (i.e.., several km resolution) estimates of bobwhite abundance across the U.S. for prioritizing conservation actions; however, previous spatial modeling of bobwhite distributions have focused either on regional scales (Duren et al., 2011; Roseberry and Sudkamp, 1998; Twedt et al., 2007) or coarse-scale predictions (Schindler et al., 2022). Furthermore, halting the current bobwhite decline requires identifying the environmental drivers of variation in bobwhite abundance. Bobwhite occur across a range of climate gradients and habitat types, such as pine savannas in the southeastern U.S. and rangelands in Texas (Brennan et al., 2020). This variability necessitates a spatially-non-stationary SDM for modeling regional variation in environment-abundance relationships to better inform local bobwhite management efforts. The objectives of our study are twofold. First, we assess the utility of integrating structured and semi-structured data in an abundance-based SDM to predict bobwhite abundance across the range in the United States. Second, we use a hierarchical process incorporating regional partitioning of regression coefficients to assess the regional drivers of bobwhite abundance for informing management actions.

2. Methods

2.1. Model resolution and input data summarization

We selected 30 states across the eastern and southern U.S. for our analysis (Fig. 1). All states fell within the bobwhite range (Ziolkowski et al., 2022) and were therefore selected as the basis of the major concentration of our datasets. We overlaid a grid of 5-km x 5-km cells across the whole of our study area to estimate grid-specific abundance. We removed from analysis any grid cells with missing covariate data (see below), leaving 182,455 grid cells across the U.S.

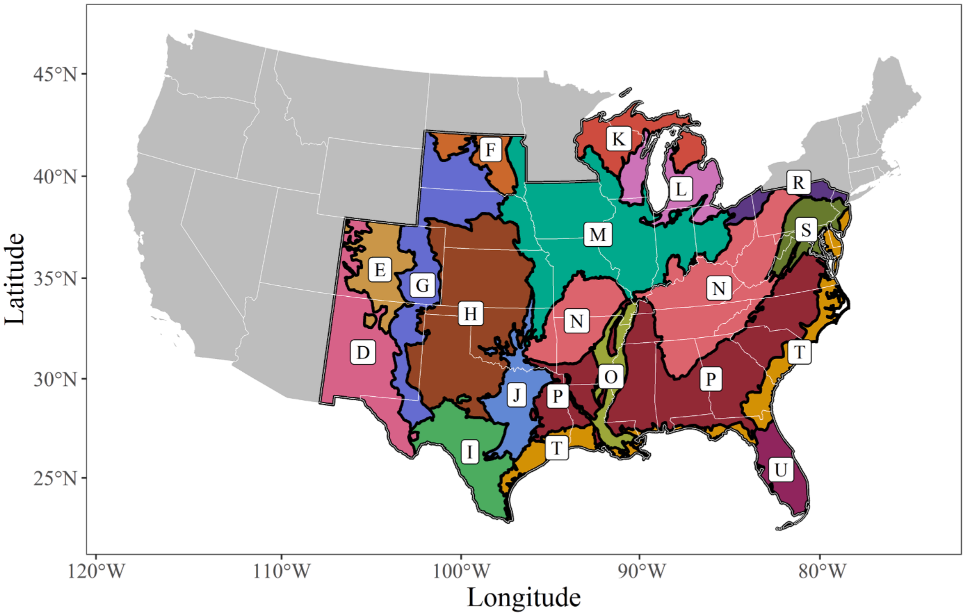

Fig. 1. Map showing the study region (colored) used to estimate the abundance and distribution of northern bobwhite (*Colinus virginianus*) across the eastern United States. Colored regions show USDA Land Resource Regions: D (Western Range and Irrigated Region), E (Rocky Mountain Range and Forest Region), F (Northern Great Plains Spring Wheat Region), G (Western Great Plains Range and Irrigated Region), H (Central Great Plains Winter Wheat and Range Region), I (Southwest Plateaus and Plains Range and Cotton Region), J (Southwestern Prairies Cotton and Forage Region), K (Northern Lake States Forest and Forage Region), L (Lake States Fruit, Truck Crop, and Dairy Region), M (Central Feed Grains and Livestock Region), N (East and Central Farming and Forest Region), O (Mississippi Delta Cotton and Feed Grains Region), P (South Atlantic and Gulf Slope Cash Crops, Forest, and Livestock Region), R (Northeastern Forage and Forest Region), S (Northern Atlantic Slope Diversified Farming Region), T (Atlantic and Gulf Coast Lowland Forest and Crop Region), and U (Florida Subtropical Fruit, Truck Crop, and Range Region).

2.2. *Dataset selection and processing*

2.2.1. *Structured dataset*

We used BBS data as our structured dataset (Ziolkowski et al., 2024). As part of BBS, volunteer observers with previous experience identifying birds by sight and sound perform roadside sampling routes each year from May – early July to survey bird abundance. Routes are ∼40 km long with 50 stops spaced ∼0.8 km apart. Observers perform a 3 min, 400 m radius point count at each stop, recording all species seen or heard. BBS route establishment was performed based on a stratified random design, with approximately 3000 routes surveyed annually in North America (Ziolkowski et al., 2022). For our analysis, we used data from the years 2018, 2019, and 2021 (data from 2020 were missing due to public health restrictions imposed on field collection during the COVID-19 Pandemic). The raw data consist of surveys across all 50 stops/route and the geographic location of the start of each route. We used a shapefile of BBS route paths, generated stops at 0.8 km intervals from the starting point along each route path, and associated these 50 stops with their corresponding survey data (for further details, see Appendix A). Each stop was assigned to a 5 km x 5 km grid cell based on its geographic location. Each survey was also associated with two covariates affecting detection probability: the number of passing cars and the presence or absence of excessive background noise (excluding car noise) during the survey duration. No more than 18 stops were surveyed per grid cell in each calendar year.

2.2.2. *Semi-structured dataset*

We used eBird as our semi-structured dataset (Sullivan et al., 2009). eBird, administered by the Cornell Lab of Ornithology, maintains a citizen-science database wherein users can submit checklists detailing the number of individuals of each species they observe. eBird represents a massive dataset on bird abundance, with over 1 billion bird observations from across the world (www.ebird.org); however, the opportunistic nature of data collection means that eBird data is generally of lower quality than BBS (Pacifici et al., 2017). eBird employs many quality-control filters, such as removing unrealistically high bird counts or observations of species in places and times of year in which they are unlikely to occur, but observers vary widely in experience and identification skills (Sullivan et al., 2009). Each checklist is associated with geographic coordinates and information about survey type (e.g., incidental observations, stationary count, travelling count, etc.) and effort (duration and distance traveled, if applicable); however, unlike BBS, the exact survey area of eBird checklists is often not known precisely. Furthermore, the semi-structured nature means that the spatial and temporal coverage of eBird is dependent on where and when observers submit checklists. eBird is thus spatially biased towards cities and easily-accessible areas (Johnston et al., 2021; Sullivan et al., 2009).

We performed a series of data processing steps to reduce the influence of potential biases in the eBird dataset. Data were first filtered to only include complete checklists, i.e., only those surveys in which the observer recorded all species detected. We also filtered data based on observer effort to only include checklists < 5 h in duration, < 5 km in distance traveled, and checklists with < 10 observers (Schindler et al., 2022). We then subset to only checklists that occurred during May and June of 2018, 2019, and 2021 to align with the years and periods of BBS data collection. Finally, we used the geographic coordinates reported by each checklist to assign it to its corresponding 5 km x 5 km grid cell. We then randomly selected up to 50 checklists per grid cell for each calendar year to reduce the effects of spatial autocorrelation in the eBird dataset (Johnston et al., 2021). For each checklist in this final pre-processed dataset, we also retained survey information, including the duration (in minutes), distance traveled (in km), and checklist type (stationary or traveling).

2.3. *Environmental covariates*

We used a suite of covariates to model the impacts of environmental variation and land use on spatial variation in abundance of bobwhite

(Table B.1). These covariates were thematically grouped into three categories: climate, land cover and structure, and land use and disturbance. Covariate layers were processed using a combination of the Google Earth Engine Python API (Gorelick et al., 2017) and R (R Core Team, 2020). As abundance data were summarized at the level of the 5 km x 5 km grid cell, all environmental covariates were smoothed at 5 km. All the covariate values at the center of each 5 km x 5 km grid cell were used to model grid cell-level bobwhite abundance estimates. No environmental variables were correlated ($|r| < 0.6$) across the range and all were standardized prior to analysis.

2.3.1. Climate

Climate variables included mean daily maximum temperature, mean daily precipitation, and the mean number of days with snow depth greater than 2.5 cm (hereafter, max temperature, precipitation, and snow days, respectively). The first two climate variables were derived from NASA's Daymet v4 dataset (Thornton et al., 2020) spanning the years 2016 to 2021. We first calculated the pixel-wise mean climate values across all years and then smoothed surfaces by calculating the pixel-wise focal mean using a circular kernel with a 5-km radius. The snow days dataset was derived using the National Snow and Ice Data Center's Snow Data Assimilation System (SNODAS) data product (National Operational Hydrologic Remote Sensing Center 2004; https://nsidc.org/data/G02158/versions/1). For each year from 2016 to 2021, we downloaded daily snow-depth rasters and reclassified as 1 if the pixel had a recorded depth of 2.5 cm or greater and 0 otherwise. Then for each calendar year, we calculated the number of relevant snow days as the pixel-wise sum of all 365 daily rasters. Finally, we calculated the pixel-wise mean value across all years to derive a final covariate.

2.3.2. Land cover and structure

We included land cover variables that captured the mean proportional cover of broad vegetation classes hypothesized to affect bobwhite abundance. We calculated the percent cover (within a 5-km radius of each pixel) of lands classified as row crop, grassland, pasture, deciduous forest, evergreen forest, mixed forest, and water/wetland (hereafter, row crop, grassland, pasture, deciduous, evergreen, mixed, and water cover, respectively) based on the National Land Cover Dataset (NLCD) releases for 2016 and 2019. The percentage cover layers for each land use type were then averaged across the two years. We also used Rangeland Analysis Platform (RAP) land cover datasets (Allred et al., 2021) spanning the years 2016 to 2021 to derive the proportional cover of shrubs and bare ground.

2.3.3. Land use and disturbance

We quantified mean human land use intensity using layers described in detail in Suraci et al. (2023) and based on a procedure originally developed by Theobald (2013). These layers integrate multiple datasets to estimate the intensity of disturbance at each location (i.e., raster pixel) across the landscape for three categories of human disturbance: urbanization, transportation, and energy development (hereafter, urban, transport, and energy intensity, respectively). Values for each disturbance type range between 0 and 1 and are based on underlying datasets quantifying human land use circa 2016.

