How to build a biodiverse city: environmental determinants of bird diversity within and among 1,581 cities

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Abstract

Cities are novel environments compared with the evolutionary history of the species that reside within them. Collectively, cities and their fauna can be thought of as ecosystems, recognized as playing a critical role in supporting global biodiversity, but they are fundamentally a combination of old species surviving or thriving in a new environment, and the mechanisms and underlying processes which support biodiversity within cities have not been investigated at broad macroecological scales. We aimed to understand — at a broad macroecological scale — how biodiversity responds both among and within cities. We integrated > 5 million eBird citizen science observations with remotely sensed landcover products throughout 1,581 cities within the continental United States. We first investigated the species-area relationship as it pertains to cities and compared the slope of this relationship to randomly sampled polygons. Second, we investigated how biodiversity responds to an urbanization gradient at the level of localized bird observations. We found strong support for the longstanding species-area relationship theory: geographically larger cities had greater species richness. Surprisingly, the species-area relationship was greater in cities when compared to the overall relationship for randomly sampled polygons in the study region (continental United States), which included many different land use and land cover types. Our finding suggests that diverse and heterogeneous cities play a significant role in supporting biodiversity. We also found that there is a consistent threshold where the level of urbanization begins to profoundly and negatively affect biodiversity. Critically, urban planning at the city-scale and at a local-scale (e.g., neighborhood) should focus on preserving attributes of water and tree-cover for increased biodiversity to keep as much of the city as possible above this threshold value.

Keywords: citizen science; species-area relationships; spatial scales; urbanization; urban ecology; eBird; biodiversity

Introduction

Cities first appeared on planet earth ~ 6000 years ago, while the evolutionary history of most bird species which currently reside within them dates back 1-10 million years (McKinney 2002, Weir and Schulter 2007, Nemeth and Brumm 2009, McDonnell and Hahs 2015). Because of the relative lack of time for species to evolve and speciate within cites, it is unsurprising that cities generally have negative impacts on local biodiversity (McKinney 2006, 2008, Šálek et al. 2015), including species richness (Blair 1996, Chace and Walsh 2006, Concepción et al. 2016), species diversity (Blair and Launer 1997, Wang et al. 2001), phylogenetic diversity (Knapp et al. 2012, 2017, Ricotta et al. 2012), and functional diversity (Pavao-Zuckerman and Coleman 2007, Pauw and Louw 2012, Nock et al. 2013), resulting from the conversion of natural habitat into urbanized land (Ferenc et al. 2014), with associated ecological disturbances; e.g., light-pollution (Hölker et al. 2010), noise-pollution (Duarte et al. 2011, Davies et al. 2017), or habitat fragmentation (Delaney et al. 2010, Dubois and Cheptou 2017).

Despite the overall negative impacts of urbanization on biodiversity (McDonald et al. 2013), urban areas are increasingly recognized for their ability to support biodiversity (Kühn et al. 2004, Baldock et al. 2015, Goertzen and Suhling 2015, Kowarik and Lippe 2018), sometimes including threatened species (Ives et al. 2016), and are even seen as opportunities for conservation (Dearborn and Kark 2010, Aronson et al. 2017, Lepczyk et al. 2017). One of the most generalized principles in ecology (MacArthur and Wilson 1963, 2001), also applicable to the relationship between cities and biodiversity (Ferenc et al. 2014, Beninde et al. 2015) is the species-area relationship. This relationship probably reflects the scaling effects taking place in cities, including a positive relationship between city size and amount of green area (Fuller and

Gaston 2009). This ecological relationship can result in an oxymoronic relationship: *larger geographic cities have more species*. Large geographic cities, however, are not a "solution" to maintaining biodiversity within urban environments. Even accounting for geographic area relationships, not all cities support biodiversity equally. Indeed, biodiversity responds to urbanization inconsistently among cities (Chamberlain et al. 2017); sometimes non-linearly (Lepczyk et al. 2008, Batáry et al. 2018) and sometimes with a peak at intermediate levels of urbanization (Callaghan et al. 2019c). Importantly, some cities are more species-rich than others (Ferenc et al. 2014). Understanding how biodiversity responds to urbanization processes — both within and among cities — can ultimately help influence conservation and policy decisions of local relevance (Evans et al. 2009, Fuller and Gaston 2009, Aronson et al. 2014), with a focus on preserving biodiversity within these expanding ecosystems. From a policy-relevant perspective (Sutherland et al. 2006, Puppim de Oliveira et al. 2011), a more nuanced understanding of the effects of city size on biodiversity is needed. Specifically, we need to fully understand: (1) how a given city compares with cities of similar size; and (2) whether city size thresholds (e.g., Garaffa et al. 2009) exist, which influence biodiversity negatively or positively.

