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A citizen science approach to evaluating US cities for biotic homogenization

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Background. Cities around the world have converged on structural and environmental characteristics that exert similar eco-evolutionary pressures on local communities. However, evaluating how urban biodiversity responds to urban intensification remains poorly understood because of the challenges in capturing the diversity of a range of taxa within and across multiple cities from different types of urbanization.

Methods. Here we utilize a growing resource—citizen science data. We analyzed 66,209 observations representing 5,209 species generated by the City Nature Challenge project on the iNaturalist platform, in conjunction with remote sensing (NLCD2011) environmental data, to test for urban homogenization at increasing levels of urban intensity across 14 metropolitan cities in the United States.

Results. Based on community composition analyses, we found that while urban homogenization occurs to an extent, urban biodiversity is often much more a reflection of the regional specificity of taxa. On the other hand, we also found that the most commonly observed species are often shared between cities and are non-endemic and/or have a distribution facilitated by humans. This study highlights the value of citizen science data in answering questions in urban ecology.

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Abstract

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Introduction

Cities around the world exist in a range of environmental contexts, yet because of the requirements and preferences of their human inhabitants, they share commonalities such as landscape fragmentation, altered water and resource availability, and high densities of fabricated structures and impervious surfaces that alter climate (Rebele, 1994). With this ecological homogenization (Groffman et al., 2014) come potential consequences on the biodiversity of the organisms that live in and around cities. Plants have been found to bloom earlier in city centers due to the urban heat island effect (Mimet et al., 2009), bird migratory patterns have shifted to take advantage of resource availability (Tryjanowski et al., 2013), and invasive species can be more prominent because of increased rates of species introductions (Tsutsui et al., 2000). While such modifications are still relatively recent on an evolutionary time scale, phenotypic changes have been observed across taxa on a global scale as eco-evolutionary consequences of urbanization (Alberti, 2015). Understanding such changes can help us to better plan for future ecological dynamics in cities, such as predicting population vulnerability to invasive species or minimizing human-wildlife conflicts, such as property damage or health hazards (ex. disease vectors).

Common ecological metrics such as species richness and abundance have shown mixed results in urban environments. A review of 105 studies on species richness along urban to rural gradients demonstrated inconsistent patterns, with some studies finding that species richness decreases with higher urban intensification, while other studies found the opposite (McKinney, 2008). Often, this greater than expected species richness can be largely attributed to non-native species (McKinney, 2008), highlighting the importance of additionally considering shifts in community composition. The commonality and spread of urban specialists has led to concerns of urban biotic homogenization, the idea that on a global scale, the biodiversity of cities show convergence and the cascading impacts this could have for conservation through reducing beta diversity (Clavel, Julliard & Devictor, 2011; Pearse et al., 2018).

A challenging aspect to measuring urban homogenization is gathering sufficient data to cover the variation in ecological communities within and between cities. Within city biodiversity levels can vary greatly by neighborhood (Sushinsky et al., 2013). To address this, cities have frequently been examined along rural to urban gradients, although this method has been criticized for its oversimplification of features and the vagueness of definitions that makes comparisons between cities difficult (McDonnell & Hahs, 2008). Broad terminology like "urban" can refer to dense downtown built-up environments, residential neighborhoods, industrial areas, or parks. Even within a single type, such as residential neighborhoods, factors such as socioeconomic demographics or landscape legacy can contribute to even more local habitat heterogeneity (Leong, Dunn & Trautwein, 2018).

One solution to capturing all this variation and exploring patterns of biodiversity across geographically disparate cities is to utilize data generated through public engagement. Broadly referred to as citizen science (although we emphasize that one need not be a citizen of any nationality to participate), this process involves public collaboration with professional scientists in ways that help our understanding of the natural world (Ballard et al., 2017). Citizen science data collection overcomes the challenges of accessing private land and can be scaled up to cover multiple cities with relative ease (Spear, Pauly & Kaiser, 2017). There are obvious challenges such as collection biases and identification quality that need to be accounted for (Isaac et al., 2014), but citizen science is a potentially valuable tool that can be used far beyond science engagement or exploring expanding species distributions.

Here we examine patterns in urban biodiversity across 14 metropolitan areas in the United States using data generated by the general public. We take a multi-scale approach to examine urban biotic homogenization both between and within cities. Specifically, we ask 1) how biodiversity is shared across cities in different regions; and 2) whether the effect of biotic homogenization gets stronger as urbanization intensifies.

Materials & Methods

The City Nature Challenge is a citizen science initiative started by the California Academy of Sciences and the Los Angeles Museum of Natural History that utilizes the iNaturalist platform to encourage users to photograph urban nature during a bioblitz in late April. For the 16 cities that participated in 2017 (San Francisco CA, Los Angeles CA, Seattle WA, Salt Lake City UT, Austin TX, Houston TX, Dallas TX, Duluth, MN, Minneapolis MN, Chicago IL, Nashville TN, Miami FL, Raleigh NC, Washington DC, New York NY, and Boston MS) we accessed all available City Nature Challenge data from for all years available. Next, we filtered all observations to include “Research Grade” only, which is defined by the iNaturalist platform as being verifiable with a photograph and having reached a species identification consensus by at least 2 users in the iNaturalist community (more details available at inaturalist.org). We further filtered these observations to only include those observations that had open and un-obscured geocoordinates (geoprivacy both by user choice and for species with a conservation status are maintained on the iNaturalist platform). Because this reduced the number of available observations, we excluded the cities of Duluth and Nashville from further analyses. The 14 included metropolitan areas (Figure 1) cover a range of geographic and environmental diversity. There were a range of number of observations between cities, highlighting the disproportionate sampling effort, with Miami having the fewest observations at 1,011 and the San Francisco Bay Area having the most at 15,733. The average number of observations of the 14 cities was 5,077 +/-3817. Differences in collecting effort are addressed in our analyses.

All data and scripts used for the following analyses can be found at https://github.com/mishoptera/cnc.

Biotic homogenization across cities

We identified which species were found in the majority of the cities to see how this widespread group compared with the total pool of observations. We also divided the dataset by major taxa: 4 plant groups (monocots, dicots, ferns, and conifers), 6 animal groups (birds, insects, reptiles, amphibians, mammals, and gastropods), and an “other” category to allow for better comparisons between similar taxa.

