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Phylogenetic homogenization of bee communities across ecoregions

Tina Harrison¹  | Jason Gibbs² | Rachael Winfree¹

¹Department of Ecology, Evolution, & Natural Resources, Rutgers University, New Brunswick, New Jersey

²Department of Entomology, University of Manitoba, Winnipeg, Manitoba, Canada

Correspondence

Tina Harrison, Department of Ecology, Evolution, & Natural Resources, Rutgers University, New Brunswick, NJ 08901, USA.
Email: tinaharrison09@gmail.com

Abstract

Aim: Land use change reorganizes local communities, resulting in complex changes in biodiversity at larger scales. The biotic homogenization hypothesis predicts that the replacement of sensitive loser species with widespread winner species will lead to loss of beta diversity and ultimately loss of regional diversity at multiple levels of ecological organization. We ask if land use is associated with biotic homogenization patterns in bee communities at two large spatial scales, using both species and phylogenetic dissimilarity indices.

Location: North-eastern USA (New Jersey, New York and Pennsylvania).

Time period: 2013–2015.

Major taxa studied: Superfamily Apoidea (bees).

Methods: We sampled bee communities from replicated sites in forest, agriculture and urban land use types within a large spatial extent spanning four distinct ecoregions. We compared pairwise compositional dissimilarity within and between ecoregions, using both species and phylogenetic dissimilarity indices. We also investigated how compositional difference is related to geographic distance between sites.

Results: Forested, agricultural and urban landscapes did not differ detectably in either mean pairwise species dissimilarity or slope of distance-decay. Dissimilarity among both agricultural and urban bee communities increased with geographic distance. However, urban landscapes had significantly lower phylogenetic pairwise dissimilarity, indicating strong phylogenetic homogenization at within- and between-ecoregion scales.

Main conclusions: We did not detect bee species homogenization in agricultural or urban land use types. However, urban land use was associated with phylogenetic homogenization across a large regional extent. Urban bee communities are dominated by closely related species that maintain beta diversity at the species level, but contribute to low phylogenetic beta diversity relative to forest and agricultural bee communities. We observed similar levels of homogenization at landscape and regional spatial extents, despite inter-site distances differing by an order of magnitude between these scales. Further urbanization could result in loss of bee biodiversity and evolutionary history at multiple spatial scales.

KEYWORDS

agriculture, beta diversity, biodiversity, biotic homogenization, ecoregion, land use, phylogenetic beta diversity, phylogenetic diversity, pollinator, urban

1 | INTRODUCTION

The conversion of natural habitats to human use is currently the largest driver of species decline and extinction (Pereira et al., 2010). Understanding how biodiversity responds to human land use is therefore a key challenge for ecologists (Tschamntke et al., 2012). Most studies, including those seeking to estimate biodiversity loss at large spatial and temporal scales, have focused on species richness measured at the community scale, or alpha diversity (McGill, Dornelas, Gotelli, & Magurran, 2015). The relatively fewer studies that track species identities show that land use change also drives large shifts in species composition resulting from a combination of loss and decline of sensitive species and increases in species that thrive in anthropogenic habitats (Mayfield et al., 2010; McGill et al., 2015; Winfree, Bartomeus, & Cariveau, 2011). These gains in anthropogenically associated species may compensate for species loss at the local scale (Dornelas et al., 2014; Vellend et al., 2016). At the same time, however, communities within an anthropogenic landscape may exhibit lower variability in species identities among communities (i.e., lower beta diversity) relative to communities in natural landscapes (Karp et al., 2012; Laliberté et al., 2010). Because regional species diversity is a product of alpha diversity and beta diversity (Jost, 2007), loss of beta diversity can drive regional declines in species richness, even in cases where local richness has increased (Smart et al., 2006). Thus, beta diversity is particularly critical for assessing how land use affects diversity at the large regional and biogeographic scales that are most relevant for preserving species (Socolar, Gilroy, Kunin, & Edwards, 2015).

