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Research article

Anthropogenic habitat modification causes nonlinear multiscale bird diversity declines

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Anthropogenic habitat modification is a leading contributor to biodiversity change, but it is unclear what factors, including scale, influence the magnitude of change. Changes in species richness and its scaling relationship across an anthropogenic gradient can be influenced by changes in the total number of individuals in each sample, the species abundance distribution, and/or the spatial arrangement of conspecific individuals. Here, we integrated continental-scale citizen science data on bird occurrences across the contiguous United States – from eBird – with an analytical framework capable of dissecting the aforementioned biodiversity components to quantify bird diversity changes along an anthropogenic landscape habitat modification gradient. We found an overall decline in bird diversity along an anthropogenic modification gradient, with peak levels of bird diversity at low to moderate levels of modification. The magnitude of biodiversity change was greater at gamma than at alpha scales and was most strongly associated with a declining number of individuals along the anthropogenic gradient. Spatial species turnover was lower at higher impacted sites, but this was also due to the sampling of fewer individuals rather than changes in spatial species patchiness. Our results suggest that local-scale management can promote bird diversity, especially at the natural–rural–suburban interface. Management efforts (e.g. managing natural habitat or preserving urban greenspaces against development) should be focused on creating, restoring, and preserving resources (e.g. nesting habitat, foraging resources) necessary for a large number of individuals, as this is the primary influence of diversity change along an anthropogenic gradient.

Keywords: anthropogenic modification, beta diversity, biodiversity scale, biodiversity, birds, citizen science, eBird, urban ecology



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Introduction

Anthropogenic habitat modification is a leading contributor to biodiversity change in space and time (Newbold et al. 2015, Díaz et al. 2018). Species' pools within anthropogenically modified habitats are often constrained – taxonomically, functionally, and phylogenetically – when compared with unmodified habitats (Aronson et al. 2014, Nowakowski et al. 2018). The consequences of anthropogenic modification are apparent across taxa (Piano et al. 2020), negatively impacting abundance (Doherty et al. 2020), movement (Tucker et al. 2018), and phylogenetic and functional diversity (Sol et al. 2020). As urban and agricultural areas continue to expand (Liu et al. 2020) concomitantly with production landscapes such as forestry and mining (Curtis et al. 2018), mitigation of such negative consequences necessarily relies on quantifying the components underlying biodiversity that are most heavily impacted by anthropogenic modification.

Birds are one of the most well-studied taxa as a result of their appeal and conspicuousness, as well as their status as ecological indicators (Fraixedas et al. 2020). As a result, a large body of research has highlighted patterns of bird abundance and diversity (Butchart et al. 2004, Lepczyk et al. 2017a), as well as how it changes along anthropogenic gradients such as urbanization (Palacio et al. 2018, Carvajal-Castro et al. 2019, Korányi et al. 2021) and agriculture (Donald et al. 2006, Teillard et al. 2015, Olivier et al. 2020). Generally, studies have shown that bird diversity declines along these gradients (Blair 1996, Sol et al. 2017a, 2020). At the same time, some studies have found little influence of urbanization on bird diversity (Korányi et al. 2021), with no trend in species richness, abundance, or biomass along an urbanization gradient (Chamberlain et al. 2017). Others have even shown an increase in bird diversity along an urbanization gradient (Clergeau et al. 1998, Batáry et al. 2018, Filloy et al. 2019). Changes in bird diversity along an urbanization gradient can depend on the type of biome (Filloy et al. 2019) or can be modulated by the amount of urban green areas and corresponding resource availability (de Castro Pena et al. 2017, Callaghan et al. 2019, Planillo et al. 2021). Another general pattern that has emerged is the higher likelihood of exotic species colonizing and thriving in urban environments (Clergeau et al. 2006, Sol et al. 2017a) leading to different species assemblages along an urbanization gradient (Mbiba et al. 2021). Different species assemblages can lead to different functional composition, with 20% less functional diversity in urban environments compared with surrounding natural habitats (Sol et al. 2020).

To date, the majority of research quantifying bird diversity responses to anthropogenic gradients has focused on species richness at a single spatial scale (McKinney 2008, Reis et al. 2012, Piano et al. 2020) with fewer studies quantifying different components of diversity at multiple scales (Sol et al. 2014, 2020, Carvajal-Castro et al. 2019). This is unsurprising due to the ease of measurement and interpretation of species richness (Gotelli and Colwell 2001, Magurran and McGill 2010). However, species richness is limited

as a measure of diversity change (Fleishman et al. 2006, Hillebrand et al. 2018, Chase et al. 2018) because it is highly sensitive to spatial scale and it may obscure changes in different components of community structure, such as the total and relative abundances of species (e.g. evenness and rarity). For example, previous research has shown the importance of considering multiple components of diversity such as species richness as well as abundance evenness (Andrade et al. 2018, Sol et al. 2020), functional diversity (Mbiba et al. 2021), or abundance and biomass (Chamberlain et al. 2017). The spatial scale in which data are collected (e.g. alpha or gamma scales) could further influence our understanding of diversity changes along an anthropogenic gradient as it is expected birds can use different habitats throughout the landscape which may buffer changes in diversity at the local (i.e. alpha) scales (Hiron et al. 2015, Kale et al. 2018) in impacted environments. Similarly, it is expected that diversity changes may manifest differently at different spatial grains as coarser grain sizes have a greater likelihood of capturing a greater percentage of the anthropogenic gradient being sampled.

