DISSERTATION

HOW COMMON BIRD POPULATIONS RESPOND TO THEIR ENVIRONMENT ACROSS SPECIES AND SCALES

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ABSTRACT

HOW COMMON BIRD POPULATIONS RESPOND TO THEIR ENVIRONMENT ACROSS SPECIES AND SCALES

A hallmark of the Anthropocene is widespread declines in biodiversity. Conservation research, attention, and resources largely have been directed toward supporting populations of rare species because their small population sizes and often specialist habitat or resource needs make them at increased risk of extinction. However, multiple studies have described population declines in common species across diverse taxa and regions. These losses are far from trivial as common species likely contribute disproportionately to ecosystem structure, function, and integrity due to their abundance and biomass within ecological communities. They also are the species people tend to experience most in their daily lives and can provide important connections to nature, which have demonstrated benefits for mental health and well-being. Due to a traditional focus on rarity in conservation, we lack understanding of how many common species respond to their environment, especially across the extent of their distributions. Birds are unique in that they are the subject of long-term citizen science monitoring programs that have generated rich datasets across extraordinary temporal and spatial extents. Here, I leveraged data from local to continental avian citizen science programs to investigate population responses to the environment for common species across multiple scales.

Eastern Screech-Owl (*Megascops asio*) is one of the most common and generalist owls within its range across the eastern half of the United States. In Fort Collins, Colorado, the city's natural areas department uses the species as an indicator of riparian forest health. The species is

poorly studied, however, in the western and more arid portion of its range and no quantitative data exist for the species in Colorado. In 2013, Bird Conservancy of the Rockies, a local bird conservation organization, developed a citizen science monitoring program for Eastern Screech-Owl to better understand the species' occupancy dynamics in an understudied portion of its range and to help inform the city's management of natural space. Using data from 2013–2021, I fit an auto-logistic occupancy model in the Bayesian framework to examine whether tree cover, vegetation structure, and/or winter or breeding season climate were associated with Eastern Screech-Owl breeding season occupancy along the Fort Collins section of the Cache La Poudre River. I found approximately 30% of sites were occupied by in a given year and that occupancy was positively associated with site-level variation in vegetation height. Heterogeneity in vegetation height previously had not been identified as an important habitat component for Eastern Screech-Owl, but may benefit the species by generating more diverse microhabitats for prey species or a variety of perching sites from which to hunt. This finding also provides a tangible management target the city's natural areas department could use to support the local Eastern Screech-Owl population (e.g., prioritizing planting native species of different heights within restoration areas along the river).

Beyond Colorado, bird populations have experienced widespread declines across North America since the 1970s, especially common species. Global disturbances like land conversion have been proposed as drivers of these declines. A key question, however, is whether commonness itself may mediate population responses to land cover change. Rare species may be more sensitive to land cover change than common species because of these species' small population sizes, limited ranges, and narrow habitat requirements. Nevertheless, more individuals may be lost from common species because common species are typically widespread

and thus their populations may experience greater pressure from land conversion. To quantify avian population responses to land cover change along a gradient from rare to common species, I used generalized linear mixed-effects models fit in the frequentist framework to relate species-level avian abundance at North American Breeding Bird Survey routes in 2016 to commonness, change in land cover surrounding each route between 2001 and 2016, and amount of land cover in 2001 (i.e., initial amount of land cover). I fit two models to data for all species (n = 282 species): one focused on natural land cover (all forest, shrubland, grassland/herbaceous, and wetland classes combined) and one on different types of human land cover (development, agriculture, and pasture). Across a gradient of commonness, I found species differentially responded to initial amount of but not change in natural land cover; superabundant and common species were most abundant where initial natural land cover was low whereas less common and rare species were most abundant where it was high. Species did differentially respond across a gradient of commonness to change in human land cover. Gain in developed lands was associated with declines in abundance for all birds, gain in agriculture was associated with increases in common but declines in rare birds, and loss of pasture was associated with declines in rare but increases in common birds. These findings suggest that conservation action or policy targeted only toward rare or threatened species may not maintain populations of common species and that landscapes can become too developed even for species that tolerate human disturbance. The latter finding was particularly surprising because developed areas surveyed by the North American Breeding Bird Survey largely comprised less intense types of developed spaces, like exurban and suburban environments (e.g., neighborhoods with parks, trees, golf courses), where common species often are assumed to thrive. Additional research into understanding how developed areas could better support common species is merited given projections of continued

land conversion to development. Ultimately, just as multiple land cover types are needed to support human populations, policy that fosters diversity in land cover at large extents also may best support the full suite of common to rare birds.

Common species that have invaded across continents can be excellent case studies for gaining better understanding of the ecological niche because they are abundant and by definition non-native species have entered new geographic space. Recent research attention has been directed toward determining whether species conserve or shift their niche upon entering new geographic space – i.e., the niche conservatism hypothesis. This hypothesis often is tested by quantifying and comparing the boundaries and/or breadth of a species' niche space in its native and invaded ranges. An outstanding question is whether a species responds differently to its environment in original versus new geographic space. I fit generalized linear mixed-effects models in the frequentist framework to examine whether abundance of two common invasive species – House Sparrow (*Passer domesticus*) and European Starling (*Sturnus vulgaris*) – responded differently to land cover, climate, and elevation in their native European versus invaded North American ranges. I found differences in abundance responses between the native and invaded ranges for both House Sparrow and European Starling, as well as differences in environmental range limits. These species generally were more sensitive to land cover in their native than invaded ranges, though variation occurred by species and land cover type. House Sparrow and European Starling were detected at higher elevations, at cooler and warmer average temperatures, and in areas with wetter breeding seasons in North America compared to Europe. My finding that two widespread, common, and invasive species responded differently to some components of their environment in their native versus invaded ranges calls into question the assumption that niches are conserved over space and time. More research attention is needed toward understanding species' responses within the interior of their niche space, in addition to defining its boundaries. With this more nuanced and comprehensive examination of the niche concept, we can improve our ability to predict how biological communities will be sensitive or resilient to ongoing global change.

Ultimately, I found common species did not respond to their environment in entirely predictable ways. Moreover, the ecological insight that emerged from my research into how common species respond to their environment and niche space would not have been possible without the local and continental long-term avian citizen science monitoring programs from which I used data. While valid concerns have been raised about the quality of data collected from citizen science programs, studies increasingly have found such data to be credible and robust, especially when standardized survey protocols are used and volunteers are formally trained. Citizen science is a particularly powerful framework for generating ecological data for common species given the logistical and financial unfeasibility of using systematic surveys for species with generally large distributions. Yet, developing comprehensive conservation strategies for common species remains challenging due to extensive knowledge gaps of these species' population dynamics and drivers and because these species occur across landscapes that are ecologically, politically, socioeconomically, and culturally diverse. Research that engages diverse stakeholder groups, including agencies and organizations that design and implement policy and management decisions, and is directed toward identifying how populations respond to land cover and climate change, will be critical for helping keep common species common.

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PREFACE

My dissertation work was conducted with multiple collaborators and will be submitted to different peer-reviewed scientific journals with independent and varied formatting requirements. Consequently, I use “we” instead of “I” when describing the research in my dissertation chapters and each chapter may be formatted differently.

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CHAPTER 1. EASTERN SCREECH-OWL RESPOND POSITIVELY TO INCREASED VARIATION IN VEGETATION STRUCTURE AT ITS WESTERN RANGE EDGE

Summary

Many common bird species have experienced substantial population declines, but the habitat needs of such species remain poorly quantified due to a focus on rarity and the prevention of extinction within traditional conservation research. Citizen science offers a powerful framework for studying common birds as these species may be more familiar to participants and/or easier to detect. Citizen science programs targeted toward informing local management also could provide data to support management decision-making while being cost-efficient. To this effect, we used a citizen science program designed for the monitoring of Eastern Screech-Owl (*Megascops asio maxwelliae*) to quantify occupancy dynamics in an understudied portion of its range, Fort Collins, CO. Using data from this program, we fit an auto-logistic occupancy model in the Bayesian framework to examine whether tree cover, vegetation structure, and/or winter or breeding season climate were associated with Eastern Screech-Owl breeding season occupancy from 2013–2021 along a river corridor in the western edge of its range. We found only site-level variation in vegetation height was associated with occupancy in our system, and that this relationship was positive. Heterogeneity in vegetation height previously has not been identified as an important habitat component for Eastern Screech-Owl but may benefit the species by generating more diverse microhabitats for prey species. This finding also provides a tangible management target that could be used to support the local owl population, such as prioritizing planting native species of different heights within restoration areas along the river. Ultimately, our study demonstrates the power of place-based citizen science to contribute to the

body of scientific knowledge and its utility for understanding the habitat needs of common species.

Introduction

Due to their abundance and biomass, common birds can contribute disproportionately to ecosystem services, structure, and functioning (Gaston et al. 2018; Baker et al. 2019). Yet, they are not immune to anthropogenic pressures on biodiversity. Recent evidence has demonstrated striking population declines for common bird species across continents (Inger et al. 2015; Schipper et al. 2016; Rosenberg et al. 2019; Burns et al. 2021). Despite these concerning trends, common birds generally have received less research attention than uncommon species due to a focus on rarity and the prevention of extinction within traditional conservation policy and practice (Gaston and Fuller 2008; Gaston 2010, 2011). Thus, the habitat needs of many common birds remain poorly quantified. The many emerging and ongoing programs that engage volunteers to collect ecological observations hold exceptional potential for advancing understanding of shifts in abundance, distribution, and habitat requirements of common species in a changing world (Silvertown 2009).

Citizen science, referenced here as institution-led scientific research whereby biological observations are collected by persons without formal scientific training (and unrelated to citizenship status; Silvertown 2009; Cooper et al. 2021), has a long history of monitoring and revealing ecological insight about birds in North America (Butcher 1990; Sauer et al. 2017). Hundreds of publications have been produced from analyzing The North American Breeding Bird Survey and the Audubon Christmas Bird Count (the latter being the longest-running citizen science bird monitoring program in the world; Butcher 1990; Sauer et al. 2017); a more-recent citizen science platform for birds, eBird, recently surpassed 1 billion observations (Team eBird 2021). Avian citizen science monitoring programs also have been used successfully to understand patterns of occurrence and abundance of common birds at local scales (Nagy et al. 2012; Jimenez et al. 2021).

Beyond pure monitoring, citizen science could be designed to address environmental management questions driven by local communities and municipalities (Aceves-Bueno et al. 2015; Estes-Zumpf et al. 2022). Agencies across levels of government (i.e., from local to federal) must conduct wildlife management in alignment with environmental regulations but rarely (if ever) have the financial or human resources to monitor all species of management or conservation concern. Engaging non-scientists in the monitoring of common species of management concern could provide data to support management decision-making while enhancing community members' scientific literacy and connections to their local environment (Aceves-Bueno et al. 2015; Estes-Zumpf et al. 2022). The practice also could generate partnerships between management agencies and community members or organizations to manage communal resources more efficiently.

The City of Fort Collins, Colorado (hereafter, the City) engaged in such a partnership with Bird Conservancy of the Rockies (hereafter, Bird Conservancy), a local conservation non-profit organization, in 2013 to monitor Eastern Screech-Owl (*Megascops asio maxwelliae*) along the stretch of the Cache la Poudre River that runs through the City (Sparks 2014). Because cottonwood trees (Populus spp.) are a preferred nesting species for Eastern Screech-Owl (Ritchinson et al. 2020), the City uses the species as an indicator for riparian forest health in Fort Collins (Roberts et al. 2017). Although Eastern Screech-Owl is a common species, its ecological requirements are poorly studied in the western and more arid portion of their range (which includes Fort Collins). Through this citizen science program, Bird Conservancy sought to better understand the biology of a common species within the organization's local community, and the City sought to better understand how their management of natural space along the Cache la Poudre River could affect the local Eastern Screech-Owl population. The program also has facilitated regular communication between Bird Conservancy and the City's Natural Areas Department about Eastern Screech-Owl and vegetation management along the Cache la Poudre River.

We used data from Bird Conservancy's long-term citizen science monitoring program to examine what environmental factors were associated with Eastern Screech-Owl occupancy over 9 breeding seasons along a river corridor in the western edge of its range. We hypothesized that vegetation characteristics and climate would be important drivers of occupancy for the species, so we modeled how occupancy was influenced by percent tree cover, variation in vegetation height, average minimum winter and breeding season temperature, and average cumulative winter precipitation (Nagy et al. 2012; Ritchinson et al. 2020). We predicted Eastern Screech-Owl occupancy would increase with percent tree cover, as reported in other portions of their range (Nagy et al. 2012; Ritchinson et al. 2020). We also predicted that occupancy would increase with variation in vegetation height, which has not previously been explored but could be associated with greater access to prey (Zulla et al. 2022). We predicted occupancy would decrease with lower minimum winter and breeding season temperatures and higher winter precipitation because previous research suggests Eastern Screech-Owl will make long movements following extreme winters and that cold temperatures in summer increase desertion rate of nests (Ritchinson et al. 2020).

Methods

Study species and area

Eastern Screech-Owl is one of the most common and generalist owl species in the eastern United States (Ritchinson et al. 2020). It is a permanent resident and secondary cavity nester that uses a wide variety of treed environments, from mature forest to urban and suburban parks. Cottonwoods are a preferred nesting species for the owl and it has been associated specifically with riparian forest in parts of its range. The species also readily uses human environments; it can occur at higher densities in suburban than rural areas and will successfully nest in anthropogenic features like buildings, mailboxes, and nest boxes (Ritchinson et al. 2020). It is primarily nocturnal and a sit-and-wait predator, relying more on eyesight than hearing to forage from subcanopy perches for small invertebrate and vertebrate prey primarily on the ground in areas with sparse understory vegetation (Ritchinson et al. 2020). Eastern Screech-Owl is socially and genetically monogamous and breeds between February and June. The species' population trend is thought to be increasing at the scale of its distribution (Rosenberg et al. 2019), but populations in portions of the species' northern and northwestern range are considered vulnerable (i.e., at moderate risk of extirpation; NatureServe 2022).

The Bird Conservancy citizen science monitoring program for Eastern Screech-Owl occurs along a 33.8-km stretch of the Cache La Poudre River that runs through the City of Fort Collins, Colorado (Figure 1). Fort Collins is a small city with an estimated population size around 168,500 in 2021 (United States Census Bureau 2021). Vegetation along the surveyed stretch of the Cache la Poudre river ranges from mature riparian forest, dominated by plains cottonwoods (Populus deltoides ssp. monilifera), boxelder (Acer negundo), and various species of willows (Salix spp.), to non-native grasses (Poudre River Trail Corridor 2022). Land ownership along the river is a mix of public and private and includes agriculture, storm water management, active gravel mining, and City-owned and managed natural spaces (City of Fort Collins Natural Areas Department 2022). Mean daily temperature ranged from ~-5°C to 3°C in January and from ~21°C to 25°C in July from 2013–2021 (Colorado State University 2022). Long-term average annual precipitation is ~41 cm (1981–2010), with most of the precipitation occurring in April–August (Western Regional Climate Center 2022).

Study design and citizen science monitoring

The Eastern Screech-Owl monitoring program was designed to quantify occupancy along the focal stretch of the Cache La Poudre River in Fort Collins (Sparks 2014). The river was divided into 500-m2 segments and sampling units were selected using a spatially balanced sampling scheme. Although sampling units were relatively evenly distributed across private and public land, most of the program's sampling units occurred on natural areas owned and managed by the City due to a lack of permission to survey on many private lands. Citizen scientists were trained on a standardized protocol developed by Bird Conservancy to conduct 10-minute playback surveys for Eastern Screech-Owl. Surveyors would use a portable speaker to alternate playing an Eastern Screech-Owl breeding call with silence and record any Eastern Screech-Owls detected from the center of each sampling unit. Surveyors would not conduct or would end a survey early if a Great Horned Owl (Bubo virginianus) was detected (a main predator of Eastern Screech-Owl; Ritchinson et al. 2020). Sites were surveyed three times in 2013 and four times in 2014–2021 between March and June. Fifty-one sites total were surveyed since 2013, though not all sites were surveyed in all years. We used data from a total of 1084 surveys from 2013–2021 in our analyses.

Vegetation and climate data

To examine what habitat factors were associated with Eastern Screech-Owl occupancy, we quantified the proportion of tree cover and variation in vegetation height within 250-m-radii buffers surrounding the centroid of each sampling unit (to correspond to the 500 m2 sampling unit). We used the Rangeland Analysis Platform dataset to quantify tree cover, which is an annual remotely-sensed layer of continuous tree cover at a 30-m2 spatial resolution (Allred et al. 2021). Because tree cover in this layer is continuous (i.e., pixel values range from 0 – 100% tree cover) and we wanted to calculate a proportion of tree cover within our sample units, we converted the continuous tree layer to a binary layer where a tree pixel was one with ≥ 10% tree cover. We then calculated the proportion of tree pixels within each sample unit in each year. We considered a threshold of ≥ 10% tree cover to be appropriate for our study because Eastern Screech-Owl readily use areas with low tree cover (Nagy et al. 2012; Ritchinson et al. 2020). We also conducted sensitivity analyses using different threshold values to convert the continuous tree cover data to binary and models produced similar results (Appendix A Figure A1). To quantify variation in vegetation height, we used a mosaicked vegetation height layer generated from LiDAR data collected by the Northern Colorado Geospatial Consortium in 2013 (0.5 m2 spatial resolution) to calculate the standard deviation of vegetation height within our focal buffers (Guo et al. 2017). We did not have LiDAR data for eight sites, so we specified a prior in our model for all LiDAR values from our sites and estimated the hyperparameters of that prior to maximize information from our observed data (Kéry and Royle 2016a). We considered the LiDAR data to represent vegetation structure over the course of our study because tree cover in our study area remained relatively stable over the 9 breeding seasons of our study and LiDAR data were not collected after 2013 (R. Sparks, personal communication).

Previous research found that Eastern Screech-Owl will move long distances following severe winters and that nest desertion is more likely following cool temperatures and heavy rain events in summer (Ritchinson et al. 2020). Thus, we considered average winter minimum temperature, average winter cumulative precipitation, and average breeding season minimum temperature as components of climate that could influence Eastern Screech-Owl occupancy. We did not consider average breeding season cumulative precipitation because research suggests individual rain events during the breeding season rather than precipitation over an extended period of time affects Eastern Screech-Owl nest desertion (Ritchinson et al. 2020), and we did not have data on individual weather events for our study area. We used Daymet to compile our climate variables, which is an annual climatological dataset for the United States at a 1-km2 spatial resolution (Thornton et al. 1997; Thornton et al. 2020; Thornton et al. 2021). Because the spatial resolution of our climate data was larger than that of our sampling unit (1 vs. 0.5 km2, respectively), we chose to compile our climate variables at the level of our study area. To do this, we added 1 km to the northern, eastern, southern, and western-most site centroids, created a rectangle that encompassed our study area from those modified coordinates, and averaged daily minimum temperature and summed daily precipitation within this extent for our focal temporal periods. Thus, our climate variables represented annual conditions across our study area (i.e., were not at the level of a site). We considered the breeding season to be March 1–June 15 (Ritchinson et al. 2020) and winter to be November 1– February 28 (or 29 for a leap year) preceding the breeding season.