Biotic homogenization with increasing urban intensification

After seeing how biodiversity was shared between cities, we asked whether the biotic homogenization effect was stronger with increasing urbanization intensity. Based on geographic coordinates, we linked all observations with a NLCD2011 land cover classification from the Multi-Resolution Land Characteristics Consortium (MRLC). Assessed nationwide at a 30 x 30m resolution, every pixel is assigned one of 16 land cover classifications, four of which are forms of developed land with increasing urbanization intensity (developed-open space, developed-low intensity, developed-medium intensity, developed-high intensity; further details in Table 1). We collapsed the remaining land cover classifications into “water”, “agricultural”, and “natural”. As we were only interested in comparing increasing levels of urbanization against the natural land use type, we excluded any observations that were classified as having occurred within agricultural or water pixels.

We then analyzed the relative influence of level of urban intensification and city on community composition. We built Bray-Curtis dissimilarity matrices comparing the species composition of each level of urbanization within each city and conducted PERMANOVA (Permutational Multivariate Analysis of Variance) analyses with 999 iterations nested by city (and then also city nested by level of urbanization) (R package *vegan*, (Oksanen et al., 2015)). We visualized community composition using NMDS (Non-Metric multi-Dimensional Scaling) with 100 restarts. We applied a stress cut-off of 0.20; if stress was >0.20, we considered the NMDS plot to be unreliable.

Next, we approached biotic homogenization from an individual species level to explore whether any species benefitted from increasing urban intensity. We focused on species that had over 100 observations to prevent potential biases associated with rarity, and created two different but complementary metrics--a “City Accumulation Metric” and an “Averaged Ranking Metric”. The City Accumulation Metric (CAM) quantified the number of cities a species was found in for each of the 5 levels of increasing urbanization intensity, with the assumption that the urban specialists should accumulate a higher city count in higher intensity land cover types than the more natural land cover types which would vary greatly based on local environmental conditions. The Averaged Ranking Metric (ARM) was a way to compare species relative to similar taxa based on rank rather than using absolute number of observation comparisons to help mitigate potential biases of different levels of collecting effort between cities and between land use types. We calculated the rank of a species within its taxa group for each land cover type for each city, then all rankings within each land cover type were averaged across cities. Here, urban specialists would be expected to have a higher averaged rank in the high intensity land cover types because they should make up a larger proportion of the population than in the more surrounding natural areas. Based on these metric values, we calculated a linear model slope for each species’ City Accumulation and Averaged Ranking metrics. A positive slope for the City

Accumulation Metric indicated species were found in more cities as urban intensity increased. Similarly, the slope for the Average Ranking Metric tracks higher-placed rankings with higher urban intensity. More details for these metrics can be found in Supplementary Materials.

Results and Discussion

Biotic homogenization across cities

We analyzed 66,209 citizen science research grade iNaturalist observations across 14 US metropolitan areas. Overall, dicots, the largest plant group, were overwhelmingly the most observed (59.6%) and had the most species (52.4%). The next most observed groups were birds (12.8%), monocots (8.7%), and insects (8%). However, despite making up only 8% of the observations, insects actually made up 18.4% of the total species diversity. Birds, on the other hand, made up only 7.8% of the diversity, meaning they have a higher proportion of number of observations per species.

Of the 5,209 observed species, 100 were found in the majority (8 or more) of the cities, (Table 2) and were primarily birds and dicots (36 each), and a few mammals (7), insects (7), and reptiles (4). There was only one widespread species each for amphibians, monocots, and conifers, and no representative species for gastropods or ferns. Although only 1.9% of the total species diversity, these cosmopolitan species made up 21.4% of the total observations. Two birds, the rock dove and American crow, were the only species observed in each of the 14 cities. Ten additional species were observed in 13 cities each—7 of which were also birds (red-winged blackbird, mallard, great blue heron, turkey vulture, house sparrow, American robin, and mourning dove), but also one dicot (common dandelion), one insect (Asian lady beetle), and one mammal (common raccoon).

Taxa varied in how cosmopolitan they were as a group (here defined as being found in the majority of our cities). Mammals and birds had the highest proportions of cosmopolitan species (10.6% and 10.1% respectively). On the opposite end of the spectrum, insects and dicots had a much smaller proportion of their species observed in the majority of cities (0.83% and 1.5% respectively). Our findings that cities comprise a few cosmopolitan species with a mix of many local species complement other findings that the majority of urban species are still local species (Aronson et al., 2014).

However, these cosmopolitan species accounted for the majority of observations for mammals (55.2%) and birds (64.8%), and even made up a large proportion of observations for insects (25.3%) and dicots (15.7%). While it is possible that these patterns could also be explained by cosmopolitan species being more recognizable to people (and therefore more frequently identified, leading to an inflation in the proportion of observations for these groups), the substantial proportion of cosmopolitan species could also be indicative of a downward trend of relative abundance native species populations in cities. Previous multi-city studies of biotic homogenization have relied on species lists (Aronson et al., 2014), which can not capture shifts in community composition. With mass species declines in tropical and temperate ecosystems

(Hallmann et al., 2017; Lister & Garcia, 2018), such findings of cosmopolitan species making up such a large portion of the community relative to native species merit further investigation.

Biotic homogenization with increasing urban intensification

We next focused on the varying degrees of urban intensification within cities to explore whether the effect of biotic homogenization grows stronger the as a landscape becomes more developed. We found significant differences in community composition with varying levels of urban intensity land cover types (nested by city; Table 3) in our PERMANOVA analysis. Community composition was also influenced by city (nested by land cover types; Table 4). These patterns were consistently found in analyses that included all taxa, plants only, and animals only. Though communities varied according to land cover type and city, city generally explained more of the pattern than did land cover type.