Throughout the bobwhite range, and especially in ecosystems like pine savannas, fire has been used as a key management technique for improving bobwhite habitat due to its ability to suppress woody encroachment and stimulate the growth of important food plants (Greenfield et al., 2003; McGrath et al., 2017). However, excessive fire activity can lead to greater predation risks and habitat removal (Rosche et al., 2021). We estimated the frequency of fires between 2006 and 2021 in each 5 km x 5 km grid cell using the Monitoring Trends in Burn Severity (MTBS) Burned Areas Boundaries Dataset (available at https://www.mtbs.gov/direct-download). We then tabulated, for each 5 km x 5 km grid cell, the total number of burn perimeters that it intersected, providing a coarse estimate of fire frequency.

2.4. Model description

We utilize a generalized linear model (GLM) framework for modeling bobwhite abundance, as this class of models has been successfully utilized to integrate multiple data sources for abundance-based SDMs (Schindler et al., 2022; Strebel et al., 2022). Waldock et al. (2022) found that simple GLMs (i.e., relating observations directly to the latent abundance state with a single data source likelihood) generally had lower predictive accuracy than machine-learning methods; however, data integration, hierarchical dependencies, non-stationarity, and imperfect detection are all straightforward to incorporate with GLMs (Doser et al., 2024; Kéry et al., 2010; Pacifici et al., 2017; Strebel et al., 2022). Importantly, GLMs allow for estimation of easily interpretable regression coefficients for assessing species' environmental responses and for informing management decisions.

2.4.1. State process

We used a hierarchical Bayesian framework to develop and fit a model jointly analyzing the BBS and eBird datasets through the integration of a common state process but utilizing different observation processes for the different datasets. Both datasets jointly estimate the latent abundance state ($N_{i,t}$) representing bobwhite abundance in 5 km x 5 km grid i in year t based on an intercept ($b0$), environmental covariate effects (βcov), and year effects ($\beta year$). We accounted for non-stationarity in bobwhite responses to environmental gradients through hierarchical regional partitioning of $b0$, βcov, and$\beta year$ (Smith and Edwards, 2021). We modeled βcov and $\beta year$ as varying by USDA Land Resource Regions (LRR, Fig. 1). LRRs are subset into 4 – 64 USDA Major Land Resource Areas (MLRA) over the study area. In total, our study area was divided into 17 LRR and 159 MLRA. We allowed $b0$ to vary based on MLRA to accommodate finer-scale variation in abundance. Grid-level abundance was then modeled as:

$$N_{i,t} \sim Poisson\left(\lambda_{i,t}\right) \tag{1}$$

$$log\left(\lambda_{i,t}\right) = b0\left[MLRA_{\mathrm{i}}\right] + \beta cov\left[LRR_{\mathrm{i}}\right]X_i + \beta year\left[LRR_{\mathrm{i}}\right]_t \tag{2}$$

where $b0[MLRA_{\mathrm{i}}]$ represents the MLRA-specific intercept for grid i, $\beta cov[LRR_{\mathrm{i}}]$ is a vector of LRR-specific covariate effects for grid i, X_i is a matrix of environmental covariates, and $\beta year[LRR_{\mathrm{i}}]_t$ is the LRR-specific year effect for grid i in year t. We incorporated quadratic effects of fire frequency and the land cover and structure covariates to allow for non-linear effects on abundance (Table B.1). $\beta year$ was set to 0 for the first year of the study (2018). We modeled values of $b0$ for MLRA m as arising from a Normal process around a corresponding LRR-specific mean:

$$b0_m \sim Normal\left(\mu.b0^{\mathrm{LRR}}\left[LRR_m\right], \sigma.b0^{\mathrm{LRR}}\left[LRR_m\right]\right) \tag{3}$$

We then modeled values of $\mu.b0^{\mathrm{LRR}}$ for LRR l as arising from a Normal process with a global mean and standard deviation:

$$\mu.b0_l^{LRR} \sim Normal(\mu.b0, \sigma.b0) \tag{4}$$

We modeled hierarchical effects on βcov and $\beta year$ in a similar manner as *eq*.4. We note that this modeling framework does not explicitly model spatial autocorrelation but will partially account for spatial autocorrelation through MLRA-specific intercepts and LRR-specific coefficients. We chose this model formulation to enable estimation of clearly-interpretable covariate effects within ecologically relevant geographic regions for informing local bobwhite management.

2.4.2. BBS detection process

Observers record all birds detected within a 400-m radius on BBS surveys, meaning that each BBS stop surveys only 2 % of the area of a 5 km x 5 km grid. As we used covariates to model abundance at the grid-level, we assumed a common abundance across BBS stops within a grid and year. We therefore modeled abundance ($N_{i,t}^{BBS}$) at BBS stops in grid i

in year t as:

$$N^{BBS}_{i,t} \sim Binomial\left(0.02, N_{i,t}\right) \tag{5}$$

We then modeled the number of bobwhite detected on BBS survey j in grid i in year t ($y^{BBS}_{j,i,t}$) as a realization of a Binomial process based on $N^{BBS}_{i,t}$ and the BBS detection probability ($p^{BBS}_{j,i,t}$). $p^{BBS}_{j,i,t}$ was modeled based on survey-level covariates of the presence or absence of extraneous background noise ($noise_{j,i,t}$) and number of passing cars ($car_{j,i,t}$), such that the BBS likelihood was specified as:

$$y^{BBS}_{j,i,t} \sim Binomial\left(p^{BBS}_{j,i,t}, N^{BBS}_{i,t}\right) \tag{6}$$

$$logit\left(p^{BBS}_{j,i,t}\right) = b0^{BBS} + b1^{BBS}noise_{j,i,t} + b2^{BBS}car_{j,i,t} \tag{7}$$

2.4.3. eBird detection process

In contrast to BBS, the area surveyed on eBird checklists is often not known precisely. We therefore modeled observed bobwhite counts ($y^{eBird}_{e,i,t}$) on checklist e in grid i in year t directly as a function of grid-level abundance and the eBird detection probability ($p^{eBird}_{e,i,t}$). $p^{eBird}_{e,i,t}$ was modeled as a function of checklist type (a binary variable with $type_{e,i,t} = 0$ for stationary checklists), duration ($time_{e,i,t}$), and distance ($dist_{e,i,t}$). We only included the distance covariate as an interaction with checklist type because distance is only informative for traveling counts (i.e., will always be 0 for stationary counts).

$$y^{eBird}_{e,i,t} \sim Binomial\left(p^{eBird}_{e,i,t}, N_{i,t}\right) \tag{8}$$

$$logit\left(p^{eBird}_{e,i,t}\right) = b0^{eBird} + b1^{eBird}type_{e,i,t} + b2^{eBird}time_{e,i,t} + b3^{eBird}dist_{e,i,t}type_{e,i,t} \tag{9}$$

We standardized all continuous detection covariates prior to analysis.

2.5. Model implementation

We implemented SDMs in NIMBLE (de Valpine et al., 2017) via R v. 4.1.1 (R Core Team, 2020). We drew posterior samples from three Markov chain Monte Carlo (MCMC) chains of 200,000 iterations, with burn-in phases of 40,000 iterations and thinning rates of 25. We evaluated convergence through visual assessments of trace plots. The model took approximately 71 h when run in parallel with 3 cores on a 4th Generation AMD EPYC™ processor. Unless otherwise noted, we report medians and 95 % credible intervals of posterior samples in the Results. A summary of posterior samples is provided in Table C.1.

2.6. Validation

To assess the efficacy of data integration, we ran three versions of the model: (1) the fully integrated model, (2) an eBird-only model, and (3) a BBS-only model. We assessed out-of-sample prediction performance for each model as in Strebel et al. (2022) by randomly removing some grids from each dataset as validation datasets. We ensured adequate spatial coverage by randomly removing ~10 % of grids for each dataset in each LRR. In total, we used 1369 grids for BBS and 4565 grids for eBird as validation datasets. We fit the models on the training data (without the validation data, see Results) and used the posterior samples of $b0$, βcov, the average across years of $\beta year$, and the cell-specific covariate values at each grid cell in the validation dataset to predict the expected abundance (λ^{exp}_i) at each grid cell via Eq. (2). We then calculated the predicted counts on BBS validation surveys via *eqs. 5 – 7* and the predicted counts on eBird validation surveys via *eqs. 8 – 9* using the respective survey-level detection covariates. We then calculated the root mean squared prediction error (RMSPE) between the observed and predicted counts. We also assessed the effect of the regional partitioning of regression coefficients by running a spatially-stationary model, i.e., replacing $\beta cov[LRR_i]$ with the global mean for the covariate effect ($\mu.\beta cov$) in Eq. (2), which we refer to as the spatially-stationary integrated model. The spatially-stationary integrated model still incorporated regional partitioning of the intercept and year effects, just not the covariate effects.

2.7. Predicting abundance across the range

We predicted λ^{exp}_i at each of the 182,455 cell across the study area for each of the four scenarios (integrated model, eBird-only model, BBS-only model, and spatially-stationary integrated model) as described in Section 2.6. Most detected birds in the BBS and eBird data are likely to be males, as both datasets were collected during the early breeding season when males are easily-detectable (i.e., calling to defend territories and attract mates). We therefore assumed λ^{exp}_i to assess male bobwhite abundance in a given grid cell. We converted to density by multiplying λ^{exp}_i by 2 (assuming a 50/50 sex ratio) and dividing by the area of the grid cell (2500 ha). We set an upper limit on bobwhite abundance for all λ^{exp}_i predictions. We enforced this limit because predictions would occasionally (<0.01 % of posterior predictions) predict unrealistically high abundance (e.g., millions or billions of birds in a grid cell) in preliminary analyses; these mainly occurred with positive quadratic covariate effects and grid cells with extreme covariate values. Bobwhite densities can reach 6.6 birds/ha in areas of high-quality habitat (Brennan et al., 2020), corresponding to a maximum possible male abundance of 8250 in a 5 km x 5 km grid cell (assuming a 50/50 sex ratio). In a preliminary analysis without an upper limit, posterior samples of λ^{exp}_i at grid cells in the training data never exceeded 3000. Setting an upper limit on λ^{exp}_i is therefore likely to only affect predictions and not model estimation. Bobwhite form aggregations during the non-breeding season with minimum sizes of ~ 8 individuals (Brennan et al., 2020); therefore, we defined the bobwhite range as including grid cells with $\lambda^{exp}_i \geq 8$ (0.0032 birds/ha). We provide a table of median predicted bobwhite density for each MLRA in Table D.1.

3. Results

Our final training dataset consisted of 136,610 eBird checklists and 175,823 BBS surveys from 41,810 and 12,412 grid cells, respectively. These surveys generated 33,739 bobwhite detections in the eBird dataset and 16,752 detections in the BBS dataset. Analysis of trace plots suggested adequate convergence for detection, global mean intercept, and covariate parameters; however, model convergence was limited for a few of the MLRA-specific intercepts and LRR-specific covariate effects. Limited convergence seemed to occur most frequently in areas containing both very high and very low density (such as LRRs I and T) or for environmental covariates which exhibited limited variability in the LRR (such as snow days in the southern LRRs).

