



Modeling eighteen years of community science data reveals extensive recolonization of bobcats in Illinois, USA

Javan M. Bauder · Kirk W. Stodola ·
Thomas J. Benson · Craig A. Miller ·
Maximilian L. Allen

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Abstract

Context Many terrestrial mammals have undergone substantial distribution changes in recent decades; yet collecting broad-scale occurrence data for carnivores is difficult due to their low densities and cryptic behaviors. Carnivore observations from community (i.e., citizen) science programs can be a potentially valuable approach for understanding changes in carnivore distributions over long time periods.

Objectives We used 18 years of bobcat (*Lynx rufus*) observations collected by archery deer hunters (i.e., participants) across Illinois, USA, to estimate spatiotemporal patterns in occurrence and determine how landscape features influenced patterns of recolonization.

Methods We developed Bayesian spatial and non-spatial multi-scale dynamic occupancy models to estimate county-level occupancy, persistence, and colonization and participant-level occupancy. We modeled county-level parameters as a function of

multiple a priori landscape covariates and compared model predictive performance using cross-validation. **Results** Our non-spatial occupancy model had greater predictive support than our spatial occupancy model. Mean annual statewide county-level occupancy increased from approximately 0.43–0.83 while mean annual participant-level occupancy increased from approximately 0.07–0.28. Bobcats were primarily restricted to southern Illinois during the early 2000s but by 2018 occurred throughout western and southern Illinois. Landscape covariates had relatively weak effects on model parameters.

Conclusions Our study illustrates how community science observations analyzed with hierarchical occupancy models can be used to model spatiotemporal changes in species distributions. Bobcats have recolonized much of Illinois, but this colonization was not strongly mediated by county-level landscape features at the scales we measured.

Keywords Bobcat · Distribution · *Lynx rufus* · Occupancy · Expansion · Recolonization · Spatial occupancy model

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J. M. Bauder (✉) · K. W. Stodola · T. J. Benson ·
C. A. Miller · M. L. Allen
Illinois Natural History Survey, Prairie Research Institute,
University of Illinois, 1816 S. Oak Street, Champaign,
IL 61820, USA
e-mail: jbauder@arizona.edu

Introduction

Many carnivores, including grizzly bear (*Ursos arctos*), tiger (*Panthera tigris*), and leopard (*Panthera pardus*), have declined during the last two centuries due to habitat loss and fragmentation and

human-caused mortality for predator control or consumptive use (Laliberte and Ripple 2004; Ripple et al. 2014; Jacobson et al. 2016; Wolf and Ripple 2017; Marneweck et al. 2021). However, other carnivores, including golden jackal (*Canis aureus*), lion (*Panthera leo*), gray wolf (*Canis lupus*), European otter (*Lutra lutra*), and European pine marten (*Martes martes*), have increased in abundance in recent decades due to conservation measures including reductions in human-caused mortality (Arnold et al. 2012; Blackburn et al. 2016; Chapron et al. 2014; Sainsbury et al. 2019). Carnivore responses to human landscape alterations are often varied and may depend on life history traits (Sévêque et al. 2020; Suraci et al. 2021), landscape composition and configuration (Nickel et al. 2020), and the existing carnivore community (Wang et al. 2015; Rota et al. 2016). Mosaics of natural and human-modified habitats (e.g., urban and agriculture) may provide increased food resources (Bateman and Fleming 2012) or shelter from larger carnivores (Moll et al. 2018). Medium-sized carnivores (i.e., mesocarnivores) often benefit from the absence of larger carnivores and their ability to exploit human-modified landscapes (Hody and Kays 2018; Jachowski et al. 2020). Increased carnivore abundance can have cascading effects on ecological communities and systems (Estes et al. 2011; Ripple et al. 2014) and potentially lead to increased needs for managing human-wildlife conflict (Raithel et al. 2017; Lennox et al. 2018) and societal pressures for sustainable harvest (White et al. 2015). Successfully managing the ecological, economic, and societal aspects of carnivore conservation therefore requires an accurate understanding of the patterns and causes of dynamic carnivore distributions.

Wildlife managers and conservationists need to understand species distribution changes across relatively broad spatiotemporal extents (Jones 2011) as these are often the extents at which management decisions are made (Mason et al. 2006; Apollonio et al. 2010). However, systematic monitoring programs that would provide this type of understanding are often logistically and financially challenging to implement over broad spatiotemporal extents, even when collecting only occurrence (i.e., detection/non-detection) data (Farhadinia et al. 2018). This difficulty is particularly true for many carnivore species that are cryptic and occur at low densities (O’Connell et al. 2006). Community science (i.e., citizen science) may

offer alternative means for collecting large amounts of occurrence data across broad spatiotemporal extents (Devictor et al. 2010; Dickinson et al. 2010), and can be used to monitor carnivores (Mueller et al. 2019; Rafiq et al. 2019). Such community science data can be particularly valuable for modeling dynamic species distributions by allocating sampling effort along shifting distribution margins where low densities or imperfect species detection may make detections by formal standardized surveys untenable (Crum et al. 2017; Molinari-Jobin et al. 2018).

Hierarchical occupancy models provide substantial flexibility to account for multiple sources of variation within community science data to accurately model temporally dynamic species distributions. Like all field-based data, community science data suffers from imperfect detection, and failure to account for imperfect detection can result in biased or misleading inferences (Kery et al. 2010, 2013). Many community science programs use repeated site visits, that when analyzed using hierarchical occupancy models can account for imperfect detection (Kery et al. 2010). Hierarchical occupancy models are particularly well suited for investigating range dynamics by modeling changes in site occupancy using first-order Markov processes and site colonization and extinction parameters (i.e., occupancy at time t is dependent upon occupancy status at time $t-1$ (MacKenzie et al. 2003; Royle and Kéry 2007). This approach is particularly useful for species with expanding and contracting ranges because site occupancy dynamics are likely spatially dependent such that sites near previously occupied sites will have higher colonization probabilities (Hanski 1999; Bled et al. 2011; Heard et al. 2013; Saura et al. 2014). Imprecise locations in citizen science data can create challenges for modeling species-habitat relationships (Bauder et al. 2021), but multi-scale occupancy models permit the estimation of occupancy across multiple spatial scales (Nichols et al. 2008; Mordecai et al. 2011) thereby maximizing the information content of the data.

