Homogenizing effects of cities on North American winter bird diversity

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Abstract. Urbanization is widespread throughout the United States and Canada. Studies at different scales have shown mixed consequences of urban areas for ecological communities and biodiversity. Here, we use geographic data on urban extent and survey data from the Christmas Bird Count to investigate the influence of urbanization on winter bird diversity over a continental scale. We compared the alpha (local richness) and beta diversity (turnover with distance) of 42 urban bird communities to nearby non-urban communities. We investigated the processes underlying beta diversity between non-urban and urban sites by comparing the frequency of occurrence in species and variability in relative abundances across sites. Alpha diversity was statistically indistinguishable between urban and non-urban sites when controlling for latitude. Community similarity decreased less rapidly over distance in urban compared to non-urban sites, indicating that spatial homogenization from urbanization results in lower beta diversity. Eighteen species of non-native or native generalists occurred across all urban sites, whereas no species occurred in all non-urban sites. Mean-variance scaling of relative abundance shows that species in urban sites maintained similar levels of community dominance across space compared to non-urban sites. The widespread presence of urban species is likely due to similarity in habitats among cities compared to nearby non-urban sites. The decreased variability in relative abundance of urban species is possibly due to urban resource subsidies (e.g., bird feeders, garbage, and irrigation) and shelter (e.g., landscaping, buildings, and microclimates). The increased occurrence of widespread species in cities and less variation in relative abundances across urban sites contribute to the homogenizing effect of cities on avian communities.

Key words: alpha diversity; beta diversity; Christmas Bird Count; cities; citizen science; community similarity; distance-decay; macroecology; species richness; Taylor’s power law; urban ecology.

INTRODUCTION

Cities are a prominent presence on North American landscapes. The consequences of urbanization for ecological communities and biodiversity are unclear. On the one hand, the destruction of natural habitats due to urban development can have negative impacts on native species (Czech et al. 2000). Urban cores, for example, have lower bird diversity than surrounding natural areas as native species are replaced by few, often non-native, species that are associated with humans (Marzluff 2005). Urban cores, however, make up only a small fraction of the total urban extent. Urban areas are
comprised of a patchwork of human-dominated habitats ranging from buildings and roads to parks and suburban residential areas. On the other hand, such heterogeneous landscapes may favor certain species and promote local diversity (e.g., Smith 2003, Atchison and Rodewald 2006). Indeed, at intermediate to large spatial scales, species richness increases with human population density, in part because non-native species are added to the local species pool (Sax and Gaines 2003, Pautasso 2007). So the overall effects of urbanization on bird communities are complicated, and differences in scale and methodology between studies have likely contributed to mixed results (Pautasso 2007).

Over larger spatial scales, the environmental conditions of urban landscapes may be more similar to each other than to adjacent natural landscapes (Groffman et al. 2014), likely supporting similar species. In addition, high human densities may be associated with greater concentrations of resources that are similar across space and stable through time. These resources, such as food, water, and shelter, could provide a buffer against environmental conditions and support similar species at similar abundances irrespective of geographical location. In fact, food subsidies have been shown to increase the abundance of urban specialists (McKinney 2002). In the temperate zone, resource subsidies should be especially important during winter, when food is often scarce and energy demands for thermoregulation are high due to cold temperatures (Root 1988).

Here, we use geographic land cover data and surveys from the Christmas Bird Count (CBC) to understand the effects of urban areas on bird diversity across North America. We use the CBC instead of other inventories (e.g., Breeding Bird Survey and e-bird) to specifically gain insights into the role urban areas play in buffering species from winter conditions. We investigated how land alteration processes affect local species richness (alpha diversity), and species turnover (beta diversity) between urban and non-urban winter bird communities. Due to the heterogeneity of urban habitats, we expected urban sites to have higher alpha diversity than non-urban sites (Prediction 1). Due to similarity in landscape features and resource availability across urban sites, we expected beta diversity to be lower across urban relative to non-urban sites (Prediction 2). To understand the processes contributing to the spatial pattern in beta diversity, we investigated the frequency of species occurrences across urban and non-urban sites. Because of the similarity in habitats across urban sites, we expected to see the widespread occurrence of some non-native and native generalists across urban areas (Prediction 3). If the greater and more stable resources facilitated by cities provide a buffer that favors particular species against environmental uncertainty, then we would expect to see lower variation in relative abundances across urban sites compared to non-urban sites (Prediction 4).