Recently the measurement of biodiversity (MoB) framework was developed to provide deeper insights into the factors underlying diversity (Chase et al. 2018, McGlinn et al. 2019, 2021), and this framework has the potential to help decipher bird diversity responses along anthropogenic gradients. The MoB framework specifically targets three components of community structure that can influence diversity (Chase et al. 2018, McGlinn et al. 2019, 2021): 1) the total number of individuals in a given sample (Newbold et al. 2015, Andrade et al. 2018, Jokimäki and Huhta 2000) – if anthropogenic modification influences the numbers of individuals (e.g. if food, nest sites, or predation is altered), we would expect it to also influence the numbers of species via the sampling process (i.e. fewer individuals will result in lower diversity), 2) the species abundance distribution (Clergeau et al. 1998, 2006, Tryjanowski et al. 2015, Leveau 2019) – if anthropogenic modification disfavors some species from the pool, and/or favors others (e.g. if certain species tolerate or thrive in human-dominated systems, while others suffer), this will also influence the relative numbers of different species in a given area (e.g. human-dominated systems are less even); and 3) the spatial arrangement of conspecific individuals (Natuhara and Imai 1996, Sol et al. 2014, Marcacci et al. 2021) – if anthropogenic modification influences how individuals are spatially distributed (e.g. degraded sites have high contrast environments leading to strong spatial patchiness and low diversity), then this can potentially impact diversity across a modification gradient. By understanding how these different components are linked to biodiversity change, a more complete picture of how biodiversity is responding to anthropogenic change can be quantified.

The purpose of our study is to examine how bird diversity changes across the continental United States due to an anthropogenic modification gradient using the MoB framework. To ask these questions we leverage citizen science data, a complementary approach to standardized surveys designed to quantify biodiversity change. Specifically, we tested whether a

diversity-human impact gradient emerged due to differences in the total number of individuals, evenness, or aggregation (Fig. 1A) using the eBird dataset for the continental United States. We expected that there would be a unimodal relationship between species richness and an anthropogenic gradient (sensu Batáry et al. 2018, Callaghan et al. 2019) because of the different niches that are created at intermediate levels of ‘disturbance’ where disturbance is anthropogenically modified habitats which lead to increased habitat heterogeneity (Oliveira-Hagen et al. 2017, Fahrig et al. 2019). We also asked how two aspects of spatial scale influenced the effect of an anthropogenic modification gradient on bird diversity. First, we investigated the differences in alpha, beta, and gamma diversity. Second, we investigated the influence of the chosen grain size (i.e. size of a grid, or observational unit) when assessing the diversity-gradient relationship.

Material and methods

To quantify how bird diversity, and its underlying components, varied along a gradient of anthropogenic habitat modification, we 1) compiled bird abundance data from the eBird citizen science dataset which includes abundance and identity of birds from observational surveys across the continental United States (Sullivan et al. 2014); 2) compiled data on anthropogenic habitat modification (Kennedy et al. 2019); and 3) estimated diversity metrics (Table 1) that allowed us to disentangle the influence of total and relative abundances

(rarefied richness, evenness) at two spatial extents (alpha and gamma). Data were aggregated across our study extent into hexagonal grid cells. We repeated analyses for data aggregated at different grains, ranging in size from 0.1 to 1. Each step is described in more detail below.

Bird abundance data

We compiled bird data from the eBird citizen science dataset (eBird basic dataset: ebd_vrs_May2020) to aggregate bird diversity records and quantify bird diversity across the continental United States (where the majority of eBird data exists). eBird enlists volunteer birdwatchers to submit ‘checklists’ (i.e. a list of all bird species and the abundance of each species) of the birds they hear and/or see while birdwatching. For each checklist, the spatiotemporal coordinates are automatically appended. A checklist can either be marked ‘complete’, where the observer is reporting all the birds they were able to identify, or ‘incomplete’. Data quality is controlled through a semi-automated process with pre-defined filters of expected birds and bird species counts in a given region, and if a species or count exceeds these filters it is checked by regional expert volunteers before being integrated in the dataset. Nevertheless, there exist biases and potential ‘outliers’ in eBird data. Therefore, we further subsetted the eBird dataset to checklists that met the following criteria: 1) only complete checklists (to remove incomplete checklists that did not fully sample the community); 2) only stationary checklists (to remove the potential of not knowing where birds were