Bobcats (*Lynx rufus*) in Illinois, USA, provide an excellent case study with which to use community science data to model broad-scale carnivore distributions to quantify the recolonization of their former range. Bobcats declined markedly in the Midwest USA, including Illinois, due to large-scale loss of forest and prairie to agriculture and potential over-exploitation following European settlement in the

mid-1800s (Cory 1912; Mohr 1943; Larivière and Walton 1997; Woolf and Hubert 1998). Recreational harvest of bobcats in the Midwest USA was largely prohibited during the 1970s (Woolf et al. 2000) and bobcats subsequently began recolonizing the region (Woolf et al. 2002; Linde et al. 2012; Prange and Rose 2020). However, the extent of recolonization remains poorly documented. For example, bobcats were largely restricted to southern Illinois and the Mississippi and Illinois River corridors in western Illinois at the beginning of the millennium (Woolf et al. 2002) yet subsequent occurrence patterns are poorly understood. In 2016, the population of bobcats in Illinois was deemed sufficiently recovered to allow recreational harvest (Jacques et al. 2019). It is therefore important to understand both the past and current distribution of bobcats within Illinois to inform harvest regulations.

Bobcats within the Midwest USA are positively associated with natural land covers, including forest, grassland, and wetland, and negatively associated with row-crop agriculture (Woolf et al. 2002; Tucker et al. 2008; Linde et al. 2012; Clare et al. 2015; Popescu et al. 2021). Whereas some studies have found negative associations between bobcats and human development (Riley et al. 2003; Ordenana et al. 2010; Lesmeister et al. 2015), others have found more varied responses to human development and activity (Wang et al. 2015; Wait et al. 2018; Nickel et al. 2020). Bobcats in this region are also positively associated with natural habitat heterogeneity and edge (Preuss and Gehring 2007; Tucker et al. 2008; Linde et al. 2012; Wait et al. 2018) that may increase foraging opportunities and prey abundance (Litvaitis et al. 1986). However, forest and prairie cover in Illinois remains low relative to pre-European settlement levels (Iverson 1988; Walk et al. 2010). In highly altered landscapes, remnant patches of natural habitat may be important in promoting carnivore movement and recovery (Kramer-Schadt et al. 2004; Suraci et al. 2020; Popescu et al. 2021). However, carnivores (Hawley et al. 2016), including bobcats (Johnson et al. 2010; Hughes et al. 2019), have high dispersal potential and dispersing individuals may show lower habitat selectivity compared to resident adults (Elliot et al. 2014). These dispersal tendencies may mitigate the effects of anthropogenic landscape change for recovering carnivores and permit recolonization through relatively less connected landscapes.

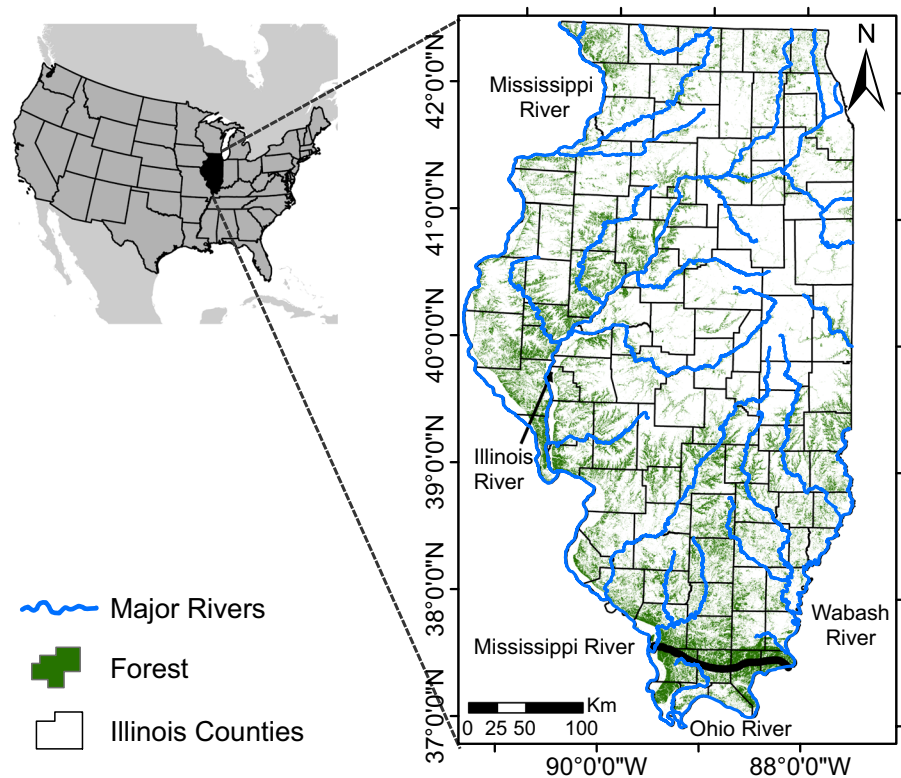
We examined the spatiotemporal patterns of occurrence and colonization for bobcats in Illinois to describe the extent of recolonization and determine how landscape features may have influenced this process. Specifically, we analyzed 18 years of statewide observations by archery deer hunters using spatial and non-spatial multi-scale dynamic occupancy models to account for multiple sources of variation and uncertainty. We hypothesized that, given expansion of occurrence of bobcats across the Midwest and USA (Roberts and Crimmins 2010), their occupancy would increase during our study at multiple spatial scales. Our second hypothesis was that changes in occupancy for bobcats would reflect habitat suitability and therefore predicted occupancy, colonization, and persistence for bobcats would have positive relationships with natural land cover amount and heterogeneity and have negative relationships with anthropogenically disturbed habitats (i.e., agriculture and urban land covers). Our third, and alternative, hypothesis was that high dispersal potential would result in temporal patterns of occupancy for bobcats that was largely independent of landscape features. We accordingly predicted relatively weak relationships between occupancy, colonization, and persistence and landscape features and stronger empirical support for our occupancy model incorporating the spatial arrangement of occupied sites.