The loss of beta diversity due to anthropogenic change is known as biotic homogenization (McKinney & Lockwood, 1999; Olden & Rooney, 2006). Biotic homogenization can result from the replacement of sensitive, specialized and endemic species by widespread, disturbance-adapted species that are the 'winners' in a human-dominated world (Olden, 2006). These winner species may be exotic, but more commonly belong to a regionally native species pool of species with characteristics pre-adapted to anthropogenic habitats, including dietary generalism and high dispersal rates (Aronson et al., 2014; Mayfield & Daily, 2005). These characteristics are also associated with high site occupancy rates and large species range sizes, leading to compositional homogenization of the communities they dominate (Tabarelli, Peres, & Melo, 2012). Anthropogenic communities may also be homogenized relative to natural communities if they are assembled from a relatively small regional pool of winner species (Karp et al., 2012), or if they are filtered by similar environmental conditions replicated across a naturally environmentally heterogeneous region (Goffman et al., 2014). These mechanisms of biotic homogenization in anthropogenic landscapes are not mutually exclusive, may be differently important at different scales or for different taxa in the same region (Burkle, Myers, & Belote, 2015), and cannot be reliably separated based on community data alone (Dormann, Freund, & Schaefer, 2017).

As expected under strong environmental filtering, winner species tend to represent non-random subsets of the regional pool of species

traits and phylogenetic lineages (Frishkoff, Karp, Gonigle, Hadly, & Daily, 2014; Knapp, Kühn, Schweiger, & Klotz, 2008; Mayfield et al., 2010; Sol, Bartomeus, Gonzalez-Lagos, & Pavoine, 2017). Despite the inclusion of phylogenetic diversity in a few recent studies of biotic homogenization in plants and birds (Frishkoff et al., 2014; Sol et al., 2017; Winter et al., 2009), such studies are still too few and too taxonomically narrow to draw general conclusions (Vellend et al., 2016). Anthropogenically driven loss of phylogenetic beta diversity, or phylogenetic homogenization, can occur independently from species homogenization (Graham & Fine, 2008). For example, urban areas can support species-rich plant communities; however, they tend to be a subset of closely related, functionally similar, urban-tolerant species (Knapp et al., 2008). Phylogenetic homogenization represents a loss of evolutionary diversity, which is a primary conservation concern (Frishkoff et al., 2014; Vamosi & Wilson, 2008). It may also drive loss of trait or functional turnover across a region, insofar as species traits tend to be phylogenetically correlated at a study's particular spatial and taxonomic scales (Cavender-Bares, Kozak, Fine, & Kembel, 2009; Webb, Ackerly, McPeck, & Donoghue, 2002; Winter et al., 2009).

Any change in species or phylogenetic beta diversity attributed to human land use must be defined against a baseline of beta diversity in natural habitats. As natural communities tend to diverge with increasing geographic and environmental distance (distance-decay; Soininen, McDonald, & Hillebrand, 2007), there is more scope for detecting biotic homogenization when comparing more distant communities. In contrast, at smaller scales, patterns of compositional change can be complex and human land use can produce both homogenization and differentiation (Figure 1a). Therefore, to fully understand the effects of land use on regional diversity, researchers need to test for biotic homogenization at multiple spatial scales simultaneously (Olden & Poff, 2003). To date there are few such studies, and they have all focused on similar systems, namely bird or plant communities in tropical forest as compared with recently converted agriculture (Arroyo-Rodríguez et al., 2013; Karp et al., 2012; Laurance et al., 2007; Solar et al., 2015; Tabarelli et al., 2012). Loss of spatially structured turnover can occur when anthropogenic land use removes natural dispersal barriers (McKinney & Lockwood, 1999), disturbs species-sorting processes (Vellend et al., 2007), filters habitat specialists and promotes habitat generalists (Devictor et al., 2008), and removes natural environmental gradients by creating similar environmental conditions over a large area (Goffman et al., 2014). Biotic homogenization that is stronger at larger spatial scales indicates a flattening of the natural distance-decay relationships that underpin how biodiversity accumulates across space (Anderson et al., 2011).

