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Human-associated species dominate passerine communities across the United States

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Abstract

Aim: Human development and agriculture can have transformative and homogenizing effects on natural systems, shifting the composition of ecological communities towards non-native and native species that tolerate or thrive under human-dominated conditions. These impacts cannot be fully captured by summarizing species presence, as they include dramatic changes to patterns of species abundance. However, how human land use patterns and species invasions intersect to shape patterns of abundance and dominance within ecological communities is poorly understood even in well-known taxa.

Location: Conterminous United States.

Time period: 2010–2012.

Major taxa studied: Passeriformes.

Methods: We analyse continental-scale monitoring data to study the proportional abundance of non-native and native synanthropic species within passerine bird communities. Synanthropic species are those that benefit from an association with humans. We estimate how the amount and configuration of human development and agriculture relate to the degree to which human-associated species dominate passerine communities across the continent.

Results: Human-associated species comprised the majority of detected passerine individuals across two-thirds of bird surveys. Non-native and synanthropic species responded differently to land cover and reached highest relative abundance in different portions of the continent. The proportional abundance of synanthropic birds increased rapidly with development, but was not related to the configuration of land cover. The proportion of non-native individuals was higher when intensively-used land cover was more aggregated.

Main conclusions: Even low amounts of intensively-used lands were associated with a dramatic reshaping of passerine communities, with consequences for patterns of relative abundance across the continent.

KEYWORDS

habitat fragmentation, habitat loss, land cover, non-native species, synanthropic species

1 | INTRODUCTION

Urbanization and agriculture strongly impact biodiversity (Newbold et al., 2015), but some species, both non-native and native, thrive in human-dominated landscapes (Aronson et al., 2014; Fischer, Schneider, Ahlers, & Miller, 2015; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). Non-native species respond to changes in human land use patterns and can reduce native species' richness and abundance through competition, hybridization, and disease transmission (MacDougall & Turkington, 2005; Martin-Albarracin, Amico, Simberloff, & Nuñez, 2015). Native synanthropic species (Johnston, 2001) can be similar to non-native invasive species in that they expand their distributions with a growing human footprint (Essl et al., 2019; McCune & Vellend, 2013). Together, non-native and synanthropic species contribute to biotic homogenization across space and time (McKinney, 2006). Those populations that have increased in abundance during the Anthropocene are as species rich as those that have declined (Dornelas et al., 2019), a pattern that can lead to stable local species richness despite striking changes in community composition (Dornelas et al., 2014; Magurran et al., 2018). Combined with the recognition that a major facet of biodiversity loss is the declining population size of many native species (Ceballos, Ehrlich, & Dirzo, 2017; Hallmann et al., 2017; Young, McCauley, Galetti, & Dirzo, 2016), this has led to an increasing focus on monitoring patterns of organisms' abundance over space and time (Hillebrand et al., 2018). If community-level shifts towards human-associated species are a global signature of biodiversity impacts, understanding the drivers of these species' relative abundance within communities will be critical for assessing and managing the consequences of global change, including land conversion to urban and agricultural uses.

Even common species, both native and non-native, are rare in most places where they occur (Brown, Mehlman, & Stevens, 1995; Hansen et al., 2013), and the resulting variation in abundance provides an opportunity to understand species and community-level responses to human modification of land cover. Human impacts on land cover are often characterized along two major axes: land cover composition, which reflects the amount of habitat, and land cover configuration, which captures patterns of adjacency, patch size, and isolation – features commonly lumped under the rubric of habitat fragmentation (Fahrig, 2003). Habitat quality is a third major axis, but is more difficult to quantify at broad scales (Johnson, 2007). While habitat loss is an undisputed driver of negative ecological impacts (Jantz et al., 2015), the effects of habitat fragmentation are a focus of ongoing debate. Specifically, studies that isolate the effects of fragmentation from those of habitat loss have often found weak or even positive ecological impacts of fragmentation (Fahrig, 2017). These findings have been controversial, and experimental studies have found support for negative effects of fragmentation on biodiversity (Fletcher et al., 2018; Haddad et al., 2015). Studies have also evaluated the consequences of human land use intensification, which is typified in a spatial analysis by a low diversity of land cover types, and is associated with declining organismal abundance and an increase in generalists over specialists (Benton, Vickery, & Wilson, 2003; Donald, Green, & Heath, 2001; Gámez-Virués et al., 2015).

Bird communities exemplify how patterns of relative abundance arise from species-specific responses to land cover (Flather & Sauer, 1996; Lepczyk et al., 2008), but the landscape drivers of compositional shifts towards human-associated species are poorly understood. Recent studies have highlighted the declining abundance of common birds, a loss that is not captured by community-level richness and diversity (Inger et al., 2015; Rosenberg et al., 2019; Schipper et al., 2016). Non-native species comprise only about 3% of urban bird species globally (Aronson et al., 2014), and only two non-native passerines, the European starling (*Sturnus vulgaris*) and the house sparrow (*Passer domesticus*), are widespread in the conterminous United States (U.S.). However, both non-native and native human-associated birds have higher relative abundance in agricultural and developed areas (Callaghan et al., 2019; Lepczyk et al., 2017). Compared with non-native species, the land cover associations of native synanthropic birds have received little attention (Wood et al., 2014), and for both groups the roles of land cover composition, configuration, and diversity are unclear. Therefore, improving our understanding of the conditions under which human-associated species dominate avian communities could provide targets for land use planners and land managers.

Our objective was to evaluate how land cover attributes were associated with the relative abundance of non-native and synanthropic passerines across the conterminous U.S. We hypothesized that amount of intensively-used lands would be the primary factor shaping the proportional abundance of these bird groups across large spatial extents (Flather & Sauer, 1996). Specifically, we predicted that both non-native and native synanthropic birds would increase in relative abundance with the proportion of land cover in developed and agricultural classes (Wood et al., 2014). Non-native and synanthropic species are widely regarded as generalist species (Ehrlich, 1986; Johnston, 2001), which may be relatively insensitive to the arrangement of land cover (Villard & Metzger, 2014). We therefore predicted weak effects of land cover configuration. We predicted that proportional abundance of both focal groups would increase with the diversity of land cover types within developed and agricultural classes, but could decline with diversity of natural and semi-natural cover types due to higher relative abundance of native non-synanthropic species (Julliard, Clavel, Devictor, Jiguet, & Couvet, 2006).

2 | METHODS

2.1 | Avian data

We analysed patterns of abundance of Passeriformes within the conterminous U.S. based on North American Breeding Bird Survey (BBS; Pardieck et al., 2017) data from 2010–2012. Each BBS route

consists of fifty 3-min counts arranged along roadsides at intervals of approximately 0.8 km. We focused on Passeriformes because they are a monophyletic group of diurnal landbirds within which non-native, native synanthropic, and native non-synanthropic groups are each represented across the conterminous U.S. We analysed a 3-year period of data to balance the trade-off between minimizing year-to-year variability due to sampling and unrelated variation in population sizes while maximizing survey route sample size. We centred the 3-year period on the data collection year (2011) for land cover information. We included standard routes that had been surveyed in all three focal years, had spatial information on the route path, and met BBS acceptability criteria (n = 1,649). These BBS filtering criteria identify routes with acceptable survey date, starting time, finish time, weather conditions and observer skill, and serve to limit variation due to these factors (O'Connor et al., 2000; Robbins, Bystrak, & Geissler, 1986). We analysed data at the route level, summing avian counts across all stops within the route.