Methods

Study area

Our study area included the entire state of Illinois which we describe in detail in Bauder et al. (2020) but briefly recount here. Illinois landscape composition varies latitudinally with the Chicago metropolitan area occurring in the northeast, intensive row-crop agriculture (primarily corn and soybean) dominating the northwest and central regions, and forest-agriculture mosaics with moderate topographic relief prevalent in southern Illinois (Fig. 1). Private lands make up over 95% of all Illinois (Prairie State Conservation Coalition 2022) and approximately 75% of Illinois is used for agriculture (U.S. Department of Agriculture 2017). The composition of Illinois' land covers did not change markedly during our study. Statewide elevation ranged from 85–380 m above sea level.

Fig. 1 Map of major river drainages and contemporary (2008) forest cover in Illinois. Northern boundary of the estimated distribution of bobcats during the 1970s is indicated by the thick black line (modified from Woolf and Hubert 1998)



Monthly minimum, maximum, and mean temperatures during our study ranged from -36.1 to 29.6 °C, -23.7 to 41.2 °C, and -11.7 to 28.5 °C, respectively. Monthly minimum, maximum, and mean precipitation totals ranged from 0–1 cm, 24–42 cm, and 5–11 cm, respectively, with most precipitation falling April through October as rain (Illinois Climate Network 2022).

Data collection

We used observations of bobcats from participating archery deer hunters during 2001–2018. Hunters were randomly sampled from adult Illinois residents who purchased archery permits, with the same hunters often participating multiple years. We sampled with replacement annually to replace hunters removed from the sample for non-participation. Hunters selected in the program (hereafter participants) received a standardized data sheet (i.e., species checklist) in the mail prior to the start of the archery deer hunting season (1 October) and collected data through 14 November as described in Bauder et al. (2021). Specifically, during each hunting event, participants

recorded the date, county hunted, time period (AM or PM, hereafter period), number of hours hunted, and number of target wildlife species (including bobcats) seen. We excluded incomplete or potentially erroneous records from subsequent analyses but did not otherwise subset our data. Although the number of participants hunting per county varied spatiotemporally, our hierarchical Bayesian model fully propagates parameter uncertainty due to sampling error from poorly sampled counties. We assumed that each participant hunted within the same general area within a given county during a given year. We believe this is a reasonable assumption given the prevalence of stand-based archery deer hunting (92.3% of surveyed archery deer hunters during 2015; C. Miller, unpublished data) and private land hunting within Illinois (> 80% of all archery deer hunters hunted exclusively on private lands in 2017, C. Miller unpublished data). We therefore considered multiple periods from the same hunter in the same county as repeated site visits.

Occupancy model

We combined previous applications of multi-scale (Nichols et al. 2008; Mordecai et al. 2011), spatial (Chandler et al. 2015; Zylstra et al. 2019), and dynamic (MacKenzie et al. 2003; Royle and Kéry 2007) occupancy models to model changes in occupancy of bobcats over time while accounting for imperfect detection. We accounted for the hierarchical nature of our data by modeling county- (ψ) and participant-level (θ) occupancy where the latter represented the probability that a bobcat was present within the effective sampling area of participant j conditional upon bobcats occurring within county i during year t such that:

$$z_{i,t} \sim \text{Bernoulli}(\psi_{i,t})$$

$$u_{i,t,j} | z_{i,t} \sim \text{Bernoulli}(\theta_{i,t,j})$$

The latent occupancy states for counties and participants are denoted by z and u , respectively. We then included an observation process assuming imperfect detection by participant j across period k so that detection probability was modeled as:

$$y_{i,t,j} | u_{i,t,j} \sim \text{Bernoulli}(p_{i,t,j,k})$$

We modeled ψ during the first year directly as a Bernoulli variable: $z_{i,1} \sim \text{Bernoulli}(\psi_{i,1})$. We then estimated county-level occupancy during all subsequent years as a function of county-level probability of persistence (ϕ) if a county was occupied ($z_{i,t}=1$) and probability of colonization (γ) if a county was unoccupied ($z_{i,t}=0$):

$$z_{i,t+1} | z_{i,t} \sim \text{Bernoulli}(\gamma_{i,t}(1 - z_{i,t}) + \phi_{i,t}z_{i,t})$$

Colonization and persistence are likely to vary depending on the proximity and arrangement of occupied sites (Hanski 1999). Bobcats likely recolonized Illinois from the southernmost counties (Woolf and Hubert 1998; Woolf et al. 2002). We therefore estimated pairwise colonization probabilities (ρ) between all counties using a Gaussian distance-decay function (Chandler et al. 2015). Under this model, the probability that county i becomes colonized by at least one individual from county j during year t is:

$$\rho_{i,t} = \rho_0 \exp(-d_{ij}^2 / (2\sigma^2)) z_{i,t}$$

where ρ_0 is a baseline colonization probability which can be modeled as a function of covariates and d_{ij}^2 is the Euclidean distance between the centroids of counties i and j . Counties in Illinois were generally similar in size (mean=1410 km², SD=578 km², range=415–3065 km², coefficient of variation=41.0%) so we did not expect biases from larger counties having more distant centroids. The scale parameter (σ) determines the colonization probability decay rate. This parameterization ensures that county i cannot be colonized by individuals from county j if the latter is unoccupied (i.e., $z_{j,t}=0$). We then calculated the cumulative probability of colonization for county i between years t and $t+1$ based on the occupancy status of and distance from all Illinois counties as:

$$\gamma_{i,t} = 1 - \prod(1 - \rho_{i,j,t})$$

The spatial arrangement of occupied counties could also influence persistence such that counties neighboring occupied counties have a higher probability of becoming recolonized immediately after becoming unoccupied (Hanski 1999). To incorporate such spatial effects on persistence we included a pseudo-rescue effect as: $\phi_{i,t} = 1 - \epsilon_{i,t}(1 - \gamma_{i,t})$ to allow occupied counties to become unoccupied (i.e., extinct) and subsequently recolonized between years t and $t+1$ (Chandler et al. 2015; Sutherland et al. 2014).