These results, which suggest that urban biodiversity is to some degree city specific but also tied to particular levels of urbanization, become more clear when visualized in the NMDS plots. All NMDS plots showed overlap between the different levels of urbanization in an ordered way along the urbanization spectrum, in that more similar levels of urbanization also share more similar communities (Figure 2a). Plants exhibited a slightly different pattern from animals, with the plant communities observed in the highest levels of urban intensification having the greatest differentiation, opposite to the pattern that would be expected if urban homogenization were occurring (Figure 3). This contrasts with a previous study that found that across cities, cultivated yards tended to be more similar to one another compared to the similarity of their associated natural areas across cities (Pearse et al., 2018), which could be due to being unable to differentiate between cultivated and spontaneous vegetative growth observations. The iNaturalist platform discourages the recording of cultivated plants and animals, although there is an option to indicate if an observation contains a captive or cultivated species. However, of all the observations, only one record had that label--a desert willow plant outside an elementary school in a Dallas suburb.

We found that communities, regardless of level of urban intensification, within the same city were found close together on the NMDS plots—a pattern further reinforced by region (Figure 2b). For example, all three Texan metropolitan cities (Houston, Dallas, and Austin) were grouped near one another, as were the cities along the Atlantic (Boston, New York City, and Washington DC) and Pacific Coasts (Seattle, San Francisco, and Los Angeles). Miami, being more geographically isolated and environmentally distinct than the other cities was relatively far on the plot from the other cities. Such findings complement what we had found on the between cities comparison, where urban communities are largely a reflection of the local regional community, with a few cosmopolitan species. This regional clustering was found for both plants and animals. Animal communities overall were more similar between cities than plant communities, perhaps because of their mobility and ability to respond relatively quickly to land cover changes.

Because of the regional patterns we observed, we reran the community composition analyses for all taxa in a series of city triads of increasing distance. Specifically we focused on the Texas group (Houston, Dallas, and Austin), Atlantic Coast group (New York City, Boston, and Washington DC), Pacific Coast group (Seattle, Los Angeles, and San Francisco), and a fairly widespread Central United States group (Salt Lake City, Minneapolis, and Chicago). Unsurprisingly, the PERMANOVA tests showed that as environmental region became less of an explanatory factor, and importance of land cover type increased (Table 3 & Table 4). Further, the triads that covered a smaller geographic area (Texas and Atlantic coast groupings) had greater R^2 values than the more geographically spread out triads (Pacific Coast and Central United States groupings), indicating that as environmental and geographic context becomes more similar, the role of urban intensification becomes more prominent.

The communities of each level of urban intensification appeared to be ordered along increasing levels of urbanization, but the highest levels of urbanization were more distinct from the other land cover types in these regional triad-based NMDS plots (Figure 4) than was found previously. For the Atlantic and Pacific Coast cities, there appeared to be a longitudinal gradient, with the cities falling in the geographic middle (New York City and San Francisco respectively) having all of their land cover community compositions falling between the community compositions of cities that were more north and south. Further supporting our findings from the PERMANOVA analyses, the distinctness of communities from each land cover type were more evident in those triads that have cities that are geographically closer to one another. In other words, as environmental context becomes less variable, levels of urbanization become more important in defining the community composition.

We looked deeper into these patterns at the individual species level, finding that the directionality and magnitude of species' slopes for the City Aggregation and Averaged Ranking metrics generally supported one another—in that species that accumulated more cities in the higher intensity urban land cover types also tended to have higher averaged rankings in the higher intensity urban land cover types. Many species demonstrated a preferential association for either natural or high-intensity urban areas across all the cities they were found in. In general, we found that those species that favored higher intensity urban land cover tended to be non-natives, having origins in Europe, North Africa, and South Africa (ex. common dandelion, white clover, common ivy, house sparrow, rock dove, common starling). Conversely (and expectedly), those that were found to favor more natural sites are native to North America (ex. poison ivy, Virginia creeper, northern cardinal).

Among the widespread cosmopolitan species we identified in the between cities comparison, we expected there to be a preferential association for the higher intensity land use types. There were in fact several species that showed this pattern–such as the house sparrow and rock dove. However, just as many widespread species leaned toward the less disturbed natural land cover types – such as the white tail deer (Figure 5). Rather it seems there are multiple human-associated mechanisms that act at different scales. Human transportation networks, as well as agriculture and other human directed habitat shifts have facilitated species introductions and expanded species ranges, while urbanization has created unique habitats that allow particular species to thrive. While humans are a common denominator, species that benefit from range expansions do not necessarily also benefit from urbanization.

The western honey bee is an example of a species that varied greatly in which land cover type it "favored"—it was most frequently observed in the highest intensity urban land cover types in Washington DC and Los Angeles, the natural land cover types for Austin, and somewhere along the urbanization spectrum for everywhere else. The honey bee was found in every city except Minneapolis and Seattle, and was most frequently observed in the Texan and Californian cities. Pollinators, and honey bees in particular, have been shown to be sensitive to climatic differences (Gordo & Sanz, 2006; Bartomeus et al., 2011), and the varying environmental conditions between cities in April could explain why the honey bee was not found in the two northernmost cities and most abundant in the more southern ones. Further, the "snapshot" approach of the City Nature Challenge captures cities at different points in their seasonal progression, as bee abundance phenology is known to vary between land cover types (Leong et al., 2016).

Many frequently observed species are also invasive species—such as garlic mustard. While originally introduced to North America from Europe, it thrives in the forest understory (Stinson et al., 2006). It was particularly abundant in Boston, New York, and Washington D.C., where it was found across all land cover types. Because there are many ongoing efforts to control this species (Nuzzo, 1999; Blossey et al., 2001), it will be important for land managers to consider that urban landscapes could also act as reservoirs maintaining sizeable populations of this species.

Our methodology utilizes within city and land cover type community composition and ranking metrics to avoid biases based on "collecting effort." However, there remain other challenges in teasing apart patterns reflecting ecological dynamics and natural history versus artifacts associated with data collected opportunistically by members of the public that currently limit ways in which we can interpret our findings. For example, species with the most observations are often not truly the most abundant species in cities, rather they are the easiest to photograph and identify (hence, the "overrepresentation" of bird taxa). Insects and other small taxa that are more difficult to photograph and identify are almost certainly under recorded. Many species were rarely observed—2435 of the 5,209 total species included in the dataset were singleton/doubletons, meaning they were only observed once or twice. Although we can assume that most species should be relatively equally photographable and identifiable across land cover types, we recommend using multiple approaches to make comparisons "within the biases", such as focusing on community composition and nonparametric statistical methods as we have done here.