We defined non-native species as those whose expansion in the U.S. followed intentional human introduction and those that are thought to have naturally expanded their distribution into the U.S. from outside the country. The shiny cowbird (*Molothrus bonariensis*) was the only species in the latter category (Lowther & Post, 1999). Our definition of non-native excluded species that have expanded their range within the conterminous U.S. Individuals of five non-native species were represented in the data. We use the terms non-native and invasive interchangeably because European starlings and house sparrows comprised 99.9% of non-native individuals in our data (266,833 of 266,993) and can be considered invasive based on both their capacity to spread and to cause impacts.

Synanthropic species were defined based on Johnston's (2001) review of studies documenting avian responses to human modifications within natural habitats and based on frequent use of human-provided food resources (Wells, Rosenberg, Dunn, Tessaglia-Hymes, & Dhondt, 1998). Specifically, we defined synanthropic passerine species as native species categorized as full or casual synanthropes by Johnston (2001), or those that were on one or more regional Project FeederWatch top 25 lists within the conterminous U.S. for the 2010–2012 period (https://feederwatch.org/pfw/top25; last accessed December 2017). Kirtland's warbler (*Setophaga kirtlandii*) was considered synanthropic by Johnston (2001) but was excluded to distinguish between conservation-reliant and synanthropic species. These criteria were independent of land cover composition and configuration (whereas basing the synanthropic classification on an analysis of species' abundances across landscapes would have introduced circularity). Moreover, Johnston (2001) considered human modifications of natural habitats, drawing heavily from studies conducted on public lands, the vast majority of which we do not consider intensively used. Similarly, FeederWatch sites are found across a gradient of land cover types. We consider the resulting list of native synanthropic taxa (n = 65 taxa of 290 native taxa; Supporting Information Appendix S1) to be conservative, as these lists are not exhaustive and additional native species can tolerate or thrive in human-modified land cover types. Synanthropic species included several that have expanded their range within the U.S., such as house finch (*Haemorhous mexicanus*) and brown-headed cowbird (*Molothrus ater*), species exploiting human food resources, such as many Corvidae and Paridae, and species associated with early successional or disturbed habitat types, such as the horned lark (*Eremophila alpestris*).

For each route, we summed the count of non-native, synanthropic, and total passerine individuals detected across all stops over all 3 years. We defined the proportional abundance (i.e. relative abundance) of non-native passerines as the count of all non-native individuals detected divided by the total count of all passerine individuals detected. The proportional abundance of synanthropic passerines was defined as the count of all synanthropic individuals divided by the total number of native passerine individuals. Thus, non-native species were excluded from the definition of proportional synanthropic abundance in order to model these groups separately; our models and most visualizations excluded non-native species from both the numerator and denominator in our calculations of synanthropic proportional abundance. However, in Figures 1 and 2 we visualize the proportion synanthropic of all individuals, so that the proportions across the three species groups sum to 1 for clarity. Unidentified individuals (0.05%; n = 1,723 of 2,957,981 total individuals; n = 23 of 295 taxa) were included as these were identified to a taxonomic level (e.g. one of two potential species) that allowed for classification as non-native or synanthropic (Supporting Information Appendix S1). Our approach of first summing across years and then calculating a proportion did not substantially differ from averaging the proportion in each year (r > .99); our approach enabled us to also fit models assuming a binomial distribution (see below).

We focused our analyses on variation in proportional abundance beyond that which was explained by geographical variation in proportional richness of non-native and synanthropic species. To do so, we summarized the proportional richness of non-native and synanthropic passerines across space (Supporting Information Figure S1), excluding unidentified birds. Previous work has shown that both synanthropic richness and abundance increase with human development (Wood et al., 2014). However, species richness and abundance do not always vary in tandem, with studies of urbanization suggesting species richness can decline even with increases in total abundance (Chace & Walsh, 2006; van Rensburg, Peacock, & Robertson, 2009). Conversely, stable richness can mask declines in species abundance and changes in species composition (Magurran et al., 2018; Schipper et al., 2016). We included proportional richness in our models (see below) so that our estimated relationships with land cover were interpretable as effects on proportional abundance after controlling for variation in proportional richness. This inclusion also accounted for variation in the composition of the species pool across the conterminous U.S.

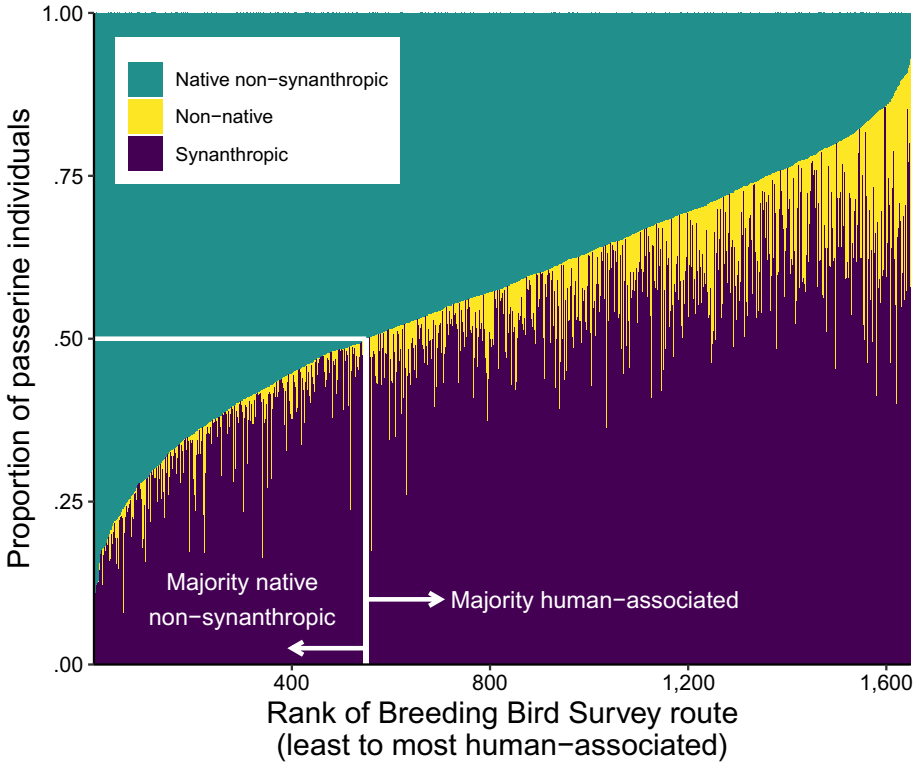

FIGURE 1 Most surveyed passerine communities across the conterminous United States were dominated by human-associated species (i.e. synanthropic or non-native). Each vertical bar represents a bird survey route, and routes are arranged along the *x* axis from a lower to higher proportion of human-associated species. More than half of all individual passerines were synanthropic or non-native species on 67% of survey routes [Colour figure can be viewed at wileyonlinelibrary.com]

2.2 | Landscape metrics

We summarized land cover data from the 2011 National Land Cover Database (Homer et al., 2015). This land cover classification has previously explained spatial variation in avian abundance and diversity (e.g. Gutzwiller, Riffell, & Flather, 2015; Lepczyk et al., 2008). We defined intensively-used land cover types as those in the developed and cultivated crop classes (i.e. classes 21–24, 82; for definitions see: https://www.mrlc.gov/data/legends/national-land-cover-database-2011-nlcd2011-legend), and natural/semi-natural land cover as that in classes with the expected natural vegetation type or lower intensity human land uses (classes 41–43, 52, 71, 81, 90, 95). We characterized land cover within a 19.7-km radius circular buffer surrounding route paths (see Supporting Information for details and sensitivity analysis). This buffer radius was half the length of a survey route and was allometrically relevant for our focal species, being approximately equal to the median (19.0 km; mean ± 1 *SD* = 21.1 ± 7.5 km) of estimated maximum natal dispersal distance based on body mass (Sutherland, Harestad, Price, & Lertzman, 2000).