Landscape covariates

We measured landscape covariates using National Land Cover Data (NLCD) from 2001, 2004, 2006, 2008, 2011, 2013, and 2016 (30-m pixels; available at <https://www.mrlc.gov> downloaded on 24 Feb 2020). We re-projected each raster to NAD83 and reclassified each raster into eight classes (Supplementary Material, Table S1). We used the R (R Core Team 2020) package LANDSCAPEMETRICS (Hesselbarth et al. 2019) to calculate the proportion of each county that was forest, grassland, agriculture, urban, and wetland, county-level patch density, mean patch area, and clumpiness index for forest, grassland, agriculture, and wetland. We used the landscape metrics from the NLCD image closest in date to each participant's observation. We calculated county-level percent stream area (i.e., stream density) using NHD

flow lines data (U. S. Geologic Survey 2020) because natural habitats within the midwestern USA may be more concentrated along riparian areas (Tucker et al. 2008). We examined our covariates for collinearity and retained a single covariate from covariate pairs where $|r| \geq 0.70$. Our final landscape covariate list included the proportion of forest cover, forest patch density, forest clumpiness index, grassland mean patch area, grassland clumpiness index, the proportion of wetland cover, wetland patch density, percent stream area, and the proportion of urban cover. Lower values of clumpiness index indicate increasingly disaggregated and decreasingly clumped patches of a given land cover class independent of patch area (McGarigal et al. 2002). Collinearity was relatively low across these covariates ($|r| < 0.70$ and variance inflation factors < 5.00 , Table S2). We z -score standardized all covariates.

Model fitting

We modeled initial county-level occupancy ($\psi_{t=1}$), persistence (ϕ), and baseline colonization (ρ_0) as logit-linear functions of the nine landscape covariates described above because landscape characteristics could affect different aspects of bobcats recolonization, particularly along the distribution margin and in highly anthropogenically modified landscapes such as Illinois. We modeled participant-level occupancy (θ) using additive Gaussian-distributed random effects of county and year because we lacked sub-county locality data for individual participants. We also modeled baseline colonization and detection (p) using a Gaussian-distributed random effect of year. We modeled persistence using a fixed linear effect of year because a random effect of year would not converge. We specifically predicted that the aforementioned parameters (except colonization) would increase as bobcats recolonized Illinois. We additionally modeled detection as a function of the number of hours hunted per period and whether a period was during AM or PM hours. Finally, to account for bobcats being most abundant in southern Illinois at the beginning of our study (Woolf and Hubert 1998; Woolf et al. 2002), we modeled initial county-level occupancy as a linear function of the Euclidean distance (km) of each county's centroid from the southernmost point in Illinois.

To evaluate the effects of spatial dependence in county-level colonization, we also fit a non-spatial

dynamic multi-scale model where we estimated county-level colonization (γ) without regards to neighboring occupancy status. We included the same covariates (fixed and random effects) in the non-spatial model as in the spatial model. To account for the hypothesized northward expansion of bobcats in Illinois within our non-spatial model, we also included distance from the southern boundary of Illinois as a covariate for all non-spatial model parameters. We compared the predictive performance of the spatial and non-spatial models using five-fold cross-validation. We randomly partitioned counties into five folds and used four folds for model training and predicted survey-level occupancy for the fifth fold. We then calculated model deviance using the observed and predicted survey-level occupancy values (Miller and Grant 2015).

We specified weakly informative priors for all parameters to account for the relative sparseness of our data and provide a degree of regularization during parameter estimation. We assessed the sensitivity of our estimated and derived parameters to prior choice and found our inferences to be consistent across different reasonable formulations for weakly informative priors. We specified a logistic prior for intercepts in regression models, $\alpha \sim \text{Logistic}(\mu=0, \sigma=1)$ (Northrup and Gerber 2018; Zylstra et al. 2019). We used Gaussian ($\mu=0, \sigma=1.648$) priors for all coefficient estimates following (Chandler et al. 2015) which provided a degree of regularization for our estimates. We used a Gamma (1,1) prior for sigma.

We fit our models in a Bayesian framework using JAGS (v. 4.3.0, Plummer 2003) called from R (v. 4.0.2, R Core Team 2020) through the package JAGSUI (v. 1.5.1, Kellner 2019, see Appendix 1 for code). We ran 25,000 adaptive iterations and 75,000 burn-in iterations across three parallel Markov chains before sampling an additional 100,000 iterations from the posterior distribution while retaining every 10th posterior sample. We visually assessed MCMC chain convergence and mixing and ensured that Gelman-Rubin statistics (\hat{R}) were ≤ 1.01 and ≤ 1.18 for all coefficient parameters in the non-spatial and spatial models, respectively (Brooks and Gelman 1998; Gelman and Hill 2006). We report means, 68% CRI (16th and 84th percentiles) and 95% CRI (2.5th and 97.5th percentiles) of parameter posterior distributions. We also calculated posterior probability values for all covariate posteriors as the proportion of posterior

samples with the same sign (positive or negative) as the posterior mean (Zylstra et al. 2019). We compared posterior probabilities between the spatial and non-spatial models using paired t-tests. We also report the mean annual statewide participant-level occupancy. Finally, we calculated the finite estimates of mean annual statewide county-level occupancy and the finite estimates of annual county- and participant-level occupancy for each county and year as derived estimates.

To better understand how our occupancy estimates reflected trends in the abundance of bobcats, we calculated an index of bobcats abundance used by the Illinois Department of Natural Resources (IDNR). Specifically, we divided the total number of bobcats seen per hunter-county per year by the total number of hours hunted per hunter-county per year. We averaged these values for each year and multiplied them by 1000 for consistency with previous estimates from IDNR. We calculated Spearman's correlation coefficient (r_s) between the annual index of bobcats abundance and each posterior estimate of mean annual statewide county-level occupancy. We also calculated r_s between our index and the finite annual participant-level occupancy for each county and year.