**Methods**

**Data**

We used winter distributions and abundances of North American birds from the Christmas Bird Count (National Audubon Society 2010). The CBC, which began in the winter of 1900–1901, is a standardized survey conducted annually from mid-December to early January at thousands of locations throughout the Americas. Although the CBC has over a century of survey records, we only used data from the time period corresponding to the available data on urban land cover (see below). Each CBC survey is conducted within a 24 km-diameter circle. Volunteer citizen scientists count all individuals seen or heard within the count circle over a 24-h period. As the number of participating volunteers is variable between locations and years, the unit of party hours is used to account for survey effort. The number of party hours for a survey is calculated by multiplying the number of volunteers present by the number of hours each participated in the survey (National Audubon Society 2010).

We included data from CBC routes based on the following criteria: the route was: (1) geographically located between 30° N and 55° N; (2) surveyed every year from 2001 to 2005 to reduce the effect of temporal variations and anomalous years; and (3) surveyed for at least 50 party hours (averaged over the 5 yr) to exclude non-urban sites with inadequate sampling effort compared to urban sites (see Appendix A, Fig. A1 for a histogram of party hours for urban and non-urban sites fulfilling these criteria).

We determined the primary land cover type for each CBC route using GIS data on urban
extent at a 500 m$^2$ cell resolution from 2001 MODIS satellite data (Schneider et al. 2009, 2010). In this data set, urban cells were defined as having greater than 50% non-vegetative, human constructed elements (e.g., roads, buildings, and runways). We only included routes that were primarily urban or “non-urban” (defined below) in our analysis to reduce the effects of urban-agriculture-wilderness heterogeneity. Sites were considered urban if the CBC survey circle was composed of at least 60% urban land cover (42 sites). A site was defined as non-urban if less than 10% of the count circle was covered by agricultural or urban areas (136 sites), although these areas are not necessarily free from human disturbance. Of 136 non-urban sites, we selected the 42 that were closest to each urban site (without replacement) to maintain equal sample sizes and similar geographic distributions between the two land cover types (see map and histogram of distances between urban and non-urban site pairs in Appendix B, Figs. B1 and B2). Water bodies larger than 500 m$^2$ were excluded when calculating land cover percentages.

**Analysis**

Alpha diversity at each site was determined using local species richness, averaged over the 5 yr time period. As latitude is known to be a strong predictor of species richness (Pianka 1966), we compared linear regressions of richness against latitude between urban and non-urban sites. A difference in $y$-intercepts would indicate a difference in alpha diversity independent of latitude. Differences in slopes would show that species richness changes over latitude at different rates between urban and non-urban sites. Significant differences were determined by calculating the 95% confidence intervals for each value (slope and $y$-intercept). Non-overlapping confidence intervals indicate that urban and non-urban categories are significantly different at the 0.05 level.

Differences in beta diversity were determined by comparing the rate of decay in community similarity over distance between urban and non-urban sites (Nekola and White 1999). Community similarity was calculated using the Horn index of overlap, averaged over the 5 yr period, which incorporates both species composition and relative abundances and does not disproportionately favor rare or common species (Jost 2007). A value of zero means that the communities are completely dissimilar and a value of one indicates that the two communities are identical.

We calculated community similarity for all pairwise comparisons of sites (a total of 861 urban and non-urban site comparisons). We then plotted the pairwise comparisons of community similarity against distances between sites. Since the decay of community similarity over distance follows an exponential function (Nekola and White 1999), we compared the slopes from regressions of log-transformed similarity and distance. A difference in slopes would indicate a difference in beta diversity between urban and non-urban sites. Again, 95% confidence intervals were used to determine significance at the 0.05 level.

Two components contribute to beta diversity: how species are shared across communities and how uniform each species’ relative abundance is across communities. We investigated the influence of both factors in determining differences in beta diversity between urban and non-urban sites. First, we calculated the percent of non-urban and urban sites in which each species occurred. To remove the effect of vagrants and other anomalous occurrences, we only included sites where a species occurred at least two out of the five years. Plotting the percent occurrence against species rank allowed us to qualitatively assess differences between urban and non-urban sites. We also identified species with the greatest difference between urban and non-urban occurrences.