Statistical analyses

We fit an auto-logistic occupancy model in the Bayesian framework to our Eastern Screech-Owl data to examine potential factors influencing occupancy while accounting for incomplete detection and potential temporal autocorrelation within sites across years (Tingley et al. 2016; Murray et al. 2021). We assumed owl observations y at site i, visit j, and year t arose from a Bernoulli distribution:

$$y_{i,j,t} \sim \text{Bernoulli}(p_{i,j,t} \times z_{i,t})$$

where the latent variable z represented the true occupancy state and equaled 0 if an owl was absent and 1 if an owl was present, and p represented the probability of detecting an owl given it was present at site i during survey j in year t. We assumed z arose from a Bernoulli distribution with probability of occupancy ψ. We used a logit link function to model z in year 1 as a function of focal covariates at site i in year 1:

$$\text{logit}(\psi_{i,1}) = \boldsymbol{\beta}\mathbf{x}_{i,1}$$

$$z_{i,1} \sim \text{Bernoulli}(\psi_{i,1}),\ t = 1$$

and for subsequent years, $t = 2, \ldots, 9$:

$$\text{logit}(\psi_{i,t}) = \boldsymbol{\beta}\mathbf{x}_{i,t} + \phi \times z_{i,t-1}$$

$$z_{i,t} \sim \text{Bernoulli}(\psi_{i,t}),\ t > 1$$

where $\boldsymbol{\beta}$ included the regression intercept and coefficients associated with our focal covariates $\mathbf{x}$ and ϕ represented whether occupancy in a given site and year was associated with occupancy at the same site in the following year (i.e., a first-order auto-regressive term; Tingley et al. 2016; Murray et al. 2021). We included proportion of tree cover, standard deviation in vegetation height, average winter minimum temperature, average cumulative winter precipitation, and average breeding season minimum temperature as our focal covariates on occupancy.

We modeled covariates on detection probability p using a logit link function. We modeled survey ordinal date and moon phase on detection because Eastern Screech-Owl may be more detectable as their breeding season progresses and the vocal behavior of other owl species has been found to correlate with moon phase (Appendix A Figure A2; Penteriani et al. 2010; Pérez-Granados et al. 2021). We calculated moon phase using the *getMoonIllumination* function in the suncalc package in R (Thieurmel and Elmarhraoui 2019; R Core Team 2021). We checked for correlations and multi-collinearity between all focal covariates using Pearson's correlation coefficient and variance inflation factors (using the *cor* function in base R (R Core Team 2021) and the *vif* function from the car package (Fox and Weisberg 2019), respectively), and did not include variables with $|r \geq 7|$ or variance inflation factors > 3 in our model. We standardized all continuous covariates prior to model fitting.

We fit the auto-logistic model using the runjags package in R (Denwood 2016; R Core Team 2021). We used uninformative logistic(0,1) priors for all parameters except the prior for the missing LiDAR data (Murray et al. 2021). We modeled the missing LiDAR data by specifying a Normal prior for all LiDAR values and estimating its hyperpriors; we used an uninformative Normal(0,10) hyperprior for the mean and an InverseGamma(1,1) hyperprior for the standard deviation (Kéry and Royle 2016). We fit our model using 4 parallel MCMC chains and an adaption phase of 1000, a burn-in phase of 50000, and a sampling phase of 100000 iterations. Chains were thinned by 10 for a total of 10000 posterior samples. We used the

Gelman Rubin statistic to evaluate model convergence and considered parameters with a Gelman Rubin statistic < 1.1 to be converged (Gelman et al. 2013). We also visually assessed trace and posterior distribution plots for all model parameters to ensure convergence. We evaluated model fit using Bayesian *p* values for discrepancy and the proportion of sites occupied *sensu* Kroll et al. (2014) and considered *p* values > 0.2 and < 0.8 to indicate good fit. We interpreted a covariate as influencing occupancy or detection if the 95% credible interval (CI) of the parameter did not include zero.

Results

One hundred fifty-eight Eastern Screech-Owls were detected on 114 surveys between 2013–2021. The mean number of owls detected per year was 18, and the annual number of owls detected ranged from 5–35. Averaged across years, ~29% (CI: 21.4–37.3%) of our study sites were occupied.

Probability of Eastern Screech-Owl occupancy increased with standard deviation in vegetation height (Figures 2 & 3), and below two standard deviations of vegetation height, predicted occupancy was less than 10% (Figure 3). Probability of occupancy was not influenced by the proportion of tree cover, average cumulative winter precipitation, or average minimum winter or breeding temperature (Figure 2). While its 95% CI included zero, the mean parameter estimate for the auto-regressive term in our model was negative (Figure 2). Neither ordinal date nor moon phase influenced the probability of detecting Eastern Screech-Owl (Supplemental Material Figure S2).

Discussion

We harnessed citizen science to examine factors influencing occupancy of the Eastern Screech-Owl in the western edge of its range. Of the vegetation and climate variables we considered, we found that standard deviation in vegetation height was the only factor correlated with owl occupancy and that this relationship was positive. Thus, nearly a decade of citizen science monitoring revealed that Eastern Screech-Owl occupancy along a western riparian corridor was positively associated with site-level heterogeneity in vegetation structure. These findings have implications for maintaining viable habitat for an important indicator species in the western extent of its range.

Previous studies on Eastern Screech-Owl occupancy have not considered the influence of vegetation structure (Ritchinson et al. 2020), but vegetation structure could influence occupancy via multiple mechanisms like prey dynamics and nesting and foraging substrates (Zulla et al. 2022). Structural heterogeneity is thought to benefit biodiversity in general by creating more niche space and thus diverse microhabitats for plant and wildlife species (Guo et al. 2017). Eastern Screech-Owl may benefit from increased structural heterogeneity because areas with higher heterogeneity in vegetation structure may be able to support a higher diversity of prey species, as was found for Spotted Owl in California (Zulla et al. 2022). Metrics of structural heterogeneity calculated from LiDAR data also have been found to predict the presence of snags (standing dead wood) and subsequently used to model woodpecker habitat (Martinuzzi et al. 2009), and higher variation in heterogeneity was associated with a higher proportion of snags (Bater et al. 2009). Thus, heterogeneity in vegetation structure could benefit Eastern Screech-Owl because it represents area with more snags and thus potential nesting sites. Finally, heterogeneity in vegetation structure could benefit Eastern Screech-Owl by providing trees of various perching heights from which to hunt. Preferred perching heights for Eastern Screech-Owl have been described only from a few areas within their range (Ritchinson et al. 2020), so whether the species exhibits variation in preferred perching height is largely unknown. Future research could explore whether owl occupancy is associated with structural heterogeneity in other portions of its range and/or mechanisms that might explain this pattern (e.g., its association with prey diversity or abundance, or prevalence of nesting or foraging sites).

Our findings regarding tree cover and the auto-regressive term were surprising as they did not align with known aspects of Eastern Screech-Owl biology (Ritchinson et al. 2020). We expected Eastern Screech-Owl occupancy to be influenced by tree cover because the species is a secondary-cavity nester and has been associated with forest cover in other parts of its range (Nagy et al. 2012). However, Eastern Screech-Owl is considered to have a broad ecological niche, uses areas with a wide range of tree cover/density in semi-urban environments (<10% to 100% forest cover, tree density of ~50–1500 trees/ha), and will readily nest on anthropogenic substrates (Ritchinson et al. 2020, Nagy et al. 2012). It is possible that Eastern Screech-Owl is less reliant on tree cover in our study area due to resource supplementation and climate mediation documented in suburban environments (Nagy et al. 2012). Regarding our finding for the auto-regressive term, a negative estimate for this parameter suggests an owl was less likely to occur at a site if it had been there the year before (~66% of sites exhibited this pattern in our data). This is surprising due to normal positive patterns of temporal autocorrelation (Murray et al. 2021) and given the species is considered highly sedentary and easily detectable via playback surveys (Nagy et al. 2012; Ritchinson et al. 2020). Additional research into the species' movement patterns, especially in understudied parts of its distribution, to explore whether the species' site fidelity varies across its range could be fruitful.

The degree to which climate influences Eastern Screech-Owl population dynamics is poorly understood. Gehlbach (2012) found Eastern Screech-Owl productivity was not associated with precipitation but increased with warmer January–February temperatures in central Texas, perhaps due to earlier availability of ectothermic prey. We thought climate might be more likely to influence Eastern Screech-Owl occupancy in our study area because it is located at the western and more arid edge of the species' range. Our finding that climate did not influence occupancy could be due to how we quantified our climate metrics, which represented average conditions across a relatively large temporal and geographic extent. A lack of relationship between occupancy and climate does align, however, with knowledge of Eastern Screech-Owl's broad ecological niche (Ritchinson et al. 2020). Moreover, severe winters have been associated with Eastern Screech-Owl movement (Ritchinson et al. 2020), but our study area did not experience a severe winter during the timeframe of our study. Eastern Screech-Owl movement also has been associated with food shortages (Ritchinson et al. 2020), which could be more common following severe weather, but this scenario may be less likely in our study area given it is suburban. Thus, climate may not be as important for the owl in our study area given the environmental buffering that can occur in suburban areas (e.g., less variable and warmer temperatures, additional/more varied food sources; Gehlbach 2012; Nagy et al. 2012).

Few studies have quantified the probability of occupancy for Eastern Screech-Owl and none have done so in the western edge of the species' range. Yet, the average proportion of sites occupied along our focal stretch of the Cache la Poudre River appears low. A study in the eastern portion of the species' distribution found that predicted probability of occupancy as a function of forest cover reached almost 100% (Nagy et al. 2012). We found average predicted probability of occupancy was higher with greater structural heterogeneity but maxed out around 55% (Figure

3). The Cache la Poudre River is one of the only continuous flowing water sources in Fort Collins, and given Eastern Screech-Owl is known both to be associated with riparian vegetation and to have higher density and reproductive performance in suburban areas (Gehlbach 2012; Ritchinson et al. 2020), we expected this river corridor to be ideal Eastern Screech-Owl habitat. Our findings suggest, however, that management by the City of Fort Collins for Eastern Screech-Owl may be merited and need to be prioritized if the species is to remain an indicator of riparian forest health for the agency.

A primary critique of citizen science is whether data collected via this framework are credible (Freitag et al. 2016; Kosmala et al. 2016; Aceves-Bueno et al. 2017). We are confident in the quality of our data for multiple reasons – volunteers were trained in data collection using a standardized protocol, were only recording presence or non-detection of a single species (i.e., they were not counting numbers of individuals, which may be more difficult to track; Jimenez et al. 2021), Eastern Screech-Owl are easily detectable via playback surveys (Nagy et al. 2012), and we explicitly modeled variation in detection probability (Kosmala et al. 2016; Aceves-Bueno et al. 2017). Furthermore, a study on Eastern Screech-Owl occupancy found almost identical detection rates between professional and citizen scientists and that occupancy models fit to the community science data well-predicted the data collected from systematic surveys conducted by professional scientists (Nagy et al. 2012). The Eastern Screech-Owl citizen science program in Fort Collins is ongoing and holds promise for assessing longitudinal effects of climate and land use change on an indicator species in a suburban landscape.

Our study highlights how citizen science can be used to reveal insight about a common bird species in an understudied portion of its range while generating community partnerships and addressing information gaps for a local environmental management agency (Estes-Zumpf et al.

2022). Citizen science could be particularly well-suited for monitoring common species, especially if such programs included formal training, given the logistical and financial infeasibility of using systematic surveys for species with generally large distributions (Aceves-Bueno et al. 2015) and that citizen scientists may be more familiar with common species. Management agencies often must operate on restricted and ever-decreasing budgets, so utilizing citizen science monitoring could help agencies better meet their regulatory requirements and management goals while being cost-efficient (Aceves-Bueno et al. 2015; Estes-Zumpf et al. 2022). Eastern Screech-Owl could be an ideal species for citizen science projects in other understudied portions of its distribution to gain a better understanding of its ecology across its range, and especially along its range edges. Ultimately, our study demonstrates the power of place-based citizen science to contribute to the body of scientific knowledge and its utility for understanding the habitat and conservation needs of common species, which urgently need research and conservation attention to mitigate current and future declines (Baker et al. 2019).

Figures

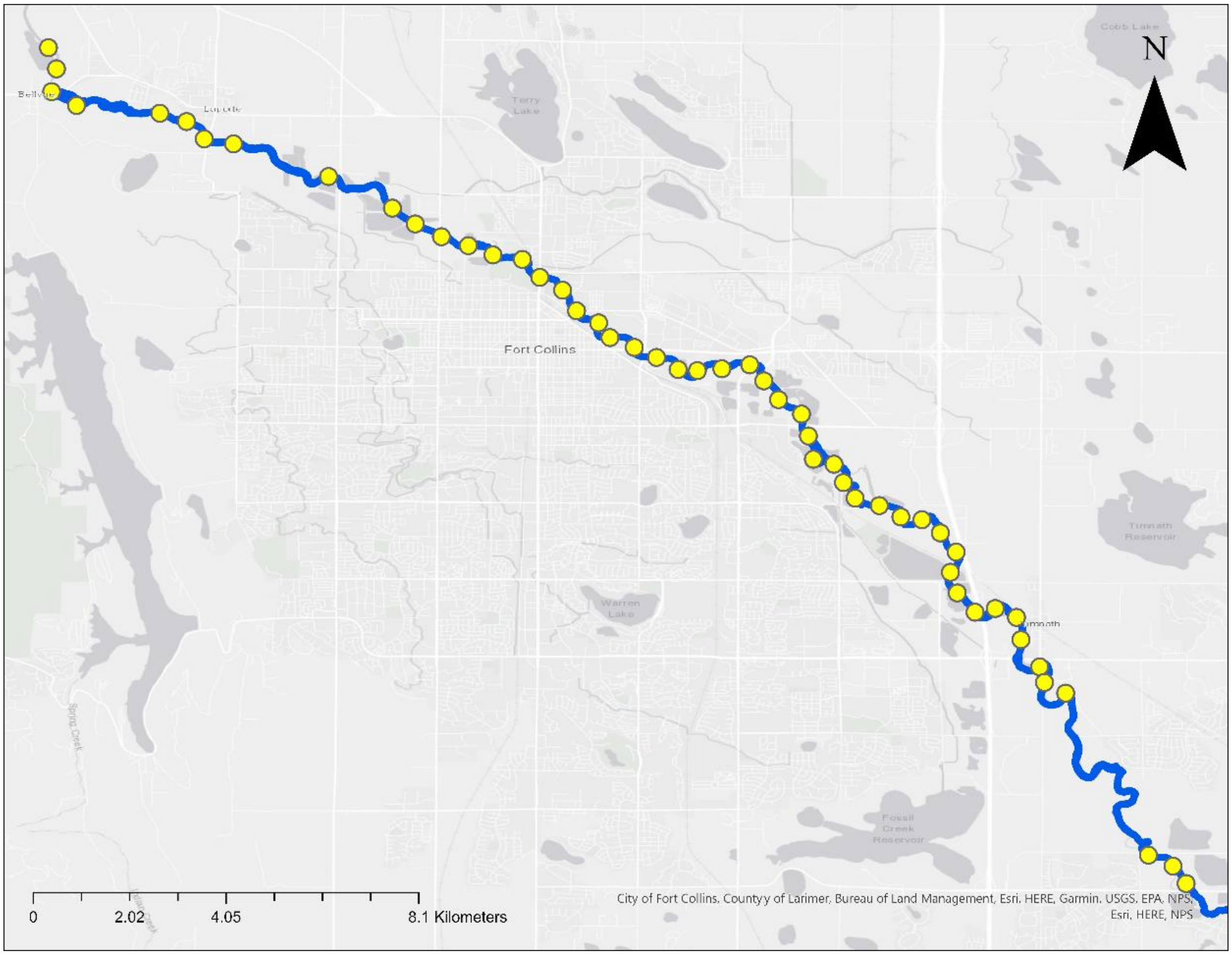

Figure 1. Monitoring sites (yellow dots) used in the Bird Conservancy of the Rockies' citizen science monitoring program for Eastern Screech-Owl along the Cache La Poudre River (blue line) in Fort Collins, Colorado from 2013–2021.

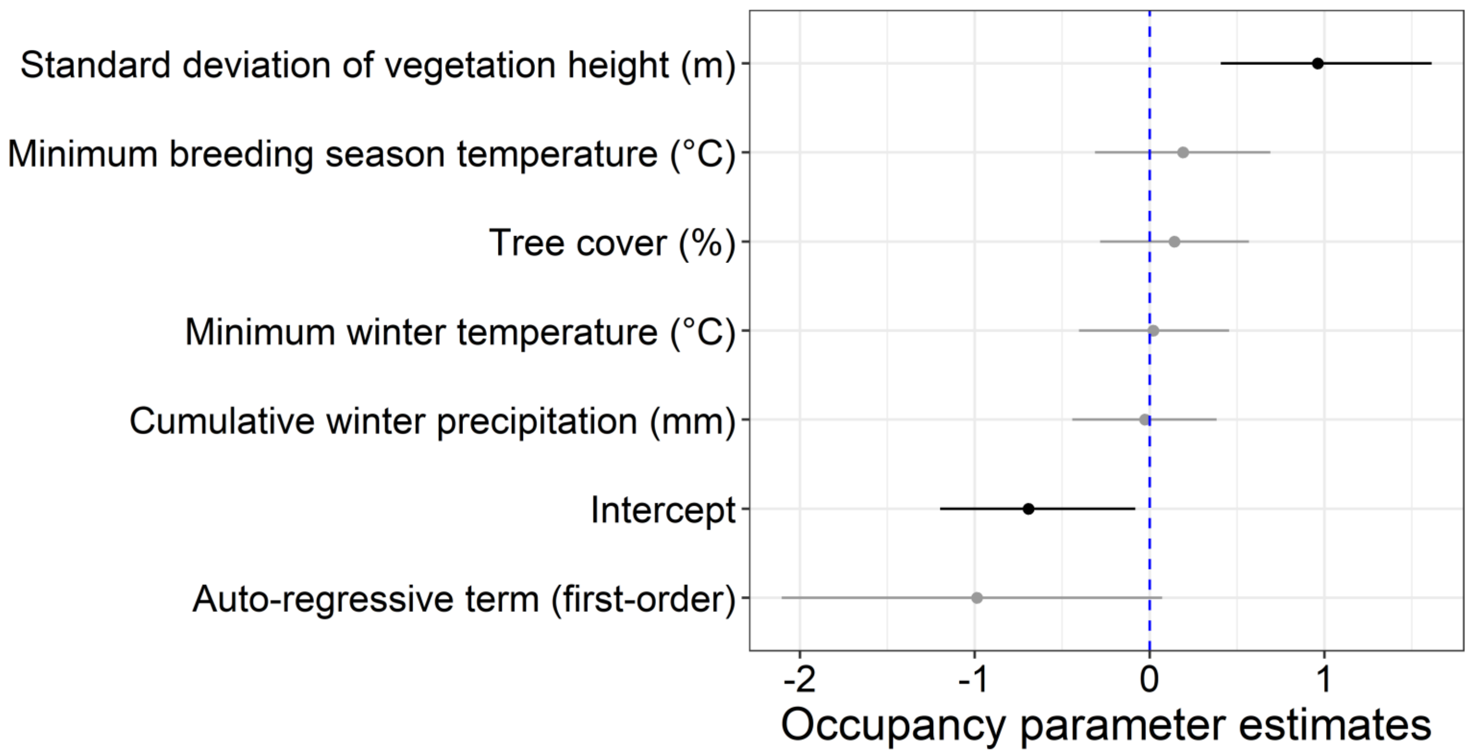

Figure 2. Means and 95% credible intervals (points and lines, respectively) of the posterior distributions of parameters associated with the occupancy process in the auto-logistic occupancy model fit to Eastern Screech-Owl data collected along the Cache la Poudre River in Fort Collins, Colorado in 2013–2021. Colors represent whether a parameter influenced Eastern Screech-Owl occupancy probability (i.e., whether the 95% credible interval of a parameter included zero; black denotes an influence, gray denotes a lack of influence). Standard deviation of vegetation height and tree cover were averages within a 250-m-radii buffer surrounding the centroid of sampling units and aimed to capture variation in occupancy over space. Temperature and precipitation variables were yearly averages across the study area and aimed to capture variation in occupancy between years at the scale of the City.