While cities may not be "natural" or "semi-natural" (Bradshaw 2003), they can be thought of as functioning ecosystems (Andersson 2006, Taylor and Hochuli 2015) with unique ecological footprints (McDonnell et al. 2009). At the broadest, macroecological sense, cities generally have some proportion of each of three main landcover types — vegetation, water, and impervious surface — all acting to influence biodiversity (Dobbs et al. 2017). Planted vegetation and water features can — but do not necessarily — provide similar macroecological functions to their "natural" or "semi-natural" counterparts (Pautasso et al. 2011, Fahrig et al. 2019). A large number of studies have investigated one or more of these habitats to understand intra-city characteristics which predict biodiversity (Dickman 1987, Cornelis and Hermy 2004, Parsons et al. 2006, Bickford et al. 2010, Hedblom and Söderström 2010, Bates et al. 2011, Fontana et al. 2011, Lizée et al. 2012, Concepción et al. 2016), but with largely inconclusive results. That is, wide variation exists among cities and associated studies, and detecting a useful signal through the noise requires a great deal of data. A recent meta-analysis (Beninde et al. 2015) found that patch area, corridors, and vegetation structure were the most significant drivers of biodiversity within cities. Protection of these remnant habitats, and associated corridors (Savard et al. 2000), is therefore critical for maintaining biodiversity within cities. Beninde et al. (2015) also concluded that local habitat variables are more important than landscape variables. Similarly, a recent global analysis (Aronson et al. 2014) found that anthropogenic factors (i.e., landcover and city age) were major drivers of bird and plant diversity among cities. Together, these results suggest that local policies within cities have the ability to influence biodiversity (Puppim de Oliveira et al. 2011).

To date, perhaps because of logistical considerations, most research elucidating the effects of cities on biodiversity has been focused on biodiversity responses *within cities* (Grimm et al. 2000, McDonnell et al. 2009), with comparative approaches *among cities* generally lacking (McDonnell et al. 2009). Moreover, studies investigating inter-city differences are limited in the number of cities being compared (e.g., Garaffa et al. 2009, Ferenc et al. 2014), possibly reflecting the geographic scope of funding or policy bodies.

One way to scale-up this type of research is broad-scale empirical data — collected by citizen scientists (Bonney et al. 2009). Such citizen science data are fundamentally enhancing our understanding of urban ecosystems, both at small (McCaffrey 2005, Callaghan and Gawlik 2015) and large (Cooper et al. 2007, Aronson et al. 2014, La Sorte et al. 2014, Callaghan et al. 2018a) spatial scales. This is most evident for birds, which have a longstanding tradition of citizen science surveys (Silvertown 2009). These data have the ability to provide generalized understanding of the impacts that cities have on biodiversity, adding to our understanding gleaned from meta-analyses (Beninde et al. 2015, Batáry et al. 2018) and systematic reviews (Marzluff et al. 2001, Marzluff 2017, Archer et al. 2019).

We use broad-scale citizen science data throughout the continental United States to better understand the relationships between city size and biodiversity responses. Birds are used as our focal taxon, given the large amount of citizen science data available reflecting their popularity with the general public (Sekercioglu et al. 2016). We integrate these citizen science data with geo-political boundaries of 1,581 cities, and assess how species richness, Shannon diversity, phylogenetic diversity, and abundance — four measures of biodiversity — respond to city size. We then specifically investigate the (1) relationship between a suite of macroecological habitats predictors (i.e., tree cover, water cover) among cities and (2) biodiversity responses within cities, along a continuous urbanization gradient.

Methods

Study-sites: cities

Cities, by definition, are largely unresolved areas of human settlement (Ferenc et al. 2014), reflecting geo-political boundaries in the sense that they are fixed areas generally controlled by a single authority. Indeed, there has been much debate about what constitutes a city and how 'urban' is defined, in an attempt to delineate urban, peri-urban, and rural areas (Marzluff et al. 2001, McIntyre et al. 2008, Moll et al. in press). The purpose of our study was to assess differences among these geo-political boundaries. As such, we relied on the U.S. Census bureau's definition of urban areas and downloaded the U.S. Census Bureau's 2017 urban areas shapefile (available here: https://www.census.gov/geo/maps-data/data/cbf/cbf_ua.html). This product defines urban areas based on population density and a suite of land-use characteristics (see more here: https://www.census.gov/geo/reference/urban-rural.html). This product treats some of the larger conurbations in the United States as one 'urban area' (e.g., New York/New Jersey). Because this is contradictory to our definition of city (i.e., a geo-political boundary capable of local-level policy relevance), these large amalgamations of urban areas (i.e., when more than one recognizable city were combined) were eliminated from analysis. We then intersected these cities with a freely available United States Cities Database (available here: https://simplemaps.com/data/us-cities), which provides information on municipal population, city population, population density, latitude, and longitude. In order for a city to be further considered for potential analysis, it had to be included in both the cities database and the U.S. Census Bureau's shapefile — after large conurbations were removed. We also focused our analysis on the contiguous United States, removing Alaska and Hawaii from consideration, with the above process resulting in a potential suite of 2,888 cities (Appendix 1).