Results

We collected data annually from participants in 100–102 of Illinois' 102 counties. The total number of participants annually ranged from 990 to 2785 (mean=1646, SD=463) and the mean number of participants per county per year was 16 (SD=10, range=1–73). The mean number of periods hunted per participant was 13 (SD=12, range=1–90) and the mean number of hours hunted per period was 2.87 (SD=0.91, range=0.10–7.00). Bobcats were recorded during 0.89% of periods (3525 of 396330 visits). Euclidean distance between county centroids ranged from 18.5 to 585.7 km (median=209.0 km).

Detection ranged from 0.02 to 0.23 across our observed range of hours hunted per period and the duration of our study (Supplementary Material, Fig. S1). Detection increased with the number of hours spent afield (mean posterior=0.26, 95% CRI=0.22–0.29, posterior probability=1.00) and was greater during AM compared to PM hours (mean posterior=-0.15, 95% CRI=-0.22– -0.08, posterior

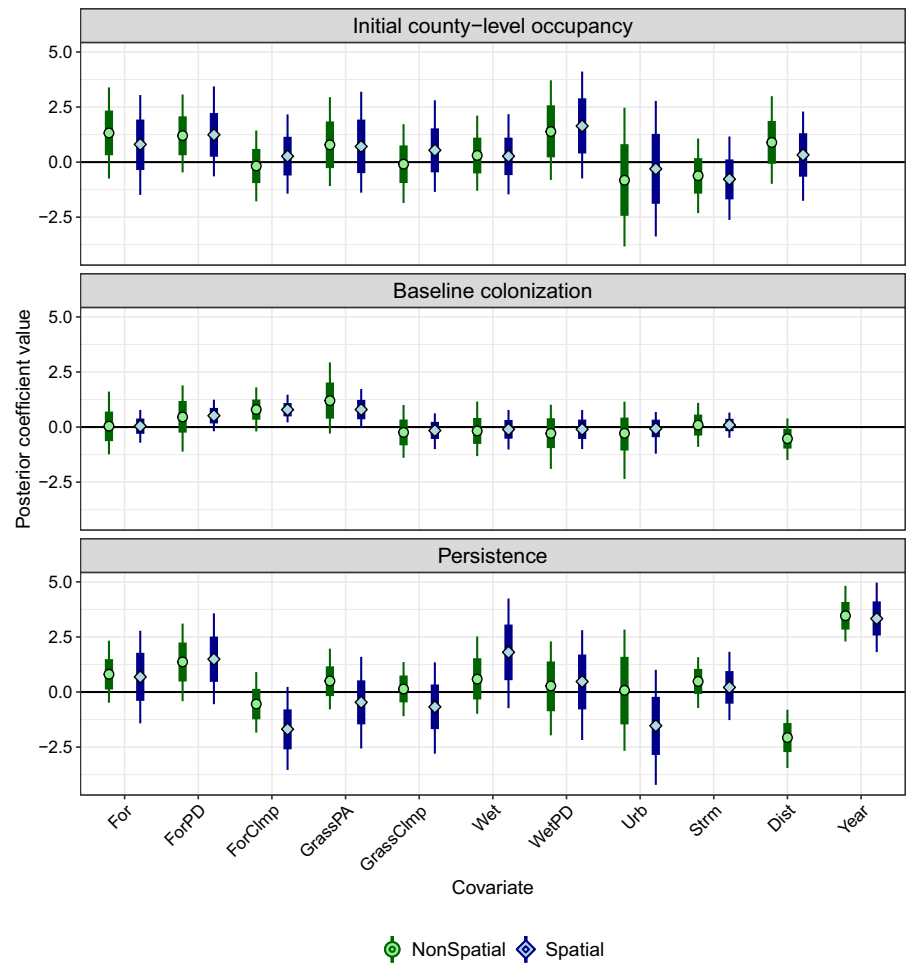
probability=1.00). There was evidence of an increasing trend in detection during our study (mean posterior of Pearson's $r=0.44$, 95% CRI=0.22–0.63, Supplementary Material, Fig. S1).

The non-spatial model had higher predictive performance than the spatial model (deviance=36768.35 vs. 37059.68, respectively; Δ deviance=291.33). We therefore present the results of the spatial model in Appendix 2 and focus the main text on the results from the non-spatial model. Landscape covariate effects on initial county-level occupancy were generally similar between the spatial and non-spatial models (median posterior probability=0.70 and 0.76, respectively; $P=0.66$; Fig. 2; Supplementary Material, Tables S3 & S4). The landscape covariates for initial county-level occupancy with the highest posterior probabilities in the non-spatial model were forest patch density, forest cover, and wetland patch density (0.92, 0.90 and 0.88, respectively) which all showed positive associations with occupancy (Fig. 2; Supplementary Material, Table S3). The relationship with distance to southern Illinois was weakly positive in the non-spatial model (mean posterior=0.89, 95% CRI=-0.99–2.99, posterior probability=0.82, Fig. 2; Supplementary Material, Table S3) in contrast to the much weaker effect of this covariate in the spatial model (posterior probability=0.64; Supplementary Material, Table S4).

Landscape covariate effects were generally weak and similar for county-level colonization in both the spatial and non-spatial model (median posterior probability=0.63 and 0.64, respectively; $P=0.48$; Fig. 2; Supplementary Material, Tables S3 & S4). However, colonization in the non-spatial model was strongly positively associated with mean grassland patch size and forest clumpiness (posterior probability=0.94 and 0.95, respectively) with a much weaker positive effect of forest patch density (posterior probability=0.74; Fig. 2). There was no evidence of a trend in colonization probability across our study (Supplementary Material, Fig. S2).