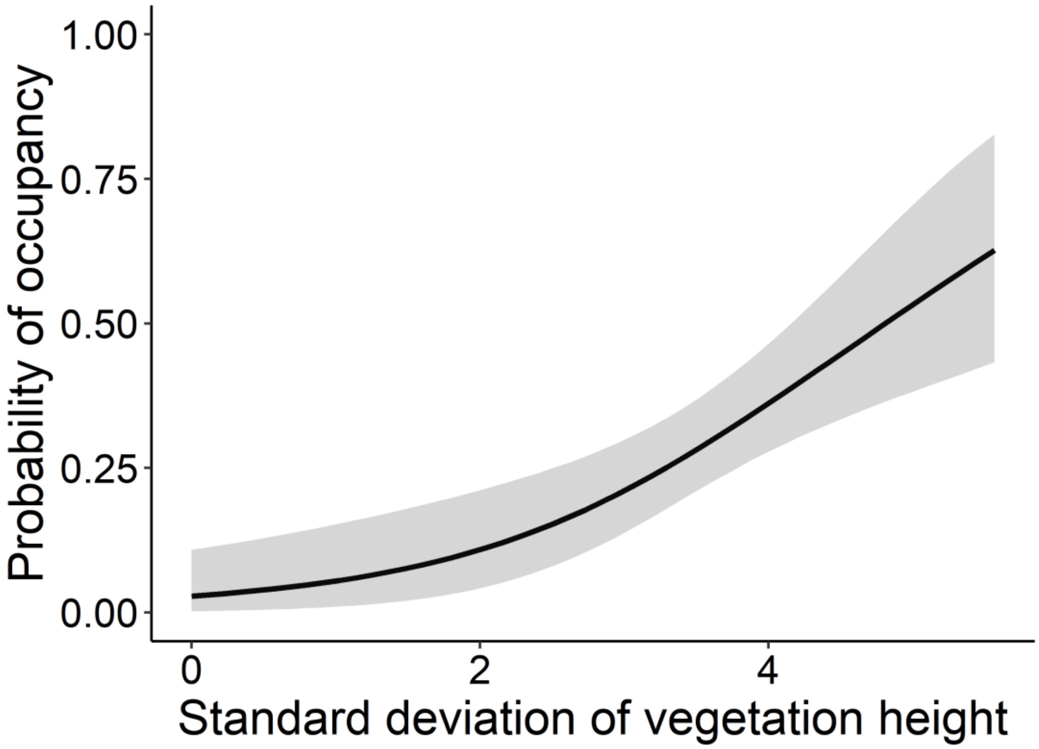

Figure 3. Predicted probability of occupancy (mean and 95% credible interval) as a function of standard deviation of vegetation height from the auto-logistic occupancy model fit to Eastern Screech-Owl data collected along the Cache la Poudre River in Fort Collins, Colorado in 2013–2021.

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CHAPTER 2. LAND COVER DIFFERENTIALLY AFFECTS ABUNDANCE OF COMMON AND RARE BIRDS

Summary

Despite continental-scale declines in bird populations, it is unclear whether common and rare species respond similarly to land cover change. Over a 15-year period in the United States, we show gain in developed lands was associated with declines in abundance for all birds, gain in agriculture was associated with increases in common but declines in rare birds, and loss of pasture was associated with declines in rare but increases in common birds. To sustain common and rare species, scientists and policymakers could leverage relationships between abundance and land cover to design conservation portfolios that support continental biodiversity.

Introduction

Widespread declines in global biodiversity have been attributed to the loss and conversion of natural land (Dirzo et al. 2014; Young et al. 2016). Recent evidence suggests 14.5% of Earth's lands (an area greater than South America) have been altered substantially by humans in the last 20 years (Theobald et al. 2020) and the global amount of urban land could increase up to 6-fold by 2100 (Gao and O'Neill 2020). Concurrent with these losses have been substantial population declines across taxa (Dirzo et al. 2014; Young et al. 2016), including common plants (Jansen et al. 2019), insects (Van Dyck et al. 2009), mammals (Lindenmayer et al. 2011), and birds (Inger et al. 2015; Schipper et al. 2016; Rosenberg et al. 2019; Burns et al. 2021). For example, recent publications have estimated over 500 million and 3 billion birds have been lost over the past 50 years in Europe and North America, respectively, with most individuals lost being from common species (Rosenberg et al. 2019; Burns et al. 2021). These losses are far from trivial as common species likely contribute inordinately to ecosystem structure, function, and integrity due to their abundance and biomass within communities (Frimpong 2018; Gaston et al. 2018; Baker et al. 2019). While rarity is generally associated with higher vulnerability to global disturbances like climate change (Foden et al. 2018), we lack knowledge of how land cover change differentially affects the abundance of common versus rare species.

Under contemporary global land cover change (Young et al. 2016; Theobald et al. 2020), a signature of global contemporary biodiversity change has been altered community composition resulting from combinations of population increases and declines (Dornelas et al. 2019). For example, shifts in avian composition can occur such that the relative abundance of human-associated species increases with the amount of developed and agricultural lands (Sofaer et al. 2020). A key question, however, is whether commonness itself may mediate responses to land cover change. Rare species may be more sensitive to land cover change than common species because of these species' more limited ability to respond to environmental change (e.g., small population sizes, limited ranges, narrow habitat requirements; Rabinowitz 1981). Nevertheless, more individuals may be lost from common species because common species are typically widespread and thus their populations may experience greater pressure from land conversion (Lindenmayer et al. 2011). Understanding how temporal changes in land cover are associated with declines in common versus rare species could inform the allocation of conservation land and resources, and shape policy and practice to mitigate further avian biodiversity loss.

To quantify responses to land cover change along a gradient from rare to common species, we used generalized linear mixed models to relate species-level avian abundance at North American Breeding Bird Survey (BBS; Sauer et al. 2017) routes to commonness and change in land cover surrounding each route. We summarized change in land cover surrounding focal routes between 2001 and 2016, a period for which consistently-derived land cover data were available (Wickham et al. 2014) and substantive change in both land cover and avian populations occurred (Di Cecco and Hurlbert 2022). We also quantified the initial proportion of land cover surrounding focal routes in 2001 because the amount of initial land cover could affect how species respond to land cover change, and recent evidence suggests legacy effects of land cover on avian populations (Haddou et al. 2022). In the absence of global change, we would expect a population's 2016 route-level abundance to be closely related to its 2001 route-level abundance, and our study asked how national-scale commonness interacted with local land cover change to alter this baseline relationship. Specifically, we modeled 2016 route-level abundance of each species as a function of its logged 2001 route-level abundance and an interaction between national commonness, route-level land cover change, and route-level initial land cover amount. We fit two models to data for all species: one focused on natural land cover (all forest, shrubland, grassland/herbaceous, and wetland classes combined) and one on different types of human land cover (development, agriculture, and pasture; see **Methods** and Appendix B Table B1).

Methods

Avian data

The North American Breeding Bird Survey is an international community science bird monitoring program in which qualified volunteer surveyors annually conduct 50 three-minute point counts spaced approximately 0.8 km apart along ~40-km routes that are oriented along roads (Sauer et al. 2017). We compiled BBS data from routes in the United States that were surveyed in all focal years, met BBS criteria for data quality (e.g., surveys occurred at appropriate times and under appropriate weather conditions), and for which spatial information exists for the route centroid (Sofaer et al. 2020). Route- and species-level abundance data were summed over three-year periods (2000–2002 and 2015–2017, hereafter 2001 and 2016 route-level abundance) to reduce stochasticity in counts (Sofaer et al. 2020). We restricted our focal dataset to non-hybrid diurnal landbird species (Rittenhouse et al. 2012; Di Cecco and Hurlbert 2022) that had a total of >100 individuals detected across all BBS routes in the United States in 2000–2002 and occurred on more than 10 routes in each of our focal time periods. We also restricted our dataset to routes on which focal species were detected in both time periods (i.e., we excluded species-route combinations where abundance was 0 in one focal time period) to avoid capturing vagrancy or extinction/colonization dynamics in our analyses. These criteria resulted in 52405 observations for 282 species (species list in Supplemental Material) from 985 routes being used in our analyses.

We quantified species' commonness at the national scale, using the natural log of each species' total abundance in the conterminous United States in 2001 (i.e., species' 2001 route-level abundances summed across all BBS routes in the conterminous United States; see Appendix B). We quantified commonness as continuous on the basis of summed species counts because continuous counts of individuals on the landscape may better capture a species' contribution(s) to ecosystem functioning or services than categorical commonness/rarity metrics (Baker et al. 2019). Our metric also was correlated with an independent measure of range size (Appendix B Figure B1; Tobias et al. 2022). While commonness was a continuous predictor in our model, we visualized our findings in terms of commonness classes for ease of interpretation: rare, less common, common, and superabundant (species with untransformed 2001 total abundances equaling 101–1000, 1001–10000, 10001–100000, and >100000, respectively). The following species' untransformed national abundances in 2001 were used to generate model predictions of abundance to represent our focal commonness classes: Virginia's warbler (*Leiothlypis virginiae*) – 975, scarlet tanager (*Piranga olivacea*) – 9489, Northern mockingbird (*Mimus polyglottos*) – 84114, and American robin (*Turdus migratorius*) – 212544 (rare, less common, common, and superabundant, respectively; see Figs 1. & 2.). We acknowledge that the ability of the BBS to detect rare species is limited because it is a road-based survey, and hence our national-scale analysis does not capture the country's most range-restricted and imperiled species.

Land cover data

We used data from the National Land Cover Database (Wickham et al. 2014) to quantify the proportion of natural and human land cover surrounding focal BBS routes in 2001 and change in the proportion of natural and human land cover between 2001 and 2016 (n = 985 routes). The National Land Cover Database is a remotely sensed land cover product that includes classifications for 16 land cover types for the conterminous United States (Wickham et al. 2014). We defined human land cover to include classes for developed land, agriculture, and pasture, and natural land cover to include all other non-water, non-barren classes (Appendix B Table B1). We quantified the initial proportion (i.e., in 2001) and change in the proportion of natural and human land cover types within 19.7-km-radii buffers surrounding route centroids, which corresponds to allometrically-estimated dispersal distances for focal species (Sutherland et al. 2000) and is commonly used to examine effects of land cover on birds using our focal datasets (Flather and Sauer 1996; Rittenhouse et al. 2012; Sofaer et al. 2020).

Modeling

We fit generalized linear mixed models using the glmmTMB package (Brooks et al. 2017) in R (R Core Team 2021) to investigate how natural and human land cover change affected avian abundance. We did not employ hierarchical models used to estimate species' trends from BBS data because these models provide estimates at scales coarser than an individual route (Sauer et al. 2017), and we were interested in the relationship between avian abundance and land cover change at the level of a route. We assumed counts arose from a negative binomial distribution and models were fit using a log link function. Our natural land cover model included logged 2001 route-level abundance and an interaction of national commonness, the initial route-level proportion of natural land cover, and change in the route-level proportion of natural land cover (Table 2). Our human land cover model included logged 2001 route-level abundance, two-way interactions of national commonness and route-level change in developed lands and national commonness and route-level change in pasture, and a three-way interaction of national commonness, the initial route-level proportion of agriculture, and change in the route-level proportion of agriculture (Table 3). The human land cover model did not include three-way interactions of national commonness and route-level land cover amount/change for developed lands and pasture because initial amount and change in these land cover types were correlated ($r > 0.7$ and < -0.7, respectively). We also explored the performance of alternative model specifications which used logged 2016 route-level abundance as the response (modeled using a Gaussian distribution) and/or untransformed (instead of logged) 2001 route-level abundance as a predictor; all models produced broadly similar results, but our models described above better met model assumptions based on diagnostic plots of residuals (Hartig

2021) and better predicted mean 2016 route-level abundance values for each visualized commonness class than the alternative model specifications (Supplemental Material).

In addition to our focal covariates (commonness and land cover), both models included fixed effects for the Bird Conservation Region within which a route is located and whether a route was surveyed by a first-year observer in 2000–2002 or 2015–2017. We included Bird Conservation Regions, which are areas in North America with similar avian communities, ecosystems, and management issues used for avian conservation planning (NABCI 2014), to account for regional variation in avian abundance beyond that explained by land cover (Sofaer et al. 2020). We included a fixed effect for first-year observer because evidence suggests first-year observers detect fewer species/individuals than more experienced observers (Kendall et al. 1996). We also included random effects for species and route in both models to account for variation in abundance within a species across routes and within routes across species, respectively.

We standardized all continuous covariates and checked for multicollinearity among covariates using the *vif* function in the car package (Fox and Weisberg 2019) prior to fitting models.

Results

Across a gradient of commonness, species differentially responded to initial amount of but not change in natural land cover (Figure 4, Table 1), and differentially responded to change in human land cover (Figure 5, Table 2). Superabundant and common species were most abundant where initial natural land cover was low, whereas less common and rare species reached greatest abundances where it was high (Figures 4 & Appendix B Figure B2b.). For human land cover types, BBS routes largely lost pasture and gained developed land and agriculture (Appendix B Figures B3 & B4a.). Species declined at similar rates with increases in developed land, and the small effect of rarity was sensitive to model specification (Figures 5 & Appendix B Figure B7). Superabundant species increased most with increases in agriculture (Figure 5). Abundance also varied by commonness, change in agriculture, and the initial amount of agriculture (Appendix B Figures B4 & B5). Rare species increased while superabundant species declined most with increases in pasture (Figure 5).

Discussion

Our results reveal that commonness can explain avian responses to initial land cover and change in land cover at a national scale. Landscapes dominated by natural land cover better supported the abundance of rare compared to common species. The trend that routes largely lost pasture and gained agriculture and developed land aligns with global patterns of land conversion and associated consequences for biodiversity – for example, grassland and farmland bird populations have declined most of any avian guild across two continents (Inger et al. 2015; Rosenberg et al. 2019; Burns et al. 2021). Change in human land cover types better explained patterns in avian abundance than changes in natural land cover. Because species responded differently to changes in human land cover, linking the type of land conversion likely to occur to conservation goals for common and rare species in a given landscape could help predict the consequences of habitat gain and loss for avian populations.

Understanding how rare versus common species respond to land cover and land cover change has complex and important implications for developing national and international land use policy that sustains both people and biodiversity. For people, natural environments are critical sources of ecosystem services (e.g., clean water, air; Sandifer et al. 2015) and support mental health and well-being (Sandifer et al. 2015; Ugolini et al. 2020; Pouso et al. 2021; Richardson and Hamlin 2021). Yet, agricultural and pasture lands are critical for feeding the global human population (Tilman and Clark 2014), and cities often provide more economic opportunity (Li et al. 2019) and can support environmental efficiencies lacking in less urbanized areas (Newman 2006). For biodiversity, natural environments often are the most species rich (Gray et al. 2016) and home to the least common species (Cooper et al. 2019). Yet, we also found that common but not rare species benefited from loss of pasture and gains in agriculture. Importantly, gain in developed land was associated with declines for all species regardless of commonness. Therefore, landscapes can become too developed even for species that tolerate human disturbance, as is also suggested by declines in non-native bird species in North America (Rosenberg et al. 2019) and common bird and butterfly species in Europe (Van Dyck et al. 2009; Burns et al. 2021). Just as multiple land cover types are needed to support human populations, policy that fosters diversity in land cover types at large extents also may best support the full suite of common to rare birds.

The conservation community largely has been focused on rare species' conservation for decades. Such efforts have been critical for preventing extinctions and saving threatened species (Rodrigues 2006). Addressing the conservation crisis unfolding for common species, however, will require utilizing different conservation paradigms than those past (Baker et al. 2019; Ellison 2019). Our findings reveal how abundances of rare and common species respond to land cover change and suggest that conservation action or policy targeted only toward rare or threatened species may not maintain populations of common species. Developing comprehensive conservation strategies that engage diverse stakeholder groups, including agencies and organizations that lead policy and planning for urban and working lands, will be particularly critical for common species as they occur across ecologically, politically, socioeconomically, and culturally diverse landscapes. We acknowledge that incorporating common species into more traditional conservation paradigms is challenged by limited conservation funding (McCarthy et al. 2012) and knowledge gaps about common species' population dynamics and drivers (Baker et al. 2019). Yet, because of their outsized role in ecosystems (Gaston and Fuller 2008; Baker et al. 2019) and their contributions to human well-being (Frimpong 2018; Prūse et al. 2020), investments in keeping common species common could pay dividends for nature and people. When a species like the passenger pigeon, which numbered in the billions, can go extinct in a human lifetime, the persistence of the world's most abundant species cannot be taken for granted (Lindenmayer et al. 2011).

Figures

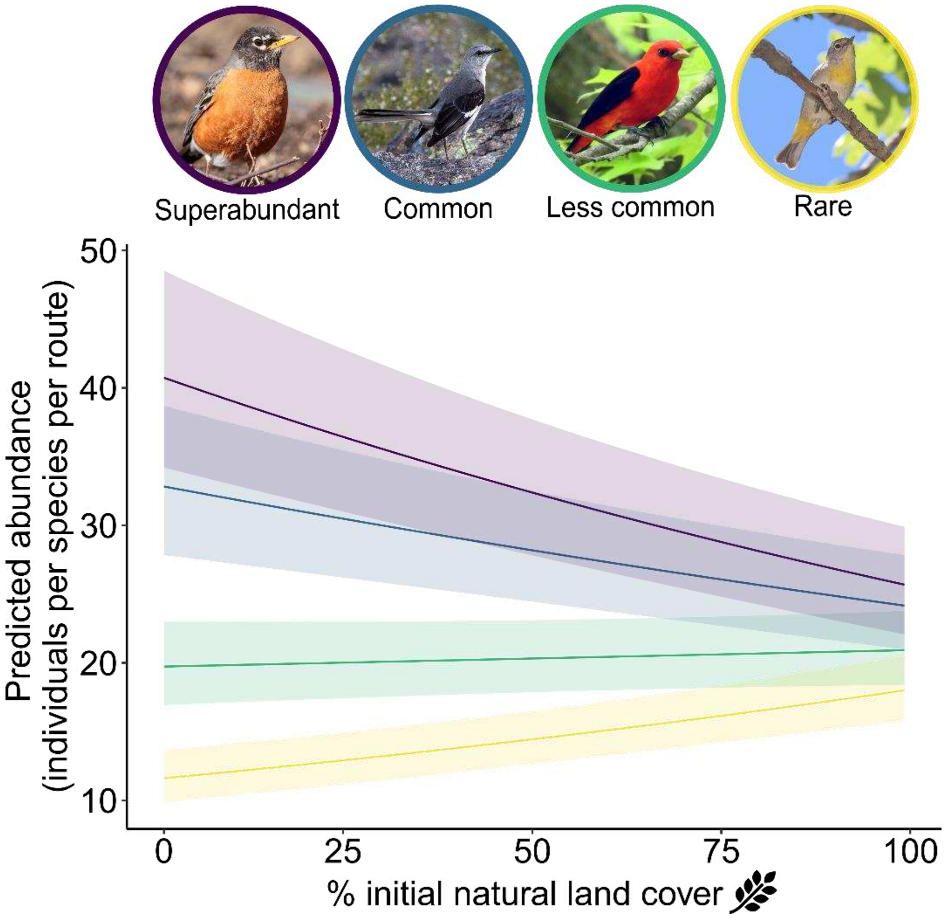

Figure 4. Predicted abundance in 2016 (means and 95% confidence intervals for counts summed across 2015–2017) as a function of commonness and the proportion of natural land cover surrounding focal North American Breeding Bird Survey (BBS) routes in the conterminous United States in 2001 (n = 985). Commonness was defined based on each species' total abundance across all BBS routes in the United States in 2000–2002. Colors represent example species with different orders of magnitude of total abundance: superabundant (over 100000 individuals; American robin), common (10001–100000 individuals; Northern mockingbird), less common (1001–10000 individuals; scarlet tanager), and rare (101–1000 individuals; Virginia's warbler). All photos are in the public domain.