Bird data

We used eBird data to estimate biodiversity among cities. eBird is a successful citizen science project (Sullivan et al. 2009, 2014, Wood et al. 2011, Callaghan and Gawlik 2015), initiated in 2002 by the Cornell Lab of Ornithology. The database hosts > 600 million observations, freely accessible to researchers and practitioners (https://ebird.org/data/download). eBird works by enlisting volunteer birdwatchers who submit bird observations in the form of checklists — defined as a list of birds seen and/or heard in a particular area at a particular time. An extensive network of regional volunteers (Gilfedder et al. 2018) use their local expertise to create filters that flag potential submissions as unusual in nature: either unexpected species or abundances of species. If an observation trips a filter, then it is reviewed before inclusion in the database. We downloaded the eBird basic dataset (version ebd_relDec-2018), and filtered for observations from January 1st, 2010 to December 31st, 2018, aligning with the period of richest data and minimizing the likelihood that city boundaries would have changed substantially in that period of time. For our analysis, we applied an additional set of filters to the eBird data to remove potential outliers from the entire potential pool. Checklists were excluded if they were incomplete, did not follow the stationary, random, or travelling protocols, or if they did not meet standard duration and distance criteria (e.g., La Sorte et al. 2014, Johnston et al. 2015, Callaghan et al. 2017). Additionally, if multiple observers submitted an eBird checklist together (i.e., a ‘shared’ checklist), then we randomly sampled one of those checklists to include in analyses. All seabirds were eliminated from analyses because our question of interest applied to terrestrial bird diversity.

Joining cities and eBird data

For each of the 2,888 potential cities, we extracted all eBird checklists which met our criteria above (Appendix 1). Cities which had a minimum of 50 checklists were included in downstream analyses, leaving us with a total sample of 1,581 cities (Figure 1a; Appendix 1). Fifty checklists was the threshold chosen because it is a conservative minimum needed to produce adequate community characterization (Callaghan et al. 2017). Additionally, variation in the number of checklists per city was accounted for in downstream analyses (see below).

Response variables

At the city-level, we calculated one response variable: the total number of species reported among all checklists. At the checklist-level, we calculated four response variables of biodiversity. For any checklist which met our criteria above, we calculated: (1) the species richness — i.e., total number of species; (2) total abundance — i.e., the sum of all abundance estimates; (3) Shannon diversity — i.e., Shannon diversity index using the vegan package (Oksanen et al. 2010); and (4) phylogenetic diversity — a measure of biodiversity incorporating the phylogenetic difference among species (Faith 1992), using the picante package in R (Kembel et al. 2010). Not all checklists provided all response variables; eBird participants can add an ‘X’ to signify presence of a species without an abundance estimate on an eBird checklist, and as such, checklists which included an ‘X’ were included only for the species richness and phylogenetic diversity analyses, which were dependent only on presence/absence. Such checklists were excluded for abundance and Shannon diversity analyses, which were dependent on abundance estimates.

Predictor variables

City-specific habitat attributes

We used Google Earth Engine (Gorelick et al. 2017) and the U.S. Census Bureau's delineations of urban areas to extract habitat attributes for each city (*sensu* Callaghan et al. 2018a). Using globally-derived datasets at a 30-m resolution, from multi-temporal time series of both MODIS and Landsat satellite imagery, we calculated the following for each city: (1) the mean tree cover (Sexton et al. 2013); (2) the proportion of water cover; and (3) the average annual composite (2014-2018) enhanced vegetation index (EVI) — an optimized version of NDVI which better accounts for the sensitivity in high biomass regions (Huete et al. 2002). Additionally, for each city, we calculated the distance from the coastline.

Checklist-specific attributes

In addition to city-specific attributes, we also assigned each eBird checklist a relative value of urbanization, on a continuous scale. To do so, we used VIIRS night-time lights (Elvidge et al. 2017), and assigned each eBird checklist the mean night-time lights value within a 5 km buffer of that checklist (*sensu* Callaghan et al. 2019a). The 5 km buffer was chosen to encompass potential spatial biases in selected sampling locations of the eBird checklists and the results of species-specific responses to urbanization is robust to buffer size (Callaghan et al. 2019b). Night-time light level is highly correlated with the level of urbanization and is commonly used in remote sensing studies (Pandey et al. 2013, Zhang and Seto 2013, Ma et al. 2015, Stathakis et al. 2015, Elvidge et al. 2019), thus making it a representative proxy for urbanization levels. Three example cities representing night-time light values and the max, mean, and median night-time light values for those cities are shown in Figure 1b. However, we note that the night-time light level is only one representative continuous measure of urbanization, and others (e.g., percent impervious surfaces, human population density) could be used in its place. Each checklist was also assigned the mean tree cover, proportion of water, and the average annual composite (2014-2018), using the methods described above, within a 5-km buffer.

Statistical analysis

Predicting species richness at the city scale

We first explored the general relationship between total species richness in a city and the area of the city (log-transformed) using a linear model with weights for the total number of checklists. To contextualize these results, we compared the slope of this city relationship with that of randomly assigned polygons within all land use and land cover types. We assigned 25,000 randomly located points within the study area using the 'sf' package in R and the size of each polygon was determined from a random sample of the city-size frequency distribution. Of the potential points assigned, 12,446 buffered polygons fell within the United States and of this set 1,284 met our criteria for a minimum of 50 eBird checklists.