Surrounding each route, we calculated land cover composition (i.e. amount of intensively-used land cover), defined as the proportion of land cover in intensively-used classes (Supporting Information Figure S2a). We measured diversity of land cover types within intensively used classes and, separately, within natural/semi-natural land cover classes using Simpson's diversity index with finite correction (Magurran, 2004; Supporting Information Figure S3). As a measure of land cover configuration, we used the clumpy index of aggregation (McGarigal, Cushman, Neel, & Ene, 2002) – hereafter, we use the terms configuration and aggregation interchangeably. Previous work has highlighted the clumpy index as a useful metric for assessing habitat fragmentation in a manner not confounded by the amount of the focal habitat class in the landscape; it has been found to be weakly correlated with habitat amount and highly correlated with habitat interspersion for both simulated and real landscapes (Neel, McGarigal, & Cushman, 2004; Wang, Blanchet, & Koper, 2014). We analysed the aggregation of intensively-used cover types (Supporting Information Figure S2b), which was positively correlated with aggregation of natural land cover types (r = .78). High aggregation corresponds to low fragmentation.

2.3 | Statistical methods

We estimated four models: (a) beta regression of the proportion of synanthropic individuals with our full covariate set, (b) zero-inflated beta regression of the proportion of non-native individuals with our full covariate set, (c) a change point logistic regression model of the proportion of synanthropic individuals in which the only covariate was the proportion of intensively-used land cover, and (d) a change point logistic regression model of the proportion of synanthropic

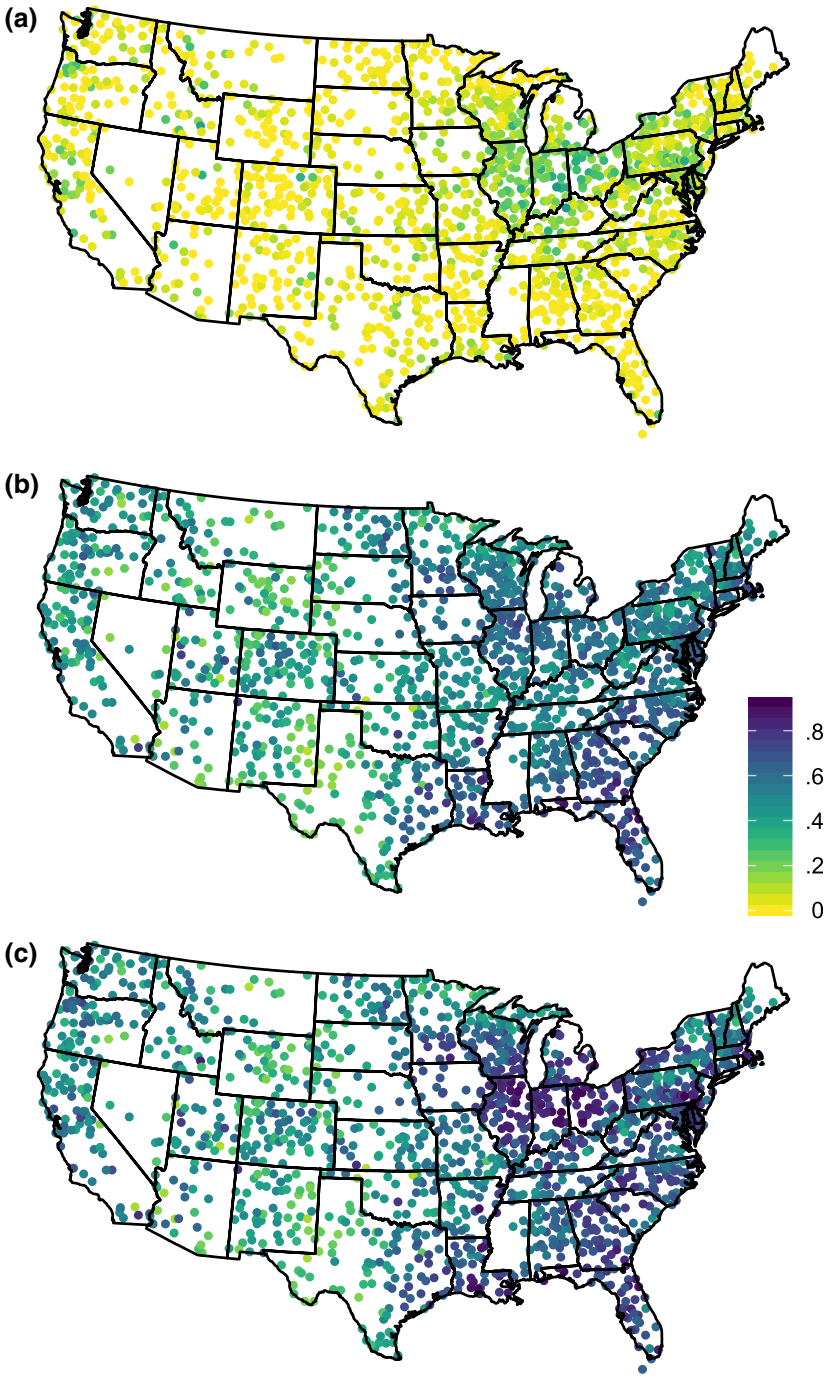

FIGURE 2 (a) Non-native, (b) synanthropic, and (c) total human-associated proportions of the passerine community differed across the conterminous United States. Non-native individuals had higher proportional abundance in some regions (e.g. Midwest) but comprised a smaller proportion of the avian community compared with synanthropic individuals (scales are consistent across panels). Native synanthropic individuals accounted for the majority of all detected passerines at over half of survey locations. Human-associated (non-native + synanthropic) individuals reached their highest proportional abundance in the Midwest and in portions of the Southeastern U.S. and East Coast [Colour figure can be viewed at wileyonlinelibrary.com]

individuals with our full covariate set. The beta distribution was selected because it has support for response values between 0 and 1, and hence is appropriate for modelling proportions. A change point regression approach was selected because it explicitly estimates the covariate value at which the relationship between the covariate and response variable changes (i.e. the change point), with a confidence interval surrounding the estimate.

Our covariate set included four landscape metrics (the proportion, aggregation and diversity of intensive land cover, and the diversity of natural cover types), proportional richness of the focal group (non-native or synanthropic) on the route, whether a first-year observer (with potential lower detection probabilities; Kendall, Peterjohn, & Sauer, 1996) conducted the survey in any of the 3 years, and the Bird Conservation Region containing the route centroid. Bird Conservation Regions are areas of North America within which avian communities, habitats, and management issues are similar, and are used for collaborative conservation planning (Bird Studies Canada & NABCI, 2014). Bird Conservation Region was included to account for and estimate regional variation in the proportion of human-associated species, beyond that explained by landscape metrics. Our study encompassed 30 Bird Conservation Regions across the conterminous U.S. Previous work has shown that landscapes surrounding BBS routes are collectively similar in land cover composition to the Bird Conservation Regions in which

they are located (Veech, Small, & Baccus, 2012). All continuous covariates were standardized prior to model fitting. Collinearity among covariates was sufficiently low for inclusion of all variables within each model (maximum $r < .6$).