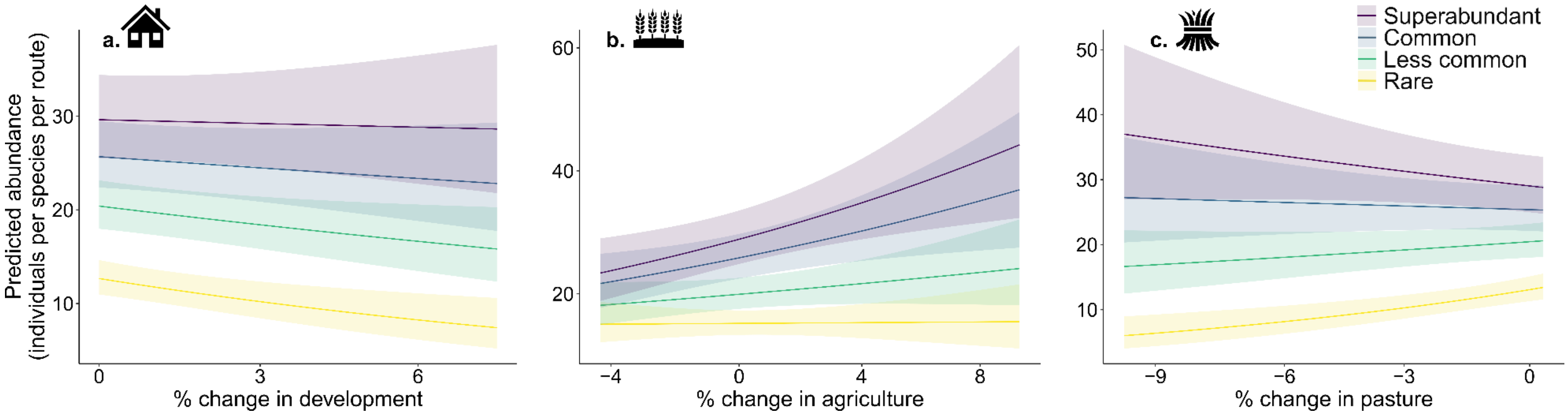

Figure 5. Predicted abundance in 2016 (means and 95% confidence intervals for 2015–2017) as a function of commonness and change in (a.) developed land, (b.) agriculture, and (c.) pasture surrounding focal North American Breeding Bird Survey routes in the conterminous United States. Colors represent example species across the commonness gradient, as in Figure 4. Change in agriculture interacted with the amount of initial agriculture, and was plotted at the mean proportion of agriculture surrounding a route in 2001 (~20%).

Tables

Table 1. Standardized coefficient estimates (means and 95% confidence intervals [CI]) of fixed effects from the natural land cover model for avian abundance (individuals per species per route) on North American Breeding Bird Survey routes in 2015–2017. Abundance was modeled using a negative binomial distribution and the intercept represents abundance in 2015–2017 in Bird Conservation Region (BCR) 5 on a route that was surveyed by a non-first-year observer. Initial amount of land cover refers to land cover in 2001. Total abundance refers to a species' route-level abundances summed across all BBS routes in the conterminous United States. Bolded text indicates fixed effects with statistically significant effects on abundance ($\alpha = 0.05$).

Fixed effects	Mean	CI	z value	p value
Intercept	1.398	(1.269, 1.527)	21.08	< 0.0001
Initial amount of natural land cover (%)	-0.018	(-0.051, 0.015)	-1.06	0.2874
Change in natural land cover (%)	-0.013	(-0.035, 0.009)	-1.13	0.2599
Commonness (logged total abundance in 2000–2002)	0.188	(0.157, 0.219)	11.55	< 0.0001
Initial amount of natural land cover * change in natural land cover	-0.003	(-0.03, 0.024)	-0.23	0.8219
Initial amount of natural land cover * commonness	-0.071	(-0.079, -0.063)	-16.96	< 0.0001
Change in natural land cover * commonness	0.002	(-0.006, 0.01)	0.63	0.5284
Initial amount of natural land cover * change in natural land cover * commonness	-0.003	(-0.013, 0.007)	-0.57	0.5664
Logged route-level abundance in 2000–2002	1.459	(1.447, 1.471)	224.47	< 0.0001
BCR9	0.031	(-0.116, 0.178)	0.42	0.6768
BCR10	-0.065	(-0.226, 0.096)	-0.8	0.4235
BCR11	0.053	(-0.119, 0.225)	0.61	0.5423
BCR12	-0.191	(-0.352, -0.03)	-2.32	0.0202
BCR13	-0.1	(-0.278, 0.078)	-1.1	0.2705
BCR14	-0.273	(-0.438, -0.108)	-3.26	0.0011
BCR15	-0.085	(-0.383, 0.213)	-0.56	0.5739
BCR16	-0.061	(-0.206, 0.084)	-0.83	0.4085
BCR17	-0.006	(-0.186, 0.174)	-0.06	0.9512
BCR18	0.286	(0.119, 0.453)	3.38	0.0007
BCR19	-0.025	(-0.201, 0.151)	-0.27	0.7835
BCR20	0.065	(-0.196, 0.326)	0.49	0.6249
BCR21	-0.097	(-0.279, 0.085)	-1.04	0.2973
BCR22	-0.216	(-0.367, -0.065)	-2.8	0.0052
BCR23	-0.221	(-0.374, -0.068)	-2.83	0.0046
BCR24	-0.115	(-0.264, 0.034)	-1.51	0.1308

BCR25	-0.309	(-0.556, -0.062)	-2.45	0.0143
BCR26	0.015	(-0.199, 0.229)	0.14	0.8917
BCR27	-0.202	(-0.343, -0.061)	-2.8	0.0051
BCR28	-0.164	(-0.297, -0.031)	-2.42	0.0155
BCR29	-0.154	(-0.311, 0.003)	-1.93	0.0541
BCR30	-0.179	(-0.344, -0.014)	-2.13	0.0331
BCR31	-0.499	(-0.707, -0.291)	-4.69	< 0.0001
BCR32	-0.067	(-0.283, 0.149)	-0.61	0.5387
BCR33	-0.108	(-0.357, 0.141)	-0.85	0.3929
BCR34	-0.244	(-0.46, -0.028)	-2.22	0.0265
BCR35	-0.105	(-0.291, 0.081)	-1.11	0.2681
BCR37	0.086	(-0.251, 0.423)	0.5	0.6155
First-year observer	0.047	(0.004, 0.09)	2.12	0.0342

Table 2. Standardized coefficient estimates (means and 95% confidence intervals) of fixed effects from the human land cover model for avian abundance (individuals per species per route) on North American Breeding Bird Survey routes in 2015–2017. Abundance was modeled using a negative binomial distribution and the intercept represents abundance in 2015–2017 in Bird Conservation Region (BCR) 5 on a route that was surveyed by a non-first-year observer. Initial amount of land cover refers to land cover in 2001. Total abundance refers to a species' route-level abundances summed across all BBS routes in the conterminous United States. Bolded text indicates fixed effects with statistically significant effects on abundance ($\alpha = 0.05$).

Fixed effects	Mean	CI	z value	p value
Intercept	1.376	(1.247, 1.505)	20.71	< 0.0001
Commonness (logged total abundance in 2000–2002)	0.183	(0.152, 0.214)	11.28	< 0.0001
Change in developed land cover (%)	-0.021	(-0.043, 0.001)	-1.87	0.0611
Initial amount of agriculture (%)	0.015	(-0.016, 0.046)	0.98	0.3279
Change in agriculture (%)	0.033	(-0.002, 0.068)	1.84	0.0662
Change in pasture (%)	0.012	(-0.021, 0.045)	0.74	0.4578
Change in developed land cover * commonness	0.011	(0.003, 0.019)	2.68	0.0074
Initial amount of agriculture * change in agriculture	0.016	(-0.009, 0.041)	1.27	0.2031
Initial amount of agriculture * commonness	0.049	(0.041, 0.057)	11.65	< 0.0001
Change in agriculture * commonness	0.015	(0.003, 0.027)	2.62	0.0088
Change in pasture * commonness	-0.026	(-0.036, -0.016)	-4.9	< 0.0001
Initial amount of agriculture * change in agriculture * commonness	-0.024	(-0.034, -0.014)	-5.08	< 0.0001
Logged route-level abundance in 2000–2002	1.461	(1.449, 1.473)	224.82	< 0.0001

BCR9	0.029	(-0.118, 0.176)	0.39	0.6939
BCR10	-0.067	(-0.224, 0.09)	-0.83	0.4069
BCR11	0.01	(-0.168, 0.188)	0.11	0.9119
BCR12	-0.185	(-0.344, -0.026)	-2.28	0.0228
BCR13	-0.06	(-0.234, 0.114)	-0.67	0.5037
BCR14	-0.259	(-0.422, -0.096)	-3.13	0.0018
BCR15	-0.082	(-0.376, 0.212)	-0.55	0.5832
BCR16	-0.063	(-0.204, 0.078)	-0.87	0.3842
BCR17	-0.033	(-0.211, 0.145)	-0.36	0.7197
BCR18	0.271	(0.102, 0.44)	3.17	0.0015
BCR19	-0.033	(-0.211, 0.145)	-0.36	0.7217
BCR20	0.075	(-0.184, 0.334)	0.57	0.5707
BCR21	-0.041	(-0.221, 0.139)	-0.45	0.652
BCR22	-0.193	(-0.35, -0.036)	-2.42	0.0153
BCR23	-0.177	(-0.332, -0.022)	-2.25	0.0243
BCR24	-0.087	(-0.236, 0.062)	-1.15	0.2489
BCR25	-0.283	(-0.528, -0.038)	-2.25	0.0243
BCR26	0.057	(-0.159, 0.273)	0.52	0.6007
BCR27	-0.179	(-0.32, -0.038)	-2.48	0.0132
BCR28	-0.135	(-0.266, -0.004)	-2.01	0.0444
BCR29	-0.098	(-0.255, 0.059)	-1.22	0.224
BCR30	-0.095	(-0.258, 0.068)	-1.14	0.2539
BCR31	-0.44	(-0.648, -0.232)	-4.17	< 0.0001
BCR32	-0.051	(-0.265, 0.163)	-0.47	0.6376
BCR33	-0.086	(-0.333, 0.161)	-0.68	0.4945
BCR34	-0.228	(-0.44, -0.016)	-2.1	0.0357
BCR35	-0.104	(-0.288, 0.08)	-1.11	0.2656
BCR37	0.143	(-0.192, 0.478)	0.84	0.403
First-year observer	0.045	(0.002, 0.088)	2.05	0.0409

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CHAPTER 3. INVASIVE POPULATIONS SHOW NICHE DIVERGENCE VIA DIFFERENCES IN ENVIRONMENTAL SENSITIVITIES AS WELL AS EXPANSION OF RANGE LIMITS

Summary

Recent attention has been directed toward testing the niche conservatism hypothesis, which predicts that species conserve their niche upon entering new geographic spaces. This hypothesis often is tested by quantifying and comparing species' niche boundaries and breadth between their native and invaded ranges. An outstanding question, however, is whether the sensitivity of species' responses to their environments differs between original and new geographic space. We fit generalized linear mixed effects models to examine whether abundance of two common invasive species – House Sparrow and European Starling – responded differently to land cover, climate, and elevation in their native European versus invaded North American ranges. We found differences in abundance responses between the native and invaded ranges for both House Sparrow and European Starling, as well as differences in environmental range limits. Changes in abundance along gradients of land cover were generally stronger in the native than invaded range, though variation occurred by species and land cover type. House Sparrow and European Starling were detected at higher elevations, at cooler and warmer average temperatures, and in areas with wetter breeding seasons in North America compared to Europe. Our findings call into question the assumption that niches are conserved over space and time. We suggest a more comprehensive examination of the niche concept that includes exploring variation in occupancy, abundance, and demography under similar environmental conditions between native and invaded ranges. Deepening the study of niche conservatism within niche

boundaries would improve our ability to predict how biological communities will be sensitive or resilient to ongoing global change.

Introduction

After centuries of study, fundamental questions about the ecological niche remain (Grinnell 1917; Hutchinson 1957). Recent attention has been given to whether species conserve or shift their niche upon entering new geographic space – i.e., the niche conservatism hypothesis (Liu et al. 2020b; Bates and Bertelsmeier 2021). Support for this hypothesis is mixed, perhaps in part due to limitations in how niche shifts are identified and interpreted (Liu et al. 2020b; Bates and Bertelsmeier 2021). Most previous studies have defined and compared the boundaries of niche space using ecological niche or species distribution models and/or principal components analyses fit to occurrence data (Liu et al. 2020b; Bates and Bertelsmeier 2021). Such approaches provide valuable insight into whether the boundaries of species niches shift, expand or contract in novel environments. However, differences in species' distributional patterns can occur not only due to processes that determine niche boundaries but also as a function of how species respond to environments representing the interior of their niche space. An outstanding question is whether the a species' responses to its environment differs between original and new geographic space (Hierro et al. 2017).

While typical approaches to examining niche conservatism focus on occurrence information (Liu et al. 2020b; Bates and Bertelsmeier 2021), a species' demographic responses to its environment may not mirror those of distribution or occupancy (Bohner and Diez 2020; A. Lee-Yaw et al. 2021). Substantial evidence suggests abundance, in particular, can be decoupled from occupancy or areas of high habitat suitability (Baer and Maron 2020; Jiménez-Valverde et al. 2020; Sporbert et al. 2020). Recent evidence of population declines in common species across taxa also has highlighted how species can lose substantial numbers of individuals while maintaining stable distributions (Baker et al. 2019; Rosenberg et al. 2019; Burns et al. 2021). Consequently, considering abundance alongside distributional responses to the environment is critical both for understanding niche dynamics and for applied conservation and management (e.g., to mitigate ecological impacts from climate change or invasive species; Baker et al. 2019).

An implicit assumption of the niche conservatism hypothesis is that species respond to their environment similarly in their original and new geographic space (Figure 6a). Yet, multiple mechanisms could explain why a species' niche boundaries may appear similar but response sensitivity differs between original and novel geographic space, or vice versa (Figure 6b & c). For example, enemy or competitive release could result in abundance being more strongly associated with an environmental variable in novel compared to original geographic space, both under niche conservatism or a shift (Figure 6b & d; Woodburn and Sheppard 1996; Williams et al. 2010). Alternatively, abundance could be more strongly associated with an environmental variable in new compared to original range space due to exploiting novel food resources (Figure 6b). Wild boars (*Sus scrofa*), for instance, utilize more animal and fungal matter in their invaded versus native range (Ballari and Barrios-García 2014). Even if a species' niche boundaries differ between the original and novel geographic space, this pattern does not definitively suggest how the species responds to its newly-occupied niche space. Local adaptation to climate in novel geographic space could explain why a species may occur across a wider range of conditions in novel geographic space but respond similarly to a given climatic variable (Figure 6c).

Invasive species have been recognized as excellent test cases to explore niche dynamics because it is explicit that they have entered novel geographic space (Sax et al. 2007; Gallien and

Carboni 2017). Invasive species also are important drivers of global change and biodiversity loss (Clavero et al. 2009; McClure et al. 2018; Pysek et al. 2020). Studying how invasive species respond to their non-native environment could inform how native species may respond to global change, and indeed similar methodological approaches are used to predict where invasive species may spread and how native species may respond to climate change. Moreover, evidence suggests variation in the abundance of invasive species in their invaded versus native ranges – some species achieve notably higher abundances in their invaded ranges while others do not (Hansen et al. 2013; Parker et al. 2013; Hierro et al. 2017). Interestingly, some invasive species have also recently experienced notable population declines in their native ranges (Burns et al. 2021), raising the question of whether species are thriving in invaded ranges but declining in native ranges under similar climatic and land cover contexts. This suggests pertinent and important questions remain about how invasive species utilize niche space.

To test for niche conservatism in how abundance responds to environmental conditions in original and novel geographic space, we examined whether abundance-environmental responses (hereafter, response curves) of two common invasive species differed between their native and invaded ranges. Specifically, we modeled the abundances of House Sparrows (*Passer domesticus*) and European Starlings (*Sturnus vulgaris*) from data collected across the species' native ranges in Europe and invaded ranges in North America (Sauer et al. 2017; European Bird Census Council & BirdLife International 2019). House Sparrow and European Starling are excellent species for investigating potential response differences because they are common and widespread in both their native and invaded ranges and abundance data for them exist across Europe and North America (Sauer et al. 2017; European Bird Census Council & BirdLife International 2019; Cabe 2020; Lowther and Cink 2020). They also likely are in the postcolonization phase of their invasion in North America as they were introduced over 100 years ago and now occur across the continent (Hofmeister et al. 2021). Given some evidence of local adaptation to temperature clines and/or precipitation in North America (Schrey et al. 2011; Hofmeister et al. 2021), we expected response curves to abiotic factors would differ between Europe and North America for House Sparrow and European Starling. Because both species are habitat and diet generalists and strongly associated with humans (Cabe 2020; Lowther and Cink 2020), we expected response curves for habitat-specific variables would be similar between their native and invaded ranges.

Methods

Study species

House Sparrow and European Starling are small passerines native to Eurasia that have invaded every continent except Antarctica. Both species are strongly human-associated; their habitats are comprised entirely of human-modified environments (e.g., pasture, agriculture, urban areas; Cabe 2020; Lowther and Cink 2020). It is speculated that this trait has been a main contributor to their invasion success. In North America, both species were first introduced in the mid- to late-1800s and occurred across the continent approximately 50–70 years after their first introductions (Robbins 1973; Linz et al. 2007). They currently are some of the most common and abundant species and are known to negatively impact native biodiversity and human livelihoods in North America (e.g., they can outcompete native cavity nesters, spread Salmonella bacteria in cattle feedlots through their feces; Avery and Tillman 2005). Yet, despite being strongly human-associated, common, and invasive, House Sparrow and European Starling have experienced substantial population declines in the last 50 years in their native ranges in Europe and invaded ranges in North America (Rosenberg et al. 2019; Burns et al. 2021). In Europe, country-level declines primarily have been attributed to reduced food availability due to agricultural intensification (Donald et al. 2006), though recent evidence suggests declines of House Sparrow in urban areas in Europe may be due to disease (Dadam et al. 2019). Drivers of declines for these species in North America largely are unknown, though some evidence suggests House Sparrow reproduction is negatively affected by lead pollution in urban areas (White et al. 2022).

Avian data

We used data from two international breeding bird monitoring programs – the Pan-European Common Bird Monitoring Scheme (PECBMS; European Bird Census Council & BirdLife International 2019) and the North American Breeding Bird Survey (Sauer et al. 2017) – to quantify the abundance of House Sparrows and European Starlings in their native and invaded ranges, respectively. PECBMS is a volunteer-based monitoring program that has operated since the early 2000s (European Bird Census Council and BirdLife International 2019). Methodologies vary somewhat by monitoring scheme (Appendix C Table C1) and data from all participating countries are collated to produce national and supranational trends (European Bird Census Council & BirdLife International 2019). The North American Breeding Bird Survey is a volunteer-based bird monitoring program that began in the eastern United States in the 1960s and now covers southern Canada, the United States, and northern Mexico. Each North American Breeding Bird Survey route contains 50 stops spaced approximately 0.8 km apart at which qualified volunteer surveyors conduct three-minute unfixed-radius point counts (Sauer et al. 2017).