Conclusions

Our findings provide some support for biotic homogenization, although no single species was recorded in the highest level of urbanization across all cities. While we find that community composition is significantly impacted by degree of urban intensification, the role of geographic and environmental region seems to have a much larger role in determining communities. Urban biodiversity is a mix of local natural biodiversity and introduced species that are closely associated with humans. These novel “hybrid ecosystems,” with both local regional filters and the human influences of dispersal and resources are a growing reality in many parts of the world, and are continually changing with species adapting to exploit them (Kowarik, 2011). It has been suggested that cities can act as reservoirs for native biodiversity (Pearse et al., 2018). Conversely, natural areas can also be impacted by the diversity of species in the cities that they border.

Despite the complexity of urban biodiversity dynamics, this work demonstrates the power of using citizen science data in urban landscapes. The data from the City Nature Challenge provide an opportunity to look at diverse species occurrences across many cities during the same snapshot of time in a manner that has not been possible before. The opportunistic nature of citizen science data is comparable to natural history collections in many ways (Spear, Pauly & Kaiser, 2017), yet with an additional factor of being focused in urban landscapes. Further, citizen science data makes up a large proportion of GBIF data and is continuing to grow at a fast rate. There are many potential future questions to explore with this data, particularly as this dataset continues to grow and in conjunction with other large environmental datasets.

While we focused our efforts using a subset of available iNaturalist observation data from the City Nature Challenge and the levels of urbanization from the National Land Cover Database, there are many more environmental and geopolitical datasets available that can be used to explore patterns in urban biodiversity. Expanding our scope to include all iNaturalist observations and museum collection specimen data could help untangle some of the complexity that we observed. Future work can also pursue broader ecological questions such as the role of climate change on urban biodiversity, phenological shifts, city connectedness, links with socioeconomics, the historical legacies of cities, and how these patterns change over time.

Finally, beyond the value that citizen science data can provide in allowing us to ask questions that would have been impossible to previously explore, the collection of these data engages the broader public in the ecological and environmental world around them in a meaningful way. An engaged network of citizen scientists is a built-in audience for science communication, making citizen science a valuable tool to increase the relevancy of environmental research. The “mundane everyday biodiversity” in cities is now known to be an important contributor to city resident well-being and health. Concerns about the growing disconnect between city residents and nature can be combated (Schuttler et al., 2018) with increased awareness and participation in decision-making to build healthier and happier cities.

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Figure 1

Map of included City Nature Challenge cities.

The 14 cities are color grouped into five major regions: East, Midwest, South, Southwest, and West. The size of the circle markers represent the relative number of observations coming from each city. Miami had the fewest observations (1,011) and the San Francisco Bay Area had the most (15,733). The average number of observations of the 14 cities was 5,077 +/- 3,817.

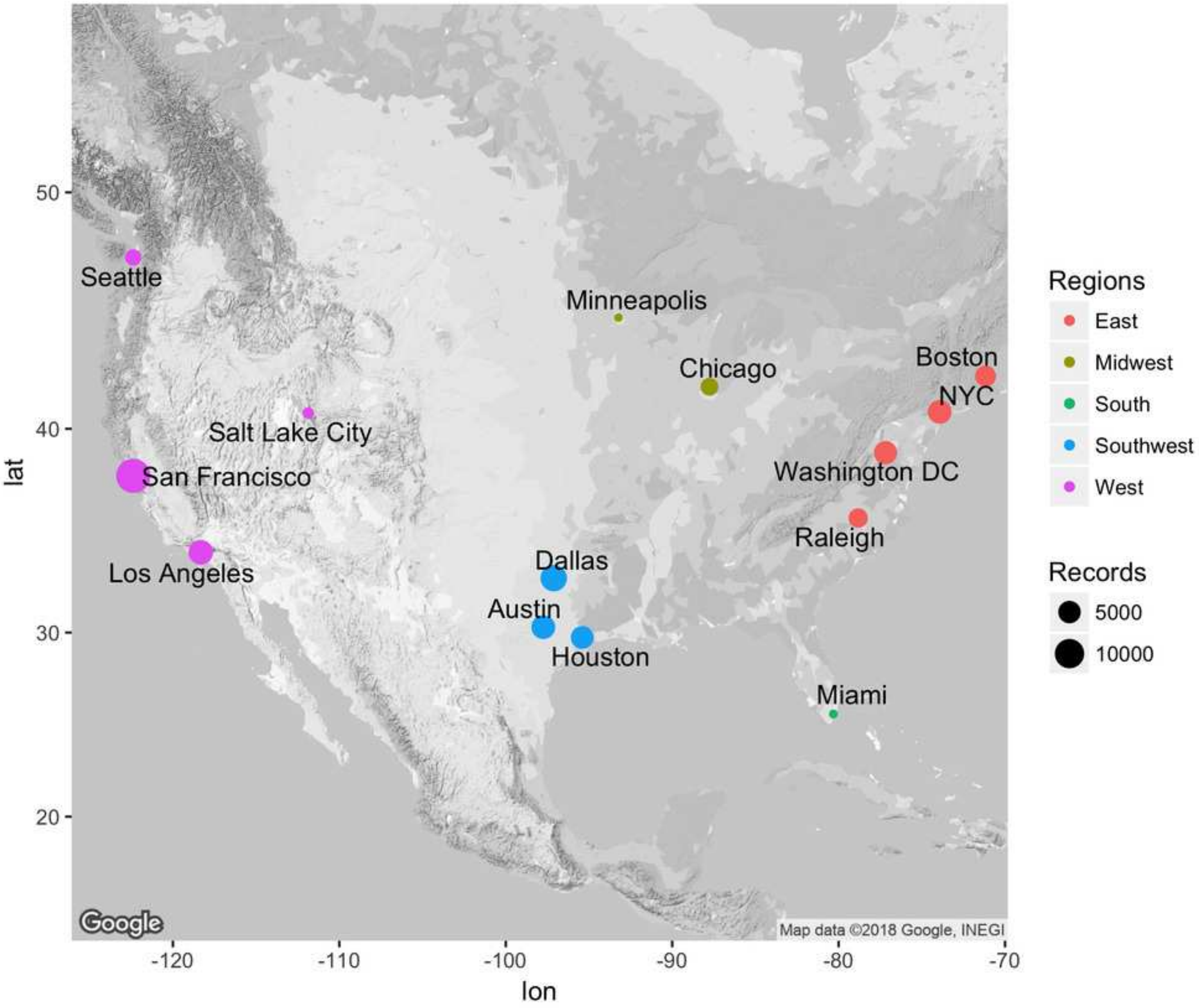


Figure 2

Community composition NMDS plots with all taxa included.