We modelled the proportion of synanthropic individuals on BBS routes with a generalized linear model assuming a beta distribution with a fixed dispersion parameter. We used a logit link function, and estimated the model in the betareg package (Cribari-Neto & Zeileis, 2010) in R (R Core Team, 2018). Sensitivity analyses confirmed that estimated coefficients and predicted values were similar based on this model, a Bayesian implementation of beta regression, and logistic regression. The logistic regression was implemented such that the number of synanthropic individuals was the number of successes and the number of native non-synanthropic individuals was the number of failures; this yielded similar coefficient estimates but unrealistically small confidence intervals, presumably because of the much larger sample size implied by the number of individuals detected.

Our model for the proportion of non-native individuals assumed a zero-inflated beta distribution. Zero-inflation was included because the beta distribution does not support zeros, and on 169 of 1,649 BBS routes no non-native individuals were detected. This model was estimated using the zoib package (Liu & Kong, 2018) in R, which implements Bayesian zero-inflated beta regression models via rjags (Plummer, 2016). We used a logit link and a diffuse normal prior for each regression coefficient; results were very similar when using ridge-like shrinkage priors. We drew samples from three Markov chains, with 10,000 iterations per chain, a burn-in period of 5,000 iterations, and a thinning period of five after burn-in. Mixing and convergence were assessed with trace plots, autocorrelation plots and the potential scale reduction factor, implemented via the coda package (Plummer, Best, Cowles, & Vines, 2006). This model yielded very similar coefficient estimates ($r = .99$) and predictions ($r = .99$) as a beta regression without zero-inflation, fit in the betareg package, that was based on a transformation to place all response values within the (0, 1) interval (Smithson & Verkuilen, 2006). Coefficient estimates from beta regression models were exponentiated (analogous to conversion to odds ratios in a logistic regression), and can be interpreted as the change in the ratio of proportions.

As the relationship between the proportion of synanthropic individuals and the proportion of intensive land use showed a nonlinear pattern, we fit change point regression models to estimate the amount of intensive land use at which the slope of the relationship changed. Models assumed a segmented type of threshold, that is, one in which the relationship between the proportion of intensive land use and the proportion of synanthropic individuals was continuous, with a change in slope (Fong, Huang, Gilbert, & Permar, 2017). We considered two models: the first contained only the proportion of intensive land use, while the second included a linear fixed effect of each of the other variables we considered in our beta regression model of synanthropic proportional abundance. Change point models assumed a binomial distribution, where the number of successes was the number of synanthropic individuals, and failures were non-synanthropic native individuals. These models were implemented in the chngpt package (Fong et al., 2017) in R.

3 | RESULTS

Most surveyed passerine communities across the conterminous U.S. were dominated by synanthropic and non-native birds (Figure 1). Synanthropic individuals comprised a median of 55% (0.25–0.75 quantiles: 43–67%; range: 10–91%) of passerine individuals detected on BBS routes. Routes on which over half of individuals were human-associated were distributed throughout the country (Figure 2). Non-native individuals comprised a smaller overall component of passerine communities (median: 4%; interquartile range: 1–11%) but reached high proportional abundance locally (max: 48% of detected individuals). There was considerable variation in the proportion of each group within each Bird Conservation Region, with highest proportions of human-associated species in the Midwest, and generally lower proportions in the Southwest and portions of the Intermountain West (Figure 2 and Supporting Information Figure S4).

Landscapes with a higher proportion of land cover in intensive use categories had a higher proportion of both non-native and synanthropic birds (Figure 3). Similarly, the diversity of intensive land cover types was positively related to the proportion of non-native and synanthropic individuals (Figure 4). Land cover configuration affected the non-native, but not the synanthropic, proportion, with more aggregated intensive lands associated with a higher proportion of non-native individuals (Figure 3). Increasing proportional richness of each species group was associated with increasing proportional abundance (Figure 4). Diversity of natural and semi-natural land cover types had little effect on the proportion of non-native or synanthropic individuals (Figure 4).

The proportion of synanthropic individuals increased steeply at low proportions of intensive land use (Figure 3c), a pattern that reflected shifts in the avian community with increasing development (Supporting Information Figure S5). The bivariate relationship between synanthropic proportional abundance and the proportion of intensively-used lands showed a change point (Figure 3c), with synanthropic abundance increasing slowly at a higher composition of intensively-used lands, which were largely agricultural (Supporting Information Figure S5). The change point was estimated to occur at 8% [95% confidence interval (CI): 4–12%] of land cover in developed and agricultural classes. However, we saw systematic nonlinear patterns in how land cover aggregation and diversity varied with increasing intensive use (Supporting Information Figure S6), such that when all landscape metrics and other covariates were included in the model, there was little support for a change point. Specifically, in the model with all covariates, the change point in the relationship between the proportion of intensively-used land cover and synanthropic proportional abundance was estimated at a higher composition and lacked statistical support (52%; 95% CI: 1–63%). The beta regression model (i.e. without a change point) showed a