Landscape covariates had somewhat stronger effects on persistence in both the spatial and non-spatial model (median posterior probability=0.82 and 0.78, respectively; $P=0.37$). Forest patch density and forest cover had relatively strong positive effects (posterior probabilities=0.94 and 0.88, respectively) while stream area had a weaker positive effect (posterior probability=0.80; Fig. 1; Supplementary

Fig. 2 Means, 68% (thick bars), and 95% (thin bars) credible intervals (CRI) from the posterior coefficient distributions for initial county-level occupancy (ψ), colonization (ρ or γ), and persistence (ϕ) from multi-scale dynamic spatial and non-spatial occupancy models for bobcats (*Lynx rufus*) in Illinois, USA, during 2001–2018. All covariates were measured at the county-level and z-score standardized



Material, Table S4). Persistence increased strongly over the course of our study (posterior probability = 1.00). When holding all other covariates constant at their mean using the non-spatial model, persistence increased from 0.11 (95% CRI = 0.008–0.35) during 2001 to 1.00 (95% CRI = 1.00–1.00) during 2017 (Fig. 3).

Statewide county-level occupancy from the non-spatial model increased from approximately 0.43 in 2001 to 0.83 in 2018 (Fig. 4a). Eighty-seven and 73 of Illinois' 102 counties had occupancy ≥ 0.50 and 0.90, respectively, during 2018 (Fig. 5c). Mean annual statewide participant-level occupancy also increased during our study from approximately 0.07–0.28 (Fig. 4a). Our non-spatial model indicated that bobcats were predominately restricted to southern Illinois at the beginning of our study although predicted occupancy values were moderate to high in

northern Illinois. However, northward recolonization was mostly concentrated along the Mississippi and Illinois river drainages in western and central Illinois, respectively (Fig. 5). Finite annual participant-level occupancy by county between the spatial and non-spatial models were highly correlated ($r_S = 0.999$; Supplementary Material, Fig. S4). Our index of abundance for bobcats increased during our study and was highly correlated with mean annual statewide county-level occupancy (mean posterior $r_S = 0.86$, 95% CRI = 0.73–0.93, Fig. 4b). Our index was also highly correlated with participant-level occupancy from the spatial and non-spatial models ($r_S = 0.83$) albeit with substantial variation (Supplementary Material, Fig. S5).

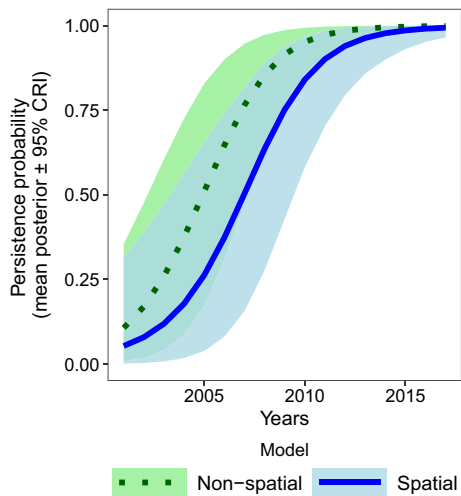


Fig. 3 Predicted county-level probabilities of persistence (mean posteriors and 95% credible intervals [CRI]) for bobcats (*Lynx rufus*) across Illinois, USA, estimated from observations by archery deer hunters during 2001–2018 from multi-scale dynamic spatial and non-spatial occupancy models

Discussion

As the distributions of both native and invasive species continue to change due to anthropogenic landscape alterations and climate change, accurate estimation of these dynamic distributions will become increasingly important for species and ecosystem management and conservation. These estimates must account for diverse sources of variation, including imperfect detection and spatiotemporal variation in species occurrence. We addressed these concerns using 18 years of community science data and hierarchical models to estimate patterns of recolonization for bobcats across a highly anthropogenically modified landscape. Our results support the hypothesis that bobcats have recolonized Illinois as county- and participant-level occupancy, county-level persistence, and detection probabilities all increased during our study. Moreover, participant-level occupancy by county was strongly correlated with an index of abundance for bobcats derived from our community science observations, although we observed substantial variation around this relationship making it unclear how well participant-level occupancy estimates may serve to monitor bobcat abundance at the county level. The apparent recolonization of bobcats in Illinois follows similar trends of mesocarnivore

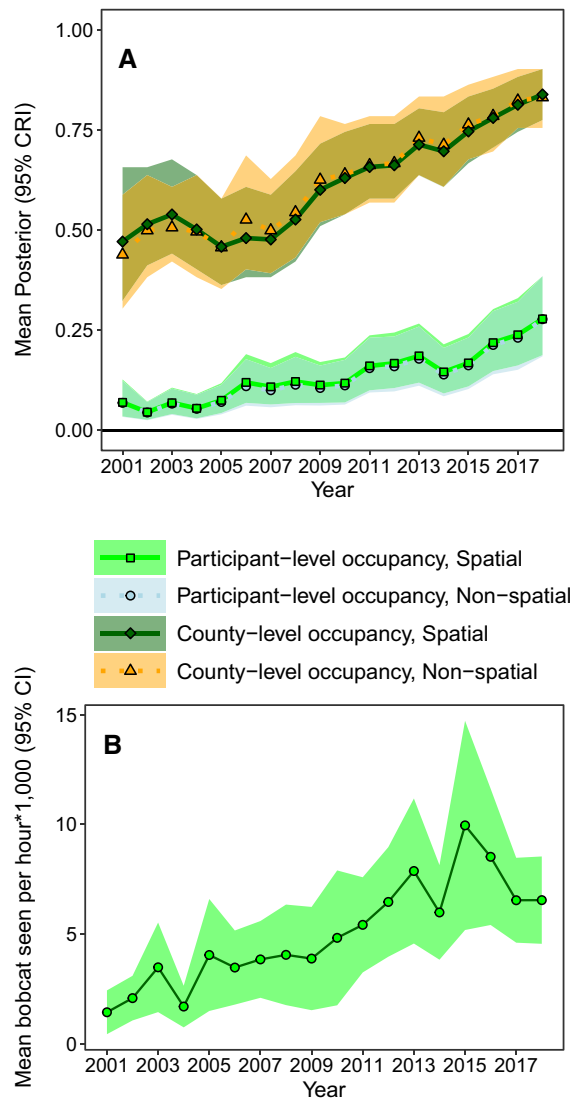


Fig. 4 **A** Finite estimates of mean annual statewide county-level occupancy and mean annual statewide participant-level occupancy ($\pm 95\%$ credible intervals) for bobcats (*Lynx rufus*) across Illinois, USA, estimated from observations by archery deer hunters using spatial and non-spatial dynamic multi-scale occupancy models. **B** Mean ($\pm 95\%$ CI) index of relative abundance of bobcats during 2001–2018. Note that the mean posteriors of annual participant-level occupancy are virtually identical for the spatial and non-spatial models

expansion around the globe (Arnold et al. 2012; Hody and Kays 2018; Molinari-Jobin et al. 2018). Our use of community science data provided consistent and substantial annual survey effort across a broad extent (approximately 150,000 km²) even in areas where bobcats were scarce or absent. This allocation