The map of predicted density revealed that the bobwhite range covers much of the eastern U.S., with the range extending to far-eastern New Mexico and Colorado along the western edge and through southern South Dakota, mid-Iowa, and northern Illinois, Indiana, and Ohio along the northern edge (Fig. 2). The predicted bobwhite range barely extended into Michigan and Pennsylvania, while no areas of Wisconsin were predicted to be viable for bobwhite (i.e., highest predicted abundance was only about 2 birds/grid cell, or 0.0008 birds/ha, in the state). Within the range, the SDM identified three major regions with high bobwhite abundance. The first region was in the southern tip of Texas (LRR I), which exhibited the highest predicted densities across the range (i.e., some grid cells reaching the maximum possible predicted density of 6.6 birds/ha). The second region encompassed the Great and Midwestern Plains (LRRs H and M), extending from northern Texas north through Nebraska and east to Kentucky and Ohio. The last major region

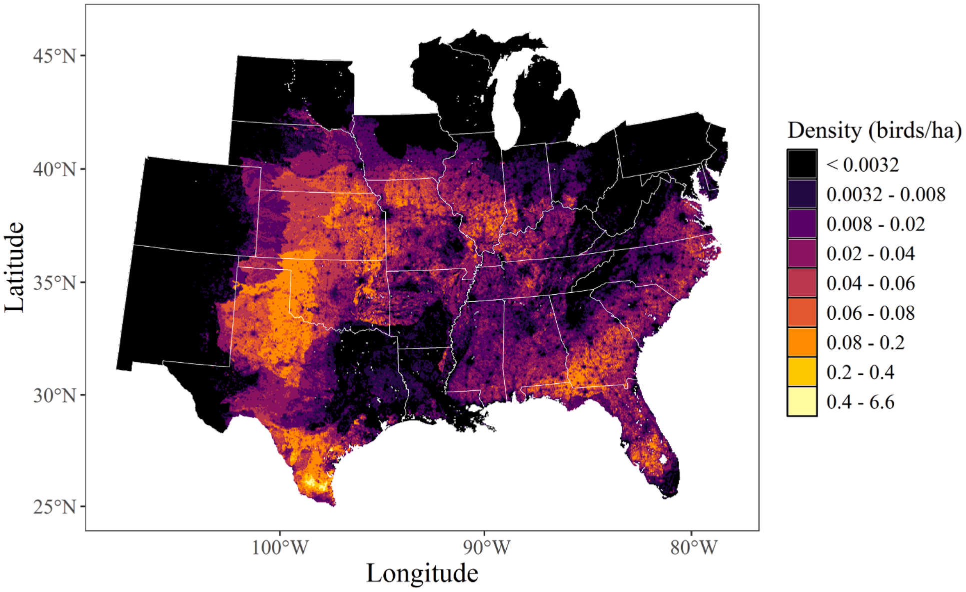

Fig. 2. Model predictions of median density (birds/ha) of northern bobwhite (*Colinus virginianus*) across the eastern United States from a species distribution model integrating North American Breeding Bird Survey and eBird data. Warmer colors represent areas of higher predicted density. Model predictions were in the form of expected abundance/grid cell, which we assumed to be largely representative of male abundance and converted to bird density based on a 50/50 sex ratio and the area of grid cells (2500 ha). Grid cells with predicted abundance < 8 birds (0.0032 birds/ha) were considered to be unviable for bobwhite persistence.

was in the southeastern U.S. and primarily encompassed the Atlantic Coastal Plain (LRRs P, T, and U). Abundance in this region was centered in southern Georgia and northern Florida, with an additional area of high abundance in central Florida, and extended north along the coastal plain to Virginia. Median predicted densities in the second and third regions reached 0.19 and 0.29 birds/ha, respectively. Predicted density was low in the Appalachian region, the Mississippi Delta, the Florida Everglades, and the Blackland Prairie/Oak Woods and Prairies regions of Texas. Coefficients of variation of predicted density were generally inversely correlated with density estimates and were highest along the edges of the range in western Colorado and New Mexico, northern South Dakota, and the Upper Peninsula of Michigan (Fig. E.1).

Predicted abundances across grid cells for the integrated SDM were generally more highly correlated with predictions from the eBird-only SDM (r^2: 0.66, 0.28 – 0.79) than the BBS-only SDM (r^2: 0.49, 0.26 – 0.61); however, uncertainty was high and the strength of correlations differed by LRR (Table F.1). Spatial predictions of bobwhite distributions were relatively similar between the integrated model and single data source models, with each predicting a similar distribution of the 3 major areas of bobwhite abundance. Despite this, predicted abundance values varied widely between the three models (Figs. 2, 3). In particular, predicted abundance values for the eBird-only model were far lower than for the integrated model. This led to a greatly diminished bobwhite range predicted from the eBird-only model compared to the integrated model (Fig. 3A), as many grid cells predicted to be occupied by the integrated model were predicted to be below the 8 bird threshold by the eBird-only model. In contrast, the spatial extent of the BBS-only model was largely similar to the integrated model; however, abundance estimates from the BBS-only model were substantially higher, especially within the three main bobwhite regions (Fig. 3B). The BBS-only model also estimated higher bobwhite density in central Texas (between southern Texas and the start of the Great/Midwestern Plains region), northeastern Louisiana, and the edge of the range on the Nebraska/South Dakota border. These relative differences in predicted local abundance led to substantial differences in estimates of total bobwhite abundance summed within the estimated range, with abundance estimates from the integrated model being between those of the eBird-only and BBS-only models. Total bobwhite abundance within the range was estimated at 8,577,291 (8,292,554–8,933,202) by the integrated model, 179,327 (122,064–258,751) by the eBird-only model, and 16,417,536 (15,626,753–17,510,721) by the BBS-only model. Out-of-sample prediction accuracy was similar between models for both the BBS (integrated RMSE: 0.48; BBS-only RMSE: 0.49) and eBird (integrated RMSE: 0.90; eBird-only RMSE: 0.90) data likelihoods; however, precision of grid-level abundance estimates was higher for the integrated model than for the single data source models after accounting for regional variation in CV (Table G.1).

LRR-specific regional partitioning of regression coefficients revealed that bobwhite responses to many environmental covariates varied across the range (Figs. H.1 – H.16). For example, snow days had a negative effect on bobwhite abundance at the northern edge of the range (e.g., LRRs F, M, L, R) but not the southern edge (e.g., LRRs I, J, P, Fig. 4, Fig. H.3). Despite the regional variation, eight environmental covariates exhibited significant linear or quadratic effects on bobwhite abundance at the global level (Fig. 5, Table C.1). Globally, abundance was positively linearly related to max temperature (1.38, 0.15 – 2.81) and row crop cover (0.45, 0.17 – 0.72) but negatively linearly related to snow days (-3.09, -5.43 – -0.90), deciduous cover (-0.34, -0.72 – -0.08), water cover (-0.16, -0.31–-0.03), and urban intensity (-0.44, -0.65 – -0.19). In particular, bobwhite abundance was predicted to be near zero when max temperatures were below 20 °C and the number of snow days were above 20 (Fig. 5). Grassland and shrub cover exhibited curvilinear relationships with abundance, having positive linear effects (grassland: 0.50, 0.28 – 0.75; shrub: 0.70, 0.08 – 1.28) and negative quadratic effects (grassland: -0.23, -0.47 – -0.07; shrub: -3.68, -6.72 – -1.24). Globally, bobwhite abundance peaked at ∼ 30 % grassland cover; however, LRRs encompassing southern Texas and the Great/Midwestern Plains (H, I, M) exhibited straight linear or quadratic increases in abundance with grassland, while other LRRs peaked between 20 – 50 % grassland cover (Fig. 4, Fig. H.5). Similarly, abundance peaked at ∼ 4 % shrub cover at the global level, but LRR-specific peaks ranged up to 30 % shrub cover (Fig. H.11).

Abundance predictions from the spatially-stationary integrated SDM were largely similar to predictions from the spatially-non-stationary integrated SDM, though the spatially-stationary integrated model generally predicted smoother range edges and higher densities in areas unlikely to be suitable for bobwhite, such as the Mississippi River Delta and the Everglades (Fig. I.1). Out-of-sample prediction accuracy of the