Here we present the first multiple-scale study testing for biotic homogenization as driven by both agricultural and urban land use. To our knowledge, this is also the first multiple-scale study to measure phylogenetic beta diversity. We investigate biotic homogenization in wild bee communities by comparing beta diversity among communities in natural forested landscapes with beta diversity among communities in two types of anthropogenic

landscapes. Forest, agricultural and urban landscapes were replicated within four north-eastern USA ecoregions, allowing us to investigate biotic homogenization at two contrasting spatial scales (5–50 km vs. 50–500 km). We chose wild bees as our study taxon because bees provide an essential ecosystem function as the main pollinators of flowering plants (Ollerton, Winfree, & Tarrant, 2011), and because they are diverse, with over 500 species in our region. Bee communities show strongly different composition across habitat types (Brosi, Daily, Shih, Oviedo, & Durán, 2008; Lichtenberg, Mendenhall, & Brosi, 2017; Winfree, Griswold, & Kremen, 2007); however, the bee literature has been slower than other fields in moving beyond alpha richness as the primary measure of communities (Winfree et al., 2011, 2007, 2011, 2007). Therefore, it is not well understood if agricultural habitats support bee beta diversity at levels found among natural habitats (Laliberté & Tylianakis, 2010), and the role of urban land use in homogenizing bee communities across larger spatial scales is virtually unknown (Baldock et al., 2015). To determine if land use is associated with biotic homogenization of bee communities, we answered two questions:

1. Is species-based beta diversity lower among anthropogenic or forest sites?
2. Is phylogenetically based beta diversity lower among anthropogenic or forest sites?

We addressed each question using beta diversity calculated at both the smaller within-ecoregion scale and larger between-ecoregion scale. Lastly, to determine if anthropogenic land use breaks down distance-decay relationships as predicted by biotic homogenization theory, we asked:

3. Does the relationship between beta diversity and geographic distance differ between anthropogenic and forest sites?

2 | METHODS

2.1 | Data collection

2.1.1 | Study design

We designed a regional-scale study containing 36 sites spatially grouped in 12 blocks, each consisting of one forested, one urban and one agricultural site (Figure 1b). The block design ensures that land use type is not confounded with geographic, environmental, or species pool gradients across our study extent, and that geographic and environmental distances among sites are comparable between land use types. The sites were located in four different ecoregions, as defined by United States Geological Survey (USGS) Level III classification, which is based on geology, climate and vegetation (Omernik, 1987). We quantified agriculture, urban and forest land cover in ArcGIS using the USGS 2006 National Land Cover Database (30-m resolution), and selected sites for which one of these three land cover types constituted $\geq 80\%$ of the surrounding land cover at a 1,500-m radius (Figure 1c). This design makes it likely that the bees we collected at each site were associated with the designated land cover type, because bees, while quite mobile in their daily foraging movements, typically fly less than 1,500 m from their nests (Greenleaf et al., 2007).

2.1.2 | Data collection

We collected bees primarily by pan trap (91% of specimens collected), which is the most unbiased way to sample a bee community (Westphal & Bommarco, 2008). In addition, we used blue vane traps (9% of specimens collected), which perform better for sampling larger-bodied bees such as *Bombus* and *Melissodes*. Because bees are attracted to flowers, flowers in the immediate vicinity of traps could bias collection rates either positively or negatively. We therefore standardized this variable by placing all of the pan traps in patches of

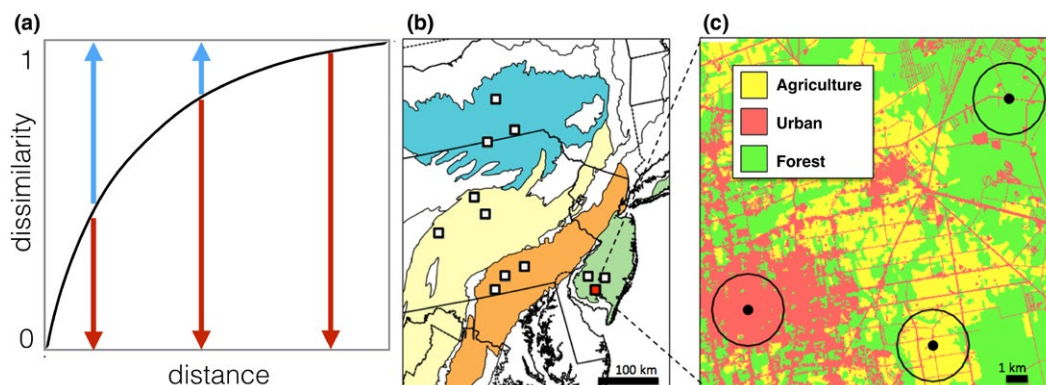


FIGURE 1 (a) The distance-decay curve in community similarity (black line) generates the expectation that there will be a greater scope for loss of dissimilarity (i.e., loss of beta diversity) at larger spatial extent (red arrows). Conversely, there is greater scope for increase in dissimilarity (i.e., gain in beta diversity) at smaller spatial scales (blue arrows). (b) We located three site blocks in each of four north-eastern US ecoregions (from north to south; blue – Northern Allegheny Plateau, yellow – Ridge and Valley, orange – Northern Piedmont, green – Atlantic Coastal Pine Barrens). (c) Each block includes a forest, agricultural and urban landscape, for a total of 36 landscapes