We modelled the difference between the slopes of the city vs. random data using a Generalized Additive Model (Wood 2017). GAMs allow for both linear predictors (including both parametric terms) and a set of smoothing functions. These models are advantageous because they allow for modelling of unknown non-linear relationships, including continuous and categorical terms, often helpful to account for parameters which are not of inherent interest, but likely influence results of the model (Rigby and Stasinopoulos 2005). The GAM was fitted using a quadratically penalized likelihood approach, with the smoothing parameters estimated via Generalized Cross

Validation, optimizing trade-off between model complexity and model fit. GAMs were fit using the mgcv package (Wood 2003, 2004, Wood et al. 2016). In our case, we fit a GAM where the response was total species richness with a parametric predictor variable for log-transformed patch area (i.e., either city or random polygon) in addition to a smooth term for the total number of lists, accounting for this inherent relationship because the number of eBird lists is highly correlated with total species richness (Appendix 2).

After we investigated the relationship between species richness and city area, we modelled the macroecological habitat predictors which influenced the biodiversity *at a given* city size using the residuals of a linear model fit between species richness and city area. The magnitude of the residual is an estimate of either under-performance or over-performance relative to other cities of similar size (Figure 2b). We then used a Generalized Additive Model where residual species richness was the response variable, with parametric terms for the distance to coast, mean EVI, mean tree, proportion of water, and an interaction between proportion of water and trees, which were standardized to ensure effect sizes were comparable. In addition, we accounted for spatial autocorrelation among cities by fitting the model with a smooth term including latitude and longitude. We first tested for correlation among predictor variables (Appendix 3) but found weak evidence of correlation so all predictors were included.

Predicting biodiversity along gradients of urbanization within cities

We were also interested in how biodiversity responds at a local-level sampling unit (i.e., eBird checklist) to a continuous urbanization gradient within cities. Using the checklist-level urbanization classification, defined above, we again used GAMs to assess these relationships among all cities. First, we employed a GAM for each of the four response variables (i.e., four separate models). These models consisted of the response variables regressed against a smooth term for our parameter of interest which was the level of urbanization. A smooth term was used as there is strong support for non-linear responses of biodiversity to urbanization gradients (e.g., Batáry et al. 2018) and we thus did not want to make assumptions about linear relationships. Other variables included in the models, to account for varying effort among checklists, included duration and distance-travelled for each checklist, fitted with a thin-plate regression spline. There is significant variation in the temporal usage of urban areas, driven by migratory species in this system (e.g., La Sorte et al. 2014), but this was not of intrinsic interest in our analysis. Therefore, we accounted for temporal autocorrelation and non-independence of eBird checklists by assigning each eBird checklist a 'season' of the year, and this was included in the model as a smoothed term with a cyclical cubic regression spline. Further, to account for possible spatial autocorrelation among cities, we included a smooth term with a thin-plate regression spline for latitude and longitude, estimating the spatial effect in the model as a smoothed 2-d function. City was treated as a random effect in these models. Each of the four response variables were fit with a gaussian family distribution, for consistency, but species richness, abundance, and phylogenetic diversity were log-transformed to meet model assumptions.

To investigate whether other checklist-level predictors were more important than the urbanness of a checklist, we repeated the analysis described above, but with urbanness treated as a parametric term, and we also included the mean EVI, mean tree cover and the proportion of water at a checklist-level as parametric terms. These four terms were scaled and centered prior to modelling, making effect sizes comparable. We were also interested in exploring urbanization gradients within cities, so we fitted separate GAMs for each city and assessed the slope of the response to urbanization. These detailed methods and corresponding results can be found in Appendix 4.

Data accessibility

All analyses were performed within the R statistical environment (R Core Team 2018), and relied heavily on the tidyverse workflow (Wickham 2017). Code and data necessary to reproduce these analyses are available in a GitHub repository and will be made available upon acceptance of this article as a permanently archived Zenodo repository.

Results

For our analysis of species richness and phylogenetic diversity, we included a total of 5,420,748 checklists from 538,466 unique localities throughout the United States. For Shannon diversity and total abundance, we analyzed 5,002,534 checklists.

Among city relationships

For the 1,581 cities included in our assessment of total species richness among cities (Figure 1a; Appendix 5), the average number of checklists was 3,220 with a median of 334, ranging from 50 — our minimum cut-off — to 171,466 (Seattle, Washington). Species richness in a city was strongly related to the size of the city (Figure 2a; t=43.348, df=1579, $p < 0.001$), with an R^2 of 0.54. This relationship accounted for the positive association between species richness in a city and the total number of eBird lists submitted (Appendix 2). When modelling this relationship using a GAM, there was also strong evidence of the same positive association ($p < 0.001$), providing robust evidence (Appendix 6). There was strong evidence ($p < 0.001$) that the slope of the city species-area relationship (m=29.81) was greater than that of random polygons (m=19.03) chosen from across the US (Figure 2a; Appendix 7). This relationship remained ($p<0.001$), after log-transforming total species richness in addition to patch area, where the slope of the city species-area relationship (m=0.11) was significantly greater than the slope of the random polygons (m=0.09).