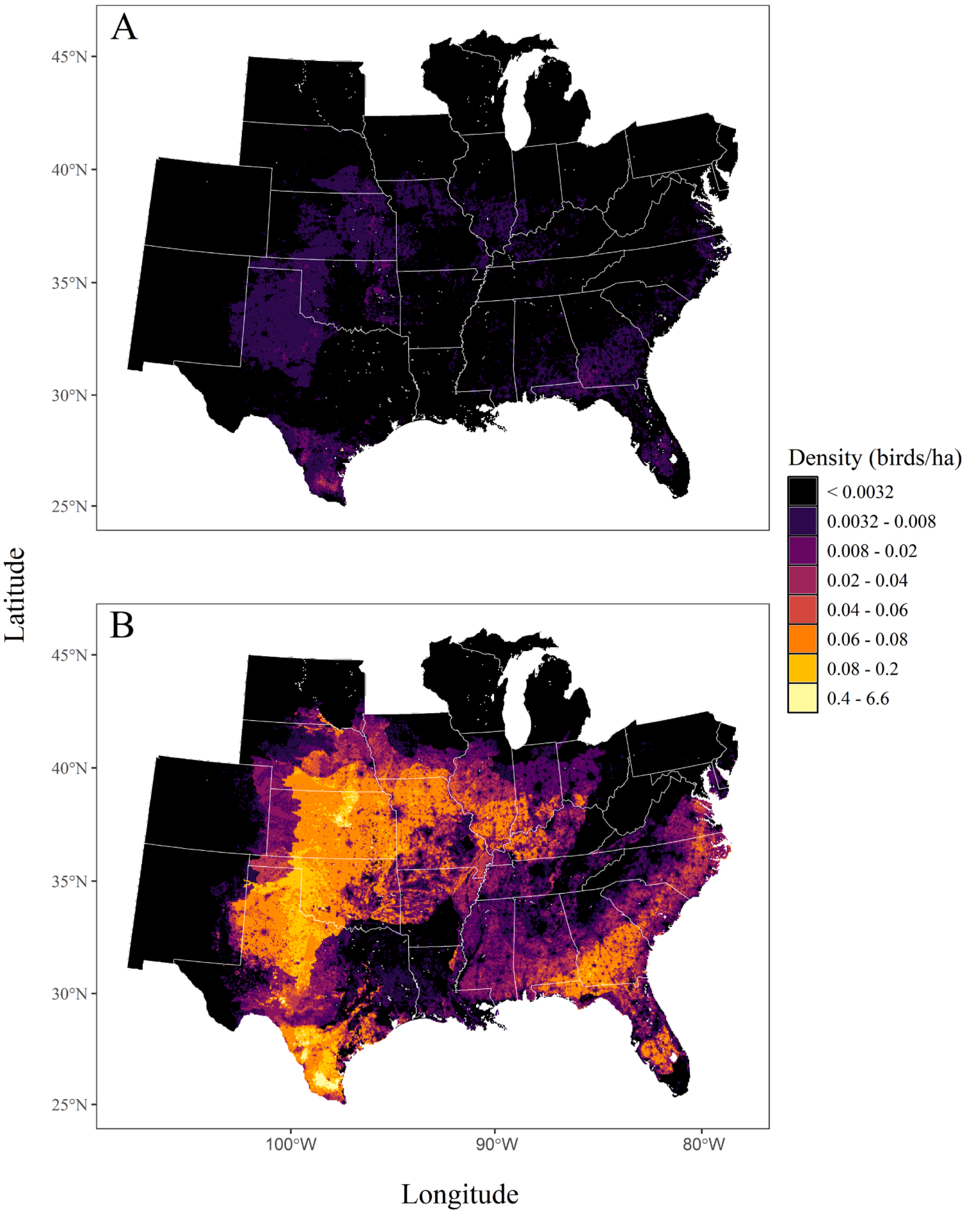

Fig. 3. Model predictions of median density (birds/ha) of northern bobwhite (*Colinus virginianus*) across the eastern United States from species distribution models fit using either only eBird data (A) or only North American Breeding Bird Survey data (B). Warmer colors represent areas of higher predicted density. Model predictions were in the form of expected abundance/grid cell, which we assumed to be largely representative of male abundance and converted to bird density based on a 50/50 sex ratio and the area of grid cells (2500 ha). Grid cells with predicted abundance $<$ 8 birds (0.0032 birds/ha) were considered be unviable for bobwhite persistence. Note that the density scale is the same as in Fig. 2.

spatially-stationary model was comparable for the BBS (RMSE: 0.48) but slightly worse for the eBird (RMSE: 0.92) data likelihoods compared to the spatially-non-stationary integrated model. Despite the relative similarities, estimated covariate effects differed substantially between the spatially-stationary and spatially-non-stationary integrated models, such that patterns from one portion of the range often masked effects in other regions with the spatially-stationary integrated model (Table C.1, Table I.2). For example, the spatially-stationary integrated model estimated a negative effect of precipitation on bobwhite abundance; however, this was mostly driven by eastern LRRs (N, P, T) while bobwhite in LRRs covering southern Texas and the Great/Midwestern Plains (H, I, M) were positively associated with rainfall (Fig. 4, Fig. H.2). Similarly, the spatially-stationary integrated model estimated a positive linear and negative quadratic effect of fire frequency on bobwhite density. This was mostly driven by effects in the southeastern U.S. (LRRs P, T) but masked a negative effect of fire frequency in southern Texas (LRR I, Fig. 4, Fig. H.16). In contrast, the spatially-non-stationary integrated model estimated non-significant global effects of precipitation and fire frequency on bobwhite abundance.

4. Discussion

We successfully developed an integrated SDM that jointly exploited the information contained in multiple, disparate datasets to predict density of bobwhite across the United States. Our prediction of the spatial extent of the bobwhite range is similar to previous estimates of bobwhite distributions (Schindler et al., 2022; Ziolkowski et al., 2022); however, our distribution map was generated at a much finer scale than previous studies. For example, our study estimated density in 5 km x 5 km grid cells while Schindler et al. (2022) estimated density within 111 km x 111 km grids. Our use of an abundance-based SDM showed that abundance was not constant across the range but was instead

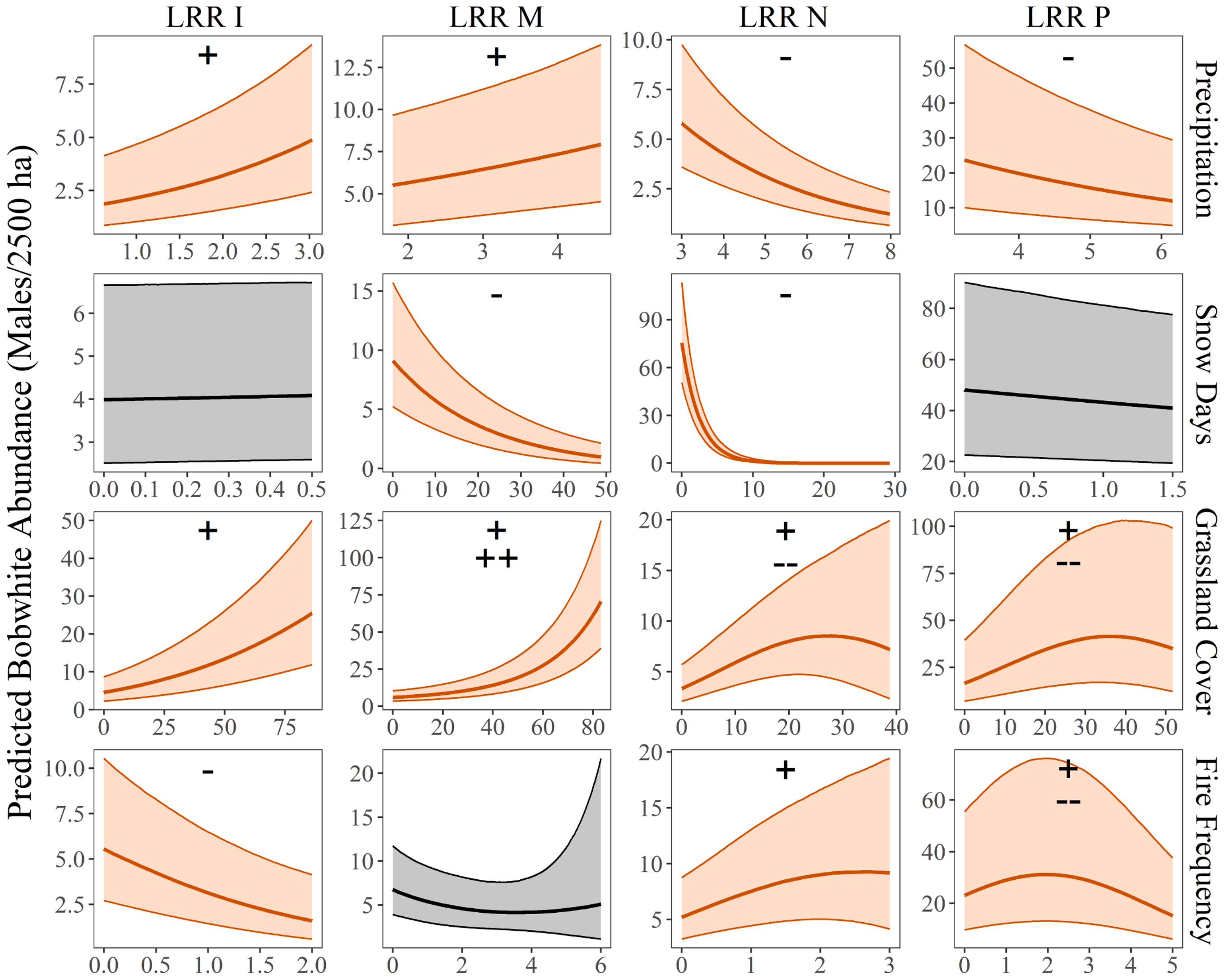

Fig. 4. Predictions for the effect of select environmental covariates on density (males/2500 ha) of northern bobwhite (*Colinus virginianus*) across select USDA Land Resource Regions (LRR) from a spatially-non-stationary species distribution model integrating eBird and North American Breeding Bird Survey data. Selected environmental covariates include mean daily precipitation (mm, top row), mean number of days with snow depth greater than 2.5 cm (snow days, second row), percentage cover of grassland (third row), and the number of recorded fires over a 16-year period (fire frequency, bottom row). Selected LRRs are I (leftmost column), M (second column), N (third column), and P (rightmost column). See Fig. 1 for a description of LRRs. Predictions are shown across the general range of covariate values observed in each LRR over the study duration and were generated using LRR-specific intercepts and year effects. Lines represent median prediction estimates across posterior samples. Predictions generally exhibited high uncertainty, especially at the high end of the covariate range, so we denote 85 % credible intervals of the model predictions (shaded region) to better visualize median trends. LRR-specific covariate effects with significant positive or negative linear effects (95 % credible intervals do not overlap 0) are denoted with symbols "+" or "-", respectively, while significant quadratic effects are denoted with double symbols. LRRs with a significant covariate effect on abundance are colored vermilion.

concentrated in three major regions, southern Texas, the Great and Midwestern Plains, and the coastal plain of the southeastern U.S. into central Florida, all of which have experienced bobwhite population declines over the past several decades (Hernández et al., 2013; Sauer et al., 2020). Conservation funding is often limited and cannot be implemented everywhere within the range; our results suggest that WLFW and other bobwhite initiatives aimed at reversing broad-scale bobwhite population declines should prioritize these three major regions for bobwhite conservation rather than lower-abundance regions (e.g., the Delmarva Peninsula or much of Mississippi, Louisiana, and northeastern Texas).

In biodiversity monitoring and ecology, multiple data sources are often available when examining the distribution of a species over a broad geographical area (Miller et al., 2019). Our SDM exploits the information from structured BBS and semi-structured eBird datasets by jointly estimating the latent grid-level abundance and allowing a separate observation process for each data source. Abundance predictions across the study area from the integrated model and the individual dataset models generally exhibited similar spatial patterns of occupancy (i.e., predicting the occurrence and distribution of the three main regions of bobwhite abundance). Out-of-sample predictive accuracy was also similar across models. The vast majority of surveys in the validation dataset consisted of either 0 (eBird: 86 %; BBS: 94 %) or 1 (eBird: 8 %; BBS: 4 %) bobwhite detections and so were largely assessing occupancy rather than abundance. Despite these similarities, the three models differed widely in absolute abundance estimates. While true abundance of bobwhite in the U.S. is not known exactly, the total range-wide abundance estimates from the eBird-only (0.17 million) and BBS-only (16 million) models are an order of magnitude lower and higher, respectively, than abundance estimates based on expert opinion from Partners in Flight (5.8 million, Rosenberg et al., 2016). eBird data had broad spatial coverage but appeared to underestimate density,