We used site-level PECBMS data to quantify abundance instead of national or supranational trends produced by the program so that we could examine factors influencing local abundance (i.e., at a site). We used North American Breeding Bird Survey data from the first stop of routes that occur on the North American mainland and met program criteria for data quality (e.g., surveys occurred at appropriate times and under appropriate weather conditions; Robbins et al. 1986; O'Connor et al. 2000). We used data only from the first stop because spatial information for the other 49 stops is not publicly available for the full dataset. We used count data from 1992–2018 for all monitoring schemes and years for which they were available to align with the temporal resolution of our land cover and climate data. For monitoring schemes that conducted multiple surveys in a breeding season, House Sparrow data were provided as a maximum count (Appendix C Table C1). For European Starling, we restricted our dataset to observations that occurred before June to better ensure we were modeling observations of adult birds only (i.e., not adults and juveniles; see **Appendix C**). For monitoring schemes that conducted multiple surveys in a breeding season, we averaged European Starling counts across survey locations within a year. This resulted in a total of 209617 observations from 17850 survey locations for European Starling and 199795 observations from 15741 survey locations for House Sparrow.

Spatial data

We generated focal land cover metrics from the European Space Agency (ESA) Land Cover CCI Climate Research product (Santoro et al. 2017). The ESA land cover product contains annual land cover data for over 20 land cover classes from 1992–2018 at a 300-m2 spatial resolution. Five classes in this product represent anthropogenic land use and thus potential habitat for House Sparrow and European Starling: four for agriculture (“cropland, rain-fed”, “cropland, irrigated or post-flooding”, “mosaic cropland/natural vegetation”, “mosaic natural vegetation/cropland”) and one for urban areas (“urban areas”; Santoro et al. 2017). To align with the most common sampling design of the monitoring schemes in Europe (Appendix C Table C1), we quantified the annual proportion of anthropogenic land cover types within 1-km-radii buffers surrounding the centroid of survey locations in Europe and the first stop of BBS routes in North America (Pellissier et al. 2020). We summed the proportions of the rain-fed and irrigated or post-flooding cropland classes to obtain the total proportion of cropland per site. We also summed the proportions of the mosaic cropland/natural vegetation and mosaic natural vegetation/cropland classes into a total proportion of mosaic cropland and natural vegetation class per site.

We used the CHELSA climate dataset, which includes global monthly precipitation and temperature data at a 30-arcsecond (~750 m2) spatial resolution from 1992–2018 (Karger et al. 2017a; Karger et al. 2017b). We calculated site-level average breeding season temperature (hereafter, temperature) as the average of monthly mean daily temperature within a 1-km-radii buffer surrounding each site from February–July for House Sparrow and March–June for European Starling (Cabe 2020; Lowther and Cink 2020). We calculated site-level cumulative average breeding season precipitation (hereafter, precipitation) as the sum of average monthly precipitation within a 1-km-radii buffer surrounding each site within the same time periods for each species.

We used the Global Multi-resolution Terrain Elevation Data 2010 dataset to quantify elevation at each site (~250-m2 spatial resolution; Danielson and Gesch 2011). We calculated elevation as the average elevation within a 1-km-radii buffer surrounding each site. We calculated all climate and elevation variables in ArcGIS Pro (2021) and all land cover variables in Google Earth Engine.

Modeling

We fit generalized linear mixed effects models to examine the sensitivity of House Sparrow and European Starling counts to land cover, climate, and elevation in Europe versus North America. We assumed bird counts arose from a negative binomial distribution and used a log link function to model the influence of focal covariates. We were unable to account for detection probability in our models as this information did not exist or was unavailable to us for most monitoring schemes, so our models provide inference on patterns of relative abundance (hereafter, abundance). To explore whether abundance responses to environmental conditions differed in the native versus invaded range, we fit 2-way interactions of continent with each of our focal land cover, climate, and elevation variables. We included a fixed effect for time surveyed (see **Appendix C**) and an offset term representing area sampled *sensu* Pellissier et al. (2020) to account for differences between monitoring schemes within and across continents. We included random effects for scheme and survey location to capture remaining variation associated with these variables that was not accounted for by our fixed effects. Correlations between covariates and variance inflation factors were checked and non-correlated covariates were standardized prior to model fitting (Fox and Weisberg 2019). We fit the model separately to data for European Starling and House Sparrow using the glmmTMB package (Brooks et al. 2017) in R (R Core Team 2021). We examined model diagnostics using the DHARMa package (Hartig 2021).

Results

We found differences in response curves between the native and invaded ranges for both House Sparrow and European Starling, as well as differences in environmental range limits (Tables 3 & 4, Figures 7 and 8). Both species' abundances decreased with elevation in Europe but did not vary with elevation in North America (Tables 3 & 4, Figure 7). European Starling abundance did not respond to temperature and increased slightly with precipitation in Europe but not in North America. House Sparrow abundance decreased with precipitation in both continents but increased more with temperature in Europe than in North America (Tables 3 & 4, Figure 7). Both species were detected across a wider range of abiotic conditions in their invaded North American than native European ranges (Figure 7). House Sparrow and European Starling were detected at higher elevations, at cooler and warmer average daily temperatures, and in areas with wetter breeding seasons in North America compared to Europe.

Response sensitivity to land cover generally was higher in the native than invaded range, with variation occurring by species and land cover type (Figure 8). Mean abundance of European Starling increased more with the proportion of all land cover types except grassland in Europe than in North America. Mean abundance of House Sparrow increased more with the proportion of cropland and urban areas in Europe than in North America. Both species responded similarly across continents to the proportion of grassland and House Sparrow responded similarly to the proportion of mosaic cropland and natural vegetation (Figure 8). In addition, land cover had a stronger effect on both species' abundances than climate and elevation (Tables 3 & 4; Figures 7 and 8).

Discussion

We found that the abundance responses of two common but declining invasive species differed across continents representing their native and non-native ranges. Both House Sparrow and European Starling responded to key components of the environment differently in Europe and North America – specifically to elevation, cropland, and urban areas. To others, like grassland, they responded similarly across continents. Models that predict and project the consequences of global change implicitly assume species respond consistently to their environment across space – i.e., niche conservatism – and hence our work has important implications for the reliability of models used to predict species' niche shifts and distributions (Liu et al. 2020a, 2020b; Bates and Bertelsmeier 2021; Rousseau and Betts 2022).

Abiotic factors are main determinants of species distributions at broad scales (Davies et al. 2007). House Sparrow and European Starling responded both similarly and differently to abiotic factors across continents. Early morphological studies on House Sparrow in North America found evidence of rapid adaptation in the species, determining that House Sparrow body size in North America followed Bergmann's rule (i.e., average body size increased with latitude; Johnston and Selander 1973) but followed the opposite pattern in Europe (Johnston and Selander 1964). Recent genetic studies comparing House Sparrow and European Starling in Europe and North America found evidence of adaptation in components of the species' genome associated with elevation, precipitation, and/or temperature, despite a lack of population structure (Schrey et al. 2011; Liebl et al. 2015; Bodt et al. 2020; Hofmeister et al. 2021). Combined, this evidence suggests House Sparrow and European Starling may respond differently to and/or occur in a wider range of some abiotic conditions in North America than in Europe due to adaptation to local climatic regimes. Yet, we found House Sparrow responded negatively to precipitation in both continents and European Starling responded negatively to precipitation in North America but not Europe. In addition, European Starling were not detected across as wide a range of precipitation conditions in our North American compared to European dataset. These patterns contrast with findings that European Starling has experienced niche expansion and House Sparrow has experienced niche unfilling in North America (Strubbe et al. 2015), but align with the species' habitat preferences as wetter areas tend to be forested and House Sparrow and European Starling prefer more open environments (Cabe 2020; Lowther and Cink 2020).

Our models reveal House Sparrow and European Starling generally are more sensitive to, and thus may be more limited by, human land cover in their native ranges than their invaded ranges. Widespread land conversion in their invaded range and behavioral plasticity could be two non-mutually exclusive explanations for these patterns. Genetic studies suggest both species quickly recovered genetic diversity following a genetic bottleneck associated with introduction due to rapid expansion (Liebl et al. 2015; Hofmeister et al. 2021), likely due to the demographic explosion resulting from enemy and/or competitor release that species can experience in novel environments. While these species may no longer be experiencing enemy release 80+ years after their colonization of the continent, House Sparrow and European Starling are exceptional in their ability to exploit agricultural and urban environments (Cabe 2020; Lowther and Cink 2020). Passerines native to Europe are believed to be more tolerant of human disturbance given the evolutionary history of these species with continental land use change that occurred in Europe thousands of years ago. European colonization of North America occurred only 300–500 years ago and transformed North American land use to resemble that of Europe, which likely created ideal habitat for House Sparrow and European Starling (and at the expense of bird species associated with pre-colonization indigenous land use; Bohning-Gaese and Bauer 1996).

Moreover, House Sparrow and European Starling exhibit high behavioral flexibility (Martin and Fitzgerald 2005; Lafleur et al. 2007). Evidence suggests both species will readily eat novel foods, and for House Sparrow, will readily feed near novel objects in their invaded ranges (Martin and Fitzgerald 2005; Lafleur et al. 2007). A study on European Starling in California found starlings foraged primarily on anthropogenic food resources, including feedlots, landfills, shipping yards, and slaughterhouses (Klug and Homan 2020). Because these species are diet generalists (Cabe 2020; Lowther and Cink 2020) and can exhibit behavioral flexibility in their food choices, they may be exploiting a wider range of foods in their invaded than native ranges. Both species did respond similarly across continents to some land cover types, however, including grassland. Grassland is key foraging habitat for European Starling (Cabe 2020), and is likely the most similar land cover type between Europe and North America of those we considered in terms of ecological structure and management.

Interestingly, we found predicted abundance of both House Sparrow and European Starling was substantially lower in North America compared to Europe. While this pattern could arise in part from the different survey methods and number of counts included in our dataset (e.g., density of survey locations was much higher in Europe compared to North America; Figure S1), we included survey effort as an offset in our models (see **Methods**). Using other independent datasets to confirm our finding of higher abundance in Europe would be interesting because many hypotheses in invasion biology assume or suggest that a species should achieve higher abundance in its invaded compared to native range (e.g., via enemy or competitor release; Parker et al. 2013). Evidence from plants and marine species suggests some species achieve higher abundances in their invaded range, but this pattern is species-specific and, like native species, even widespread invaders typically occur at low local abundance (Hansen et al. 2013;

Parker et al. 2013). In addition, the perception that House Sparrow and European Starling are extremely successful and impactful invaders in North America suggests per capita effects of these species could be higher in their invaded ranges (Callaway et al. 2011; Cabe 2020; Lowther and Cink 2020). Because our focal species are human-associated (Cabe 2020; Lowther and Cink 2020) and European colonization of North America altered indigenous urban and agricultural environments to be more like those in Europe, other species may show even more striking differences in their response curves between the native and invaded range.

Variation in how species respond to their environment across geographic space challenges the transferability of models used to quantify species' niches and distributions (Elith et al. 2010; Rousseau and Betts 2022). Recent studies have highlighted pervasive challenges with transferability and extrapolation of species distribution models (Liu et al. 2020a), with many attributing poor performance of these models to extrapolation (i.e., predicting species occurrence to areas outside of the range of environmental variables included in the data; Elith et al. 2010). Little attention has been paid, however, to how intraspecific variation in environmental responses may contribute to poor transferability (though see Collart et al. 2020; Rousseau and Betts 2022), especially when species enter novel geographic space that is within their environmental range boundaries. Indeed, Sofaer et al. (2018) found errors from species distribution models were much larger in areas with more similar conditions to where a species occurred than in more distant environmental space, which was dominated by true negatives. The reliability of species distribution models ultimately depends on consistent relationships between the species and its environment, but our findings and others suggest this is not always the case (Connor et al. 2019; Crosby et al. 2019; Rousseau and Betts 2022). Further investigation into whether and how species' response sensitivities to their environments vary is critical for improving the reliability of these widely-used models.

Understanding how species respond to the environment within their niche space will be critical under continued global change (Riahi et al. 2017). Our findings that two widespread, common, and invasive species responded differently to some components of their niche in their native versus invaded ranges calls into question the assumption that niches are conserved over space and time. We suggest that more research attention is directed toward understanding species' responses within the interior of their niche space, in addition to defining its boundaries (Bates and Bertelsmeier 2021). With this more nuanced and comprehensive examination of the niche concept, we can improve our ability to predict how biological communities will be sensitive or resilient to ongoing global change.

Figures

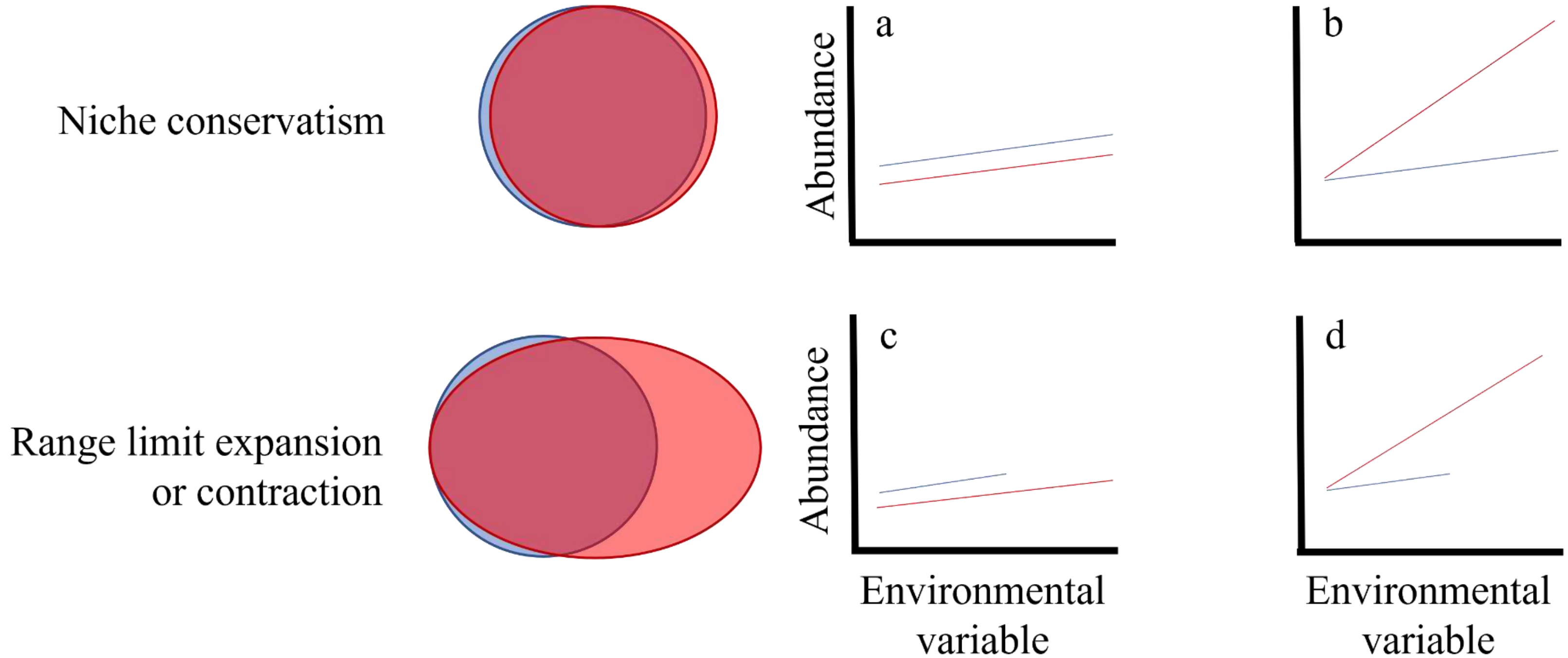

Figure 6. Four scenarios of how the sensitivity of a species' abundance could vary in original and novel geographic space (blue and red circles, respectively) under niche conservatism and niche expansion (i.e., an instance where niche dissimilarity may be detected). Whether or not a species shifts its niche in novel geographic space, it could respond to its environment similarly (a and c, with similar slopes) or differently (b and d, with different slopes) in original and novel geographic space.

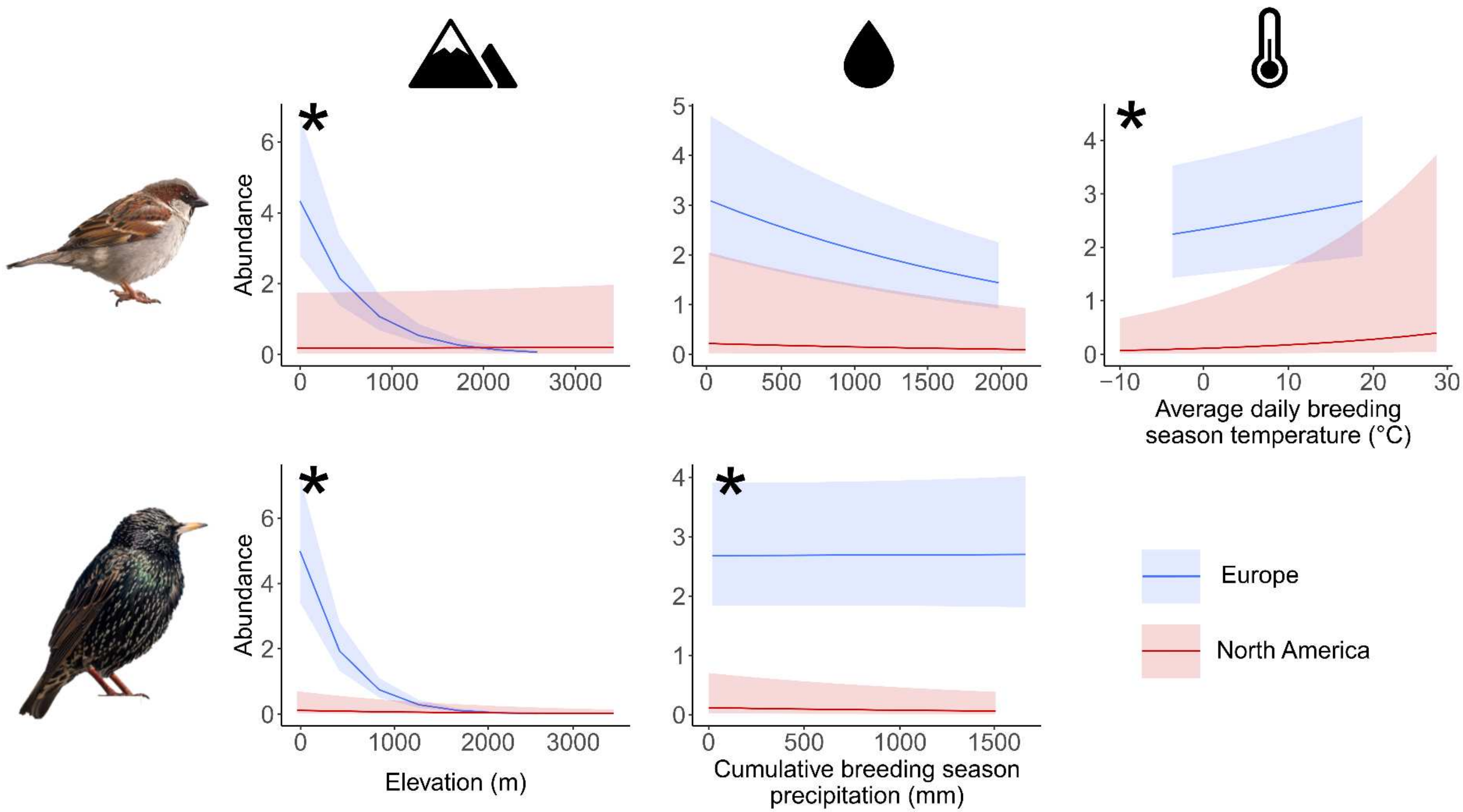

Figure 7. Predicted abundance (birds detected per square kilometer; means and 95% confidence intervals) of House Sparrow and European Starling (top and bottom, respectively) in Europe and North America as a function of elevation, precipitation, and temperature from generalized linear mixed models fit to count data for the species from the two continents from 1992–2018. Predicted abundance and 95% confidence intervals are shown within the environmental range in which each species occurred on each continent. Asterisks denote variables for which the two-way interaction of continent (Europe or North America) and the focal variable were statistically significant. Predicted abundance of European Starling as a function of temperature is not shown because the interaction nor main effect of temperature were statistically significant. The picture of House Sparrow is a derivative of "House Sparrow" by hedera.baltica and the picture of European Starling is a derivative of "European Starling [49/366]" by timsackton, both used under CC BY-SA 2.0.