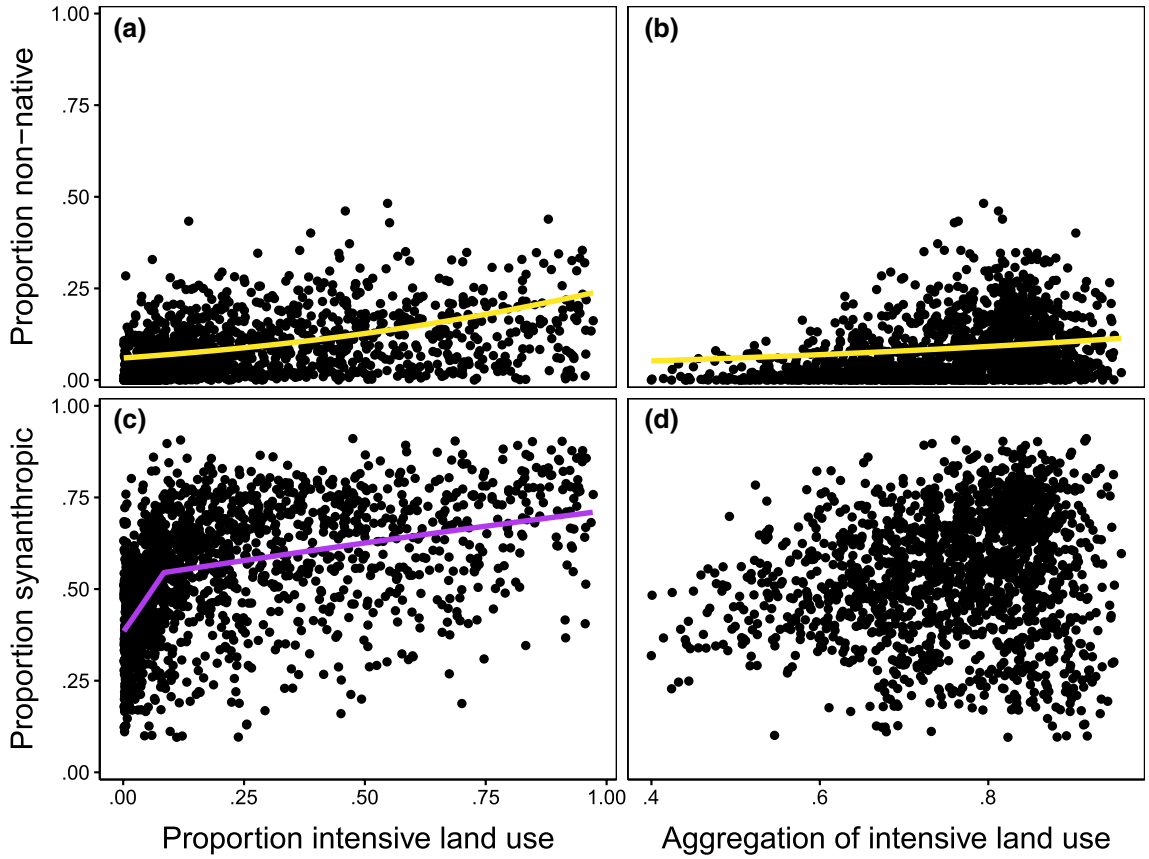

FIGURE 3 Non-native and synanthropic birds responded differentially to habitat composition (proportion of intensive land use) and configuration (aggregation of intensive land use). The proportion of non-native individuals in a community increased with an increasing proportion of intensively-used land (a) and was positively associated with aggregation of intensively-used cover types (b). In contrast, the relationship between synanthropic passerines and habitat composition was strikingly nonlinear, shifting at 8% (95% confidence interval: 4–12%) of land cover in intensive use (c), while habitat configuration had no effect on the proportional abundance of synanthropic individuals (d). Lines shown in (a, b) are predictions from zero-inflated beta regression; line in (c) shows the estimated change point relationship; no line is shown in (d) because the confidence interval on the parameter estimate included zero [Colour figure can be viewed at wileyonlinelibrary.com]

linear relationship could appropriately capture synanthropic proportional abundance (Supporting Information Figure S7). We interpreted these findings to indicate that a suite of landscape metrics were related to the composition of intensively-used lands, and that the nonlinear change-point relationship between the proportion of intensively-used lands and the proportion of synanthropic individuals arose from joint effects of multiple landscape attributes. In other words, regional variation, systematic nonlinear changes in attributes including aggregation and diversity, and associated effects on synanthropic richness, all contribute to the form of the relationship between land cover composition and synanthropic proportional abundance.

The proportional abundance of non-native and synanthropic species may be sensitive to species-specific associations with land cover, and we evaluated whether the relationship between synanthropic proportional abundance and the proportion of intensively-used lands arose due to a response of one or more particularly abundant species. We plotted proportional abundance against land cover composition for the 10 most abundant (i.e. highest total counts across the survey) synanthropic species (Supporting Information Figure S8) and the two common invasive species (Supporting Information Figure S9). The European starling and house sparrow both increased in proportional abundance with the amount of intensively-used lands (Supporting Information Figure S9a). However, relationships with land cover varied among synanthropic species and no single species showed a nonlinear relationship of the form seen across all synanthropic passerines (Supporting Information Figure S8a). When these most-abundant species were summed together, the community-wide pattern re-emerged (Supporting Information Figure S8b). This finding highlights the variability in species-specific responses and shows how proportional synanthropic abundance increases despite differences in the land cover associations of human commensualist species.

4 | DISCUSSION

Our findings support the hypothesis that human land use patterns can shape avian communities at continental scales, with the amount of intensively-used land cover being the most important landscape metric for passerine community composition. We found

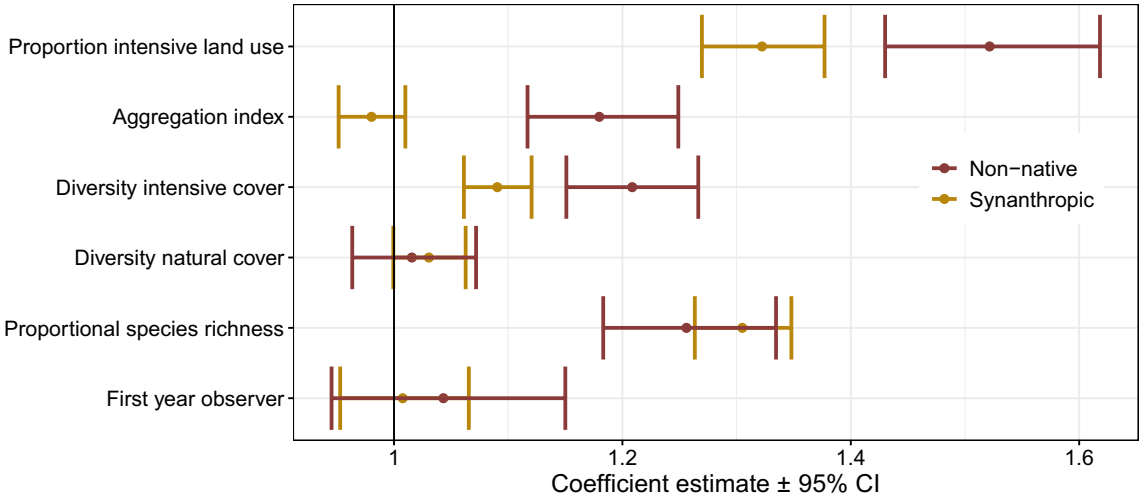

FIGURE 4 Parameter estimates and confidence intervals (CIs) from beta regression models of the proportion of non-native and the proportion of synanthropic individuals. With increases in the proportion of intensively-used land cover, the diversity of intensive land cover types, and proportional species richness, we observed an increase in the relative abundance of both non-native and synanthropic passerines. Land cover aggregation was related to non-native, but not synanthropic, proportional abundance; non-native individuals increased as intensively-used land cover types became more aggregated. Estimates were exponentiated and are interpretable as the change in the ratio of proportions (i.e. non-native : native or synanthropic : non-synanthropic); vertical line corresponds to a ratio of 1 (i.e. no effect). Note that because the proportion of non-native individuals was lower overall than the proportion of synanthropic individuals, a similar or smaller coefficient estimate in the model of the proportion of synanthropic individuals (i.e. smaller proportional change) could correspond to a larger absolute change [Colour figure can be viewed at wileyonlinelibrary.com]

that non-native and synanthropic species responded differently to the configuration of intensively-used land cover types (Figure 3), and that the relative abundance of both groups increased with the diversity of intensively-used land cover (Figure 4). We demonstrate that human-associated species now dominate surveyed passerine communities across the U.S. (Figure 1).

The relationship between synanthropic species and the proportion of intensively-used lands was nonlinear (Figure 3c). The sharp increase at low levels of intensive use arose from a strong positive association of synanthropic passerines with developed lands (Supporting Information Figure S5). Non-native passerines also increased in proportional abundance with the amount of intensively-used land, and unlike synanthropic species, had higher proportional abundance in less fragmented landscapes (Figure 3). However, complex nonlinear relationships among landscape metrics (Supporting Information Figure S6) made it difficult to isolate the impacts of each landscape attribute. For example, the aggregated nature of intensive agriculture (i.e. row crops) in the Midwestern U.S. (Supporting Information Figure S2) could underlie the relationship between fragmentation and non-native proportional abundance. Nevertheless, it is clear that low levels of intensively-used land cover, and the associated changes in aggregation and diversity, can reshape avian communities by shifting composition towards human-associated species.