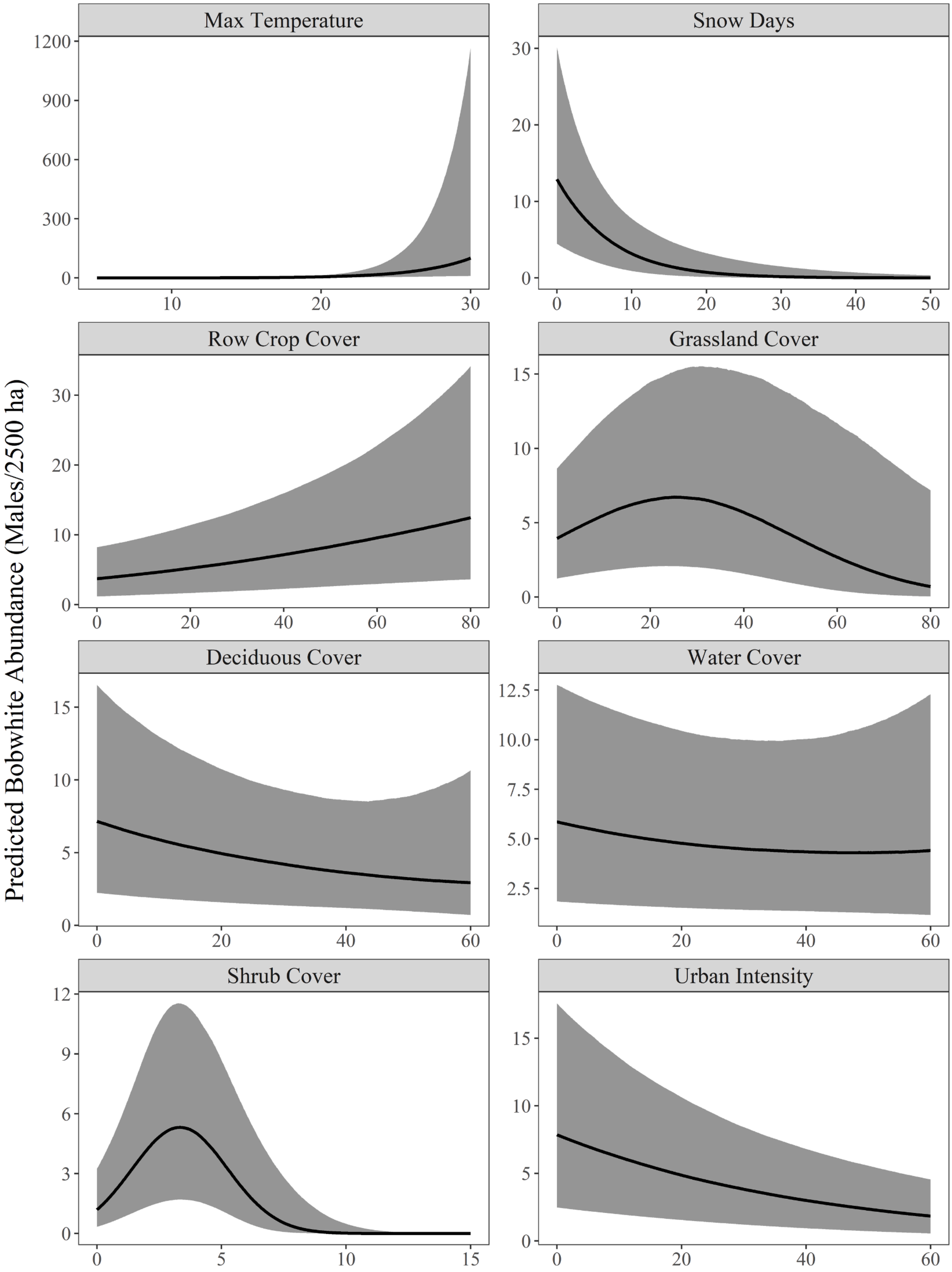

Fig. 5. Predictions of global mean covariate effects on density (males/2500 ha) of northern bobwhite (*Colinus virginianus*) in the eastern United States from a species distribution model integrating eBird and North American Breeding Bird Survey data. Predictions are shown for the six global covariates that exhibited significant (95 % credible intervals did not overlap 0) linear and/or quadratic effects on bobwhite density: mean daily maximum temperature (°C, max temperature), mean number of days with snow depth greater than 2.5 cm (snow days), urbanization intensity, and percentage cover of row crops, grassland, deciduous forest, water/wetlands (water), and shrubs. Lines represent median prediction estimates across posterior samples. Predictions generally exhibited high uncertainty, especially at the high end of the covariate range, so we denote 85 % credible intervals of the model predictions (shaded region) to better visualize median trends. Predictions were generated using the global mean intercept ($b0$) and average of year effects ($\beta year$).

likely due to the uncertainty in defining the survey area such that checklist counts had to be directly related to abundance at the 5 km x 5 km grid cell (Eq. (8)). Thus, counts on eBird surveys represent the minimum possible abundance/2500 ha, while counts from BBS surveys with known sampling area (400 m radius circle) represent the minimum possible abundance/50 ha. Checklist type, duration, and effort all had significant effects on detection probability (Table B.1); however, the eBird-only model appeared to still vastly overestimate detection probability (integrated $b0^{eBird}$: -4.23, -4.27 – -4.19; eBird-only $b0^{eBird}$: -1.67, -1.71 – -1.63, corresponding to median baseline detection probabilities of 0.014 and 0.159, respectively) and hence vastly underestimate abundance. In contrast, BBS data are associated with a known survey area but had limited spatial extent. Despite using data from over 1500 survey routes across the study area, BBS surveys were only conducted in 25 % of grids in the training dataset (compared to 84 % for eBird). In particular, BBS had limited coverage in some MLRAs, such that some of the $b0$ were likely to have been little informed by data and instead informed mostly through the hierarchical nested structure of the model. These results suggest that SDMs with complex hierarchical modeling using a single data source could be more suitable for occupancy rather than abundance analyses unless individual datasets have adequate spatial coverage and can adequately assess detection probability.

In contrast to the single data source models, integrating both eBird and BBS data with a joint-likelihood model generated a range-wide abundance estimate (8.5 million) which was much more similar to the Partners in Flight estimate. Discrepancies between our estimate and the Partners in Flight estimate may be due to the latter being based on expert opinion rather than statistical models. Alternatively, we assumed that predicted abundance was largely reflective of male abundance, so we converted to total density via a 50/50 sex ratio. Some females were likely detected on BBS and, especially, eBird surveys, such that model predictions may have represented abundance of males and some percentage of females. Multiplying this predicted abundance by 2 may therefore have led to overestimates of abundance. Regardless, data integration seemed to have greatly improved the accuracy of range-wide, and led to more precise LRR-specific, abundance estimates. In particular, the integrated model used the structured nature and defined study area of the BBS data to estimate the eBird detection process from grid cells in which both were present, and then combined this with the broader spatial extent of the eBird data to improve abundance estimation. Our work adds to a growing body of literature showing that integrating multiple datasets in an SDM framework can be a powerful tool for improving model performance (Fletcher et al., 2019; Isaac et al., 2020; Koshkina et al., 2017; Pacifici et al., 2017). Our integrated model combined the relative strengths of each data set while, at least partially, correcting for the weaknesses responsible for the poor abundance estimation with the individual data source models. Thus, our results show that data integration can be a powerful tool for overcoming the challenges associated with abundance-based SDMS (Strebel et al., 2022).

In addition to mapping predicted density across the eastern U.S., our work also shows the value of accounting for spatial-non-stationary in species' responses to environmental gradients across the range. Predicted bobwhite densities were largely similar between the spatially-stationary and spatially-non-stationary versions of the integrated SDM, suggesting that most of the spatial variation in abundance was explained by the MLRA-specific covariates rather than the regional partitioning of covariate regression coefficients. Despite this, inferences about the environmental drivers of bobwhite abundance differed greatly between the spatially-stationary and spatially-non-stationary models, with the spatially-stationary model masking many of the regional patterns observed with the spatially-non-stationary model. Regional differences in bobwhite responses were frequently observed with climate variables, including precipitation and snow days. Snow days negatively affected bobwhite abundance at the northern edge of the range but generally had little effect further south, likely reflecting northern birds living near their physiological and environmental tolerances (Brown, 1984; Holt et al., 2005). Periods of snow and cold temperatures can limit populations at the northern edge of the range through increasing energy demands, reducing food availability, and reducing overwinter survival (Janke et al., 2017; Wolske et al., 2023). Similarly, bobwhite density was positively associated with precipitation in southern Texas and the Great/Midwestern plains but was negatively related to abundance in much of the eastern U.S. Previous studies have also found positive effects of precipitation on bobwhite demography and abundance in the western portion of the range (Hernández et al., 2005; Lusk et al., 2001; Parent et al., 2016), attributable to the more arid climate. In contrast, the negative effect of precipitation on bobwhite abundance in the wetter southeastern U.S. may reflect adverse effects of extreme precipitation on recruitment and chick survival (Terhune et al., 2019). We incorporated climate variables as 6-year averages, though bobwhite populations may be more heavily affected by deviations rather than mean values (Lusk et al., 2001). Incorporating year-specific estimates of climatic variables rather than long-term averages could be implemented in future modeling efforts to potentially improve model performance.

Most land cover and land use covariates also exhibited regional variation in bobwhite responses, which could have led to incorrect inferences and management recommendations with a spatially-stationary model (Doser et al., 2024; Thorson et al., 2023). One example is the response of bobwhite to fire. Prescribed burns are frequently used to manage lands for bobwhite because they promote the growth of forbs and grasses used for food and cover, increase vegetative diversity, increase mobility, and reduce woody encroachment (Cram et al., 2002; Stoddard, 1931; Weber et al., 2022; Wellendorf and Palmer, 2009). The spatially-stationary integrated model estimated a curvilinear effect of fire frequency on bobwhite abundance. The spatially-non-stationary model, in contrast, revealed that this pattern was mostly driven by bobwhite responses in the southeastern U.S., where prescribed burns are frequently used to manage bobwhite within pine forests (Brennan et al., 2020; Jones and Chamberlain, 2004; Nolan et al., 2024; Weber et al., 2022). Assuming a spatially-stationary response to fire frequency masked a negative effect of fire in southern Texas. The more xeric conditions in this region cause vegetation to recover more slowly post-disturbance compared to in the southeastern U.S., such that frequent fires in southern Texas may prevent vegetation from recovering to a sufficient level to support bobwhite (Weber et al., 2022). Our results suggest that large-scale fires every ~ 8 – 10 years may be beneficial for bobwhite in the southeastern U.S. but are unlikely to promote bobwhite abundance in southern Texas. The optimal fire return interval of 8 – 10 years in the southeastern U.S. was surprising, as previous studies have generally found optimal prescribed fire return intervals of ~2 years for promoting bobwhite habitat in this region (McGrath et al., 2017; Weber et al., 2022; Wellendorf and Palmer, 2009). The higher optimal fire return interval in the southeastern U.S. observed in our study, and the lack of global-level fire effects for the spatially-non-stationary integrated model, may be attributable to issues of scale. Our burn data came from MTBS, which maps the distribution of large-scale fires over 202 ha in the eastern U.S. The average size of prescribed burns is usually smaller, averaging 96.7 ha in the Great Plains states (Ahamad, 2022) and 10.7 and 77.7 ha on private and public lands in the southeastern U.S., respectively (Cummins et al., 2023). Thus, our fire data did not adequately represent the distribution and frequency of small-scale prescribed burns specifically aimed at promoting bobwhite habitat and instead mostly represented wildfires. Incorporating spatial information on smaller-scale prescribed fires would likely improve inferences for future bobwhite modeling efforts.