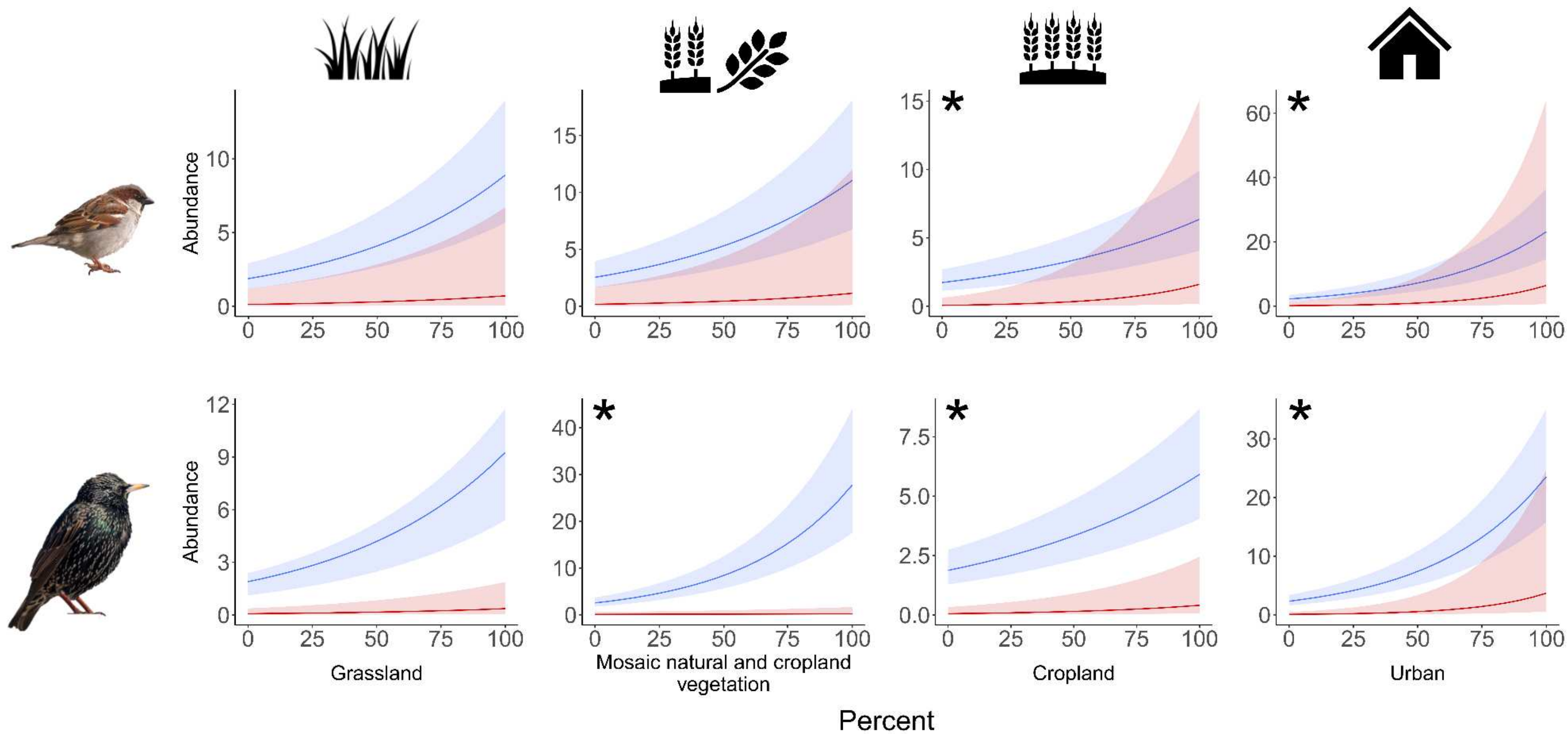

Figure 8. Predicted abundance (birds detected per square kilometer; means and 95% confidence intervals) of House Sparrow and European Starling in Europe and North America (top and bottom, and blue and red, respectively) as a function of human land cover composition within 1 km of survey sites from generalized linear mixed models fit to count data for the species from the two continents from 1992–2018. Asterisks denote variables for which the two-way interaction of continent (Europe or North America) and the focal variable were statistically significant. The picture of House Sparrow is a derivative of "House Sparrow" by hedera.baltica and the picture of European Starling is a derivative of "European Starling [49/366]" by timsackton, both used under CC BY-SA 2.0.

Tables

Table 3. Standardized coefficient estimates (means and 95% confidence intervals [CI]) of fixed effects from the model for House Sparrow relative abundance (birds detected per square kilometer) from count data from the North American Breeding Bird Survey and Pan-European Common Bird Monitoring scheme from 1992–2018. Abundance was modeled using a negative binomial distribution and the intercept represents abundance in Europe. Land cover types were calculated as proportions. Temperature was calculated as average daily breeding season temperature and precipitation was calculated as average cumulative breeding season precipitation within 1-km-radii buffers surrounding survey locations. Bolded text indicates fixed effects with statistically significant effects on abundance ($\alpha = 0.05$).

Fixed effects	Mean	CI	z value	p value
Intercept	**0.977**	**(0.537, 1.416)**	**4.35**	**<0.001**
Cropland (%)	**0.482**	**(0.445, 0.519)**	**25.24**	**<0.001**
North America	-2.649	(-4.939, -0.359)	-2.27	0.02337
Grassland (%)	**0.487**	**(0.45, 0.525)**	**25.36**	**<0.001**
Mosaic natural and cropland vegetation (%)	**0.125**	**(0.106, 0.145)**	**12.69**	**<0.001**
Urban (%)	**0.444**	**(0.418, 0.47)**	**33.38**	**<0.001**
Temperature (Celsius)	**0.040**	**(0.015, 0.066)**	**3.07**	**0.002**
Precipitation (mm)	**-0.076**	**(-0.086, -0.066)**	**-14.82**	**<0.001**
Elevation (mm)	**-0.696**	**(-0.768, -0.624)**	**-18.95**	**<0.001**
Time surveyed	0.010	(-0.274, 0.294)	0.07	0.944
Cropland * North America	**0.697**	**(0.609, 0.786)**	**15.51**	**<0.001**
Grassland * North America	0.047	(-0.049, 0.142)	0.95	0.34
Mosaic natural and cropland vegetation * North America	0.033	(-0.033, 0.1)	0.99	0.322
Urban * North America	**0.280**	**(0.176, 0.385)**	**5.26**	**<0.001**
Temperature * North America	**0.133**	**(0.079, 0.187)**	**4.84**	**<0.001**
Precipitation * North America	0.003	(-0.035, 0.041)	0.14	0.888
Elevation * North America	**0.706**	**(0.607, 0.805)**	**13.99**	**<0.001**

Table 4. Standardized coefficient estimates (means and 95% confidence intervals [CI]) of fixed effects from the model for European Starling relative abundance (birds detected per square kilometer) from count data from the North American Breeding Bird Survey and Pan-European Common Bird Monitoring scheme from 1992–2018. Abundance was modeled using a negative binomial distribution and the intercept represents abundance in Europe. Land cover types were calculated as proportions. Temperature was calculated as average daily breeding season temperature and precipitation was calculated as average cumulative breeding season precipitation within 1-km-radii buffers surrounding survey locations. Bolded text indicates fixed effects with statistically significant effects on abundance ($\alpha = 0.05$).

Fixed effects	Mean	CI	z value	p value
Intercept	**0.986**	**(0.609, 1.363)**	**5.13**	**<0.001**
Cropland (%)	**0.418**	**(0.385, 0.452)**	**24.43**	**<0.001**
North America	**-3.254**	**(-5.088, -1.42)**	**-3.48**	**<0.001**
Grassland (%)	**0.493**	**(0.459, 0.528)**	**27.96**	**<0.001**
Mosaic natural and cropland vegetation (%)	**0.187**	**(0.166, 0.208)**	**17.29**	**<0.001**
Urban (%)	**0.406**	**(0.382, 0.43)**	**33.14**	**<0.001**
Temperature (Celsius)	0.005	(-0.025, 0.036)	0.35	0.728
Precipitation (mm)	0.001	(-0.012, 0.013)	0.09	0.928
Elevation (mm)	**-0.948**	**(-1.013, -0.883)**	**-28.75**	**<0.001**
Time surveyed	0.005	(-0.287, 0.298)	0.04	0.971
Cropland * North America	**0.306**	**(0.213, 0.399)**	**6.47**	**<0.001**
Grassland * North America	0.001	(-0.103, 0.106)	0.03	0.98
Mosaic natural and cropland vegetation * North America	**-0.124**	**(-0.197, -0.05)**	**-3.31**	**0.001**
Urban * North America	**0.262**	**(0.141, 0.382)**	**4.26**	**<0.001**
Temperature * North America	-0.047	(-0.112, 0.018)	-1.41	0.157
Precipitation * North America	**-0.060**	**(-0.113, -0.006)**	**-2.18**	**0.029**
Elevation * North America	**0.739**	**(0.637, 0.841)**	**14.21**	**<0.001**

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APPENDIX A. EASTERN SCREECH-OWL RESPOND POSITIVELY TO INCREASED VARIATION IN VEGETATION STRUCTURE AT ITS WESTERN RANGE EDGE

Examination of the effect of using different thresholds for calculating tree cover on model results

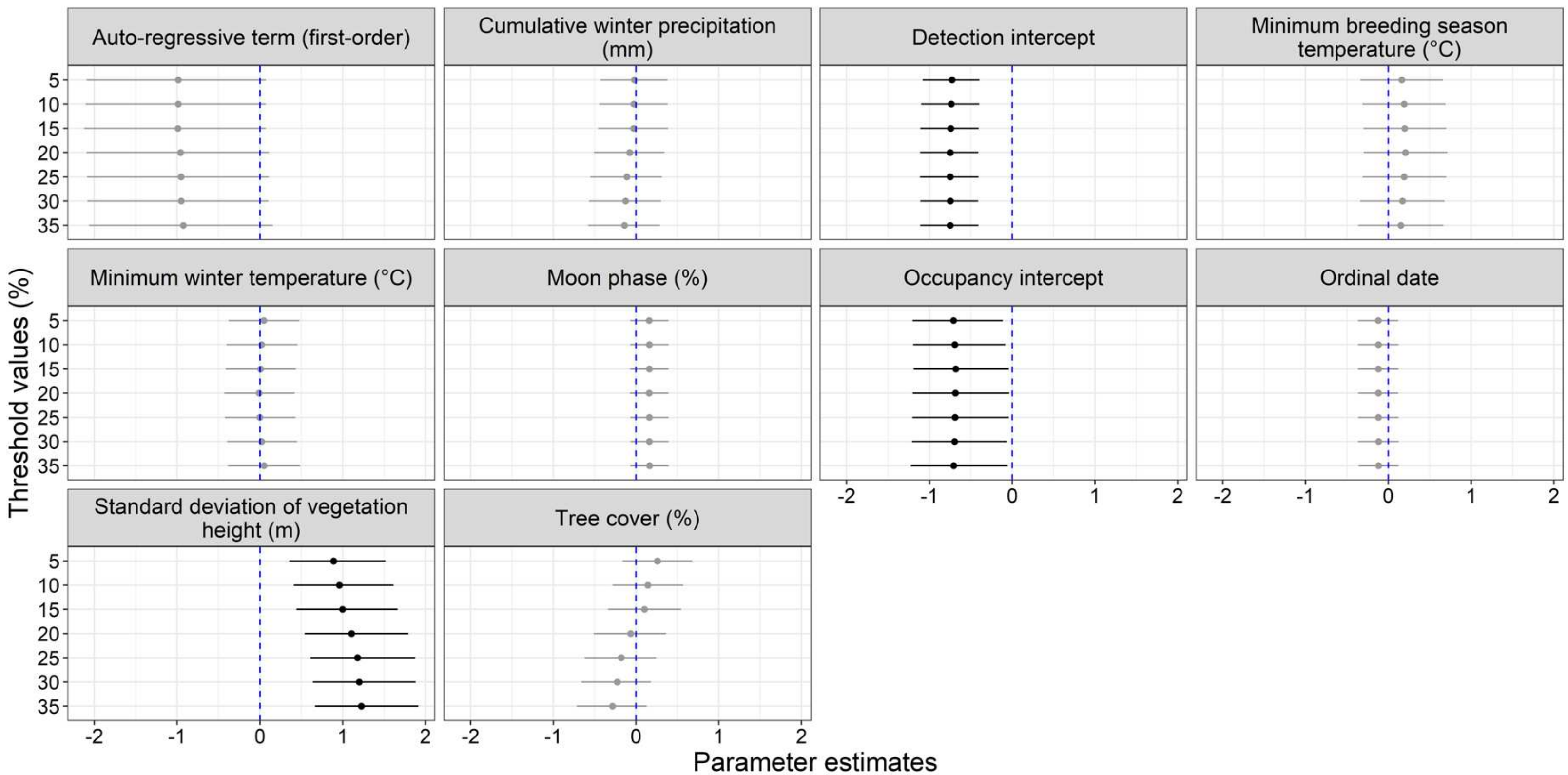

Figure A1. Means and 95% credible intervals (points and lines, respectively) of the posterior distributions of parameters (facets) in the auto-logistic occupancy model fit to Eastern Screech-Owl data collected along the Cache la Poudre River in Fort Collins, Colorado in 2013–2021. Colors represent whether a parameter influenced Eastern Screech-Owl detection or occupancy probability (i.e., whether the 95% credible interval of a parameter included zero; black denotes an influence, gray denotes a lack of influence). Standard deviation of vegetation height and tree cover were averages within a 250-m-radii buffer surrounding the centroid of sampling units. Temperature and precipitation variables were yearly averages across the study area. Across threshold values, parameter estimates were largely the same and credible intervals consistently did or did not include zero – i.e., the interpretation of whether a given parameter influenced occupancy or detection was consistent.

Results for detection

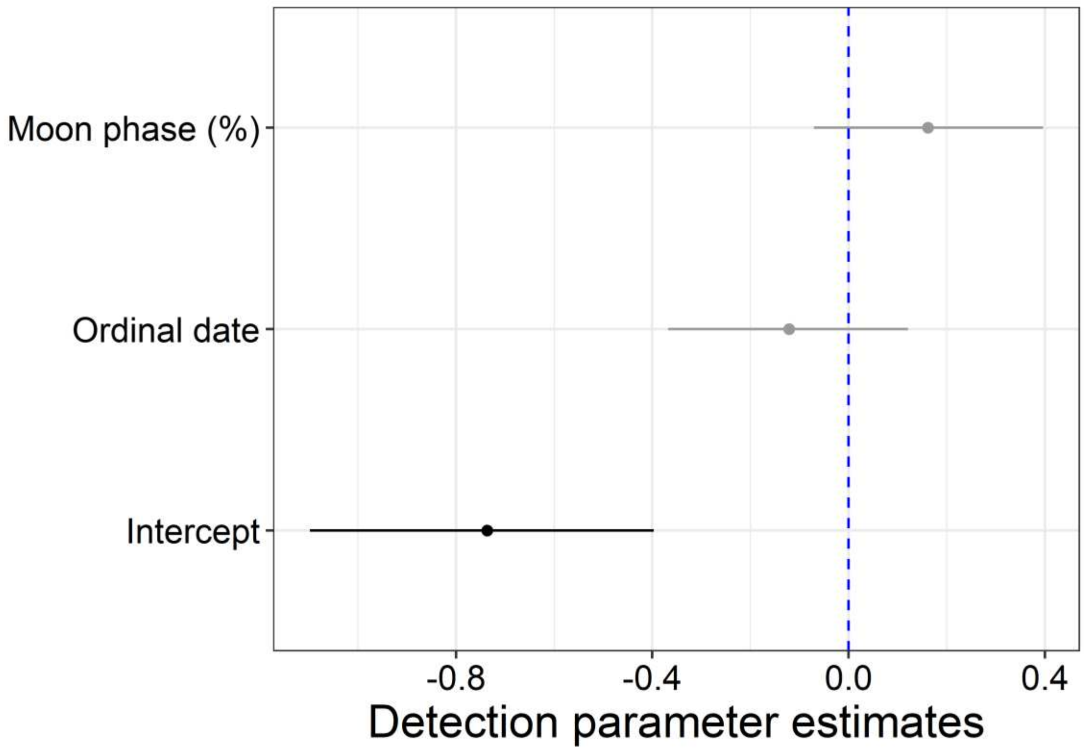

Figure A2. Means and 95% credible intervals (points and lines, respectively) of the posterior distributions of parameters associated with the detection process in the auto-logistic occupancy model fit to Eastern Screech-Owl data collected along the Cache la Poudre River in Fort Collins, Colorado in 2013–2021. Colors represent whether a parameter influenced Eastern Screech-Owl detection probability (i.e., whether the 95% credible interval of a parameter included zero; black denotes an influence, gray denotes a lack of influence).

APPENDIX B. LAND COVER DIFFERENTIALLY AFFECTS ABUNDANCE OF COMMON AND RARE BIRDS

Figures

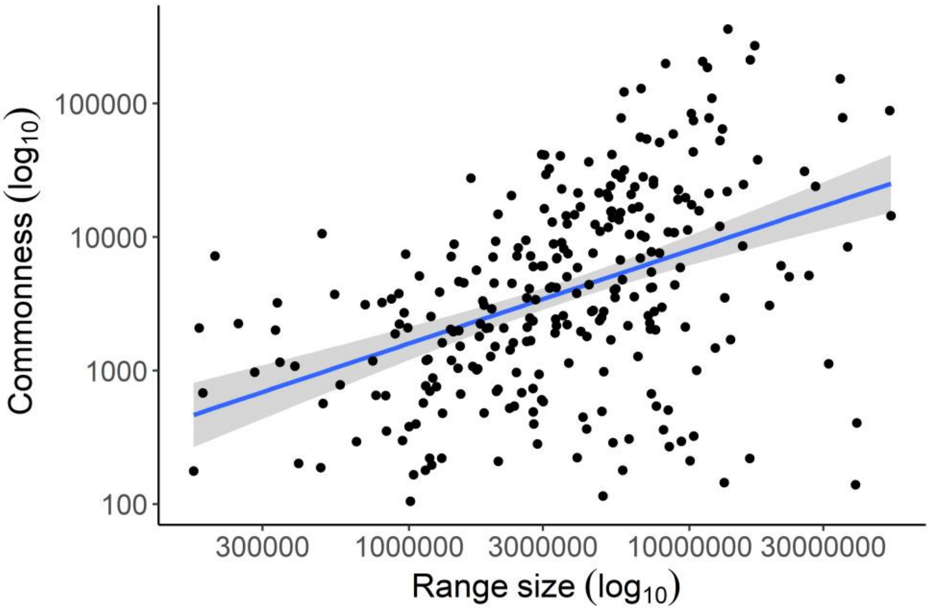

Figure B1. Relationship between commonness (species' total abundance summed across all North American Breeding Bird Survey routes surveyed in 2001 in the United States) and an independent metric of species' range sizes (meters) from the AVONET database (n = 279 species; three species were included in our dataset that were not present in AVONET; Tobias et al. 2022). Commonness and range size were log_{10}-transformed for ease of visualization. In the main analyses, commonness was transformed using the natural log.