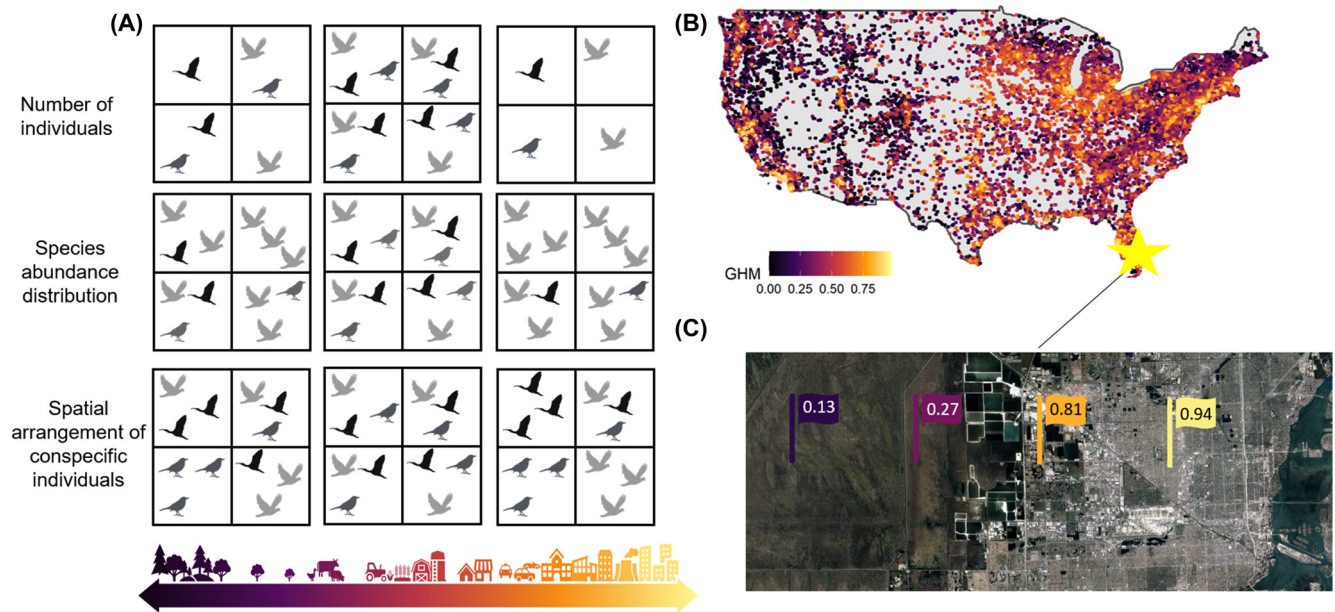


Figure 1. (A) Our hypothetical expectations of diversity responses along an anthropogenic modification gradient showing a nonlinear response, where the number of individuals, the evenness of the community, or the spatial aggregation, from top to bottom respectively, peak at intermediate levels of global human modification (GHM). (B) A map of our study area and the 92 774 potential eBird checklists used in our analysis with the associated GHM gradient shown, highlighting some of the cities visible with the high GHM values in yellow. (C) Contextualization of the GHM scores using an example gradient from southeastern Florida, where values range from low (in natural areas such as the Everglades) to high (in built up areas surrounding Miami, Florida).

Table 1. Different diversity metrics and the components of community structure that they capture and control for. SAD effects are due to changes in richness due to changes in species evenness and/or the size of the species pool, N effects refer to changes in richness due to variation in the number of individuals sampled, aggregation effects refer to changes in richness due to variation in how individuals are spatially distributed (clumped, random, or overdispersed).

Family of metric	Metric	Number of individuals sampled (n)	Component controlled for	Component captured
Diversity	Species richness	max n of each sample	none	SAD, N, and aggregation
	Evenness	n=2	N	SAD (sensitive to common species) and aggregation
	Rarified species richness	n=15	N	SAD (sensitive to common and rare species) and aggregation
Turnover	Beta species richness	Regional n vs average local n	none	SAD, N, and aggregation
	Beta evenness	n=2	N and SAD (evenness and size of pool)	Aggregation (sensitive to common species)
	Beta rarified species richness	n=15	N and SAD (evenness component)	Aggregation (sensitive to size of species pool)

observed on a given checklist); 3) conducted by one observer (to remove the potential of multiple observers leading to increased diversity estimates); 4) that lasted between 20 and 30 minutes in duration (to subsample to a similarly sampled time period); 5) had abundance estimates for every species (to remove checklists where abundance estimation was not possible); and 6) had at least 15 individuals (to ensure that estimates of diversity were not too constrained). We constrained the duration of birdwatching to between 20 and 30 min to account for the heterogeneous nature in bird observations in regards to the time spent birdwatching – our goal was to subset the data to relatively homogenous sampling, as the Measurement of Biodiversity framework was designed for standardized sampling units (see [McGlenn et al. 2019](#) for further details). We acknowledge that there can still be differences in birds observed between 20 and 30 min birdwatching events, but as the different observation times were spread across the modification gradient (Supporting information), we assume this bias is systematic and thus would not affect our results and conclusions. We excluded nocturnal owls (i.e. Strigidae, Tytonidae) and most seabirds (i.e. Stercorariidae, Alcidae, Sulidae, Procellariidae, Hydrobatidae and Oceanitidae) from our analyses. To limit the influence of intra-annual changes in urbanization preference among birds ([Callaghan et al. 2021a, b](#)), we only investigated bird diversity during the breeding season, defined as May, June, July and August. Only eBird checklists conducted in the breeding season of 2015, 2016 and 2017 were used in analyses in order to best temporally match our measure of anthropogenic modification.

We stratified analyses by Bird Conservation Regions (BCRs; Supporting information). BCRs represent biogeographical boundaries that encompass relatively unique bird assemblages and biogeography ([Bird Studies Canada and NABCI 2014](#)). We assume that a BCR approximates the biogeographic species pool for that region, and thus each BCR is independent of other BCRs and thus our analysis was stratified by BCRs to avoid geographic variation in the species pool. Within each BCR, we used individual eBird checklists as an estimate of local-scale (alpha) diversity, and aggregated

those into landscape-scale (gamma) measures of diversity using hexagonal grids (Supporting information). These hexagonal grids ranged in size from 0.1 (~ 80 km²) to 1 (~ 8000 km²; Supporting information).

Anthropogenic habitat modification

To quantify the extent of anthropogenic habitat modification, we used the global human modification (hereafter GHM) index ([Kennedy et al. 2019](#)). The GHM index has a native resolution of 1 km² and ranges from 0 (generally remote areas with little human impact) to 1 (highly anthropogenically modified environments). The index is a cumulative representation of 13 anthropogenic stressors representing five major categories: human settlement, agriculture, transport, mining and energy production, and electrical infrastructure. The GHM index is strongly correlated with other measures of anthropogenically modified environments such as human population density and night-time lights ([Liu et al. 2021](#)). We used Google Earth Engine ([Gorelick et al. 2017](#)) to extract the GHM index at each eBird checklist's location, rather than all of the pixels encompassed by the gamma scale grid cell, which provided a more representative sample of what environments the birds encountered. For example, many of the checklists in highly modified landscapes were located in urban parks which contrast strongly in GHM from the typical urban landscape that is captured in the encompassing gamma scale grid cell. We assumed that the bias among grid cells in how GHM was sampled by eBird checklists was constant across our study area, despite the overall level of modification differing throughout our study area. To further ensure that our estimates of GHM were representative at the gamma scale grid cell we used a bootstrapping procedure.