Bobwhite populations also responded strongly to coverage of deciduous forest and grassland across the range. Bobwhite abundance was negatively related to deciduous forest cover, an effect which was relatively consistent across the LRRs spanning the three high-abundance regions (Fig. H.7). Bobwhite habitat requirements include an intermixing of grasses, herbaceous plants, and shrub cover (Brennan et al., 2020); however, encroachment by deciduous hardwoods can shade out the plant communities on which bobwhite rely (Peitz et al., 1997; Welch et al., 2004). Furthermore, forests and forest edges can harbor a higher abundance of bobwhite predators such as hawks (Seckinger et al., 2008; Thompson et al., 2014). Our results are consistent with previous bobwhite research showing that closed-canopy deciduous forests are unsuitable habitat for bobwhite (Ford et al., 2025; Howell et al., 2021; Lohr et al., 2011) and that hardwood management is likely to be broadly useful for promoting bobwhite habitat across the range (Palmer and Sisson, 2017; Ransom et al., 2008). The effect of grassland cover on bobwhite abundance was more complex. We found a global-level positive linear effect of grassland cover across the range, which is unsurprising given that bobwhite are frequently considered a grassland species and have been found to be positively associated with many other grassland bird species (Crosby et al., 2015; Riffell et al., 2008; Rosenblatt et al., 2022). Grassland cover was positively related to abundance in south Texas and the Great/Midwestern Plains; however, grassland cover in the eastern and southeastern U.S. also exhibited a negative quadratic relationship with bobwhite abundance. Bobwhite abundance in this region peaked at ∼ 20–30 % grassland cover, roughly corresponding to the optimal grassland cover for bobwhite along BBS routes reported by Roseberry and Sudkamp (1998). The decline in bobwhite abundance at higher grassland covers in this region could reflect bobwhite avoidance of large monocultures of exotic grasses such as fescue (*Lolium arundinaceum*). Our landcover data came from NLCD, which cannot discriminate between cover of native and non-native grasses (Olimb et al., 2018). Non-native grasses generally provide inadequate food and vertical structure, such that bobwhite often avoid non-native grass monocultures (Barnes et al., 1973; Hernández et al., 2013; Sands et al., 2012). The predictive accuracy of our model and the estimated effects of grassland cover would likely be improved through separating the effects of coverage of native vs. non-native grasses on bobwhite abundance, though we are not aware of any maps of native grass coverage across the entire study area.

Data integration in ecology has become a widespread approach to improve predictive power of SDMs over the past several decades (Emmet et al., 2023; Isaac et al., 2020; Miller et al., 2019). Our study provides an important example showing how structured and semi-structured data collected at different spatial scales and under different observation protocols can be integrated via a joint-likelihood framework to improve abundance estimation and, at least partially, correct for the limitations of individual datasets for abundance modeling. Our approach provides a flexible modeling framework for incorporating detection probability and hierarchical regional-partitioning of regression coefficients into abundance-based SDMs. Future efforts could focus on refining covariate values used in the models, such as incorporating yearly climate values or including measures of landscape structure (e.g., interspersion or contagion; Guthery, 1997; Roseberry and Sudkamp, 1998). We anticipate that our results will be broadly useful for informing local management decisions and for prioritizing areas of conservation action across the range, as is being implemented with the NRCS Areawide Networks to Connect Habitat and Optimize Resiliency (ANCHOR) program (Costanzo et al., 2025). Furthermore, regression coefficients from our model can be used to predict changes in the abundance and distribution of bobwhite based on future broad-scale conservation actions or climate change (Guisan et al., 2013; Porfirio et al., 2014). While we focused specifically on bobwhite, our modeling framework is likely to be applicable for modeling the environmental predictors of species distributions across a broad range of taxa.

CRediT authorship contribution statement

William B. Lewis: Writing – review & editing, Writing – original draft, Visualization, Validation, Formal analysis, Data curation. **Sprih Harsh:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis. **Patrick Freeman:** Writing – review & editing, Investigation, Data curation. **Victoria Nolan:** Writing – review & editing, Methodology. **Justin Suraci:** Writing – review & editing, Investigation, Data curation, Conceptualization. **Bridgett E. Costanzo:** Writing – review & editing, Funding acquisition, Conceptualization. **James A. Martin:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors have no conflicts of interest to report.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2025.111265.

Data availability

All data used in this manuscript are publicly available through eBird (Cornell Lab of Ornithology, National Audubon Society) and the North American Breeding Bird Survey (United States Geological Survey, Environment & Climate Change Canada). Formatted data and R and NIMBLE code for running the statistical model are archived on GitHub via Zenodo (DOI: 10.5281/zenodo.15441562).

References

Ahamad, M.G., 2022. Practice cost and size differences in invasive plant management strategies: an empirical analysis of US Great Plains states. Environ. Chall. 7. https://doi.org/10.1016/j.envc.2022.100474.

Allred, B.W., Bestelmeyer, B.T., Boyd, C.S., Brown, C., Davies, K.W., Duniway, M.C., Ellsworth, L.M., Erickson, T.A., Fuhlendorf, S.D., Griffiths, T.V., Jansen, V., Jones, M. O., Karl, J., Knight, A., Maestas, J.D., Maynard, J.J., McCord, S.E., Naugle, D.E., Starns, H.D., Twidwell, D., Uden, D.R., 2021. Improving Landsat predictions of rangeland fractional cover with multitask learning and uncertainty. Methods Ecol. Evol. 12, 841–849. https://doi.org/10.1111/2041-210X.13564.

Amburgey, S.M., Miller, D.A.W., Campbell Grant, E.H., Rittenhouse, T.A.G., Benard, M. F., Richardson, J.L., Urban, M.C., Hughson, W., Brand, A.B., Davis, C.J., Hardin, C. R., Paton, P.W.C., Raithel, C.J., Relyea, R.A., Scott, A.F., Skelly, D.K., Skidds, D.E., Smith, C.K., Werner, E.E., 2018. Range position and climate sensitivity: the structure of among-population demographic responses to climatic variation. Glob. Chang. Biol. 24, 439–454. https://doi.org/10.1111/gcb.13817.

Ashcroft, M.B., King, D.H., Raymond, B., Turnbull, J.D., Wasley, J., Robinson, S.A., 2017. Moving beyond presence and absence when examining changes in species distributions. Glob. Chang. Biol. https://doi.org/10.1111/gcb.13628.

Barnes, T.G., Madison, L.A., Sole, J.D., Lacki, M.J., 1973. An assessment of habitat quality for northern bobwhite in tall fescue-dominated fields. Source: Wildl. Soc. Bull. 23, 231–237.

Boersch-Supan, P.H., Robinson, R.A., 2021. Integrating structured and unstructured citizen science data to improve wildlife population monitoring. bioRxiv 2021.03.03.431294.

Brennan, L.A., 1991. How can we reverse the northern bobwhite population decline? Wildl. Soc. Bull. 19, 544–555.

Brennan, L.A., Hernandez, F., Williford, D., 2020. Northern Bobwhite (*Colinus virginianus*). In: Poole, A.F. (Ed.), Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.norbob.01.

Brown, J.H., 1984. On the relationship between abundance and distribution of species. Am. Nat. 124, 255–279.

Costanzo, B.E., Brennan, E.J., Olimpi, E.M., Suraci, J.P., 2025. ANCHOR: An opportunity to change landscape connectivity networks and conservation delivery at-scale in the U.S. Land 14, 385. https://doi.org/10.3390/land14020385.

Cram, D.S., Masters, R.E., Guthery, F.S., Engle, D.M., Montague, W.G., 2002. Northern bobwhite population and habitat response to pine-grassland restoration. J. Wildl. Manage. 66, 1031–1039.

Crosby, A.D., Elmore, R.D., Leslie, D.M., Will, R.E., 2015. Looking beyond rare species as umbrella species: northern Bobwhites (*Colinus virginianus*) and conservation of grassland and shrubland birds. Biol. Conserv. 186, 233–240. https://doi.org/10.1016/j.biocon.2015.03.018.

Cummins, K., Noble, J., Varner, J.M., Robertson, K.M., Hiers, J.K., Nowell, H.K., Simonson, E., 2023. The Southeastern U.S. prescribed fire permit database: hot spots and hot moments in prescribed fire across the Southeastern U.S.A. Fire 6, 372. https://doi.org/10.3390/fire6100372.

Dallas, T.A., Hastings, A., 2018. Habitat suitability estimated by niche models is largely unrelated to species abundance. Glob. Ecol. Biogeogr. 27, 1448–1456. https://doi.org/10.1111/geb.12820.

de Valpine, P., Turek, D., Paciorek, C.J., Anderson-Bergman, C., Lang, D.T., Bodik, R., 2017. Programming with models: writing statistical algorithms for general model structures with NIMBLE. J. Comput. Graph. Stat. 26, 403–413. https://doi.org/10.1080/10618600.2016.1172487.

Doser, J.W., Kéry, M., Saunders, S.P., Finley, A.O., Bateman, B.L., Grand, J., Reault, S., Weed, A.S., Zipkin, E.F., 2024. Guidelines for the use of spatially varying coefficients in species distribution models. Glob. Ecol. Biogeogr. 33, 1–13. https://doi.org/10.1111/geb.13814.

Duren, K.R., Buler, J.J., Jones, W., Williams, C.K., 2011. An improved multi-scale approach to modeling habitat occupancy of northern bobwhite. J. Wildl. Manag. 75, 1700–1709. https://doi.org/10.1002/jwmg.248.

Emmet, R.L., Benson, T.J., Allen, M.L., Stodola, K.W., 2023. Integrating multiple data sources improves prediction and inference for upland game bird occupancy models. Ornithol. Appl. 125, 1–13. https://doi.org/10.1093/ornithapp/duad005.

Fletcher, R.J., Hefley, T.J., Robertson, E.P., Zuckerberg, B., McCleery, R.A., Dorazio, R. M., 2019. A practical guide for combining data to model species distributions. Ecology. 100, 1–15. https://doi.org/10.1002/ecy.2710.

Ford, J.M., Tucker, A.M., Janke, A.K., Harms, T.M., Wilson, R.O., 2025. Effects of northern bobwhite habitat management on avian species of conservation concern. Ecol. Indic. 172. https://doi.org/10.1016/j.ecolind.2025.113310.

Franklin, J., 2023. Species distribution modelling supports the study of past, present and future biogeographies. J. Biogeogr. 50, 1533–1545. https://doi.org/10.1111/jbi.14617.

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., Moore, R., 2017. Google Earth Engine: planetary-scale geospatial analysis for everyone. Remote Sens. Env. 202, 18–27. https://doi.org/10.1016/j.rse.2017.06.031.