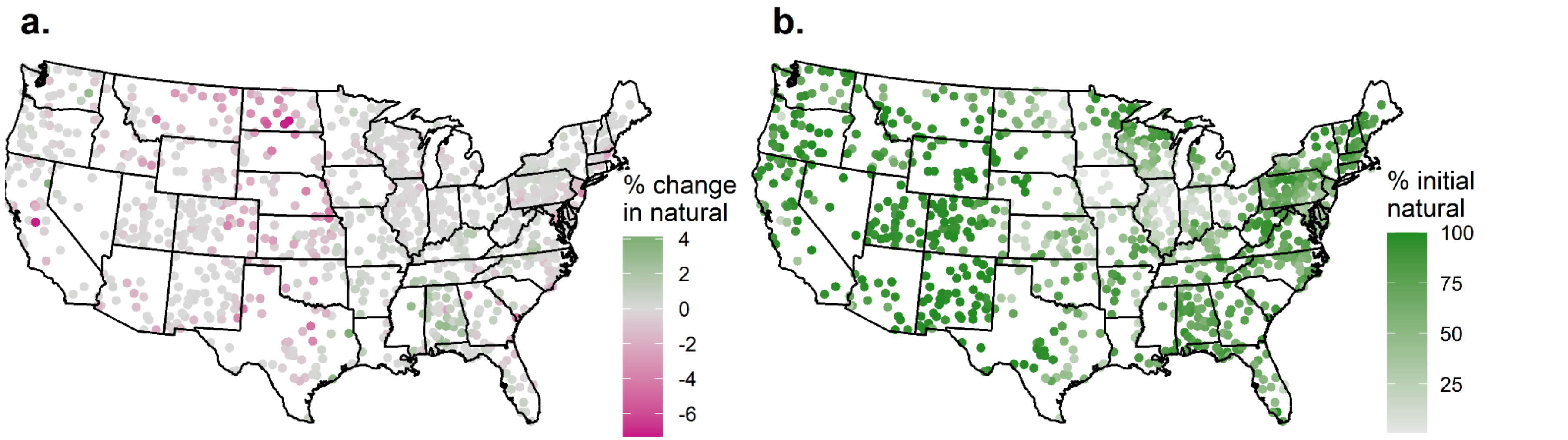

Figure B2. North American Breeding Bird Survey route centroids for which avian abundance data (individuals per species per route) were compiled between 2000–2002 and 2015–2017 (n = 985), colored by percent change in the proportion of natural land cover between 2001 and 2016 and initial proportion of natural land cover in 2001 (a. and b., respectively) within a 19.7-km-radii buffer surrounding the route.

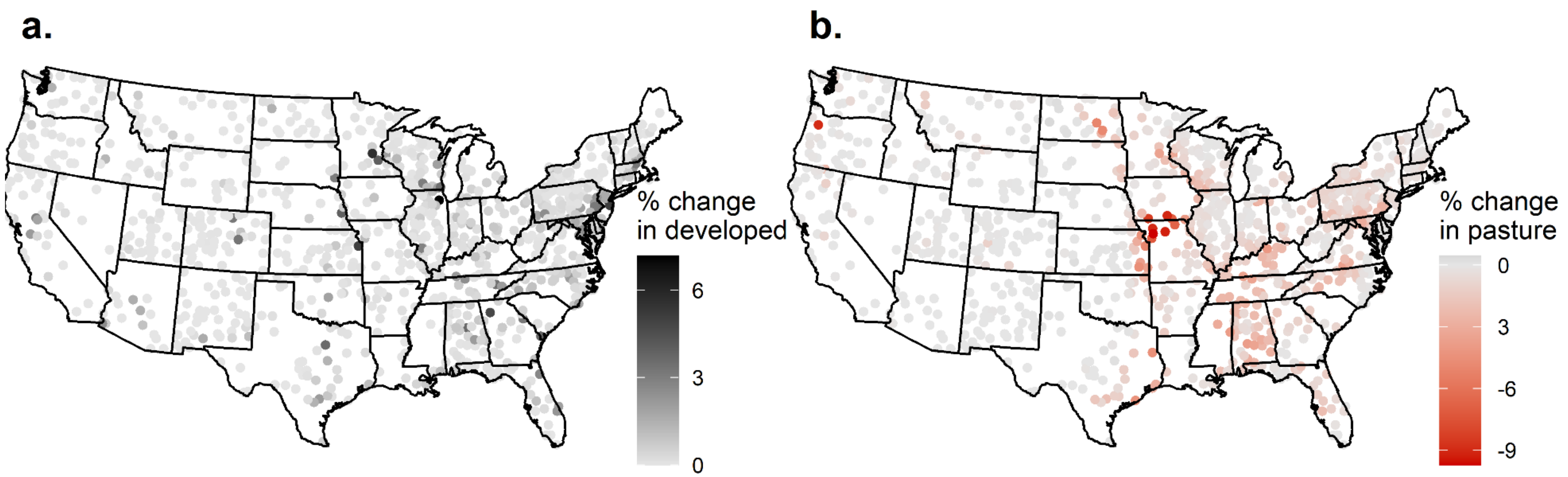

Figure B3. North American Breeding Bird Survey routes for which avian abundance data (individuals per species per route) were compiled between 2000–2002 and 2015–2017 (n = 985), colored by percent change in development or pasture between 2001 and 2016 (a. and b., respectively) within a 19.7-km-radii buffer surrounding the route.

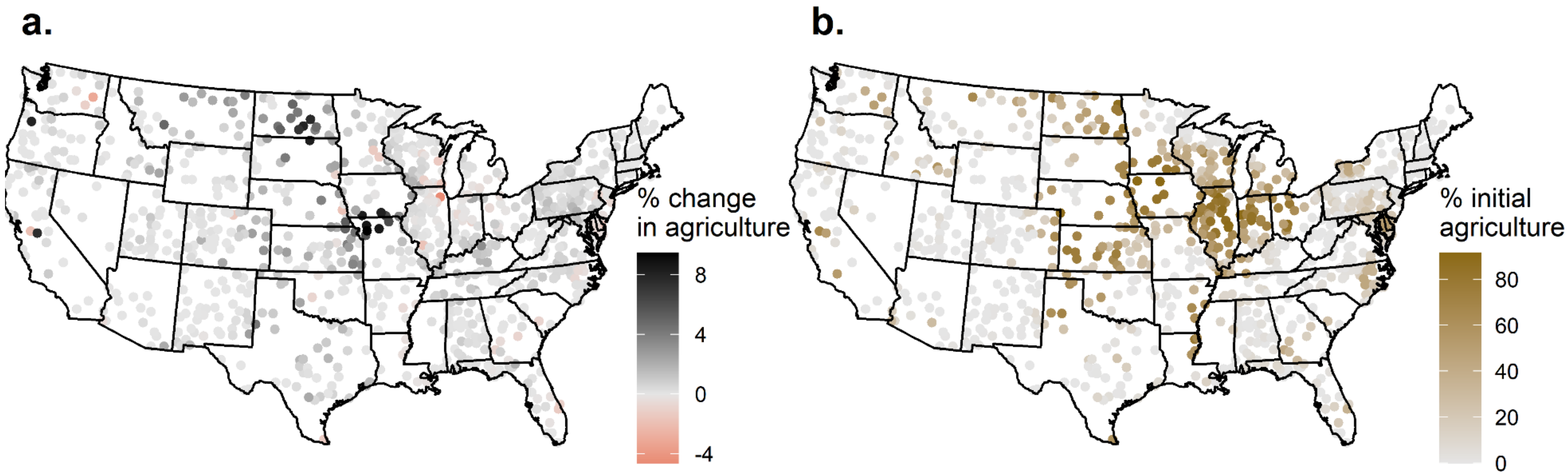

Figure B4. North American Breeding Bird Survey routes for which avian abundance data (individuals per species per route) were compiled between 2000–2002 and 2015–2017 (n = 985), colored by percent change in the proportion of agriculture between 2001 and 2016 and initial proportion of agriculture in 2001 (a. and b., respectively) within a 19.7-km-radii buffer surrounding the route.

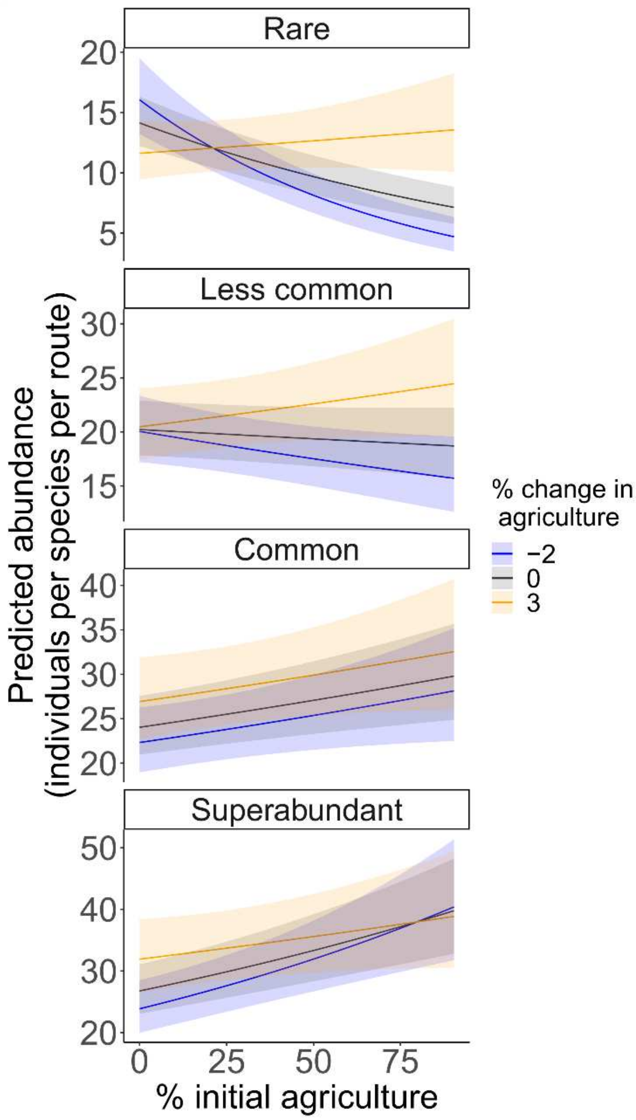

Figure B5. Predicted abundance in 2016 (means and 95% confidence intervals for counts summed across 2015–2017) as a function of commonness (facets), the initial proportion of agriculture (i.e., in 2001), and change in agriculture (colors; values represent the mean [0] and +/- two standard deviations [-2 and 3]) surrounding focal North American Breeding Bird Survey routes between 2001 and 2016 in the conterminous United States (n = 985 routes).

Tables

Table B1. Land cover classes from the 2001 and 2016 National Land Cover Database summarized within 19.7-km-radii buffers surrounding focal North American Breeding Bird Survey routes in the conterminous United States (n = 985 routes). Numbers in parentheses correspond to the value associated with a given land class in the National Land Cover Database.

Focal land cover types	**NLCD classes**
Natural	Deciduous forest (41); evergreen forest (42); mixed forest (43); shrub/scrub (52); grassland/herbaceous (71); woody wetlands (90); emergent herbaceous wetlands (95)
Development	Developed, open space (21); developed, low intensity (22); developed, medium intensity (23); developed, high intensity (24)
Agriculture	Cultivated crops (81)
Pasture	Pasture/hay (82)

Alternative model specifications

In addition to the models described in the main text, we fit two alternative specifications of the natural and human land cover models – generalized linear mixed models with a negative binomial distribution, 2016 route-level abundance as the response variable, and untransformed (instead of logged) 2001 route-level abundance as a predictor (alternative model 1), and linear mixed models using logged 2016 route-level abundance as the response variable and logged 2001 route-level abundance as a predictor (alternative model 2). Results largely were consistent across all models for the two-way interaction of commonness and change in pasture and the three-way interaction of commonness, change in agriculture, and initial amount of agriculture (i.e., in 2001). Results for the three-way interaction of commonness, change in natural land cover, and initial amount of natural land cover and the two-way interaction of commonness and change in development were more sensitive to model specification (Appendix B Figures B6 and B7, respectively). For the natural land cover model, the three-way interaction of commonness, change in land cover, and initial proportion of land cover was not statistically significant in the main model or alternative model 2 (Appendix B Figures B6a. and B6c., respectively), but was statistically significant in alternative model 1 (Appendix B Figure B6b.). For the human land cover model, the two-way interaction of commonness and change in development was statistically significant in the main model and alternative model 2 (Appendix B Figures B7a. and B7c., respectively), but not in alternative model 1 (Appendix B Figure B7b.). The decline in abundance with gain in developed lands was similar across commonness groups even when statistically significant (i.e., perhaps not biologically significant), and we place our emphasis on interpreting larger effects. Overall, these alternative model specifications yielded broadly similar results to but poorer patterns in the residuals or did not well predict mean 2016 route-level abundance per commonness class compared to the models described in the main text. Thus, we interpreted the models with untransformed 2016 route-level abundance as the response variable and logged 2001 route-level abundance as a predictor. Future studies could investigate the pattern for common and superabundant species shown in Appendix B Figures B6b. and B6c., where route-level abundance appears to vary by initial amount of and change in natural land cover.

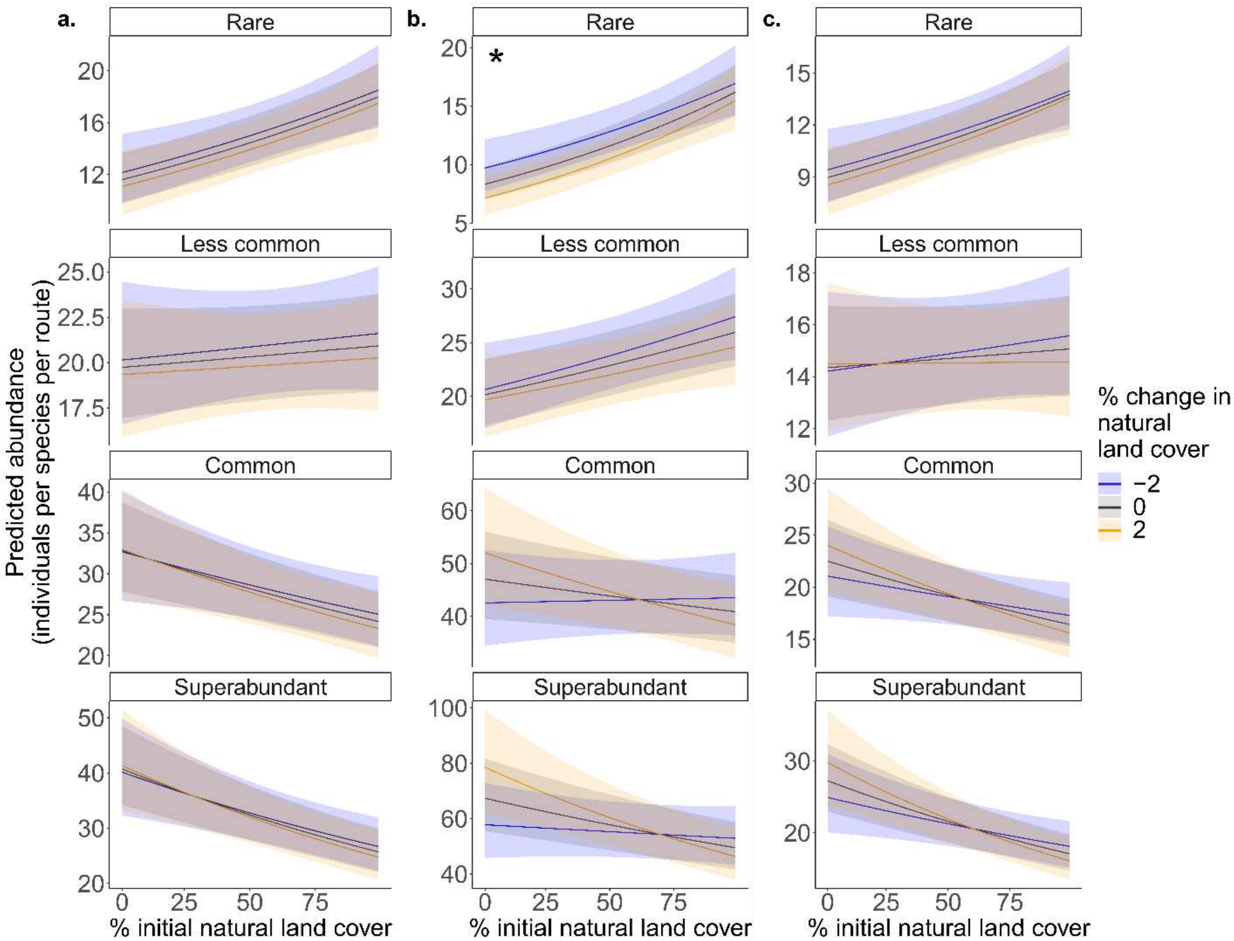

Figure B6. Predicted abundance in 2016 (means and 95% confidence intervals for 2015–2017) as a function of commonness (facets), change in natural land cover between 2001 and 2016 (colors), and the initial proportion (i.e., in 2001) of natural land cover surrounding North American Breeding Bird Survey routes in the conterminous United States (n = 985 routes) for the main natural land cover model and two alternative model specifications. Specifically, predicted abundances are shown from the main natural land cover model with 2016 route-level abundance as the response variable and logged 2001 route-level abundance as a predictor (a.), a model with 2016 route-level abundance as the response variable and untransformed 2001 route-level abundance as a predictor (alternative model 1; b.), and a model with logged 2016 route-level abundance as the response variable (modeled using a Gaussian distribution) and logged 2001 route-level abundance as a predictor (alternative model 2; c.). Asterisks denote models for which the interaction of commonness, change in natural land cover, and initial amount of natural land cover was statistically significant ($\alpha = 0.05$). Alternative model specifications (predictions shown in b. and c.) yielded similar results to the model interpreted in the main text (predictions shown in a.).