Mean–variance scaling relationships were evaluated to compare how stable relative abundances were across urban vs. non-urban sites. We plotted log-transformed variance in relative abundance of each species against log-transformed average relative abundance across all sites (Taylor 1961). A difference in $y$-intercept would indicate a difference in variation in species relative abundances across urban sites, with less variation indicating that species have similar dominance across communities, irrespective of geographic location. Confidence intervals at 95% were used to determine significant differences in $y$-intercept at the 0.05 level.
results

Alpha diversity
Species richness decreased at similar rates over latitude in urban (slope = −5.5, 95% CI = [−7.3, −3.7]) and non-urban sites (slope = −5.3, 95% CI = [−6.6, −4.0]) (Fig. 1). Species richness in urban sites (y-int. = 316.7, 95% CI = [244.0, 389.3]) tended to be higher across latitudes than non-urban sites (y-int. = 287.3, 95% CI = [234.3, 340.2]), but the difference was not significant as indicated by overlapping confidence intervals (Fig. 1).

Beta diversity
Community similarity decayed over distance more quickly in non-urban sites (slope = −0.51, 95% CI = [−0.58, −0.44]) than in urban sites (slope = −0.16, 95% CI = [−0.20, −0.13]), indicating lower beta diversity across urban communities (Fig. 2). Eighteen species occurred across all 42 urban sites for at least 2 yr of the 5 yr time period. No species were found across all non-urban sites (Table 1; see full species lists in Appendix C, Tables C1 and C2). Frequency of occurrence was greater in urban sites across all ranks except for the rarest species (Fig. 3). There were some notable characteristics among the species that had the greatest difference in occurrences between non-urban and urban sites. The species that occurred more often in urban locations tended to be aquatic species, whereas those occurring more often in non-urban sites had variable habitat requirements (Table 2; see Appendix D, Table D1).

Variance in relative abundance scaled similarly with mean relative abundance across urban (slope = 1.78, 95% CI = [1.76, 1.81]) and non-urban sites (slope = 1.79, 95% CI = [1.76, 1.81]). However, variance was significantly lower across urban sites (y-int. = 0.06, 95% CI = [−0.05, 0.17]) than non-urban sites (y-int. = 0.29, 95% CI = [0.18, 0.39]) for a given relative abundance (Fig. 4).

Discussion
Urbanization had an effect on beta but not alpha diversity of North American winter bird communities. Contrary to Prediction 1, urban and non-urban sites had similar avian richness (alpha diversity) after controlling for latitude. Previous
studies investigating the effects of urbanization on species richness have produced mixed results. Most small scale studies along urban–rural gradients have shown that avian diversity decreases with increasing settlement (reviewed by Marzluff 2001). This has been documented across many taxa, including mammals, herptiles and various invertebrates (reviewed by McKinney 2008). However, other studies along urban–rural gradients have shown a peak in avian diversity in areas of low human settlement, including urban-fringe zones where forest fragments or riparian corridors are present (e.g., Smith 2003, Hansen et al. 2005, Atchison and Rodewald 2006). This disparity in diversity patterns at smaller scales may be due to differences in how urban–rural gradients are delineated in each study, as well as geographical location, pre-existing ecological features, and the unique historical and economic circumstances of each city (McKinney 2008). At intermediate to large spatial scales studies have found that species richness increases with increasing human population density (e.g., Sax and Gaines 2003). In our study, the standardized shape and area of the CBC survey sites differ from most urban gradient studies. Furthermore, we only tested two antipodal land use types, “non-urban” and “urban,” rather than including varying levels of disturbance along the latitudinal gradient. So, the scale of CBC survey areas, the types of sites we selected, and the varied

| Urban          | f   | Non-urban | f      |
|----------------|-----|-----------|--------|
| Dark-eyed Junco| 1   | Dark-eyed Junco | 0.976  |
| Downy Woodpecker | 1  | Downy Woodpecker | 0.952  |
| European Starling| 1  | European Starling | 0.952  |
| House Sparrow  | 1   | House Sparrow | 0.952  |
| Northern Flicker| 1  | Hairy Woodpecker | 0.929  |
| Rock Pigeon    | 1   | Rock Pigeon   | 0.905  |
| Ring-billed Gull| 1  | Mourning Dove  | 0.905  |
| American Goldfinch | 1 | American Goldfinch | 0.905  |
| Mallard        | 1   | Mallard      | 0.857  |
| Red-tailed Hawk| 1   | Red-tailed Hawk | 0.857  |
| American Crow  | 1   | American Crow | 0.857  |
| Canada Goose   | 1   | White-breasted Nuthatch | 0.857  |
| Sharp-shinned Hawk | 1 | Brown Creeper  | 0.857  |
| Cedar Waxwing  | 1   | Golden-crowned Kinglet | 0.833  |
| American Robin | 1   | American Robin | 0.833  |
| Belted Kingfisher| 1 | Song Sparrow   | 0.833  |
| **House Finch**  | 1  | **House Finch** | 0.810  |
| Cooper’s Hawk  | 1   | Blue Jay     | 0.786  |

Notes: † House Finches, though native to western North America, were introduced to the east coast in the 1940s and as a result are non-native throughout much of their current range (Able and Belthoff 1998).