There was very strong evidence that the proportion of water within a city ($p < 0.001$) influenced the residual species richness, and strong evidence ($p < 0.05$) for the influence of trees on residual species richness, when modelling the residuals from the linear model (Figure 2b). But importantly, the effect size for proportion of water was three times that of trees (Figure 3). The distance to the coast, the mean EVI, and the interaction between trees and water had no noticeable effect on residual species richness (Figure 3).

Urbanization gradients

Biodiversity of birds declined strongly with increased urbanization at the scale of individual bird observations (Figure 4). For each of the response variables (species richness, Shannon diversity, phylogenetic diversity, and abundance), there was a clear 'threshold' at a certain urbanization level, which corresponded to a VIIRS night-time lights (i.e., radiance value) of approximately 80 nW $cm^{-2}sr^{-1}$ (Figure 4). However, the maximum VIIRS night-time lights (Appendix 8) only reaches above this threshold for 363 (~23%) cities. Further, the mean VIIRS night-time lights (Appendix 8) among all cities reaches a maximum of 45 nW $cm^{-2}sr^{-1}$ (New Orleans, Louisiana). However, there is a positive relationship between the area of a city and the maximum VIIRS night-time lights (Appendix 8). When urbanization level was included as a parametric term, along with water, tree, and EVI, urbanization level consistently had the most negative influence on biodiversity, and water had the least effect on biodiversity, although most effects were in the negative direction. See Appendix 9 for full model results.

Discussion

We used > 5 million bird lists in > 1,500 cities to provide a generalized understanding of city-level influences on biodiversity among and within cities. Cities — with their diverse and heterogeneous habitats (Callaghan et al. 2019c) — clearly play an important role in supporting avian diversity (Dearborn and Kark 2010, Ives et al. 2016, Soanes et al. 2019), even when compared with randomly sampled patches incorporating natural areas. We also found strong evidence that at a city-level the proportion of water, and to a lesser extent, tree cover, significantly predict residual species richness. There was little evidence that city size influenced the biodiversity response to urbanization gradients: biodiversity responses to urbanization within a city does not respond consistently among cities. Although cities can support significant levels of biodiversity, we did find evidence of a distinct threshold which negatively impacted biodiversity responses, consistent among cities. Critically, urban planning at the city-scale and at a local-scale (e.g., neighborhood) should focus on preserving water attributes and tree-cover for increased biodiversity. This mechanistic understanding should underpin the effective conservation of birds in urban environments.

The significant relationship between the number of species in a city and the size of a city (Fig. 1b & Appendix 6) confirms previous studies (MacGregor-Fors et al. 2011, Ferenc et al. 2014, Beninde et al. 2015). This is best explained by the species-area relationship (Connor and McCoy

1979, Scheiner 2003), whereby larger cities likely have a more diverse subset of ecological communities within their bounds as well as more greenspace and a heterogeneous environment to support numerous bird communities (Fuller and Gaston 2009). Given the positive relationship between plant species richness and tree cover with bird diversity (Pautasso and Dinetti 2009, Trollope et al. 2009), these larger cities probably also have a greater regional species pool (Oertli et al. 2002). Careful planning should be considered to ensure that cities — regardless of their geographic areas — continue to support diverse ecological bird communities.

For example, we found that the proportion of water cover within a city was critical, confirming the global importance of wetlands (Gibbs 2000, Dudgeon et al. 2006). The importance of wetlands in urban areas has also been recently recognized (Ehrenfeld 2000, Whited et al. 2000, Hettiarachchi et al. 2015, Palta et al. 2017). Even if remnant wetlands do not reside or are no longer present in a city, constructed wetlands are a plausible, and feasible achievement for cities (Ma et al. 2010, Blicharska and Johansson 2016). These often achieve many goals, including contact with nature, stormwater recycling, and benefits for biodiversity (Zedler and Leach 1998, Nassauer 2004, HANSSON et al. 2005). Even at small-scales (e.g., within urban greenspaces), the influence of water-bodies positively influences avian biodiversity (Callaghan et al. 2018a).

In addition to citywide analyses (discussed above), we also investigated within-city responses to urbanization gradients. Surprisingly, we found no evidence that the size of a city influenced how biodiversity responded to an urbanization gradient within a city (Appendix 4). Rather, we found large variation among cities in how biodiversity responded to urbanization, with some cities showing a negative response, others showing a positive response, and others showing little-to-no response (Appendix 4). These results confirm differential responses of biodiversity to urbanization within cities (Chamberlain et al. 2017, Batáry et al. 2018). One possible explanation for why we were unable to find strong patterns of biodiversity response compared with other studies could be because we used a continuous urbanization gradient (i.e., an explicit urbanization gradient), whereby the majority of other studies (Blair 1996, Blair and Launer 1997, Clergeau et al. 1998, Chace and Walsh 2006) rely on categorical characterization of habitats (e.g., an implicit urbanization gradient). By categorizing habitats, these studies assume that biodiversity responds similarly at similar levels of urbanization, and this may not be true. Importantly, though, our research differs from that of other research as we were only interested in investigating urbanization gradients *within* a city — the unit of potential management. Most research extends their analysis to investigate the urban-rural gradients to include the 'rural' habitats and/or 'natural' habitats which are usually outside of city-boundaries (Clergeau et al. 1998, Chamberlain et al. 2017). We also found little explanation for local-level biodiversity based on our predictor variables (Appendix 9). Taken together, these results suggest that the mechanistic processes shaping biodiversity responses within cities are inherently different, giving strength to the importance of understanding the local-level habitat influences and thus management within cities (Fernandez-Juricic and Jokimäki 2001, Melles et al. 2003, Chamberlain et al. 2004, Bryant 2006).