Urbanization and agriculture alter species assemblages, leading to the local or global loss of human-sensitive species and declines in functional diversity (Egli, Meyer, Scherber, Kreft, & Tscharntke, 2018; Ibáñez-Álamo, Rubio, Benedetti, & Morelli, 2017; La Sorte et al., 2018). Previous work has shown that patterns of biotic homogenization seen in abundance data can be more pronounced than those seen in occurrence data (La Sorte & McKinney, 2007). We found effects of land cover on the abundance of human-associated passerines, even after accounting for changes in proportional richness of non-native and synanthropic species groups (Supporting Information Figure S10). Our results are notable in light of recently documented declines in common birds, including many synanthropic species (Rosenberg et al., 2019). The positive association we found between the diversity of intensively-used cover types and the relative abundance of human-associated passerines aligns with previous studies linking agricultural intensification to the decline of farmland birds in Europe, including the house sparrow (Hole et al., 2002) and European starling (Fuller et al., 1995). Both species are non-native to the U.S. but native in Europe, where sharp declines of these and other common species have led to declining abundance and biomass of the entire avian community (Inger et al., 2015). Recent analyses point to declines in even these non-native species across the conterminous U.S. (Rosenberg et al., 2019).

Focusing on shifts in relative abundance as a bellwether of global change could provide insights into consequences for ecological services and disservices, which generally arise from abundant species (Winfree, Fox, Williams, Reilly, & Cariveau, 2015). An exception to this is cultural services, such as birdwatching, which place a premium on rarity (Gaston et al., 2018). However, an important caveat is that characterizing what the proportion of synanthropic individuals would have been in the absence of human-induced global change is difficult. Synanthropic species are widespread and many may have been relatively common regardless of human activity. In addition, passerine birds generally respond more positively than other avian taxa to urbanization (La Sorte et al., 2018). BBS routes follow roadsides and may overrepresent the proportion of non-native and synanthropic

birds, a bias that could be estimated explicitly using other datasets. Conversely, dense urban areas are somewhat underrepresented along survey routes (Veech, Ziolkowski, & Pardieck, 2017), and these areas are likely to be dominated by human-associated, if not non-native, species. Differences in detection among avian groups could also bias our results and are difficult to disentangle from variation in land cover within survey routes. Our findings were made more conservative by the inclusion of proportional non-native and synanthropic richness in our models, as we quantified the associations between proportional abundance and landscape metrics after accounting for any effects on proportional richness.

We observed high proportions of non-native and synanthropic individuals, but also considerable variation in the proportion of human-associated individuals among avian communities. This variation was observed both within each Bird Conservation Region (Supporting Information Figure S11) and for a given level of land cover composition and configuration (Figure 3). This finding raises the question of whether specific landscape attributes, species identities, or other factors can be identified that allow avian communities to maintain a relatively high proportion of native non-synanthropic individuals – or conversely, to exhibit higher vulnerability to declines of species sensitive to human land use change. Future examination of these factors could guide management and conservation strategies aimed at maintaining and recovering native non-synanthropic populations, in addition to the avian community as a whole. Synanthropic species are important to ecological communities and declines in these and other common species are a major conservation concern (Rosenberg et al., 2019). Evaluating whether our findings apply to other regions and to temporal trends will be important, as previous analyses of the reliability of space-for-time substitutions have been mixed (Bonthoux, Barnagaud, Goulard, & Balent, 2013; Flather & Sauer, 1996; La Sorte et al., 2018), and our results suggest that even a small footprint of human development can alter the avian community. Our finding that passerine communities across the conterminous U.S. are dominated by species associated with humans provides novel insights into the diverse ways that natural communities reflect human landscape modification.

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DATA ACCESSIBILITY

Data have been publicly released (Sofaer, Flather, Jarnevich, Davis, & Pejchar, 2020) https://doi.org/doi:10.5066/P9FZZU8T

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REFERENCES

Aronson, M. F. J., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., … Winter, M. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20133330. https://doi.org/10.1098/rspb.2013.3330

Benton, T. G., Vickery, J. A., & Wilson, J. D. (2003). Farmland biodiversity: Is habitat heterogeneity the key? *Trends in Ecology and Evolution*, *18*, 182–188. https://doi.org/10.1016/S0169-5347(03)00011-9

Bird Studies Canada and NABCI. (2014). *Bird conservation regions*. Published by Bird Studies Canada on behalf of the North American Bird Conservation Initiative. Retrieved August 2019 from http://www.birdscanada.org/research/gislab/index.jsp?targetpg=bcr

Bonthoux, S., Barnagaud, J.-Y., Goulard, M., & Balent, G. (2013). Contrasting spatial and temporal responses of bird communities to landscape changes. *Oecologia*, *172*, 563–574. https://doi.org/10.1007/s00442-012-2498-2

Brown, J. H., Mehlman, D. W., & Stevens, G. C. (1995). Spatial variation in abundance. *Ecology*, *76*, 2028–2043. https://doi.org/10.2307/1941678

Callaghan, C. T., Bino, G., Major, R. E., Martin, J. M., Lyons, M. B., & Kingsford, R. T. (2019). Heterogeneous urban green areas are bird diversity hotspots: Insights using continental-scale citizen science data. *Landscape Ecology*, *34*, 1231–1246. https://doi.org/10.1007/s10980-019-00851-6

Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences USA*, *114*, E6089–E6096. https://doi.org/10.1073/pnas.1704949114

Chace, J. F., & Walsh, J. J. (2006). Urban effects on native avifauna: A review. *Landscape and Urban Planning*, *74*, 46–69. https://doi.org/10.1016/j.landurbplan.2004.08.007

Cribari-Neto, F., & Zeileis, A. (2010). Beta regression in R. *Journal of Statistical Software*, *34*, 1–24.

Donald, P. F., Green, R. E., & Heath, M. F. (2001). Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society B: Biological Sciences*, *268*, 25–29. https://doi.org/10.1098/rspb.2000.1325

Dornelas, M., Gotelli, N. J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., & Magurran, A. E. (2014). Assemblage time series reveal biodiversity change but not systematic loss. *Science*, *344*, 296–299. https://doi.org/10.1126/science.1248484

Dornelas, M., Gotelli, N. J., Shimadzu, H., Moyes, F., Magurran, A. E., & McGill, B. J. (2019). A balance of winners and losers in the Anthropocene. *Ecology Letters*, *22*, 847–854. https://doi.org/10.1111/ele.13242

Egli, L., Meyer, C., Scherber, C., Kreft, H., & Tscharntke, T. (2018). Winners and losers of national and global efforts to reconcile agricultural intensification and biodiversity conservation. *Global Change Biology*, *24*, 2212–2228. https://doi.org/10.1111/gcb.14076

Ehrlich, P. R. (1986). Which animal will invade? In H. A. Mooney & J. A. Drake (Eds.), *Ecology of biological invasions of North America and Hawaii* (pp. 79–95). New York, NY: Springer-Verlag.