Measurement of biodiversity

We used the multi-metric version of the MoB framework which relies on the estimation and interpretation of complementary metrics of alpha, beta and gamma diversity ([Table 1](#), [Chase et al. 2018](#), [McGlenn et al. 2019, 2021](#)). Specifically, we computed species richness; rarefied species richness;

and species evenness. We also estimated total community abundance. Species richness was the sum of unique species observed and it is sensitive to all three components of community structure. Rarefied species richness is the expected number of species given a defined number of sampled individuals (Gotelli and Colwell 2001). We used 15 individuals as a cutoff as this was a conservative cutoff for rarefaction, and corresponded with a logical breakpoint in a histogram of the abundance on an eBird checklist across all checklists (Supporting information). As you increase the individuals to which to rarefy to, then power is lost (i.e. more replicates are lost). We did, however, find qualitatively and quantitatively similar results between an analysis of rarefied species richness with the number of individuals as 5 and 25 compared with 15 presented in the main text (Supporting information). For evenness, we used the species probability of interspecific encounter, a metric that computes the effective number of species when common species are weighted more heavily (Hurlbert 1971). PIE is the same as 1-Simpson's index, which when transformed to the effective number of species is the same as $q=2$ on the Hill number continuum (Hill 1973, Jost 2006). Intuitively, this metric of evenness corresponds to the probability that two random specimens from the species pool will be different species. Total abundance was computed as the total number of individual birds in a given sample.

These metrics are not interchangeable, but rather collectively help to comprehend the factors influencing diversity along an anthropogenic gradient (Table 1), rather than solely identifying the strongest correlates of species richness. This approach is increasingly used to understand the influence of urbanization on diversity (Piano et al. 2023). Each metric is sensitive to specific components of community structure while being less responsive to others (Blowes et al. 2022), necessitating careful interpretation of their co-variation (Hurlbert 1971, Jost 2006). For instance, rarefied richness is influenced by spatial patchiness and the species abundance distribution (SAD) but not by the total number of individuals in a sample. This does not imply that rarefied richness cannot be correlated with total abundance; rather, it indicates that such a correlation lacks informative value as rarefied richness estimates are standardized to the same total abundance for each sample. However, it is worth noting that rarefied richness can still exhibit correlation with empirical total abundance. This correlation may arise when shifts in the SAD align with changes in total abundance.

We calculated each of the above metrics at the alpha (i.e. eBird checklist level) and gamma (i.e. hexagonal grid level) scale. While the alpha-level represents the mean level of an eBird checklist, the gamma level represents the regional species pool (i.e. defined by our hexagonal grid), constructed and randomly sampled by pooling across all eBird checklists in that region. However, there was unequal sampling effort in each grid cell, with an average ranging from 2–11 checklists in a 0.1° grid cell, depending on BCR, to an average ranging from 6 to 376 checklists in a 1.0° grid cell, depending on BCR (Supporting information). Therefore,

to account for this unequal sampling, we used bootstrapping where 10 eBird checklists were randomly sampled from a grid cell to estimate gamma diversity. This was repeated 100 times. If a grid cell had less than 10 checklists, it was excluded from any potential analyses. We tested the robustness of this bootstrapping cutoff of 10 checklists by also performing this analysis for cutoffs of 30 and 50 checklists and found qualitatively similar results. We aggregated our bootstrapping results by taking the average of all 100 samples at the nearest .00 decimal place. Importantly, our analysis was not intended to estimate 'true' gamma diversity, but rather relative gamma diversity both along an anthropogenic gradient and compared with alpha diversity. Exploratory analyses, however, confirmed that at a 5 km resolution, eBird gamma diversity (i.e. total species richness of all checklists within a pixel) was positively correlated with species richness from an external source, the Breeding Bird Survey (Carroll et al. 2022, Supporting information). Finally, we computed beta diversity (β) for each diversity metric using Whittaker's (1960) multiplicative formulation: $\frac{\gamma}{\bar{\alpha}}$, where $\bar{\alpha}$ is the average of the diversity metric across all the checklists in a given grid cell. All biodiversity metrics were calculated using the `mobr` R package ver. 2.0.0 (McGlenn et al. 2019, 2021).

Statistical analysis

To statistically evaluate the relationship between the biodiversity metrics described above and GHM, we used generalized additive models (GAMs, Wood 2004, Wood et al. 2016). We used GAMs because we had an a priori expectation that the relationship between diversity and an anthropogenic modification gradient would be nonlinear (sensu Batáry et al. 2018). For all models, the response variable was the mean diversity component (species richness, rarefied species richness, evenness, or total abundance) at a given scale (i.e. alpha, gamma or beta), and the predictor variable of interest was a smooth term for anthropogenic modification gradient using a penalized cubic regression spline with 10 knots. For each model, we included a random effect for BCR, as we were not inherently interested in the variability of responses among BCRs. Models were fit for each diversity metric (e.g. species richness, rarefied species richness, total abundance) at each scale. To ensure comparability among models when visualizing our results, each model was fit using the same specification (i.e. no model selection) described above. Models were fit using the `mgcv` package (Wood 2004) and took the general form of: mean diversity component $\sim s(\text{ghm}, \text{bs}='cs', k=10) + s(\text{BCR}, \text{bs}='re')$. Results of the individual GAMs can be found in the Supporting information. To visualize and summarize our results, we predicted diversity responses using a GHM gradient from 0 to 1, by 0.01 values ($n=101$ values), where the random effect was zeroed out to represent the mean response among BCRs. We tested the effect of the sampling duration of the eBird checklists, comparing checklists sampled between 5 and 15, 20 and 30 and 50 and 60 min,

and found qualitatively and quantitatively similar results (Supporting information).

Data analysis and availability

All data analyses were conducted in R statistical software (www.r-project.org) and relied heavily on the Tidyverse (Wickham et al. 2019). Statistical significance was inferred at $\alpha < 0.05$. Code and data to reproduce these analyses are available at: <https://zenodo.org/record/8329537>.