Nevertheless, understanding local-level influences of biodiversity may only be applicable up to a certain extent: we found support for the notion that there is a distinct threshold — among all cities — at which biodiversity responds particularly negatively (~ 80 radiance value from VIIRS night-time lights). Interestingly, though, this threshold is relatively rare — only 23% of cities have a maximum VIIRS night-time lights value greater than this threshold, and no cities have a mean VIIRS night-time lights above this threshold (Appendix 8). This suggests that even within cities, biodiversity can persist relatively well — up to a certain point.

Our analysis incorporated more than 1,500 cities throughout the continental United States — a much larger sample size than previous studies. For example, previous broad-scale studies have investigated a total of 41 different cities in Europe (Ferenc et al. 2014), and a recent meta-analysis was able to include 75 cities worldwide (Beninde et al. 2015). Our large sample size was made possible because of broad-scale empirical data collected by citizen scientists (Bonney et al. 2009), a particularly useful tool to understand ecological questions within residential ecosystems (Cooper et al. 2007). Citizen science data are rapidly advancing the spatial and temporal scale of questions being asked in ecology (Theobald et al. 2015, McKinley et al. 2017). We used these data to look at broad-scales and found that our models were generally well-fit relying on these data, although there may be issues of spatial-mismatch between the scale of eBird sampling and the macro-ecological predictors we used in our analysis. We provide broad-scale patterns while also highlighting opportunities for smaller-scale research questions. First, we only investigated broad biodiversity responses, and future work should aim to understand how bird species guilds and functional groupings respond among and within cities (Devictor et al. 2008, Flynn et al. 2009, Conole and Kirkpatrick 2011). Second, future work should investigate the temporal understanding of our results, investigating intra- and inter-annual changes within urban areas (Dallimer et al. 2011, La Sorte et al. 2014). We also did not look at the habitat matrix surrounding a point — for instance, corridors could be a significant driver supporting biodiversity (Savard et al. 2000) — and future work should test our results with finer-scale mapping of habitat variables. Our workflow relies on open-access data and remotely-sensed landcover maps. As increasingly fine-scaled remote-sensing data are mapped (Pasetto et al. 2018) combined with simultaneously increasing quantity and quality of citizen science data (Wood et al. 2011, Callaghan et al. 2018b), we believe our framework provides a way to understand the mechanistic patterns shaping biodiversity trends among and within cities, globally.