Essl, F., Dullinger, S., Genovesi, P., Hulme, P. E., Jeschke, J. M., Katsanevakis, S., … Bacher, S. (2019). A conceptual framework for range-expanding species that track human-induced environmental change. *BioScience*, *69*(11), 908–919. https://doi.org/10.1093/biosci/biz101

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *34*, 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Fahrig, L. (2017). Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution, and Systematics*, *48*, 1–23. https://doi.org/10.1146/annurev-ecolsys-110316-022612

Fischer, J. D., Schneider, S. C., Ahlers, A. A., & Miller, J. R. (2015). Categorizing wildlife responses to urbanization and conservation implications of terminology. *Conservation Biology*, *29*, 1246–1248. https://doi.org/10.1111/cobi.12451

Flather, C. H., & Sauer, J. R. (1996). Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. *Ecology*, *77*, 28–35. https://doi.org/10.2307/2265651

Fletcher, R. J., Didham, R. K., Banks-Leite, C., Barlow, J., Ewers, R. M., Rosindell, J., … Haddad, N. M. (2018). Is habitat fragmentation good for biodiversity? *Biological Conservation*, *226*, 9–15. https://doi.org/10.1016/j.biocon.2018.07.022

Fong, Y., Huang, Y., Gilbert, P. B., & Permar, S. R. (2017). chngpt: Threshold regression model estimation and inference. *BMC Bioinformatics*, *18*, 454. https://doi.org/10.1186/s12859-017-1863-x

Fuller, R. J., Gregory, R. D., Gibbons, D. W., Marchant, J. H., Wilson, J. D., Baillie, S. R., & Carter, N. (1995). Population declines and range contractions among lowland farmland birds in Britain. *Conservation Biology*, *9*, 1425–1441. https://doi.org/10.1046/j.1523-1739.1995.09061425.x

Gámez-Virués, S., Perović, D. J., Gossner, M. M., Börschig, C., Blüthgen, N., de Jong, H., … Westphal, C. (2015). Landscape simplification filters species traits and drives biotic homogenization. *Nature Communications*, *6*, 8568. https://doi.org/10.1038/ncomms9568

Gaston, K. J., Cox, D. T. C., Canavelli, S. B., García, D., Hughes, B., Maas, B., … Inger, R. (2018). Population abundance and ecosystem service provision: The case of birds. *BioScience*, *68*, 264–272. https://doi.org/10.1093/biosci/biy005

Gutzwiller, K. J., Riffell, S. K., & Flather, C. H. (2015). Avian abundance thresholds, human-altered landscapes, and the challenge of assemblage-level conservation. *Landscape Ecology*, *30*, 2095–2110. https://doi.org/10.1007/s10980-015-0233-1

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., … Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, *1*, e1500052. https://doi.org/10.1126/sciadv.1500052

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., … de Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE*, *12*, e0185809. https://doi.org/10.1371/journal.pone.0185809

Hansen, G. J. A., Vander Zanden, M. J., Blum, M. J., Clayton, M. K., Hain, E. F., Hauxwell, J., … Sharma, S. (2013). Commonly rare and rarely common: Comparing population abundance of invasive and native aquatic species. *PLoS ONE*, *8*, e77415. https://doi.org/10.1371/journal.pone.0077415

Hillebrand, H., Blasius, B., Borer, E. T., Chase, J. M., Downing, J. A., Eriksson, B. K., … Ryabov, A. B. (2018). Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. *Journal of Applied Ecology*, *55*, 169–184. https://doi.org/10.1111/1365-2664.12959

Hole, D. G., Whittingham, M. J., Bradbury, R. B., Anderson, G. Q. A., Lee, P. L. M., Wilson… Krebs, J. R. (2002). Widespread local house-sparrow extinctions. *Nature*, *418*, 931–932. https://doi.org/10.1038/418931a

Homer, C., Dewitz, J., Yang, L. M., Jin, S., Danielson, P., Xian, G., … Megown, K. (2015). Completion of the 2011 national land cover database for the conterminous United States – Representing a decade of land cover change information. *Photogrammetric Engineering and Remote Sensing*, *81*, 345–354.

Ibáñez-Álamo, J. D., Rubio, E., Benedetti, Y., & Morelli, F. (2017). Global loss of avian evolutionary uniqueness in urban areas. *Global Change Biology*, *23*, 2990–2998. https://doi.org/10.1111/gcb.13567

Inger, R., Gregory, R., Duffy, J. P., Stott, I., Voříšek, P., & Gaston, K. J. (2015). Common European birds are declining rapidly while less abundant species' numbers are rising. *Ecology Letters*, *18*, 28–36. https://doi.org/10.1111/ele.12387

Jantz, S. M., Barker, B., Brooks, T. M., Chini, L. P., Huang, Q. Y., Moore, R. M., … Hurtt, G. C. (2015). Future habitat loss and extinctions driven by land-use change in biodiversity hotspots under four scenarios of climate-change mitigation. *Conservation Biology*, *29*, 1122–1131. https://doi.org/10.1111/cobi.12549

Johnson, M. D. (2007). Measuring habitat quality: A review. *The Condor*, *109*(3), 489–504. https://doi.org/10.1093/condor/109.3.489

Johnston, R. F. (2001). Synanthropic birds of North America. In J. M. Marzluff, R. Bowman, & R. Donnelly (Eds.), *Avian ecology and conservation in an urbanizing world* (pp. 49–67). Boston, MA: Springer US.

Julliard, R., Clavel, J., Devictor, V., Jiguet, F., & Couvet, D. (2006). Spatial segregation of specialists and generalists in bird communities. *Ecology Letters*, *9*, 1237–1244. https://doi.org/10.1111/j.1461-0248.2006.00977.x

Kendall, W. L., Peterjohn, B. G., & Sauer, J. R. (1996). First-time observer effects in the North American Breeding Bird Survey. *The Auk*, *113*, 823–829. https://doi.org/10.2307/4088860

La Sorte, F. A., Lepczyk, C. A., Aronson, M. F. J., Goddard, M. A., Hedblom, M., Katti, M., … Yang, J. (2018). The phylogenetic and functional diversity of regional breeding bird assemblages is reduced and constricted through urbanization. *Diversity and Distributions*, *24*, 928–938. https://doi.org/10.1111/ddi.12738

La Sorte, F. A., & McKinney, M. L. (2007). Compositional changes over space and time along an occurrence–abundance continuum: Anthropogenic homogenization of the North American avifauna. *Journal of Biogeography*, *34*, 2159–2167. https://doi.org/10.1111/j.1365-2699.2007.01761.x

Lepczyk, C. A., Flather, C. H., Radeloff, V. C., Pidgeon, A. M., Hammer, R. B., & Liu, J. (2008). Human impacts on regional avian diversity and abundance. *Conservation Biology*, *22*, 405–416. https://doi.org/10.1111/j.1523-1739.2008.00881.x

Lepczyk, C. A., La Sorte, F. A., Aronson, M. F. J., Goddard, M. A., MacGregor-Fors, I., Nilon, C. H., & Warren, P. S. (2017). Global patterns and drivers of urban bird diversity. In E. Murgui & M. Hedblom (Eds.), *Ecology and conservation of birds in urban environments* (pp. 13–33). Cham, Switzerland: Springer International Publishing.