Results

We found a generally non-linear, negative, relationship between bird diversity and anthropogenic modification across all biodiversity components – species richness, rarefied species richness, evenness, and total abundance – at both the alpha (i.e. eBird checklist) and gamma (i.e. landscape-level hexagonal grid cell) scales (Fig. 2, Supporting information). Across diversity components, we found that the magnitude of diversity loss with anthropogenic modification was proportionately greater at the gamma scale (i.e. hexagonal grid cell)

than at the alpha scale (i.e. checklist), but in general the alpha and gamma patterns tended to qualitatively resemble each other (Fig. 2). Across the ten spatial grains we examined the results were fairly consistent as well (Fig. 3, Supporting information). However, the magnitude of the effect of anthropogenic modification was greatest at the smallest gamma grain size (i.e. 0.1°) and decreased with increasing gamma grain size showing some convergence (i.e. 1.0° ; Fig. 3B).

Next, we present the results in more detail for one focal grain size (0.5°). Here, at the alpha scale (i.e. eBird checklist), the species richness (Fig. 2A) and total abundance (Fig. 2D) showed similar unimodal patterns along the anthropogenic gradient, with peaks towards the low modification end of the gradient (i.e. the more natural areas). The positive correlation between total abundance and species richness along the modification gradient suggests that changes in species richness are correlated with changes in the numbers of individuals. We examined this further by controlling for the number of individuals using rarefied species richness (Fig. 2B), and we found a general decrease with anthropogenic modification, with a tempered unimodal peak particularly at the alpha scale. Rarefied richness showed a less pronounced response to the gradient

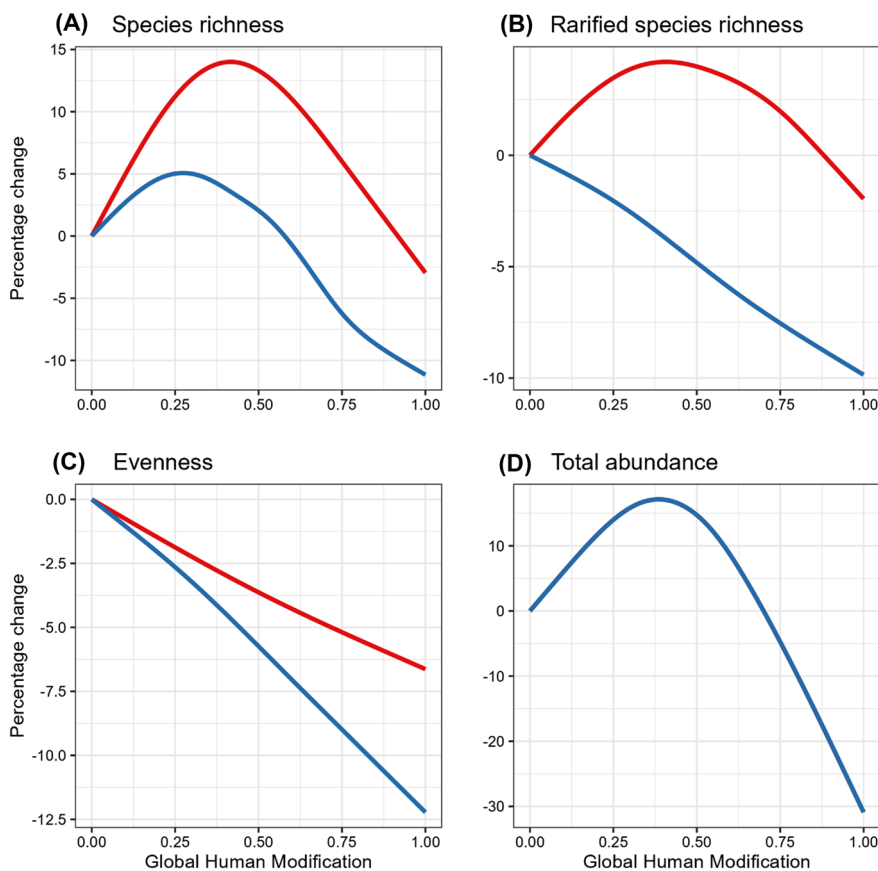


Figure 2. Grid-level results at the 0.5° grain size for gamma diversity (blue line) and alpha diversity (red line) for (A) species richness, (B) rarefied species richness, (C) evenness, and (D) total abundance. The y-axis is represented as the percentage change of the predicted biodiversity value at GHM=0, and thus, each line starts at 0 on the y-axis. Note that for total abundance, the alpha and gamma lines overlap. A version of this figure that shows the raw predicted outputs is available as Supporting information.