All 18 urban species were present throughout all urban sites (f = 1). Non-native species, highlighted in bold, were widespread across both urban and non-urban sites. See Appendix C for full species lists.
locations and biomes of our sites may have influenced our results of no differences in alpha diversity between urban and non-urban sites after controlling for latitude.

The rate of species turnover (beta diversity) was significantly lower across urban sites than non-urban sites, supporting Prediction 2. Community similarity decayed less rapidly with distance across urban areas, a trend that has been qualitatively shown in both birds and plants (McKinney 2006). Community similarity was consistently higher in urban sites, while non-urban sites showed a great deal of variation. This may be explained by the wide range of habitats that span our non-urban sites. For example, species composition turns over more quickly across montane areas (Melo et al. 2009) than in more homogenous landscapes such as northern forests.

We found that the decrease in beta diversity in urban sites was due to: (1) the widespread occurrence of some non-native and native generalists; and (2) lower variance in relative abundances across urban areas.

Eighteen species occurred across all 42 urban sites and no species were found across all non-urban sites, supporting Prediction 3. However, many of the same species were widespread across both urban and non-urban sites. The frequency of species in non-urban areas dropped off quickly with rank compared to urban sites. For example, the 18th most widespread species was present in 79% of non-urban sites, whereas in urban sites...

**Table 2. Twenty avian species with the greatest difference between urban and non-urban occurrences.**

| Urban Difference in occurrence | Non-urban Difference in occurrence |
|--------------------------------|-------------------------------------|
| Peregrine Falcon 0.667         | Common Raven 0.5                    |
| Canvasback 0.548               | Ruffed Grouse 0.452                 |
| Gadwall 0.524                  | Evening Grosbeak 0.429              |
| Double-crested Cormorant 0.524 | Pileated Woodpecker 0.381           |
| Lesser Scaup 0.476             | Wild Turkey 0.310                   |
| American Coot 0.452            | Pine Siskin 0.310                   |
| Snow Goose 0.452               | Golden Eagle 0.286                  |
| Black-crowned Night-Heron 0.452| Barred Owl 0.286                    |
| American Wigeon 0.452          | Common Redpoll 0.262                 |
| American Kestrel 0.452         | Red Crossbill 0.214                 |
| Wood Duck 0.429                | White-winged Crossbill 0.214        |
| Ring-billed Gull 0.429          | Pine Grosbeak 0.167                  |
| Mute Swan 0.405                | Northern Shrike 0.167               |
| Northern Shoveler 0.381         | Boreal Chickadee 0.143              |
| Green-winged Teal 0.381         | Gray Jay 0.143                      |
| Northern Harrier 0.381          | Prairie Falcon 0.143                 |
| Bufflehead 0.357               | Northern Goshawk 0.143              |
| Orange-crowned Warbler 0.357    | Townsend’s Solitaire 0.143          |
| Bonaparte’s Gull 0.357          | Mountain Quail 0.119                |
| Ring-necked Duck 0.357          | Northern Bobwhite 0.119             |

Notes: The “Urban” column lists the species that occurred more often in urban than non-urban areas, with the difference in frequency to the right (e.g., Peregrine Falcons occurred in 67% more urban sites than non-urban sites). The “Non-urban” column lists the top twenty species that occurred more often in non-urban than urban areas, with the difference in frequency between sites to the right. Non-native species are highlighted in bold. See Appendix D for full species list.
the frequency did not drop to 79% until the 45th most widespread species. This is apparent in the shape of the two rank-frequency curves. The frequency of occurrence for a given rank is always higher in urban areas with the exception of the rarest species. This indicates that the most widespread urban species occur across a larger portion of urban avian communities than the most widespread species in non-urban communities.

While many non-native species often associated with cities were found across all urban sites, the same species were also frequent in non-urban sites. Indeed, three of the eight species that were present in more than 90% of all non-urban sites were non-native species (Table 1). However, the sites we consider “non-urban” may have been modified by humans in some fashion that is not captured by our criteria, such as roads or logging. These modifications could also facilitate the establishment of non-native species.