Liu, F., & Kong, Y. (2018). zoib: Bayesian inference for beta regression and zero-or-one inflated beta regression. R package version 1.5.1. Retrieved from https://CRAN.R–project.org/package=zoib

Lowther, P. E., & Post, W. (1999). Shiny cowbird (*Molothrus bonariensis*), version 2.0. In A. F. Poole & F. B. Gill (Eds.), *The Birds of North America*. Ithaca, NY: Cornell Lab of Ornithology. https://doi.org/10.2173/bna.399

MacDougall, A. S., & Turkington, R. (2005). Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology*, *86*, 42–55. https://doi.org/10.1890/04-0669

Magurran, A. E. (2004). *Measuring biological diversity*. Malden, MA: Blackwell.

Magurran, A. E., Deacon, A. E., Moyes, F., Shimadzu, H., Dornelas, M., Phillip, D. A. T., & Ramnarine, I. W. (2018). Divergent biodiversity change within ecosystems. *Proceedings of the National Academy of Sciences USA*, *115*, 1843–1847. https://doi.org/10.1073/pnas.1712594115

Martin-Albarracin, V. L., Amico, G. C., Simberloff, D., & Nuñez, M. A. (2015). Impact of non-native birds on native ecosystems: A global analysis. *PLoS ONE*, *10*, e0143070. https://doi.org/10.1371/journal.pone.0143070

McCune, J. L., & Vellend, M. (2013). Gains in native species promote biotic homogenization over four decades in a human-dominated landscape. *Journal of Ecology*, *101*, 1542–1551. https://doi.org/10.1111/1365-2745.12156

McGarigal, K., Cushman, S. A., Neel, M. C., & Ene, E. (2002). *FRAGSTATS: Spatial pattern analysis program for categorical maps*. Amherst: University of Massachusetts. Retrieved from http://www.umass.edu/landeco/research/fragstats/fragstats.html

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, *127*, 247–260. https://doi.org/10.1016/j.biocon.2005.09.005

Neel, M. C., McGarigal, K., & Cushman, S. A. (2004). Behavior of class-level landscape metrics across gradients of class aggregation and area. *Landscape Ecology*, *19*, 435–455. https://doi.org/10.1023/B:LAND.0000030521.19856.cb

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., … Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, *520*, 45–50. https://doi.org/10.1038/nature14324

O'Connor, R. J., Dunn, E., Johnson, D. H., Jones, S. L., Petit, D., Pollock, K., … Welling, E. (2000). *A programmatic review of the North American Breeding Bird Survey: Report of a peer review panel*. Laurel, MD: USGS Patuxent Wildlife Research Center.

Pardieck, K. L., Ziolkowski, D. J. Jr, Link, W. A., Lutmerding, M., Campbell, K., & Hudson, M.-A.- R. (2017). *North American Breeding Bird Survey dataset 1966–2016, version 2016.0*. Laurel, MD: U.S. Geological Survey Patuxent Wildlife Research Center. Retrieved from www.pwrc.usgs.gov/BBS/RawData/

Plummer, M. (2016). rjags: Bayesian graphical models using MCMC. R package version 4-6. Retrieved from https://CRAN.R-project.org/package=rjags

Plummer, M., Best, N., Cowles, K., & Vines, K. (2006). CODA: Convergence diagnosis and output analysis for MCMC. *R News*, *6*, 7–11.

R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Robbins, C. S., Bystrak, D., & Geissler, P. H. (1986). *The Breeding Bird Survey: Its first fifteen years, 1965–1979. Resource Publication 157*. Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service.

Rosenberg, K. V., Dokter, A. M., Blancher, P. J., Sauer, J. R., Smith, A. C., Smith, P. A., … Marra, P. P. (2019). Decline of the North American avifauna. *Science*, *366*, 120–124. https://doi.org/10.1126/science.aaw1313

Schipper, A. M., Belmaker, J., Miranda, M. D., Navarro, L. M., Böhning-Gaese, K., Costello, M. J., … Pereira, H. M. (2016). Contrasting changes in the abundance and diversity of North American bird assemblages from 1971 to 2010. *Global Change Biology*, *22*, 3948–3959. https://doi.org/10.1111/gcb.13292

Smithson, M., & Verkuilen, J. (2006). A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. *Psychological Methods*, *11*, 54–71. https://doi.org/10.1037/1082-989X.11.1.54

Sofaer, H. R., Flather, C. H., Jarnevich, C. S., Davis, K. P., & Pejchar, L. (2020). Non-native and synanthropic bird data derived from 2010–2012 Breeding Bird Survey and associated landscape metrics from 2011 NLCD. U.S. Geological Survey data release. https://doi.org/10.5066/P9FZZU8T

Sutherland, G. D., Harestad, A. S., Price, K., & Lertzman, K. P. (2000). Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation Ecology*, *4*, 16. https://doi.org/10.5751/ES-00184-040116

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – Ecosystem service management. *Ecology Letters*, *8*, 857–874. https://doi.org/10.1111/j.1461-0248.2005.00782.x

van Rensburg, B. J., Peacock, D. S., & Robertson, M. P. (2009). Biotic homogenization and alien bird species along an urban gradient in South Africa. *Landscape and Urban Planning*, *92*, 233–241. https://doi.org/10.1016/j.landurbplan.2009.05.002

Veech, J. A., Small, M. F., & Baccus, J. T. (2012). Representativeness of land cover composition along routes of the North American Breeding Bird Survey. *The Auk*, *129*, 259–267. https://doi.org/10.1525/auk.2012.11242

Veech, J. A., Ziolkowski, D. J. Jr, & Pardieck, K. L. (2017). How well do route survey areas represent landscapes at larger spatial extents? An analysis of land cover composition along Breeding Bird Survey routes. *The Condor: Ornithological Applications*, *119*, 607–615. https://doi.org/10.1650/CONDOR-17-15.1

Villard, M.-A., & Metzger, J. P. (2014). Beyond the fragmentation debate: A conceptual model to predict when habitat configuration really matters. *Journal of Applied Ecology*, *51*, 309–318. https://doi.org/10.1111/1365-2664.12190

Wang, X., Blanchet, F. G., & Koper, N. (2014). Measuring habitat fragmentation: An evaluation of landscape pattern metrics. *Methods in Ecology and Evolution*, *5*, 634–646. https://doi.org/10.1111/2041-210X.12198

Wells, J. V., Rosenberg, K. V., Dunn, E. H., Tessaglia-Hymes, D. L., & Dhondt, A. A. (1998). Feeder counts as indicators of spatial and temporal variation in winter abundance of resident birds. *Journal of Field Ornithology*, *69*, 577–586.

Winfree, R., Fox, J. W., Williams, N. M., Reilly, J. R., & Cariveau, D. P. (2015). Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters*, *18*, 626–635. https://doi.org/10.1111/ele.12424

Wood, E. M., Pidgeon, A. M., Radeloff, V. C., Helmers, D., Culbert, P. D., Keuler, N. S., & Flather, C. H. (2014). Housing development erodes avian community structure in U.S. protected areas. *Ecological Applications*, *24*, 1445–1462. https://doi.org/10.1890/12-1992.1

Young, H. S., McCauley, D. J., Galetti, M., & Dirzo, R. (2016). Patterns, causes, and consequences of Anthropocene defaunation. *Annual Review of Ecology, Evolution, and Systematics*, *47*, 333–358. https://doi.org/10.1146/annurev-ecolsys-112414-054142j

BIOSKETCH

We conduct research on global change and conservation ecology, including biogeographical studies on the consequences of land use and species invasions.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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