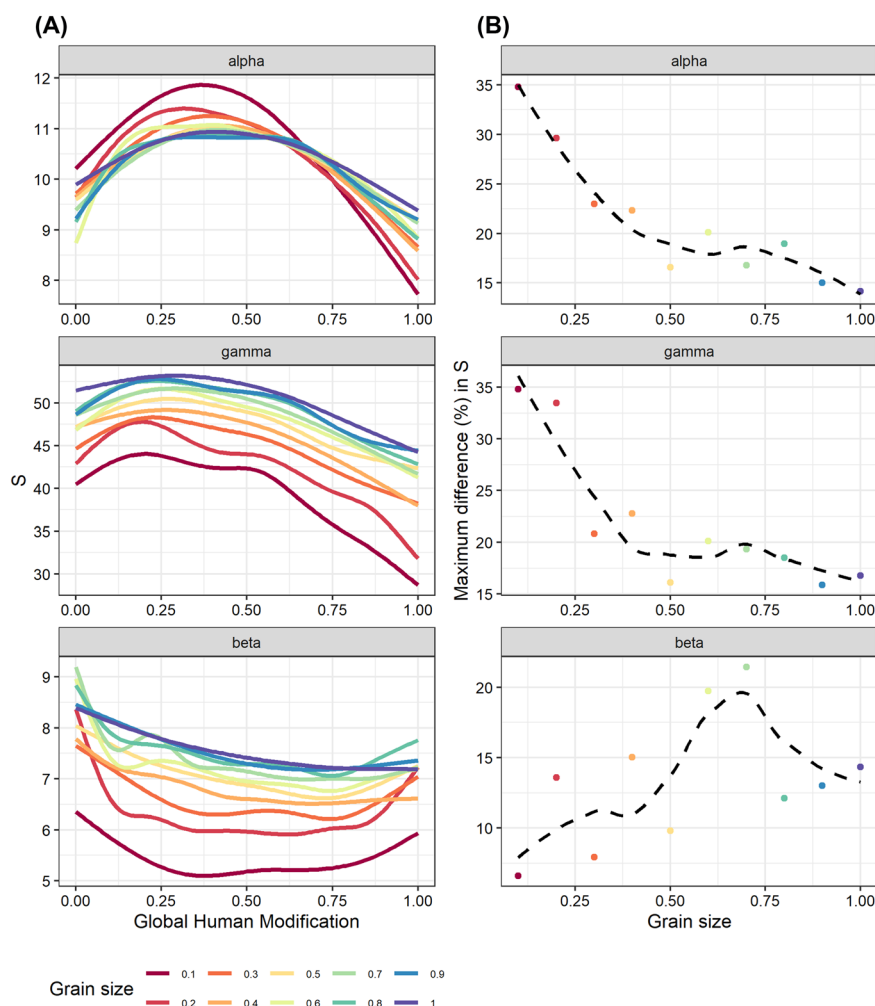


Figure 3. Results of our analysis for varying grain size, from 0.1 to 1.0 where species richness (S) was the response variable. (A) The predicted model fits from the GAMs for alpha (top), gamma (middle), and beta (bottom) diversity. (B) The maximum difference in S , measured as the difference from the 'peak' of the predicted model fit to the minimum of the predicted model fit (i.e. GHM = 1).

compared to raw species richness which lends further support to the role of the effects of total individuals in driving richness patterns along the gradient (cf. Fig. 2A–B). The shallow negative slope of rarified species richness also suggests that species evenness is decreasing along the gradient. Our examination of evenness showed a slight linear decrease along the anthropogenic gradient (Fig. 2C). These results were supported by an additional analysis that found that total abundance was most strongly correlated with species richness as opposed to evenness, supporting the notion that diversity declines are associated with a decreasing number of individuals along an anthropogenic gradient (Supporting information). However, rarified species richness and species richness were also strongly correlated suggesting a possible weaker effect of the total number of individuals, but because evenness is positively correlated with total abundance and rarified species richness is sensitive to changes in evenness, we conclude that the total number of individuals is influencing the relationship between species richness and rarified species richness.

The diversity gradients at the gamma scale (i.e. landscape-level hexagonal grid cells) were qualitatively similar to the alpha scale for species richness and evenness, but gamma did not show a strong peak like at the alpha scale. Importantly, the magnitudes of change (i.e. the predicted diversity at the beginning of the gradient compared with the end of the gradient) were proportionally stronger for the gamma than the alpha scale (Fig. 2). We again found a similar unimodal pattern in both total abundance and species richness. As at the alpha-scale, rarified species richness decreased along the anthropogenic gradient, but with less magnitude change than species richness. Evenness showed a steady decline along the anthropogenic gradient with a greater magnitude than at the alpha scale. Similar to the alpha scale, total abundance was most strongly correlated with species richness along the anthropogenic gradient, suggesting that declines in total number of individuals lead to diversity declines at the gamma scale (Supporting information).

Finally, we found a slight decrease in beta species richness along an anthropogenic gradient, and an apparent stabilizing

of beta species richness at about GHM value of 0.75 (Fig. 4). For beta evenness, we found relatively little change, although slightly less beta evenness in highly modified areas than unmodified areas with a slight nonlinear shape. And for beta rarified species richness we found relatively little change, indicating that the degree of spatial aggregation within species did not vary greatly along the anthropogenic habitat modification (Fig. 4).

Discussion

Using more than 90 000 bird surveys across the continental United States, we found strong evidence for an overall decline in bird diversity along an anthropogenic modification gradient. Our species richness results confirm the negative consequences of anthropogenic modification on bird diversity (McKinney 2006, Sol et al. 2020). We extended previous work (Clergeau et al. 1998, 2006, Sol et al. 2014, Batáry et al. 2018, Ross and Henkanaththegedara 2019, Sol et al. 2020, Morelli et al. 2021) by dissecting the potential underlying influences of diversity change across spatial scales and grains by simultaneously investigating species richness, rarified species richness, evenness and total abundance (Table 1). Bird species richness peaked at low to moderate levels of modification (i.e. natural and semi-natural areas), with slight differences between the alpha and gamma scales (Fig. 2) and this appeared to be correlated with the peak in number of individuals at this portion of the gradient both at the alpha and gamma scales. The flattening of the

diversity change signal observed in rarified species richness and evenness which both control for the numbers of individuals further supports the notion that bird diversity is largely correlated with the number of individuals. Our results suggest that the peak of individuals, and consequently species richness, happens at the natural-rural-suburban interface (Batáry et al. 2018), highlighting the importance of preserving bird diversity along the spectrum of anthropogenic modification.

We found that the magnitude of biodiversity change was greatest at the gamma scale compared with the alpha scale. Together with our results for total abundance, the various measures of beta diversity patterns (species richness, rarified species richness, and evenness; Fig. 4) suggest that spatial species turnover is lower at highly modified sites, but that rather than resulting from higher patchiness of species, this emerged because fewer individuals were found at more highly modified sites. Nevertheless, at the larger gamma scale we found moderate evidence that there were shifts in the species abundance distribution along the gradient (i.e. rarified species richness and evenness slopes were slightly negative), such that impacted sites were dominated by fewer species (i.e. less even). These findings support the literature highlighting that there are often hyper-abundant species that thrive in urban environments (Sol et al. 2017a, Hensley et al. 2019), commonly nonindigenous organisms (Sol et al. 2017b). Identifying those hyper-abundant species has important relevance for conservation and urban planning and could potentially highlight where along an anthropogenic gradient management would be best suited.