Built from a Bray-Curtis dissimilarity matrix, each point represents the community composition of a unique combination of one of the five urbanization intensity levels in one of the 14 cities. NMDS 2-D stress = 0.176. The two plots below are the same except different grouping visualizations are emphasized: in (A) points are grouped together by land cover type; in (B) points are grouped together based on city.

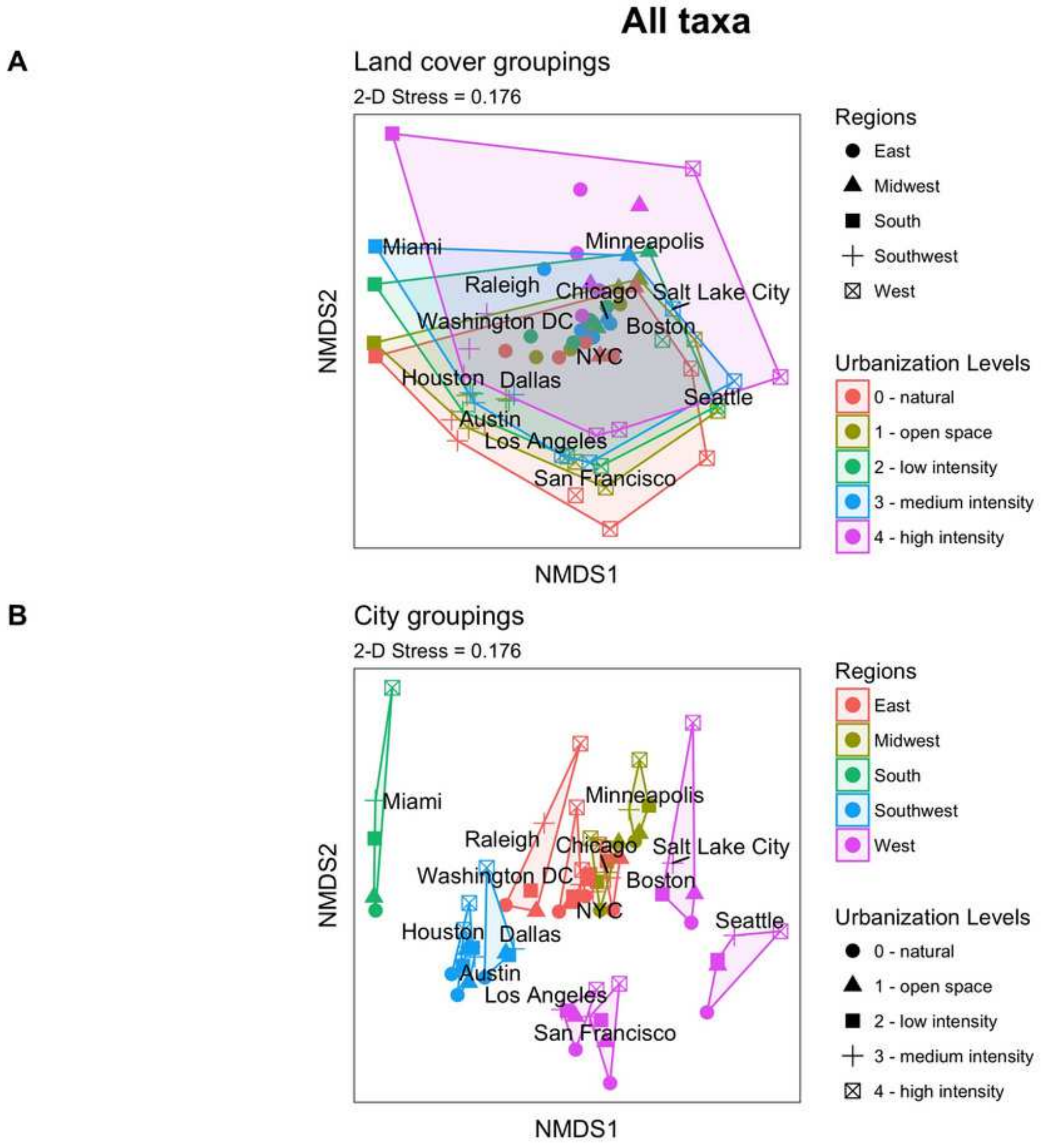
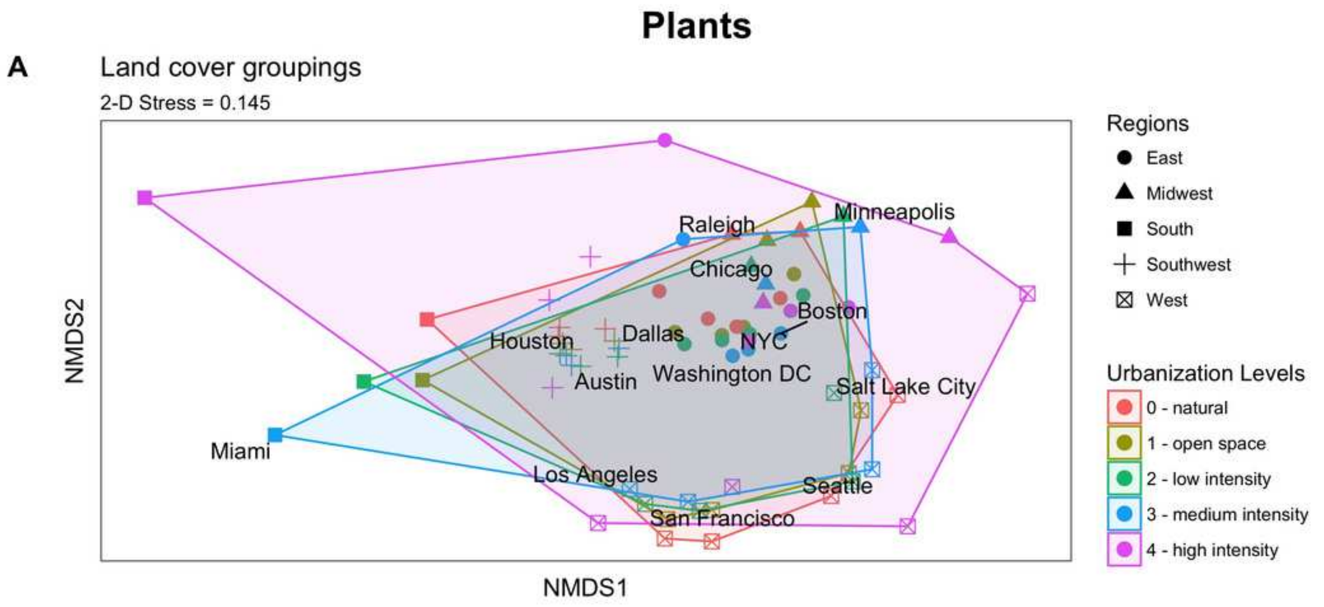