mowed grass (100–5,000 m², or 10–100 m wide when using a linear patch such as a mowed roadside). A second feature of the study design intended to reduce noise from microhabitat variables involved using four, rather than only one, sampling locations at each site. The four sampling locations were within 500 m of the site centre and therefore too close to one another to be independent, so we pooled specimens across sampling locations for each site.

For three years (2013–2015) we sampled bee communities in spring, summer and autumn, conducting one complete sampling round of all sites in 2–4 weeks depending on weather conditions. During spring rounds, we visited sites in order from south to north, in order to sample all sites at a phenologically similar time before broadleaf canopy closure. For all other sampling rounds we randomized ecoregion order, but modified this order as necessary to meet weather conditions for data collection (sunny to partly cloudy, high temperature > 18 °C, wind < 20 km per hour). In each sampling round, we set up traps at all nine sites within an ecoregion (36 sampling locations) in a single day – in an order that minimized driving distance – and took down traps in the same order the next day. All traps were therefore exposed to bee visits for a full 24 hr, thereby capturing the full range of pollinator diurnal activity. At each of the four sampling locations within a site, we set a line of six pan traps spaced 1.5 m apart, alternating white, blue and yellow, and filled with soapy water (1 tsp blue Dawn dish soap dissolved in 1 gallon water). Additionally, we haphazardly chose two of the four sampling locations within each site at which to set a blue vane trap (Springstar).

When collecting specimens, we poured trap contents through a fine-mesh strainer, transferred all insects to a Whirl-pak and added a label. All captured insects were retained in 70% ethanol as a preservative until they could be pinned and curated at Rutgers University. JG determined species identifications, except for genus *Nomada*, which were determined by Sam Droege at the USGS Patuxent Wildlife Research Center. Three unresolved species groups (bidentate *Nomada* species, *Nomada sayi-illinoense* and *Hylaeus affinis-modestus*) were treated as single species in analyses. Other unresolved species represented 1% of specimens and were removed from analysis. Honey bees (*Apis mellifera*) are a managed species in the region and we therefore removed them from analyses as well (< 5% of specimens).

No species-level phylogenies are available for the bee species of the study region. We therefore used a previously published genus-level bee phylogeny calculated from multiple protein-coding nuclear DNA sequences stored on GenBank (Hedtke, Patiny, & Danforth, 2013). We replaced genus branch tips with species polytomies of very short branch lengths.

2.2 | Analytical methods

We repeated all main analyses on two different site-by-site dissimilarity matrixes describing differences in (a) abundance-weighted community composition (i.e., using species identities), and (b) abundance-weighted phylogenetic composition (i.e., using the phylogenetic branch length). Abundance weighting allows us to focus on species that can be clearly identified as winners (anthropogenic

associates) and losers (forest associates); we do not have the statistical power to infer the winner or loser status of rare species and therefore give them minimal opportunity to influence our results. We calculated community composition dissimilarity using the Morisita–Horn index, which for each pair of sites measures the average per-site proportion of unique dominant species relative to the number of all dominant species per site (Chao & Chiu, 2016). The Morisita–Horn index ignores both singletons (species represented by one specimen from one site) and doubletons, and therefore is more stable with respect to sampling effort relative to richness-based dissimilarity indices (Barwell, Isaac, & Kunin, 2015). Our measure of phylogenetic composition dissimilarity is conceptually related to Morisita–Horn distance, and is most strongly influenced by numerically dominant taxa. For each pair of sites, we used the R package *picante* to calculate mean phylogenetic distance between pairs of specimens drawn from each site, divided by mean phylogenetic distance between all pairs of specimens in the pooled community of the two sites (Kembel et al., 2010). Values of phylogenetic dissimilarity > 1 indicate that there is greater mean phylogenetic distance between the communities than within them, that is, the communities are phylogenetically differentiated from one another.