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Figures

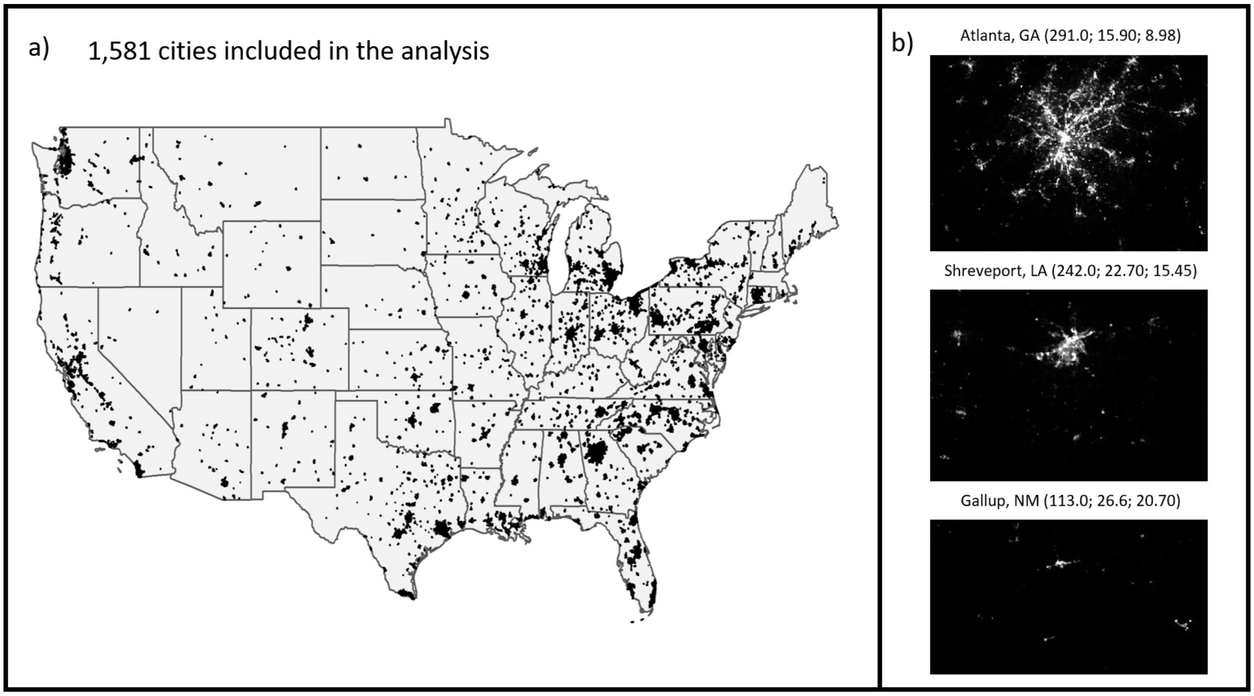

Figure 1. (a) We investigated the species richness and biodiversity variables within and among 1,581 cities throughout the continental United States. (b) Three example cities (Atlanta, Georgia; Shreveport, Louisiana; and Gallup, New Mexico) showing the visualization from space, with the city measured by VIIRS night-time lights. The max, mean, and median are shown respectively for each of these cities in parentheses after the city name. Appendix 8 further contextualizes city-wide night-time lights values.

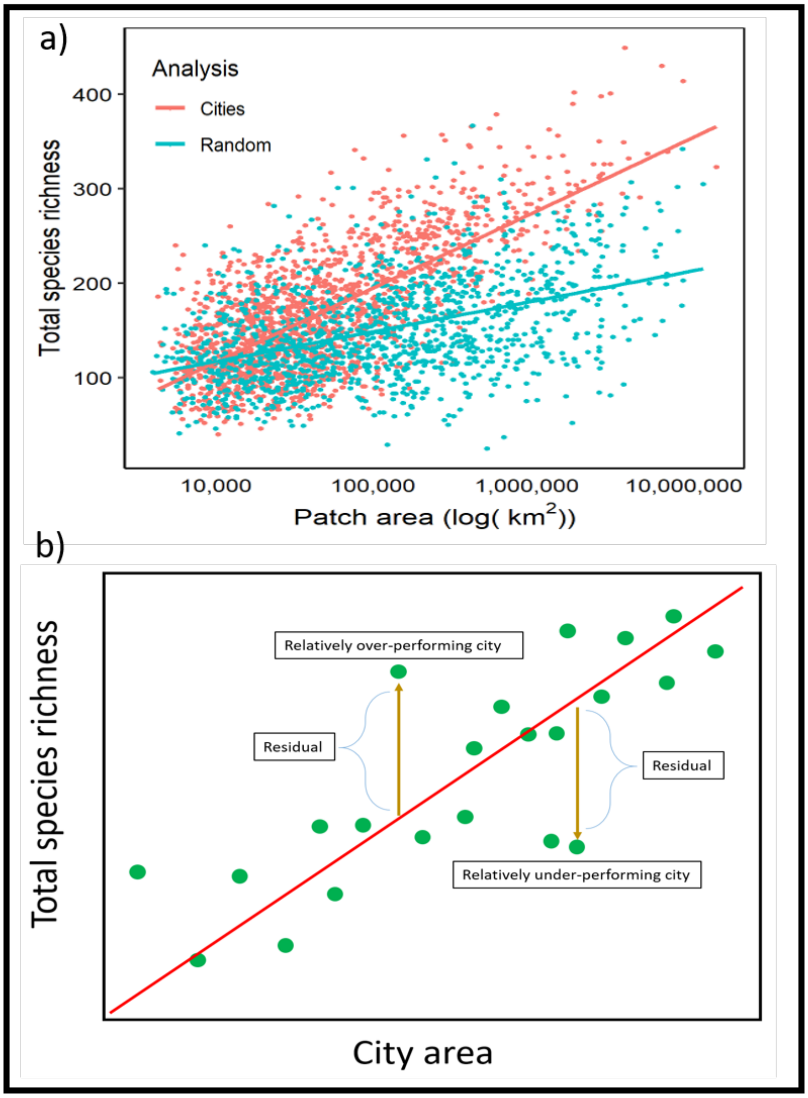

Figure 2. (a) There was a strong positive relationship (R^2=0.54) between city area and total species richness in a city (red points and line in a, above; t=43.348, df=1579, p < 0.001). This relationship was significant after accounting for the strong relationship between species richness and the total number of eBird lists (Appendix 2 & Appendix 6). There was also strong evidence (p < 0.001) that the slope of the city species-area relationship (m=29.81) was greater than that of random polygons (m=19.03) chosen from across the US; highlighting the potential value of cities for biodiversity. This relationship held after accounting for the total number of eBird checklists from each of the polygons incorporated into the analysis (Appendix 7). (b) In order to understand

which cities over-performed and under-performed based on city size, we investigated the relationship between city area and total species richness within a city by modelling the residuals, which then accounted for the significant relationship between city area and species richness. The residuals then represented cities which were ‘over-performing’ and ‘under-performing’ relative to city size.