Figure 3

Community composition NMDS plots for plants only.

Built from a Bray-Curtis dissimilarity matrix, each point represents the community composition of a unique combination of one of the five urbanization intensity levels in one of the 14 cities. NMDS 2-D stress = 0.145. The two plots below are the same except different grouping visualizations are emphasized: in (A) points are grouped together by land cover type; in (B) points are grouped together based on city.



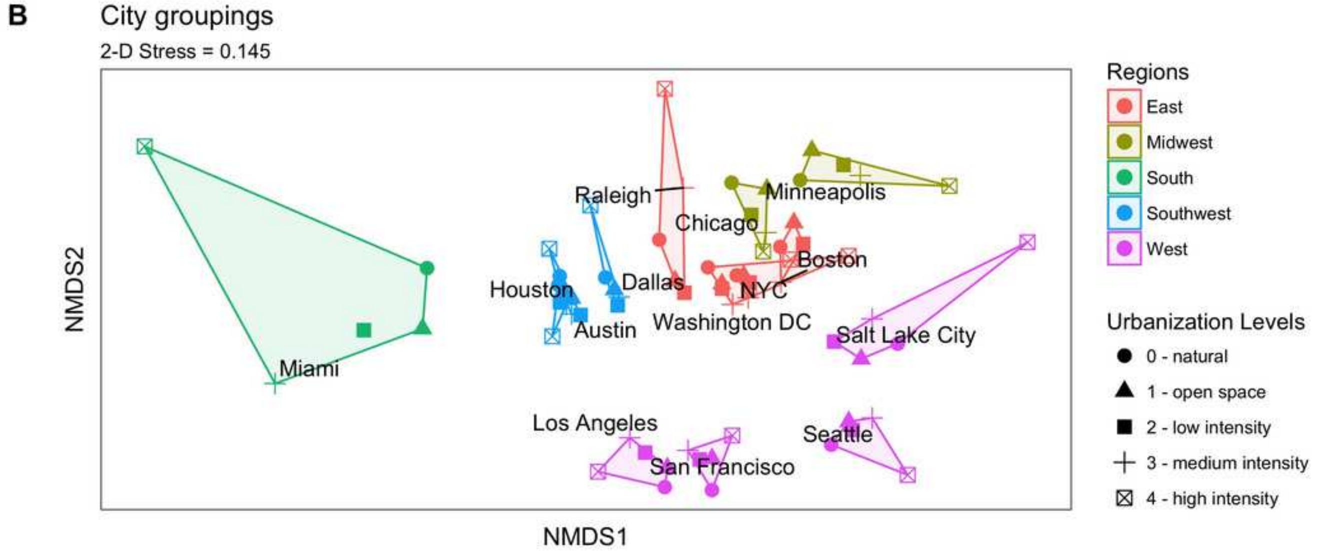


Figure 4

Community composition NMDS plots for each regional triad with all taxa included.

Built from Bray-Curtis dissimilarity matrices, each plot represents the community composition of a unique combination of one of the five urbanization intensity levels for one of the 3 focal cities for each region. Plots are in order of increasing geographic distance between cities (Texan cities are ~300 km apart, whereas the Central US cities are ~1500 km apart), and are grouped to highlight land cover type. (A) Texas (Austin, Dallas, and Houston); NMDS 2-D stress = 0.111. (B) Atlantic Coast (Boston, New York City, and Washington DC); NMDS 2-D stress = 0.0887. (C) Pacific Coast (Los Angeles, San Francisco, and Seattle); NMDS 2-D stress = 0.0367. (D) Central US (Chicago, Minneapolis, and Salt Lake City); NMDS 2-D stress = 0.0664.