Because we are using a genus-level phylogeny, which is the highest available resolution for the bee species of our region, congeneric species pairs are separated by a constant, very small positive distance (twice our chosen species polytomy branch length of 0.00005). This approach is virtually equivalent to using the original, genus-level tree and weighting by generic abundance.

The Spearman's rank correlation between our species and phylogenetic dissimilarity matrixes was low (Spearman rank correlation $\rho = .33$), indicating that the two matrixes are capturing non-redundant information about compositional differences among the communities.

2.2.1 | Is species beta diversity lower among anthropogenic sites or forest sites?

We used mean pairwise dissimilarity (MPD) among sites to calculate how sites in different land use types are differentiated within and between ecoregions. MPD is robust to the number of sampled sites, which can have a strong and unpredictable effect on multiple-site dissimilarity indexes and other classical measures of beta diversity, due to biased estimation of regional species pool size (Bennett & Gilbert, 2015). However, an important limitation of using MPD is that it does not account for species shared by more than two sites, and therefore does not accurately quantify the relationship between local and regional diversity (Baselga, 2013). For example, imagine four sites in which each pair of sites has two shared species and two unshared species, resulting in MPD = .5 (mean proportion of unshared to total species). In this situation, regional diversity could be either 6, if unshared species are unique to each site, or 4, if unshared species are shared among other site pairs (Baselga, 2013). Unfortunately, there are currently no robust techniques for estimating regional diversity from local community samples; thus we avoid doing so in this paper (Socolar et al., 2015).

If biotic homogenization is occurring within ecoregions, we expect that the mean dissimilarity calculated between pairs of sites in the same ecoregion will be higher in forest than in urban or agricultural land use types. If biotic homogenization is occurring across regions (i.e., at a larger spatial scale), then we expect that the mean dissimilarity calculated between pairs of sites in different ecoregions will be higher in forest than in urban or agricultural land use types. Because pairwise dissimilarities between all sites are not independent, we conducted a form of bootstrapping by repeated random sampling of dissimilarities, under the constraint that each site can only be represented by one dissimilarity value per sample. For each sample, we calculated mean dissimilarity for forest, agriculture and urban site pairs, and then used the results from 9,999 such draws to calculate a bootstrapped mean and 95% confidence intervals. We interpreted non-overlapping confidence intervals to indicate significant difference in mean pairwise dissimilarity between two land use types.

2.2.2 | Is phylogenetic beta diversity lower among anthropogenic sites or forest sites?

We applied the same bootstrapped MPD method described above to compare phylogenetic beta diversity between anthropogenic and forested land use types at both within- and between-ecoregion scales. To interpret the results, we additionally used an indicator species analysis to identify species associated with each land use type (De Caceres & Legendre, 2009), and plotted the abundance and location of species associated with the three land use types onto the phylogenetic tree.

2.2.3 | Does the relationship between beta diversity and geographic distance differ between anthropogenic and forest sites?

We used Mantel tests to examine how community dissimilarity increases with geographic distance within each land use type. To determine whether the relationship between community dissimilarity and distance was weaker in anthropogenic land use types, we used bootstrapped 95% confidence intervals to compare the Mantel correlations among the three land use types.

Because strong differences in alpha diversity between land use types could theoretically drive both composition and beta diversity results, we did a preliminary analysis to check for this. We calculated effective species diversity (exponential Shannon diversity index) and phylogenetic diversity (mean pairwise relatedness among all specimens captured at a site) for all sites, and compared means among land use types using ANOVA.

3 | RESULTS

3.1 | Preliminary analyses

In 3 years of sampling, we collected 13,398 specimens of 248 species. As a precursor to analysing beta diversity we calculated alpha

(site-level) diversity. At the site level, mean effective species diversity (inverse Simpson) was very similar and statistically indistinguishable among forest, agricultural and urban land use types (15, 14 and 12 dominant species per site, respectively). Phylogenetic diversity, however, was lower in urban sites than in forest (Supporting Information Figure S1a, b). Ecoregions likewise did not differ in mean effective species diversity at the alpha level, but did differ in phylogenetic diversity (Supporting Information Figure S1c, d).