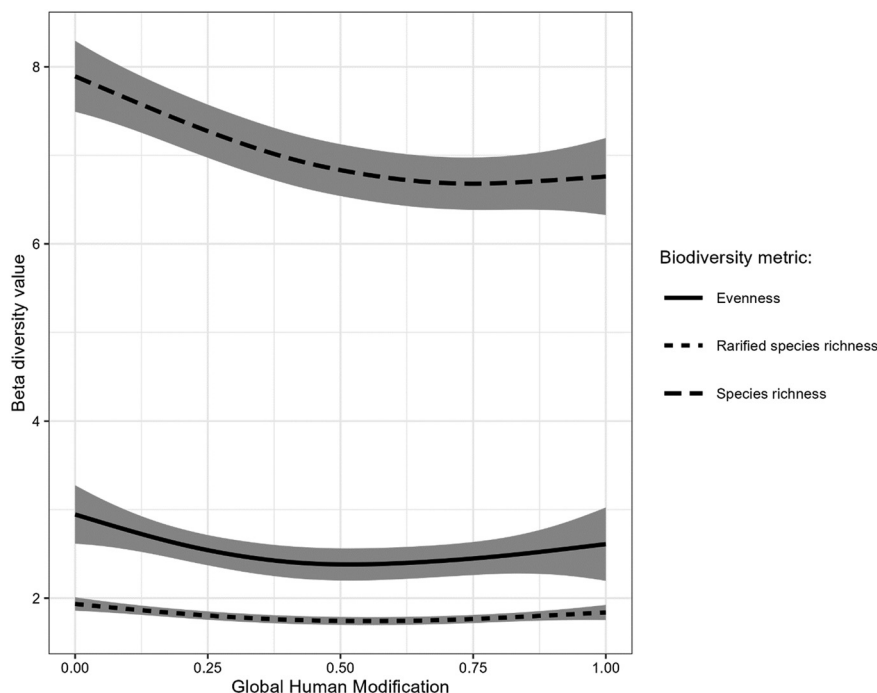


Figure 4. The beta diversity patterns for species richness (long-dashed line), evenness (solid line), and rarified species richness (short-dashed line). A beta diversity value of 1 indicates no species turnover. All lines are predicted results from generalized additive models (GAM) and the shaded area represents the 95% confidence interval surrounding those predictions.

Our results indicate that at the continental scale, variation in the number of individuals (i.e. density) plays an important role underlying patterns of changes in species richness along an anthropogenic gradient (Storch et al. 2018). In some instances, however, species richness can decline, but without a noticeable change in abundance along an urbanization gradient (Chamberlain et al. 2017) suggesting that mechanisms driving species richness and abundance are nuanced and context dependent. Changes in species richness may result from sampling – as more individuals are sampled from the regional pool, species richness inevitably increases (i.e. the more individuals hypothesis, Srivastava and Lawton 1998, Storch et al. 2018). This possibly explains why species richness can be decreasing in highly modified environments such as cities, but functional diversity can sometimes be maintained (Lee et al. 2021). We also found that the strongest decrease along the anthropogenic gradient of all diversity components was in the number of individuals. This makes sense, given that there is less habitat available for birds along an anthropogenic gradient as an increasing amount of habitat is modified by humans (e.g. agriculture, mining infrastructure, cities). For example, in agricultural habitats, there are fewer breeding bird pairs than surrounding natural areas (Heikkinen et al. 2004). Concomitantly, food and other resources also typically decrease along an anthropogenic gradient (Shochat et al. 2006), constraining the possible number of individuals as a function of the carrying capacity (Srivastava and Lawton 1998, Storch et al. 2022). We acknowledge that our framework generally assumes that the number of individuals influences species richness, but at biogeographic scales others have shown that species richness influences the number of individuals (Storch et al. 2022). There are many complexities associated with disentangling the influence of abundance from richness in studies examining diversity. While metrics such as rarefied richness control for abundance while assessing richness, there is currently no metric available that directly examines abundance while accounting for richness. This limitation poses challenges in determining the individual contributions of abundance and richness to observed patterns, particularly when changes in species richness may be driving variations in total abundance. Thus, careful interpretation is necessary when exploring the interplay between abundance and richness in shaping diversity relationships. Nevertheless, given the importance of considering the number of individuals (i.e. abundance) associating with species richness change, even when species are present in modified environments (e.g. threatened species, Ives et al. 2016), care should be taken to fully understand the abundance of these species, as opposed to just presence/absence, as some highly modified regions can act as population sinks. Future experimental work could be aimed at further disentangling the effect of abundance and richness along anthropogenic modification gradients.

Both the number of individuals and species richness showed a strong unimodal pattern across the anthropogenic gradient, with a peak generally at intermediate levels of habitat modification (Fig. 2). This is likely a result of the unimodal relationship of habitat heterogeneity (Oliveira-Hagen et al.

2017) resulting from intermediate levels of disturbance, or in this case anthropogenic modification (sensu Connell 1978). At intermediate levels of anthropogenic modification, there are likely peaks in habitat heterogeneity and productivity resulting from a mix of unique and different habitat types (e.g. pristine natural areas mixing with suburban habitats), thus supporting a higher likelihood that multiple species can coexist (Terborgh 1977, Palmer 1994, Baldi 2008, Stein et al. 2014). Indeed, using the eBird checklist sampling locations in our analysis, exploratory analysis showed that there is a peak in habitat heterogeneity at about GHM of 0.75, after which habitat heterogeneity drastically decreases at the highly modified end of the gradient (Supporting information). In contrast, at the natural end of the anthropogenic gradient, natural forest or grassland habitats may be more homogenous, leading to lower diversity, and mainly comprised of habitat specialists. Whereas in a central business district for example, with the highest possible anthropogenic modification scores, there may only be extreme generalists (i.e. human commensals such as rock pigeons and house sparrows; Palacio 2018), leading to overall lower diversity. Our results also highlight that bird diversity peaks at the natural–rural–suburban interface (Batáry et al. 2018), illustrating the importance of local biodiversity management in rural and suburban areas to maintain high levels of bird diversity (Burghardt et al. 2009, Kos et al. 2021). Nevertheless, future research should aim to confirm some of the speculation and the mechanistic understanding of how habitat heterogeneity influences bird diversity along an anthropogenic gradient.