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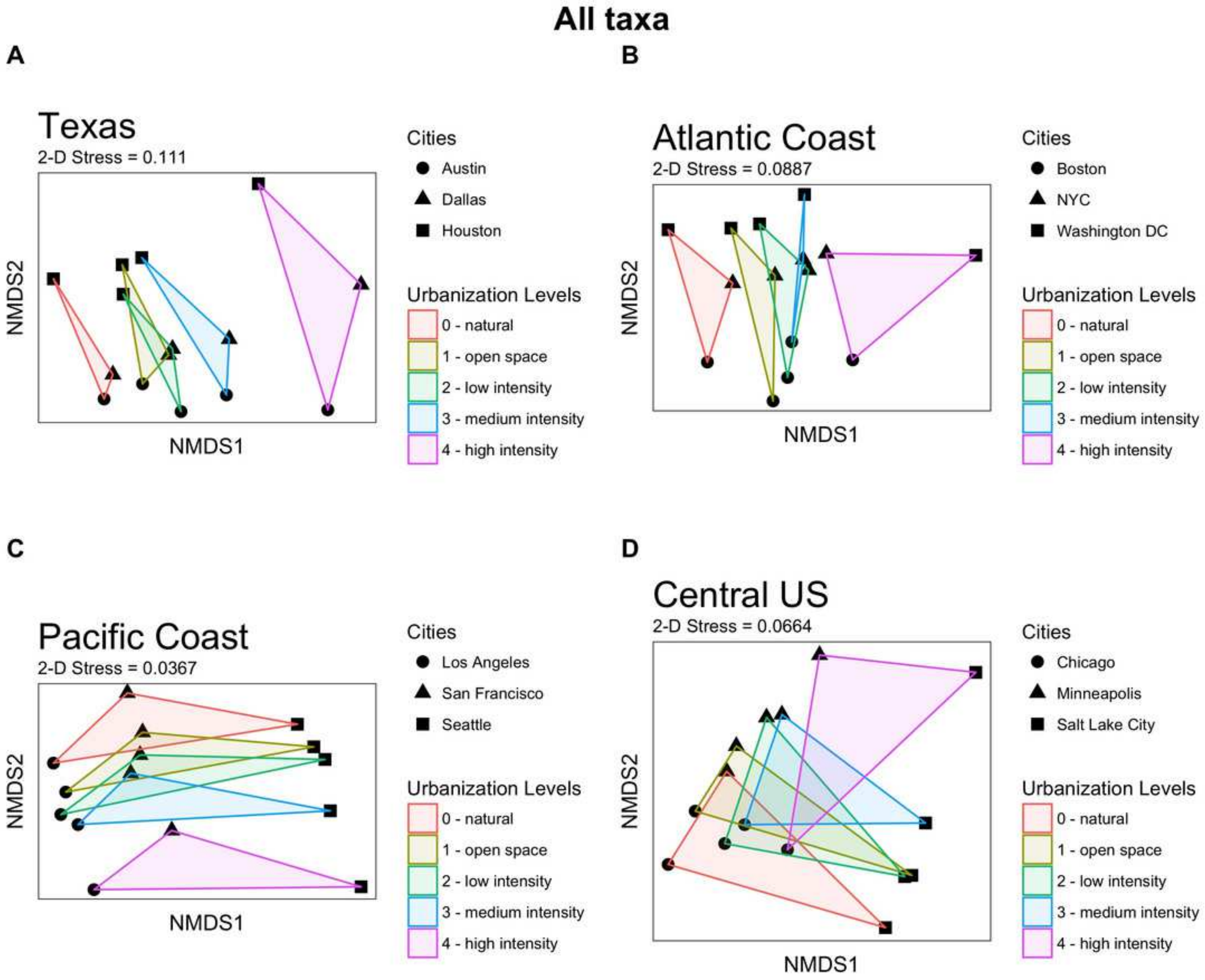
All taxa
A
Texas
2-D Stress = 0.111
NMDS2
NMDS1
Cities
Austin
Dallas
Houston
Urbanization Levels
0 - natural
1 - open space
2 - low intensity
3 - medium intensity
4 - high intensity
B
Atlantic Coast
2-D Stress = 0.0887
NMDS2
NMDS1
Cities
Boston
NYC
Washington DC
Urbanization Levels
0 - natural
1 - open space
2 - low intensity
3 - medium intensity
4 - high intensity
C
Pacific Coast
2-D Stress = 0.0367
NMDS2
NMDS1
Cities
Los Angeles
San Francisco
Seattle
Urbanization Levels
0 - natural
1 - open space
2 - low intensity
3 - medium intensity
4 - high intensity
D
Central US
2-D Stress = 0.0664
NMDS2
NMDS1
Cities
Chicago
Minneapolis
Salt Lake City
Urbanization Levels
0 - natural
1 - open space
2 - low intensity
3 - medium intensity
4 - high intensity

Figure 5

Comparison of slopes based on number of cities a species was found in.

For all species with a minimum of 100 observations, City Accumulation and Averaged Ranking metrics were calculated for each of the 5 levels of urban intensification. From these values, a linear model slope was calculated to assess the directionality and magnitude of whether a species more favored more urbanized or more natural areas. More details on the calculation of these metrics can be found in the supplementary materials. (A) City Accumulation Metric; (B) Averaged Ranking Metric. Axis is inverted to allow better comparison with (A).