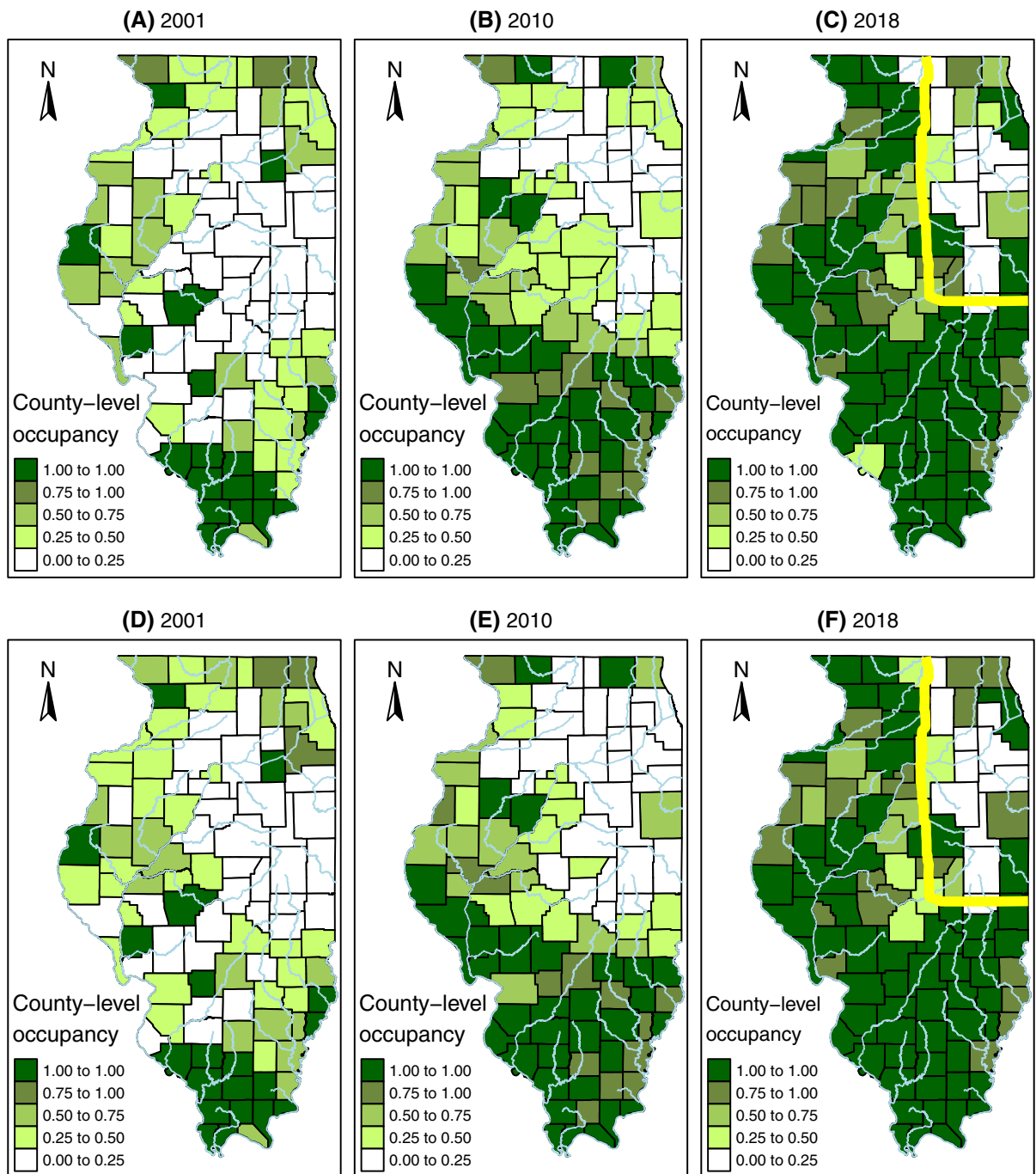


Fig. 5 Finite county-level occupancy estimates for bobcats (*Lynx rufus*) across Illinois, USA, during 2001, 2010, and 2018 estimated from observations by archery deer hunters using non-spatial (A–C) and spatial (D–F) dynamic multi-scale occupancy models. Major rivers are shown in blue. The “1.00–

1.00” bin represents counties with bobcat detections. The solid yellow line in panels C and F represents the boundary of the bobcat harvest zone with harvest prohibited in the northeast part of Illinois

of sampling effort across multiple years beyond

the margins of a species’ distribution highlight an

important advantage of community science projects over more traditional and labor-intensive sampling methods (e.g., mark-recapture, telemetry) in modeling both species range expansions and contractions (Molinari-Jobin et al. 2018). This role of community science will grow more important as climate change continues to affect biotic communities resulting in shifts in species ecological niches and subsequent range shifts (Dickinson et al. 2010).