The species that were widespread in urban areas but not in non-urban areas were mostly ducks and other aquatic species with the sole non-native species being Cygnus olor (Mute Swan) (Table 2, see Table D1). This is likely because cities are generally near natural or artificial water bodies, such as lakes, ponds, rivers, and ditches. Furthermore, supplemental feeding of waterbirds by humans and the reduction in natural predators may outweigh the negative effects of human disturbances on urban birds. For example, some waterbirds display a greater degree of habituation to areas with high levels of human development, preferring developed shorelines for activities such as resting and foraging (Traut and Hostetler 2003). The species that were more widespread in non-urban than urban areas have variable habitat requirements (e.g., forests, grasslands), but in general require large tracts of intact habitat. The species that were found only in urban areas and not in any non-urban sites (52 species total) were primarily vagrants and non-natives. The bird species that were only present in non-urban areas (49 species) also had variable habitat requirements, although many of them are habitat-specific (see Appendix C for full species lists).

The widespread occurrence of many species in urban environments is likely due to the similarity of landscape features across urban areas. As human-dominated landscapes are often more similar to each other than to adjacent undeveloped lands (Sukopp and Werner 1982), bird communities among cities have been found to be more similar than the bird communities found in adjacent natural areas (Blair 2001). The development of urban areas can cause the extirpation of native species if they are unable to adapt to these novel habitats (Czech et al. 2000). Sure enough, many studies along urban gradients have shown a decline in native bird species richness as urban activity intensifies (reviewed by McKinney 2006). However, many invasive bird species such as Sturnus vulgaris (European Starling), Passer domesticus (House Sparrow), and Columba livia (Rock Pigeon) are well adapted to urban environments. The extirpation of native species coupled with invasion by native and non-native generalists probably contributes to the decreased beta diversity we observed across urban areas.

Reduced variation in avian relative abundances across urban areas also contributed to these patterns in beta diversity, supporting Prediction 4. This could be due to similar rates of resource supply in cities compared to surrounding non-urban areas. A stable influx of resources in cities, such as food, water, heat and/or shelter, could provide a buffer against abiotic environmental uncertainty, such as water limitations in arid regions and extreme seasonality at higher latitudes. For example, several bird species have expanded their northern winter ranges due to the presence of bird feeders (Root 1988). Other subsidized food sources such as garbage and cultivated plants have been found to increase the abundance of urban exploiters (McKinney 2002). Thermal constraints are also a relevant factor for wintering birds. Microclimates have been shown to be important for reducing the energetic demands of small birds in winter (e.g., Wachob 1996). Urban ecosystems (i.e., urban heat islands) can be on average 2 °C warmer than surrounding areas due to reduced albedo and vegetation cover (Taha 1997). This allows for the presence of certain waterbirds during winter at higher latitudes by generating ice-free conditions on urban waterbodies (Adams 1994). Species best able to take advantage of these resources should be dominant in urban areas irrespective of geographic location, as shown by Jokimaki et al. (1996) in Finland.

Our results are for winter bird communities; the effects of urbanization on breeding bird communities may differ. The addition of summer migrants could change the direction or the magnitude of
our patterns depending on their ability to use urban areas for breeding. Breeding migrants rely on the summer resource pulse that occurs in temperate habitats (Fristoe 2015). If the difference in productivity between summer and winter is reduced by resource subsidies in urban areas, migrants may have fewer opportunities to breed in cities. In addition, migrants may be more sensitive to urban noise (Francis et al. 2011). Indeed, studies have shown that cities favor residents over migrants (reviewed by Chace and Walsh 2006).

Urbanization is widespread and growing. There is a need to develop a predictable science of how urban areas impact biodiversity. Here, we show how fundamental macroecological patterns of diversity can be useful tools to understand and anticipate large-scale environmental change. Our analysis reveals that urbanization results in lower beta diversity of winter bird communities across North America. This is driven by two processes: (1) increases in the occurrence of widespread species in cities; and (2) less variation in relative abundances across urban sites. These factors contribute to the homogenizing effect of urban areas on avian communities, and likely lead to similar consequences on other continents (Clergeau et al. 2006). Many of the non-natives and native generalists that occurred throughout urban sites were also widespread in non-urban sites, so understanding the processes that underlie the extended effects of cities on biodiversity in non-urban areas is warranted.

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Supporting Information
Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1216/supinfo