We found strong evidence for the importance of two kinds of spatial scale in moderating the magnitude of the effect size of the anthropogenic gradient on bird diversity, even if the qualitative patterns were similar. First, we found stronger effects of the anthropogenic gradient when bird diversity was measured at the larger, gamma scale (hexagonal grid cells) compared to the smaller alpha scale (individual eBird checklists). Such increases in the magnitude of the effect size with increasing spatial scale are expected, for example, when species area relationships diverge between communities that have fewer individuals and/or are less even (Chase and Knight 2013, Chase et al. 2018, Blowes et al. 2022). This effect could also be expected if there were a change in the degree to which anthropogenic modification influenced the intraspecific aggregation among species, as might be expected, for example, if there is variation in the degree of homogenization along the gradient. However, while we found slight changes in beta diversity along the gradient, this effect was largely reduced when we controlled for differences in the numbers of individuals (i.e. beta rarefied species richness), suggesting that there was no systematic difference in the degree to which species distributions were aggregated across the gradient, supporting other results finding little change in beta diversity in modified and unmodified areas (Petsch et al. 2021). This difference in the magnitude of the effect size between gamma and alpha scales also provides evidence that local-scale habitat attributes can positively influence bird diversity. This finding is supported by an increasing body of research demonstrating that local-level

habitat attributes are more important than landscape-level attributes for biodiversity maintenance and management, especially in urban ecosystems (Evans et al. 2009, Williams and Winfree 2013, Galitsky and Lawler 2015, Lepczyk et al. 2017a, b, Callaghan et al. 2018). Our results support recent work highlighting the value of suburban green area for supporting heterogeneous bird communities (Lerman et al. 2021). Indeed, urbanization can fail to impact bird species richness within cities and even have increased species richness compared with homogenous natural areas (Callaghan et al. 2021a, b), likely a result of heterogeneity in the surrounding local level habitat attributes (Korányi et al. 2021).

We also found a strong influence of the choice of grain size, or the spatial grain at which eBird checklists were aggregated (0.1–1.0° grain sizes) on the quantitative magnitude, but not qualitative shape, of the bird diversity response to anthropogenic habitat modification. Specifically, the degree of change in diversity from the peak diversity to the minimum diversity (at GHM = 1) – tended to be weaker at the coarser grains. This is expected in part because diversity shows a unimodal relationship and the anthropogenic gradient is strongly spatially structured; therefore, as grain size increases more of the gradient is captured within a grid cell and thus the peak in bird diversity at low to intermediate anthropogenically modified sites is diluted (i.e. the diversity gradient flattens) by including samples from low and high modified sites. Additionally, total abundance effects in which diversity is constrained by the number of individuals sampled are expected to be strongest at fine grains. Given that we found total abundance effects provided the strongest explanation for our observed diversity gradients it makes sense that finer grains show a stronger diversity gradient.

Our work extends previous results by integrating broad-scale citizen science data, allowing for a broad geographic (i.e. continental United States) and taxonomic (i.e. > 600 species) scope to decompose the influence of scale and underlying components of bird diversity change along an anthropogenic gradient. Although our community-level approach provides support to many species-specific results that have illustrated environmental filtering in urban environments (Jenerette et al. 2016, Magura et al. 2018, Uchida et al. 2021), responses to anthropogenic modification can vary by species and functional group (Galitsky and Lawler 2015). We suggest that citizen science data offer an excellent dataset that complements standardized surveys specifically designed to evaluate changes in biodiversity (Sol et al. 2014, 2017a, 2020). Such data can support new evidence to test predictions derived from more classic approaches. For example, we acknowledge that the detectability of birds can differ in different environments (e.g. a wetland compared with a forest), and we did not account for this in our analysis – something that standardized surveys can explicitly account for in survey design. However, these different environments, and corresponding biases, would be similar among BCRs and at the local scale along the anthropogenic gradient, suggesting that the biases should act in a similar direction. In other words, we anticipate that birder behavior, which leads to the different biases in large-scale citizen science data, is

consistent among BCRs and across an anthropogenic gradient. In support of this, an additional analysis (Supporting information) that used asymptotic species richness (i.e. the expected species richness given complete sampling) as a response variable was highly correlated with species richness, providing robustness that despite biases of sampling across the anthropogenic gradient our results are robust. While our analysis highlights the value of broad-scale data at decomposing biodiversity patterns, this can be further extended to more fine-scale analyses in space and time, such as differences among guilds or functional groups of species, or differences among BCRs.

Anthropogenic habitat modification is continually increasing – for example, urban land cover is expected to increase by 2–3 million km² by 2050 (Huang et al. 2019) – making it critical to understand how biodiversity responds to such habitat modifications. Here, we 1) highlighted the overall negative consequences of anthropogenic modification on bird diversity, 2) demonstrated that changes in diversity are largely associated with a decreasing number of individuals and 3) showed that the magnitude of effect was greatest at gamma compared with alpha scales. Taken together, these results illustrate that local-scale management can promote diversity, especially at the natural–rural–suburban interface. Further, efforts should be focused on creating, restoring, and preserving resources necessary to support a large number of individuals, as this is a primary influence of diversity change along an anthropogenic gradient.

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Data availability statement

Data and code are available here: <https://zenodo.org/record/8329537> (Callaghan et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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