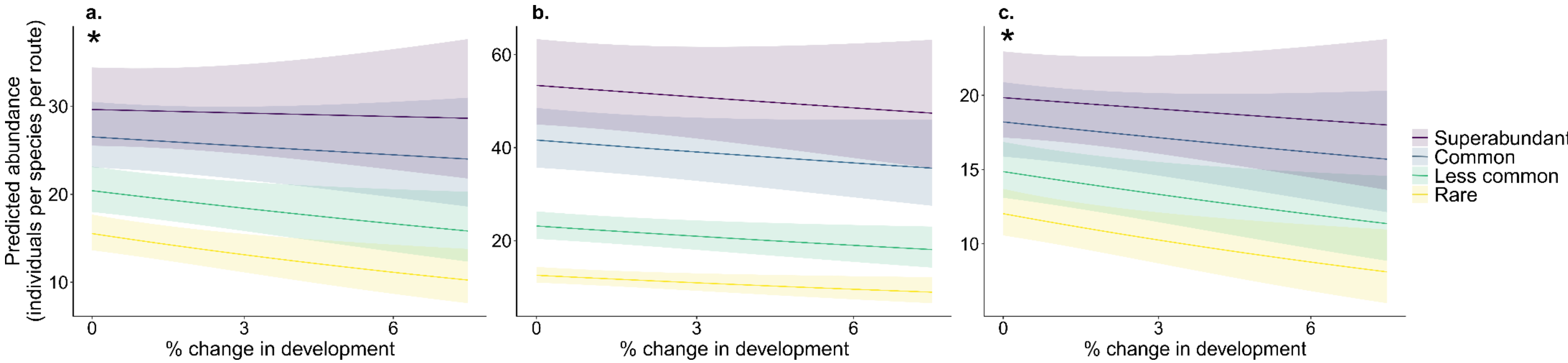

Figure B7. Predicted abundance in 2016 (means and 95% confidence intervals for 2015–2017) as a function of commonness (colors; plotted lines represent example species as in Fig 1.) and change in development surrounding North American Breeding Bird Survey routes between 2001 and 2016 in the conterminous United States (n = 985 routes) for the main human land cover model and two alternative model specifications. Specifically, predicted abundances are shown from the main human land cover model with 2016 route-level abundance as the response variable and logged 2001 route-level abundance as a predictor (a.), a model with 2016 route-level abundance as the response variable and untransformed 2001 route-level abundance as a predictor (alternative model 1; b.), and a model with logged 2016 route-level abundance as the response variable (modeled using a Gaussian distribution) and logged 2001 route-level abundance as a predictor (alternative model 2; c.). Asterisks denote models for which the interaction of commonness and change in development was statistically significant ($\alpha = 0.05$). Alternative model specifications (predictions shown in b. and c.) yielded similar results to the model interpreted in the main text (predictions shown in a.)

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Testing for spatial autocorrelation

We used the Moran's I test in the DHARMa package (Hartig 2021) in R (R Core Team 2021) to determine whether spatial autocorrelation was present in the residuals from our main natural and human land cover models (Appendix B Figure B8). Spatial autocorrelation was present in the residuals from the natural land cover model ($\alpha = 0.05$, $p = 0.036$; Appendix B Figure B8a.) but not the human land cover model ($\alpha = 0.05$, $p = 0.082$, Appendix B Figure B8b.). While the Moran's I test was statistically significant for the natural land cover model (Appendix B Figure B8a.), spatial patterns in the residuals from this model were not visually striking, and largely resembled patterns from residuals that did not show evidence of spatial autocorrelation (Appendix B Figure B8b.). Therefore, we proceeded with interpreting the natural land cover model described in the main text.

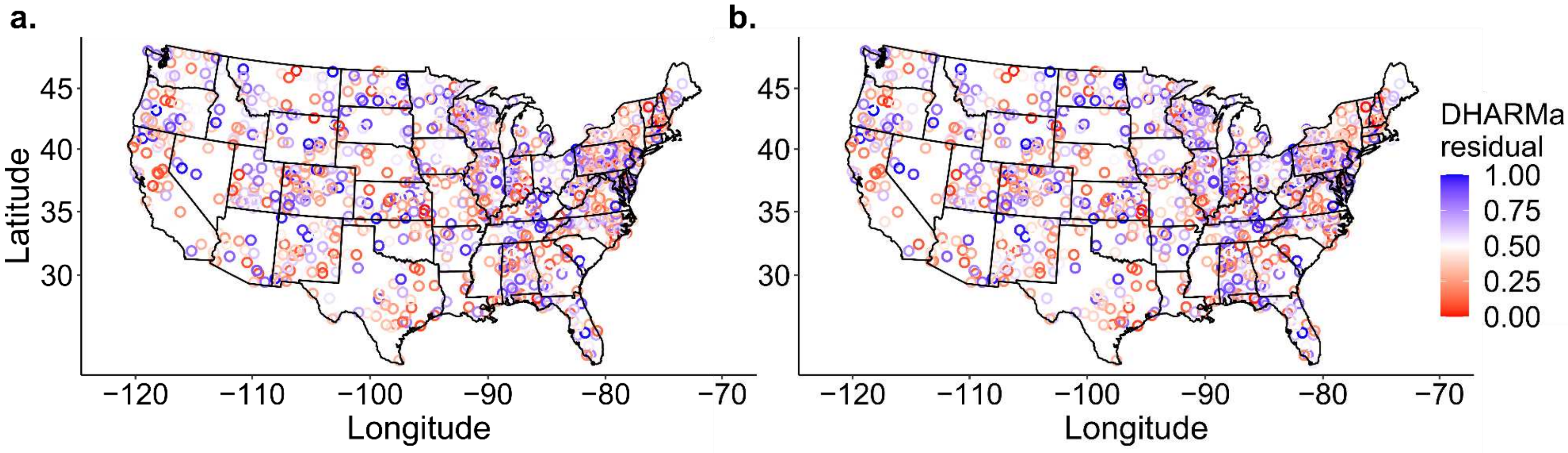

Fig. S8. Focal North American Breeding Bird Survey routes (n = 985) colored by the value of the DHARMa (Hartig 2021) residual for each route from the main natural and human land cover models (a. and b., respectively). DHARMa residuals are scaled to be between 0 and 1; a value of 0 means that all simulated values are larger than the observed value and a value of 1 means that all simulated values are smaller than the observed value.

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Hartig, F. 2021. DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models.
R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

APPENDIX C. INVASIVE POPULATIONS SHOW NICHE DIVERGENCE VIA DIFFERENCES IN ENVIRONMENTAL SENSITIVITIES AS WELL AS EXPANSION OF RANGE LIMITS

Monitoring scheme information and study area maps

Table C1. Information about monitoring schemes from which data were used to investigate House Sparrow and European Starling abundance responses to their environment in their native European and invaded North American ranges. Number of visits is the average number of surveys that occur per breeding season. Number of points is the most common number of points surveyed within a point count scheme. Total survey time is the number of points, transect length, or number of hectares surveyed (for point count, line transect, or territory mapping schemes, respectively) multiplied by the time spent surveying per sampling unit. Time surveyed is the number of visits multiplied by the total survey time per breeding season.

Scheme	Years[a]	Survey method	Number of visits	Number of points	Transect length (m)	Total survey time (minutes)	Time surveyed	Area sampled (km^2)	Number of sites - House Sparrow	Number of sites - European Starling
Austria	1998–2017	Point counts	2	10	NA	50[b]	100[b]	1.257[b]	273	340
Brussels	1992–2017	Point counts	2	1	NA	15	30	0.126	50	0
Bulgaria	2005–2016	Line transect	2	NA	1000	45	90	0.526	178	211
Catalonia	2002–2018	Line transect	2	NA	3000	135[b]	270[b]	1.326[b]	335	222
Czech Republic	1992–2018	Point counts	2	20	NA	100	200	2.513	177	224
Denmark	1992–2016	Point counts	1	15	NA	75[b]	75[b]	1.885	774	633
Estonia	1992–2016	Point counts	1	20	NA	100	100	2.513	38	42
Finland	1992–2016	Line transect	1	NA	6000	270	270	2.526	190	198
Finland	1992–2016	Point counts	1	20	NA	100	100	2.513	95	91
France	2001–2018	Point counts	2	10	NA	50	100	1.257	1945	2705
Germany	2005–2016	Line transect	4	NA	3000	135	540	1.326	956	1331
Greece	2007–2016	Point counts	2	15	NA	75	150	1.885	114	0
Hungary	1999–2016	Point counts	2	15	NA	75	150	1.885	374	530
Ireland	1998–2018	Line transect	2	NA	1000	45	90	0.526	314	401
Italy	2000–2015	Point counts	1	15	NA	75[b]	75[b]	1.885[b]	19	593

Latvia	2005–2016	Line transect	4	NA	4000	180	720	1.726	27	69
Lithuania	1994–2016	Point counts	2	20	NA	100	200	2.513	75	129
Netherlands	1992–2016	Territory mapping	7.5	NA	NA	Varies	Varies	Varies	771	1321
North American Breeding Bird Survey	1992–2018	Point counts	1	1	NA	3	3	0.126	4857	4603
Norway	2006–2017	Point counts	1	19	NA	95	95	2.388	41	73
Poland	2000–2017	Line transect	1.5	NA	1000	45	67.5	0.526	677	1036
Portugal	2004–2018	Point counts	1.5	20	NA	100	150	2.513	155	0
Romania	2006–2018	Point counts	2	10	NA	50	100	1.257	116	602
Slovakia	2005–2016	Point counts	1.5	20	NA	100	150	2.513	55	0
Slovenia	2007–2018	Line transect	2	NA	2000	90	180	0.926	113	131
Spain	1998–2016	Point counts	2	20	NA	100	200	2.513	1239	169
Sweden	1998–2017	Line transect	1	NA	8000	360	360	3.326	140	276
Switzerland	1999–2016	Territory mapping	3	NA	NA	280	840	1	131	140
United Kingdom	1994–2018	Line transect	2	NA	2000	90	180	0.926	5973	6003
Wallonia	1992–2018	Point counts	2	15	NA	75[b]	150[b]	1.885[b]	190	206

[a] All sites were not surveyed in all years, and the range of years in this column is for both species combined.

[b] Effort information varied by site for some sites in Italy, Denmark, Austria, Wallonia, Catalonia, and all sites in the Netherlands.

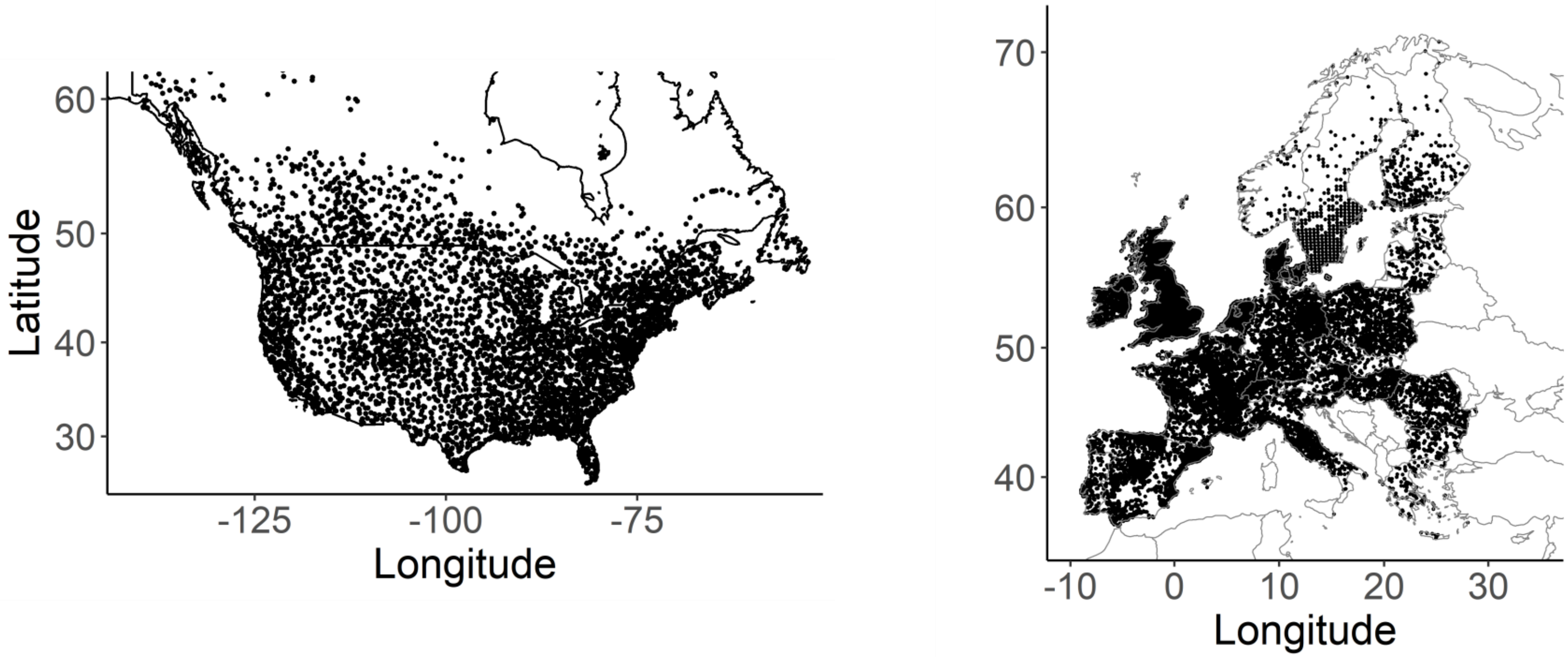

Figure C1. Focal survey locations in North America (n = 4662; left) and Europe (n = 20350; right) for House Sparrow and European Starling (combined) from which data were used to explore differences in abundance responses to the environment in the species' native European and invaded North American ranges.

Data compilation for European Starling

European Starlings in Europe aggregate into large, mobile flocks of adults and juveniles shortly after breeding. To better ensure we analyzed counts of breeding adults only, we requested survey data by date (hereafter, disaggregated data) from our focal PECBMS monitoring schemes (Table C1) and restricted our dataset to observations of European Starling that occurred before June. We received disaggregated data for European Starling from all schemes where European Starling breeds except Brussels, Greece, and Slovakia (European Starling does not breed in Portugal; Table C1). For schemes with multiple surveys per breeding season, we averaged counts across surveys and rounded values up to the nearest integer to obtain a count per survey location and breeding season (i.e., year).

Duplicate spatial locations

Some schemes had data collected from survey locations with different site IDs but the same spatial coordinates – i.e., duplicate spatial locations. If sites with duplicate spatial locations were surveyed in the same year, we averaged the counts from those sites (and rounded the value up to the nearest integer) and gave them a new site ID so that they were treated in the model as a count from a single site in the focal year. This occurred for appropriately 0.1% of our total observations for both House Sparrow and European Starling.

Testing for spatial autocorrelation

We used the Moran's I test in the DHARMa package (Hartig 2021) in R (R Core Team 2021) to determine evidence of spatial autocorrelation by year in the residuals from models of House Sparrow and European Starling abundance. Evidence of spatial autocorrelation was present in residuals for all years for both species, but the Moran's I values were consistently low (< 0.12, Table C2), so we did not account for spatial autocorrelation in our models.

Table C2. Results from Moran's I test for spatial autocorrelation by year for residuals from generalized linear mixed models for House Sparrow and European Starling abundance.

	House Sparrow				European Starling			
Year	**Observed**	**Expected**	**Standard deviation**	**p value**	**Observed**	**Expected**	**Standard deviation**	**p value**
1992	0.1308	-0.0016	0.0088	<0.0001	0.1194	-0.0014	0.0085	<0.0001
1993	0.0943	-0.0017	0.0097	<0.0001	0.1222	-0.0015	0.0091	<0.0001
1994	0.0552	-0.0005	0.0022	<0.0001	0.0696	-0.0005	0.0023	<0.0001
1995	0.0459	-0.0004	0.0020	<0.0001	0.0634	-0.0004	0.0022	<0.0001
1996	0.0531	-0.0004	0.0019	<0.0001	0.0507	-0.0004	0.0019	<0.0001
1997	0.0315	-0.0002	0.0010	<0.0001	0.0251	-0.0002	0.0010	<0.0001
1998	0.0318	-0.0002	0.0008	<0.0001	0.0251	-0.0002	0.0009	<0.0001
1999	0.0398	-0.0002	0.0008	<0.0001	0.0242	-0.0002	0.0008	<0.0001
2000	0.0397	-0.0002	0.0010	<0.0001	0.0286	-0.0001	0.0008	<0.0001
2001	0.0612	-0.0002	0.0017	<0.0001	0.0294	-0.0002	0.0014	<0.0001
2002	0.0474	-0.0001	0.0009	<0.0001	0.0296	-0.0001	0.0007	<0.0001
2003	0.0533	-0.0001	0.0008	<0.0001	0.0355	-0.0001	0.0007	<0.0001
2004	0.0532	-0.0001	0.0006	<0.0001	0.0389	-0.0001	0.0006	<0.0001
2005	0.0509	-0.0001	0.0006	<0.0001	0.0448	-0.0001	0.0005	<0.0001
2006	0.0525	-0.0001	0.0006	<0.0001	0.0539	-0.0001	0.0005	<0.0001

2007	0.0521	-0.0001	0.0006	<0.0001	0.0526	-0.0001	0.0004	<0.0001
2008	0.0569	-0.0001	0.0006	<0.0001	0.0615	-0.0001	0.0005	<0.0001
2009	0.0551	-0.0001	0.0006	<0.0001	0.0668	-0.0001	0.0004	<0.0001
2010	0.0507	-0.0001	0.0006	<0.0001	0.0690	-0.0001	0.0005	<0.0001
2011	0.0481	-0.0001	0.0005	<0.0001	0.0720	-0.0001	0.0004	<0.0001
2012	0.0504	-0.0001	0.0005	<0.0001	0.0795	-0.0001	0.0004	<0.0001
2013	0.0524	-0.0001	0.0005	<0.0001	0.0790	-0.0001	0.0004	<0.0001
2014	0.0453	-0.0001	0.0006	<0.0001	0.0780	-0.0001	0.0005	<0.0001
2015	0.0484	-0.0001	0.0006	<0.0001	0.0871	-0.0001	0.0004	<0.0001
2016	0.0528	-0.0001	0.0006	<0.0001	0.1006	-0.0001	0.0004	<0.0001
2017	0.0398	-0.0001	0.0006	<0.0001	0.1109	-0.0001	0.0005	<0.0001
2018	0.0332	-0.0001	0.0007	<0.0001	0.0850	-0.0001	0.0006	<0.0001

Testing for temporal autocorrelation

We tested for temporal autocorrelation in model residuals associated with a given survey location across years with a lag interval of one year using the timetk package (Dancho and Vaughan 2022) in R (R Core Team 2021). For each scheme and species, we calculated the percentage of survey locations for which the autocorrelation value in any year fell outside of the upper and lower bounds of uncertainty (i.e., the white noise significance bars; Table C3). Evidence of temporal autocorrelation in model residuals generally was low for both species (Table C3), so we did not account for temporal autocorrelation in our models.

Table C3. The total number of survey locations and the percentage of those that showed evidence of temporal autocorrelation (N and Percent with evidence of temporal autocorrelation, respectively) by scheme for House Sparrow and European Starling from our focal dataset. Temporal autocorrelation was examined using a lag of one year. The Brussels, Greece, and Slovakia schemes do not have information for European Starling because we did not receive disaggregated data for this species from those schemes. Portugal does not have information for European Starling because the country is outside of the species' breeding range.

	House Sparrow		European Starling	
Scheme	N	Percent with evidence of temporal autocorrelation	N	Percent with evidence of temporal autocorrelation
Austria	241	5.81	308	8.77
Brussels	50	42	NA	NA
Bulgaria	178	1.69	211	1.9
Catalonia	331	11.78	199	5.53
Czech Republic	173	12.14	218	8.72
Denmark	677	5.91	574	8.19
Estonia	37	5.4	20	5
Finland	222	9.46	233	5.15
France	1588	4.09	2180	5.05
Germany	882	4.2	1239	2.1
Greece	87	0	NA	NA
Hungary	355	4.79	499	5.01
Ireland	314	30.25	401	23.94
Italy	19	21.05	486	9.05
Latvia	22	0	53	0

Lithuania	75	1.33	127	3.15
Netherlands	497	12.68	862	11.95
North American Breeding Bird Survey	4575	22.12	4407	21.33
Norway	41	7.32	73	4.11
Poland	654	11.47	981	9.28
Portugal	127	4.72	NA	NA
Romania	116	1.72	265	0
Slovakia	38	0	NA	NA
Slovenia	111	2.7	129	3.88
Spain	1236	4.69	160	4.38
Sweden	140	19.29	276	22.83
Switzerland	131	26.72	140	14.29
United Kingdom	5830	24.55	5861	21.36
Wallonia	171	10.53	162	14.2

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