Greenfield, K.C., Chamberlain, M.J., Burger, L.W., Kurzejeski, E.W., 2003. Effects of burning and discing Conservation Reserve Program fields to improve habitat quality for northern bobwhite (*Colinus virginianus*). Am. Midl. Nat. 149, 344–353.

Guillera-Arroita, G., Lahoz-Monfort, J.J., Elith, J., Gordon, A., Kujala, H., Lentini, P.E., Mccarthy, M.A., Tingley, R., Wintle, B.A., 2015. Is my *species* distribution model fit for purpose? Matching data and models to applications. Glob. Ecol. Biogeogr. 24, 276–292. https://doi.org/10.1111/geb.12268.

Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., Regan, T.J., Brotons, L., Mcdonald-Madden, E., Mantyka-Pringle, C., Martin, T.G., Rhodes, J.R., Maggini, R., Setterfield, S.A., Elith, J., Schwartz, M.W., Wintle, B.A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M.R., Possingham, H. P., Buckley, Y.M., 2013. Predicting species distributions for conservation decisions. Ecol. Lett. 16, 1424–1435. https://doi.org/10.1111/ele.12189.

Guthery, F.S., 1997. A philosophy of habitat management for northern bobwhites. J. Wildl. Manage. 61, 291–301.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci. Adv. 1, 1–9. https://doi.org/10.1126/sciadv.1500052.

Hällfors, M.H., Liao, J., Dzurisin, J., Grundel, R., Hyvärinen, M., Towle, K., Wu, G.C., Hellmann, J.J., 2016. Addressing potential local adaptation in species distribution models: implications for conservation under climate change. Ecol. Appl. 26, 1154–1169. https://doi.org/10.1890/15-0926.

Hernández, F., Brennan, L.A., De Maso, S.J., Sands, J.P., Wester, D.B., 2013. On reversing the northern bobwhite population decline: 20 years later. Wildl. Soc. Bull. 37, 177–188. https://doi.org/10.1002/wsb.223.

Hernández, F., Hernández, F., Arredondo, J.A., Bryant, F.C., Brennan, L.A., Bingham, R. L., 2005. Influence of precipitation on demographics of northern bobwhites in southern Texas. Wildl. Soc. Bull. 33, 1071–1079. https://doi.org/10.2193/0091-7648(2005)33[1071:iopodo]2.0.co;2.

Hill, L., Hector, A., Hemery, G., Smart, S., Tanadini, M., Brown, N., 2017. Abundance distributions for tree species in Great Britain: a two-stage approach to modeling abundance using species distribution modeling and random forest. Ecol. Evol. 7, 1043–1056. https://doi.org/10.1002/ece3.2661.

Holt, R.D., Keitt, T.H., Lewis, M.A., Maurer, B.A., Taper, M.L., 2005. Theoretical models of species' borders: single species approaches. Oikos 108, 18–27. https://doi.org/10.1111/j.0030-1299.2005.13147.x.

Howell, P.E., Terhune, T.M., Martin, J.A., 2021. Edge density affects demography of an exploited grassland bird. Ecosphere 12. https://doi.org/10.1002/ecs2.3499.

Isaac, N.J.B., Jarzyna, M.A., Keil, P., Dambly, L.I., Boersch-Supan, P.H., Browning, E., Freeman, S.N., Golding, N., Guillera-Arroita, G., Henrys, P.A., Jarvis, S., Lahoz-Monfort, J., Pagel, J., Pescott, O.L., Schmucki, R., Simmonds, E.G., O'Hara, R.B., 2020. Data integration for large-scale models of species distributions. Trends. Ecol. Evol. 35, 56–67. https://doi.org/10.1016/j.tree.2019.08.006.

Janke, A.K., Terhune, T.M., Gates, R.J., Long, C.R., 2017. Northern bobwhite population responses to winter weather along their northern range periphery. Wildl. Soc. Bull. 41, 479–488. https://doi.org/10.1002/wsb.779.

Jiménez, M., Triguero, I., John, R., 2019. Handling uncertainty in citizen science data: towards an improved amateur-based large-scale classification. Inf Sci (N Y) 479, 301–320. https://doi.org/10.1016/j.ins.2018.12.011.

Jiménez-Valverde, A., Aragón, P., Lobo, J.M., 2021. Deconstructing the abundance–suitability relationship in species distribution modelling. Glob. Ecol. Biogeogr. 30, 327–338. https://doi.org/10.1111/geb.13204.

Johnston, A., Ausden, M., Dodd, A.M., Bradbury, R.B., Chamberlain, D.E., Jiguet, F., Thomas, C.D., Cook, A.S.C.P., Newson, S.E., Ockendon, N., Rehfisch, M.M., Roos, S., Thaxter, C.B., Brown, A., Crick, H.Q.P., Douse, A., McCall, R.A., Pontier, H., Stroud, D.A., Cadiou, B., Crowe, O., Deceuninck, B., Hornman, M., Pearce-Higgins, J. W., 2013. Observed and predicted effects of climate change on species abundance in protected areas. Nat. Clim. Chang. 3, 1055–1061. https://doi.org/10.1038/nclimate2035.

Johnston, A., Fink, D., Reynolds, M.D., Hochachka, W.M., Sullivan, B.L., Bruns, N.E., Hallstein, E., Merrifield, M.S., Matsumoto, S., Kelling, S., 2015. Abundance models improve spatial and temporal prioritization of conservation resources. Ecol. Appl. 25, 1749–1756. https://doi.org/10.1890/14-1826.1.

Johnston, A., Hochachka, W.M., Strimas-Mackey, M.E., Ruiz Gutierrez, V., Robinson, O. J., Miller, E.T., Auer, T., Kelling, S.T., Fink, D., 2021. Analytical guidelines to increase the value of community science data: an example using eBird data to estimate species distributions. Divers. Distrib. 27, 1265–1277. https://doi.org/10.1111/ddi.13271.

Jones, J.D.J., Chamberlain, M.J., 2004. Efficacy of herbicides and fire to improve vegetative conditions for northern bobwhites in mature pine forests. Wildl. Soc. Bull. 32, 1077–1084.

Kéry, M., Gardner, B., Monnerat, C., 2010. Predicting species distributions from checklist data using site-occupancy models. J. Biogeogr. 37, 1851–1862. https://doi.org/10.1111/j.1365-2699.2010.02345.x.

Koshkina, V., Wang, Y., Gordon, A., Dorazio, R.M., White, M., Stone, L., 2017. Integrated species distribution models: combining presence-background data and site-occupany data with imperfect detection. Methods Ecol. Evol. 8, 420–430. https://doi.org/10.1111/2041-210X.12738.

Laundré, J.W., Hernández, L., López Medina, P., Campanella, A., López-Portillo, J., González-Romero, A., Grajales-Tam, K.M., Burke, A.M., Gronemeyer, P., Browning, D.M., 2014. The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? Ecology 95, 1141–1152. https://doi.org/10.1890/13-1083.1.

Levine, J.M., Rees, M., 2002. Coexistence and relative abundance in annual plant assemblages: the roles of competition and colonization. Am. Nat. 160, 452–467.

Lohr, M., Collins, B.M., Williams, C.K., Castelli, P.M., 2011. Life on the edge: northern bobwhite ecology at the northern periphery of their range. J. Wildl. Manag. 75, 52–60. https://doi.org/10.1002/jwmg.25.

Lusk, J.J., Guthery, F.S., Demaso, S.J., Lusk, J.J., 2001. Northern bobwhite (*Colinus virginianus*) abundance in relation to yearly weather and long-term climate patterns. Ecol. Modell.

MacArthur, R.H., 1972. Geographical Ecology. Harper & Row, New York.

Maxwell, S.L., Butt, N., Maron, M., McAlpine, C.A., Chapman, S., Ullmann, A., Segan, D. B., Watson, J.E.M., 2019. Conservation implications of ecological responses to extreme weather and climate events. Divers. Distrib. https://doi.org/10.1111/ddi.12878.

McGrath, D.J., Terhune, T.M., Martin, J.A., 2017. Northern bobwhite habitat use in a food subsidized pyric landscape. J. Wildl. Manag. 81, 919–927. https://doi.org/10.1002/jwmg.21254.

Miller, D.A.W., Pacifici, K., Sanderlin, J.S., Reich, B.J., 2019. The recent past and promising future for data integration methods to estimate species' distributions. Methods Ecol. Evol. 10, 22–37. https://doi.org/10.1111/2041-210X.13110.

Nolan, V., Yeiser, J.M., Costanzo, B., Martin, M.R., Mcguire, J.L., Delancey, C.D., Lewis, W.B., Martin, J.A., 2024. Effects of management practices on Northern Bobwhite *Colinus virginianus* density in privately owned working forests across the Southeastern United States. Ecol. Solut. Evid., e12352 https://doi.org/10.1002/2688-8319.12352, 1–13.

Northern Bobwhite, Grasslands and Savannas Framework: a framework for conservation action, Working Lands for Wildlife, 2022. National Resources Conservation Service (NRCS), Washington, DC, USA.

Olimb, S.K., Dixon, A.P., Dolfi, E., Engstrom, R., Anderson, K., 2018. Prairie or planted? Using time-series NDVI to determine grassland characteristics in Montana. GeoJournal 83, 819–834. https://doi.org/10.1007/s10708-017-9805-8.

Osborne, P.E., Foody, G.M., Suárez-Seoane, S., 2007. Non-stationarity and local approaches to modelling the distributions of wildlife. Divers. Distrib. 13, 313–323. https://doi.org/10.1111/j.1472-4642.2007.00344.x.

Osborne, P.E., Suárez-Seoane, S., 2002. Should data be partitioned spatially before building large-scale distribution models? Ecol. Modell. 157, 249–259.

Pacifici, K., Reich, B.J., Miller, D.A.W., Gardner, B., Stauffer, G., Singh, S., McKerrow, A., Collazo, J.A., 2017. Integrating multiple data sources in species distribution modeling: a framework for data fusion. Ecology 98, 840–850. https://doi.org/10.1002/ecy.1710.

Palmer, W.E., Sisson, D.C., 2017. Tall Timbers' Bobwhite Quail Management Handbook. Tall Timbers Press, Tallahassee, Florida, USA.

Parent, C.J., Hernández, F., Brennan, L.A., Wester, D.B., Bryant, F.C., Schnupp, M.J., 2016. Northern bobwhite abundance in relation to precipitation and landscape structure. J. Wildl. Manag. 80, 7–18. https://doi.org/10.1002/jwmg.992.

Peitz, D.G., Tappe, P.A., Shelton, M.G., 1997. Effects of retained pine and hardwood basal areas on percent cover of plants utilized by bobwhite quail. J. Ark. Acad. Sci. 51, 144–149.