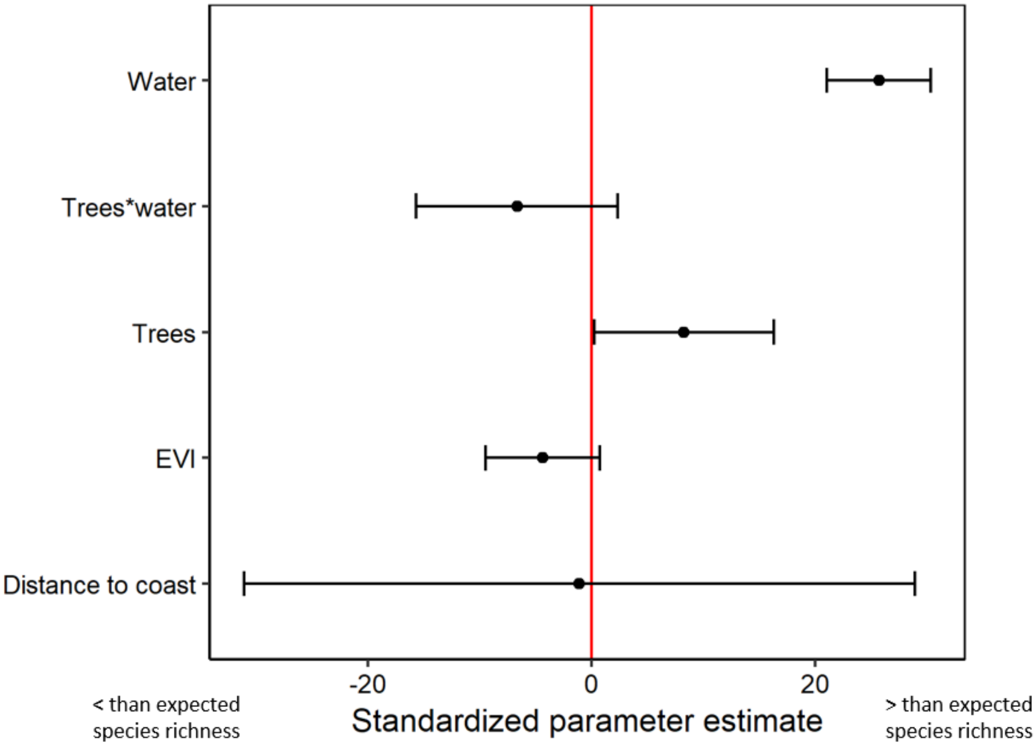

Figure 3. The standardized parameter estimates (and 95% confidence intervals) showing the relationship between residual species richness and our macroecological predictor variables. A Generalized Additive Model was used to model this relationship. Greater than the red line represents high species richness than predicted by city area alone, and less than the red line represents less species richness than predicted by city area alone.

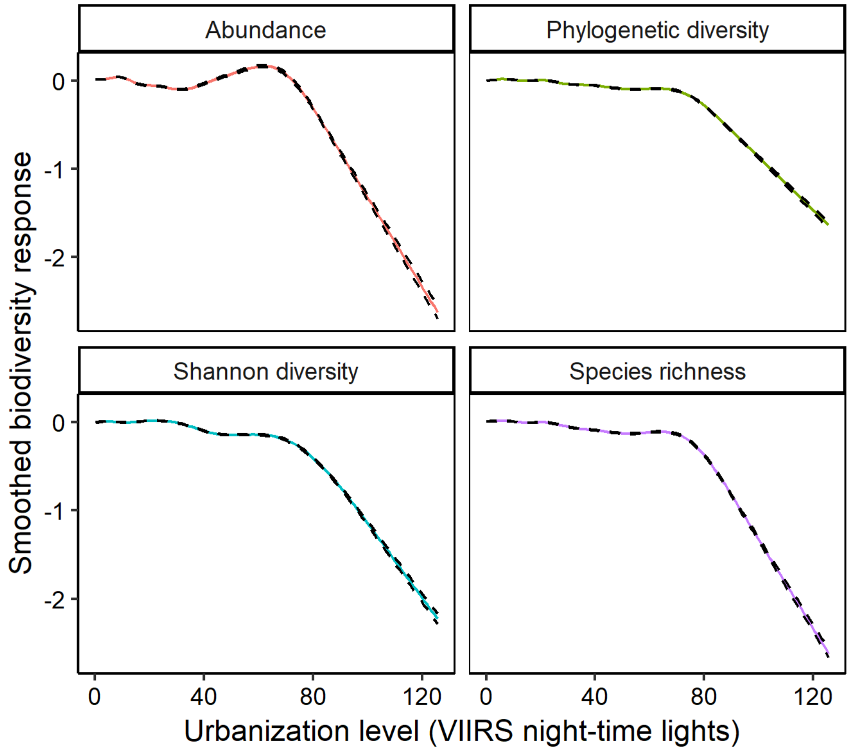

Figure 4. Smoothed response of biodiversity response variables from Generalized Additive Models (N=4), showing that a threshold exists where biodiversity significantly drops off at a local level (i.e., at the level of bird observations not a city-level), in response to urbanization. This threshold is further contextualized in Appendix 8. VIIRS night-time lights was used to represent a continuous level of urbanization and its units are: nW cm^{-2}sr^{-1}.