Biotic homogenization with urbanization intensity

A evaluated with City Aggregation Metric

B evaluated with Averaged Ranking Metric

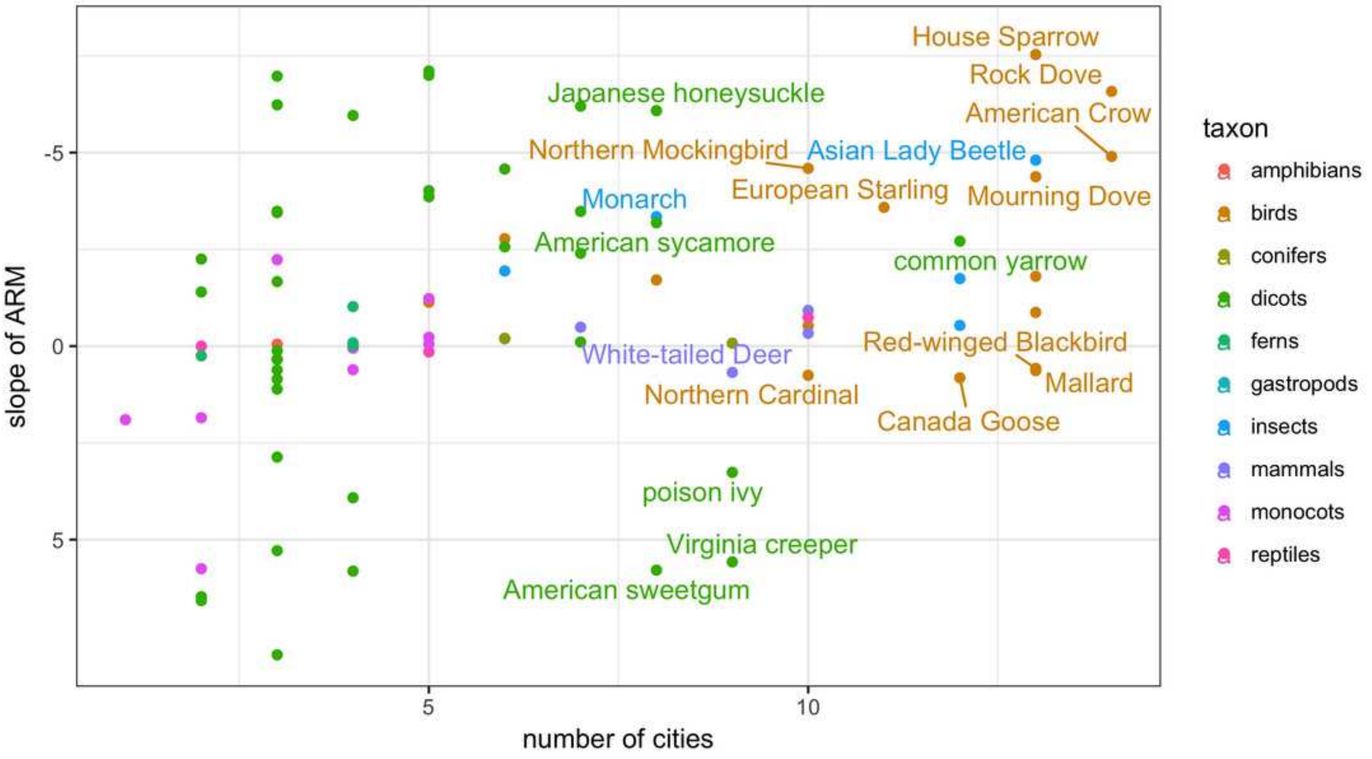

Table 1(on next page)

Urban land cover definitions table.

Descriptions of urbanization are based on MRLC’s NLCD2011 definitions (https://www.mrlc.gov/nlcd11_leg.php).

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Table 1. Urban land cover definitions table. Descriptions of urbanization are based on MRLC's NLCD2011 definitions (https://www.mrlc.gov/nlcd11_leg.php).

Code	Land Cover Type	Description
n	natural	all areas not classified as developed, agricultural, or water
d1	developed - open space	areas with a mixture of some constructed materials, but mostly vegetation in the form of lawn grasses. Impervious surfaces account for less than 20% of total cover. These areas most commonly include large-lot single-family housing units, parks, golf courses, and vegetation planted in developed settings for recreation, erosion control, or aesthetic purposes.
d2	developed - low intensity	areas with a mixture of constructed materials and vegetation. Impervious surfaces account for 20% to 49% percent of total cover. These areas most commonly include single-family housing units.
d3	developed - medium intensity	areas with a mixture of constructed materials and vegetation. Impervious surfaces account for 50% to 79% of the total cover. These areas most commonly include single-family housing units.
d4	developed - high intensity	highly developed areas where people reside or work in high numbers. Examples include apartment complexes, row houses and commercial/industrial. Impervious surfaces account for 80% to 100% of the total cover.

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Table 2 (on next page)

Taxa-based counts of species found in the majority of cities.

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Table 2. Taxa-based counts of species found in the majority of cities.

	Cosmopolitan Pool		Total Pool		Proportion Cosmopolitan	
Taxon	**num species**	**observations**	**num species**	**observations**	**num species**	**observations**
amphibians	1	81	58	725	1.72%	11.17%
birds	36	5258	355	8115	10.14%	64.79%
conifers	1	124	45	786	2.22%	15.78%
dicots	36	5696	2380	37744	1.51%	15.09%
ferns	0	0	57	869	0.00%	0.00%
gastropods	0	0	113	719	0.00%	0.00%
insects	7	1283	835	5067	0.84%	25.32%
mammals	7	938	66	1698	10.61%	55.24%
monocots	1	33	499	5527	0.20%	0.60%
reptiles	4	334	137	2123	2.92%	15.73%
other	7	430	664	2836	1.05%	15.16%
TOTALS	**100**	**14177**	**5209**	**66209**	**1.92%**	**21.41%**

Table 3(on next page)

Land cover PERMANOVA results.

We built Bray-Curtis dissimilarity matrices then conducted PERMANOVA (Permutational Multivariate Analysis of Variance) analyses with 999 iterations, nested by city. We ran tests for the entire dataset, and then for iterative subsets for each region, and for plants only and animals only.

Table 3. Land cover PERMANOVA results. We built Bray-Curtis dissimilarity matrices then conducted PERMANOVA (Permutational Multivariate Analysis of Variance) analyses with 999 iterations, nested by city. We ran tests for the entire dataset, and then for iterative subsets for each region, and for plants only and animals only.

Taxon	**Region**	**R^2**	**p**
all	All USA	0.066487768	0.001
all	Texas	0.379506898	0.001
all	Atlantic	0.31927022	0.003
all	Pacific	0.224720519	0.001
all	Central	0.249440927	0.002
plants	All USA	0.057168419	0.001
plants	Texas	0.376422835	0.002
plants	Atlantic	0.314924829	0.001
plants	Pacific	0.220314541	0.007
plants	Central	0.239500705	0.027
animals	All USA	0.077114628	0.001
animals	Texas	0.381789046	0.001
animals	Atlantic	0.317510181	0.006
animals	Pacific	0.22008025	0.014
animals	Central	0.292432443	0.007

Table 4(on next page)

City PERMANOVA results.

We built Bray-Curtis dissimilarity matrices then conducted PERMANOVA (Permutational Multivariate Analysis of Variance) analyses with 999 iterations, nested by land cover type. We ran tests for the entire dataset, and then for iterative subsets for each region, and for plants only and animals only.

Table 4. City PERMANOVA results. We built Bray-Curtis dissimilarity matrices then conducted PERMANOVA (Permutational Multivariate Analysis of Variance) analyses with 999 iterations, nested by land cover type. We ran tests for the entire dataset, and then for iterative subsets for each region, and for plants only and animals only.

Taxon	Region	R^2	p
all	All USA	0.536624661	0.001
all	Texas	0.29115619	0.001
all	Atlantic	0.352870122	0.002
all	Pacific	0.428061973	0.001
all	Central	0.378168123	0.001
plants	All USA	0.536412422	0.001
plants	Texas	0.299323329	0.002
plants	Atlantic	0.367002976	0.001
plants	Pacific	0.415719503	0.002
plants	Central	0.387824797	0.002
animals	All USA	0.522510275	0.001
animals	Texas	0.273142782	0.001
animals	Atlantic	0.337557222	0.003
animals	Pacific	0.425446902	0.002
animals	Central	0.309673791	0.001

7

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