Piirainen, S., Lehikoinen, A., Husby, M., Kålås, J.A., Lindström, Å., Ovaskainen, O., 2023. Species distributions models may predict accurately future distributions but poorly how distributions change: a critical perspective on model validation. Divers. Distrib. 29, 654–665. https://doi.org/10.1111/ddi.13687.

Porfirio, L.L., Harris, R.M.B., Lefroy, E.C., Hugh, S., Gould, S.F., Lee, G., Bindoff, N.L., Mackey, B., 2014. Improving the use of species distribution models in conservation planning and management under climate change. PLoS. One 9, 1–21. https://doi.org/10.1371/journal.pone.0113749.

Potts, J.M., Elith, J., 2006. Comparing species abundance models. Ecol. Modell. 199, 153–163. https://doi.org/10.1016/j.ecolmodel.2006.05.025.

Pulliam, H.R., 2000. On the relationship between niche and distribution. Ecol. Lett. https://doi.org/10.1046/j.1461-0248.2000.00143.x.

R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, R Foundation for Statistical Computing. https://doi.org/10.1007/978-3-540-74686-7.

Ransom, D., Lopez, R.R., Schulz, G.G., Wagner, J.S., 2008. Northern bobwhite habitat selection in relation to brush management in the rolling plains of Texas. West N. Am. Nat. 68, 186–193. https://doi.org/10.3398/1527-0904(2008)68[186:NBHSIR]2.0.CO;2.

Renner, I.W., Louvrier, J., Gimenez, O., 2019. Combining multiple data sources in species distribution models while accounting for spatial dependence and overfitting with combined penalized likelihood maximization. Methods Ecol. Evol. 10, 2118–2128. https://doi.org/10.1111/2041-210X.13297.

Riffell, S., Scognamillo, D., Burger, L.W., 2008. Effects of the Conservation Reserve Program on northern bobwhite and grassland birds. Env. Monit. Assess. 146, 309–323. https://doi.org/10.1007/s10661-007-0082-8.

Rodenhouse, N.L., Sherry, T.W., Holmes, R.T., 1997. Site-dependent regulation of population size: a new synthesis. Ecology 78, 2025–2042. https://doi.org/10.1890/0012-9658(1997)078[2025:SDROPS]2.0.CO;2.

Rosche, S.B., Moorman, C.E., Kroeger, A.J., Pacifici, K., Jones, J.G., Deperno, C.S., 2021. Effects of prescribed fire on northern bobwhite nesting ecology. Wildl. Soc. Bull. 45, 249–257. https://doi.org/10.1002/wsb.1183.

Roseberry, J.L., Sudkamp, S.D., 1998. Assessing the suitability of landscapes for northern bobwhite. J. Wildl. Manage. 62, 895–902.

Rosenberg, K.V., Kennedy, J.A., Dettmers, R., Ford, R.P., Reynolds, D., Alexander, J.D., Beardmore, C.J., Blancher, P.J., Bogart, R.E., Butcher, G.S., Camfield, A.F., Couturier, A., Demarest, D.W., Easton, W.E., Giocomo, J.J., Keller, R.H., Mini, A.E., Panjabi, A.O., Pashley, D.N., Rich, T.D., Ruth, J.M., Stabins, H., Stanton, J., Will, T., 2016. Partners in Flight Landbird Conservation Plan 2016: revision for Canada and Continental United States.

Rosenblatt, C.J., Matthews, S.N., Gates, R.J., Peterman, W.E., Shumar, M.B., 2022. Are northern bobwhites an umbrella species for open-land birds in Ohio? J. Wildl. Manag. 86, 1–22. https://doi.org/10.1002/jwmg.22141.

Sands, J.P., Brennan, L.A., Hernández, F., Kuvlesky, W.P., Gallagher, J.F., Ruthven, D.C., 2012. Impacts of introduced grasses on breeding season habitat use by northern bobwhite in the South Texas plains. J. Wildl. Manag. 76, 608–618. https://doi.org/10.1002/jwmg.305.

Sauer, J.R., Link, W.A., Hines, J.E., 2020. The North American breeding bird survey, analysis results 1966-2019. https://doi.org/10.5066/P96A7675.

Saunders, S.P., Farr, M.T., Wright, A.D., Bahlai, C.A., Ribeiro, J.W., Rossman, S., Sussman, A.L., Arnold, T.W., Zipkin, E.F., 2019. Disentangling data discrepancies with integrated population models. Ecology 100, 1–14. https://doi.org/10.1002/ecy.2714.

Schindler, A.R., Cunningham, S.A., Schafer, T.L.J., Sinnott, E.A., Clements, S.J., DiDonato, F.M., Mosloff, A.R., Walters, C.M., Shipley, A.A., Weegman, M.D., Zhao, Q., 2022. Joint analysis of structured and semi-structured community science data improves precision of relative abundance but not trends in birds. Sci. Rep. 12, 1–13. https://doi.org/10.1038/s41598-022-23603-0.

Seckinger, E.M., Burger, L.W., Whittington, R., Houston, A., Carlisle, R., 2008. Effects of landscape composition on winter survival of northern bobwhites. J. Wildl. Manage. 72, 959–969. https://doi.org/10.2193/2006-124.

Semper-Pascual, A., Burton, C., Baumann, M., Decarre, J., Gavier-Pizarro, G., Gómez-Valencia, B., Macchi, L., Mastrangelo, M.E., Pötzschner, F., Zelaya, P.V., Kuemmerle, T., 2021. How do habitat amount and habitat fragmentation drive time-delayed responses of biodiversity to land-use change? Proc. R. Soc. B: Biol. Sci. 288. https://doi.org/10.1098/rspb.2020.2466.

Smith, A.C., Edwards, B.P.M., 2021. North American Breeding Bird Survey status and trend estimates to inform a wide range of conservation needs, using a flexible Bayesian hierarchical generalized additive model. Ornithol. Appl. 123. https://doi.org/10.1093/ornithapp/duaa065.

Stoddard, H.L., 1931. The Bobwhite quail: Its habits, Preservation and Increase. Charles Scribner's Sons, New York, New York, USA.

Strebel, N., Kéry, M., Guélat, J., Sattler, T., 2022. Spatiotemporal modelling of abundance from multiple data sources in an integrated spatial distribution model. J. Biogeogr. 49, 563–575. https://doi.org/10.1111/jbi.14335.

Sullivan, B.L., Wood, C.L., Iliff, M.J., Bonney, R.E., Fink, D., Kelling, S., 2009. eBird: a citizen-based bird observation network in the biological sciences. Biol. Conserv. 142, 2282–2292. https://doi.org/10.1016/j.biocon.2009.05.006.

Suraci, J.P., Littlefield, C.E., Nicholson, C.C., Hunter, M.C., Sorensen, A., Dickson, B.G., 2023. Mapping connectivity and conservation opportunity on agricultural lands across the conterminous United States. Biol. Conserv. 278, 109896. https://doi.org/10.1016/j.biocon.2022.109896.

Terhune, T.M., Palmer, W.E., Wellendorf, S.D., 2019. Northern bobwhite chick survival and effects of weather. J. Wildl. Manag. 83, 963–974. https://doi.org/10.1002/jwmg.21655.

Theobald, D.M., 2013. A general model to quantify ecological integrity for landscape assessments and US application. Landsc. Ecol. 28, 1859–1874. https://doi.org/10.1007/s10980-013-9941-6.

Thompson, S.J., Arnold, T.W., Amundson, C.L., 2014. A multiscale assessment of tree avoidance by prairie birds. Condor 116, 303–315. https://doi.org/10.1650/CONDOR-13-072.1.

Thornton, M.M., Shrestha, R., Wei, Y., Thornton, P.E., Kao, S.-C., 2020. Daymet: daily surface weather data on a 1-km grid for North America, version 4.

Thorson, J.T., Barnes, C.L., Friedman, S.T., Morano, J.L., Siple, M.C., 2023. Spatially varying coefficients can improve parsimony and descriptive power for species distribution models. Ecography 2023, 1–13. https://doi.org/10.1111/ecog.06510.

Twedt, D.J., Wilson, R.R., Keister, A.S., 2007. Spatial models of northern bobwhite populations for conservation planning. J. Wildl. Manage. 71, 1808–1818. https://doi.org/10.2193/2006-567.

Valladares, F., Matesanz, S., Guilhaumon, F., Araújo, M.B., Balaguer, L., Benito-Garzón, M., Cornwell, W., Gianoli, E., van Kleunen, M., Naya, D.E., Nicotra, A.B., Poorter, H., Zavala, M.A., 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. Ecol. Lett. 17, 1351–1364. https://doi.org/10.1111/ele.12348.

VanDerWal, J., Shoo, L.P., Johnson, C.N., Williams, S.E., 2009. Abundance and the environmental niche: environmental suitability estimated from niche models predicts the upper limit of local abundance. Am. Nat. 174, 282–291. https://doi.org/10.1086/600087.

Waldock, C., Stuart-Smith, R.D., Albouy, C., Cheung, W.W.L., Edgar, G.J., Mouillot, D., Tjiputra, J., Pellissier, L., 2022. A quantitative review of abundance-based species distribution models. Ecography 2022, 1–18. https://doi.org/10.1111/ecog.05694.

Weber, D.A., Tanner, E.P., Terhune, T.M., Varner, J.M., Martin, J.A., 2022. Northern bobwhite and fire: a review and synthesis. Natl. Quail Symp. Proc. 9, 0–14. https://doi.org/10.7290/nqsp09v0ju.

Welch, J.R., Miller, K.V., Palmer, W.E., Harrington, T.B., 2004. Response of understory vegetation important to the northern bobwhite following imazapyr and mechanical treatments. Wildl. Soc. Bull. 32, 1071–1076.

Wellendorf, S.D., Palmer, W.E., 2009. Effects of two burn scales on northern bobwhite demographic parameters and home range size. Natl. Quail Symp. Proc. 6, 271–281. https://doi.org/10.7290/nqsp06qwx5.

Wolske, J.M., Behney, A.C., Powell, L.A., 2023. Nonbreeding season survival of northern bobwhite in northeastern Colorado. Wildl. Biol. e01126, 1–8. https://doi.org/10.1002/wlb3.01126.

Ziolkowski, D., Lutmerding, M., Aponte, V.I., Hudson, M.-A.R., 2022. North American breeding bird survey dataset 1966 - 2021. https://doi.org/10.5066/P97WAZE5.

Ziolkowski, D.J., Lutmerding, M., English, W.B., Hudson, M.-A.R., 2024. North American Breeding Bird Survey Dataset 1966 - 2023. https://doi.org/10.5066/P136CRBV.

Zipkin, E.F., Zylstra, E.R., Wright, A.D., Saunders, S.P., Finley, A.O., Dietze, M.C., Itter, M.S., Tingley, M.W., 2021. Addressing data integration challenges to link ecological processes across scales. Front. Ecol. Env. 19, 30–38. https://doi.org/10.1002/fee.2290.