Surprisingly, we did not find support for including a spatial component to our model of colonization of bobcats. The non-spatial model had greater predictive performance although statewide county-level occupancy trends were similar between the two models. Furthermore, both models predicted highest occupancy in southern Illinois with subsequent expansion largely following the major river drainages of the Mississippi and Illinois Rivers in western and central Illinois, respectively (Woolf et al. 2000, 2002). While we expected the spatial model to perform better, as unmodeled heterogeneity can lead to misleading inferences when modeling dynamic species distributions (Broms et al. 2014), we believe our use of landscape covariates accounted for some spatial heterogeneity in the colonization process. Some of our covariates had weaker effects in the spatial model which further suggests that, in the absence of a spatial component, our non-spatial model estimated greater landscape effects to account for spatial relationships in occupancy. In landscapes with marked spatial heterogeneity in land cover and high levels of landscape disturbance, landscape covariates may be sufficient to account for spatial dependencies in dynamic distributions for species associated with natural land covers. The widespread prevalence of agriculture in Illinois, particularly in central Illinois, may have allowed landscape covariates to sufficiently capture changes in bobcat distribution given this species' association with natural, particularly forest, land covers. However, both models predicted relatively high occupancy for bobcats in northeast Illinois despite a paucity of observations of bobcats in this area during the early years of our study. Bobcat observations are also scarce directly north of Illinois (i.e., southern Wisconsin) (Clare et al. 2015; Allen et al. 2019). However, bobcats were reported from these northern counties in the early 2000s (Woolf et al. 2002) and detected in the area during the intermediate years of our study.

The relatively moderate effects of landscape features on bobcat recolonization within Illinois were somewhat surprising given bobcats' association with forest (Woolf et al. 2002; Tucker et al. 2008; Clare et al. 2015; Popescu et al. 2021) and wetlands (Clare et al. 2015). Nevertheless, we did find generally positive, albeit relatively weak, effects of forest on initial county-level occupancy, colonization and persistence as we hypothesized. The positive relationship between grassland patch size and colonization is consistent with previous research showing positive associations between bobcats and grassland and grassland-forest mosaics in the Midwest (Linde et al. 2012). We suggest several non-mutually exclusive hypotheses to explain our lack of stronger landscape effects. First, there was a mismatch between the scales at which we measured landscape covariates (i.e., the county) and the scales at which our observations occurred (i.e., the participant) (sensu Bauder et al. 2021). Second, high dispersal potential in bobcats (203–288 km, Johnson et al. 2010; Hughes et al. 2019) may permit recolonization of a portion of a county that may not be indicative of the general landscape features of that county. For instance, agriculturally dominated counties may still have pockets of suitable habitat for bobcats that may act as stepping stones and therefore increase an individual's dispersal potential (Saura et al. 2014). Finally, occupancy is a relatively low-resolution state variable compared to abundance or density (He and Gaston 2000; MacFarland and Van Deelen 2011; but see Clare et al. 2015) and it may be that these finer resolution state variables show a greater response to landscape features.

Our results indicate a more restricted distribution for bobcats in Illinois than reported by earlier studies using observations from the 1980s and 1990s (Woolf et al. 2000, 2002), and we offer some potential explanations for these discrepancies. First, Woolf et al. (2000, 2002) predominately used observations from successful deer and turkey hunters and the Illinois Natural Heritage Database which likely were less systematic or rigorous than our statewide observations from archery deer hunters. Our community science data were collected from randomly selected participating hunters across the entire state with most counties having data from multiple hunters during each year. Second, we accounted for the dynamic nature of bobcat distributions within Illinois rather than pooling all observations into a single sampling event.

Pooling observations over multiple years, particularly for species with dynamic distributions and potential turnover among sampling units at the margin of the range, may overestimate a species' distribution. We therefore suggest that our distribution estimates represent a more conservative and accurate estimate, which is often ideal when managing a hunted population or species of concern.

We acknowledge four limitations to our study. First, we were unable to validate our assumption that hunters hunted in the same area within a county during a year. However, this assumption was reasonable within our study system given the prevalence of stand-based archery hunting and private land hunting in Illinois. Second, the number of participants varied widely across counties, sometimes as few as a single participant, which creates additional sampling error and could reduce parameter precision. However, our multi-scale occupancy model fully propagates this uncertainty throughout our analyses thereby fully representing the uncertainty due to uneven sampling effort. Third, community science data can sometimes have false-positives (Clare et al. 2019), and we did not account for false-positives in our model which may positively bias occupancy estimates (Royle and Link 2006; Chambert et al. 2015). Unfortunately, our sampling design and low detection rates did not allow us to estimate a false-positive rate. While bobcats are the only native felid in Illinois, domestic cats (*Felis catus*) were also observed by participants and could potentially be mistaken for bobcats. We therefore encourage additional research to estimate the false-positive rate for observations of bobcats by community scientists. Finally, modeling participant-level occupancy using random effects of county and year may have left additional heterogeneity unmodeled. Ideally, more precise participant locality could be used to obtain landscape covariates at the scale of each participant's effective sampling area which could account for within-county heterogeneity in landscape features. However, such data were unavailable for our study. Another possibility is to use of integrated modeling approaches to incorporate more precise and/or systematically collected data sources (e.g., camera trap or telemetry data; Miller et al. 2019; Gilbert et al. 2021).

Conclusion

Our research illustrates the utility of using community science programs and hierarchical occupancy models that account for the appropriate uncertainties and dependencies to estimate changes in species distributions. This is particularly important for species which are substantially expanding or contracting in geographic range, for whom traditional data collection methods are not logistically or financially feasible. Community science programs are able to obtain large samples across large spatial extents, thereby facilitating long-term monitoring efforts. For example, estimates of county-level occupancy for bobcats from archery hunter observations and hierarchical occupancy models appear valuable for monitoring statewide trends in occurrence of bobcats across Illinois. We encourage additional research exploring the utility of using counts of bobcats from archery hunters in combination with hierarchical abundance models that account for false-positives (Royle 2004; Dail and Madsen 2011) to estimate the abundance of bobcats while accounting for imperfect detection.

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Data availability The datasets used in this manuscript are available from the corresponding author on reasonable request.

Code availability The R script used for these analyses are available in the Online Supporting Information.

Declarations

Conflict of interest The authors have no conflicts of interest to disclose.

Ethical approval Surveys of archery deer hunters were conducted under approval from the University of Illinois Institutional Review Board approval (IRB 10236).

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