3.1.1 | Is species beta diversity lower among anthropogenic sites or forest sites?

Within-ecoregion scale

For the average pair of forest sites drawn from the same ecoregion, approximately half (.5) of the species were unique to one site, as measured by mean pairwise Morisita–Horn dissimilarity. The proportion of unique species was lower between average pairs of agricultural (.42) and urban (.40) sites. These estimates have wide, overlapping confidence intervals, indicating high uncertainty and no significant differences among land use types (Figure 2a).

Between-ecoregion scale

For the average pair of sites drawn from different ecoregions, the proportion of unique species was .60 (forest), .62 (agriculture) and .55 (urban). Again, these estimates are not detectably different due to wide overlapping confidence intervals (Figure 2b).

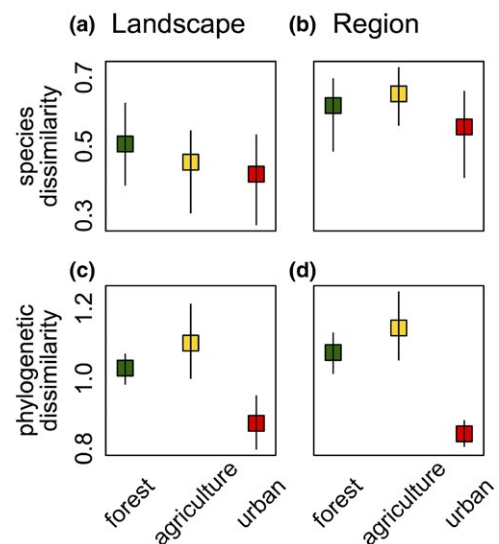


FIGURE 2 (a) Mean pairwise species dissimilarity (Morisita–Horn index) calculated between site pairs drawn from the same ecoregion. (b) Mean pairwise species dissimilarity calculated between site pairs drawn from different ecoregions. (c) Phylogenetic dissimilarity is significantly lower in urban sites at the within-ecoregion scale and (d) the between-ecoregion scale. 95% confidence intervals are calculated from iteratively bootstrapped means

3.1.2 | Is phylogenetic beta diversity lower among anthropogenic sites or forest sites?

Within-ecoregion scale

For the average pair of sites drawn from the same ecoregion, the ratio of mean phylogenetic difference between the two sites to mean phylogenetic difference among the pooled specimens of the two sites was not significantly different from one (1.0 for forest and 1.1 for agriculture). However, urban site pairs from the same ecoregion were significantly less differentiated than expected given pooled diversity (0.87; confidence interval does not include 1), and significantly less differentiated compared with forest and agricultural site pairs (Figure 2c).

Between-ecoregion scale

For the average pair of sites drawn from different ecoregions, both forest and agricultural site pairs were more differentiated than expected given pooled diversity (1.08 and 1.13, respectively; confidence intervals do not include 1), while urban site pairs were less differentiated than expected (0.08) and significantly less differentiated than forest and agricultural sites (Figure 2d).

Forest-associated species were evenly distributed among four dominant genera in four different families (Halictidae: *Lasioglossum*; Andrenidae: *Andrena*; Megachilidae: *Osmia*; and Apidae: *Nomada*). Agriculture- and urban-associated species were largely concentrated within a single family, the Halictidae, although they were found throughout the phylogeny (Figure 3).

3.1.3 | Does the relationship between beta diversity and geographic distance differ between anthropogenic and forest sites?

The relationship between species-based beta diversity and geographic distance between site pairs was significantly positive for all three land use types (Figure 4a). This indicates that the geographic extent of our study design is large enough to capture the distance-decay relationship for bee communities in the native vegetation type, forest, and thereby provides scope for the detection of biotic homogenization at regional scales (Figure 1). However, anthropogenic land use did not significantly diminish this natural gradient (Figure 4b). For phylogenetic dissimilarity, forest and urban sites showed a very weak, but significantly positive correlation with geographic distance, whereas agricultural sites did not (Figure 4c). However, the confidence intervals overlapped for all three land use types, such that the distinctions among land use types were insignificant (Figure 4d).

4 | DISCUSSION

Despite a study design that explicitly contrasted spatial scales over a 75,000 km² region, we found little difference in the strength of biotic homogenization at different spatial scales. As predicted, within

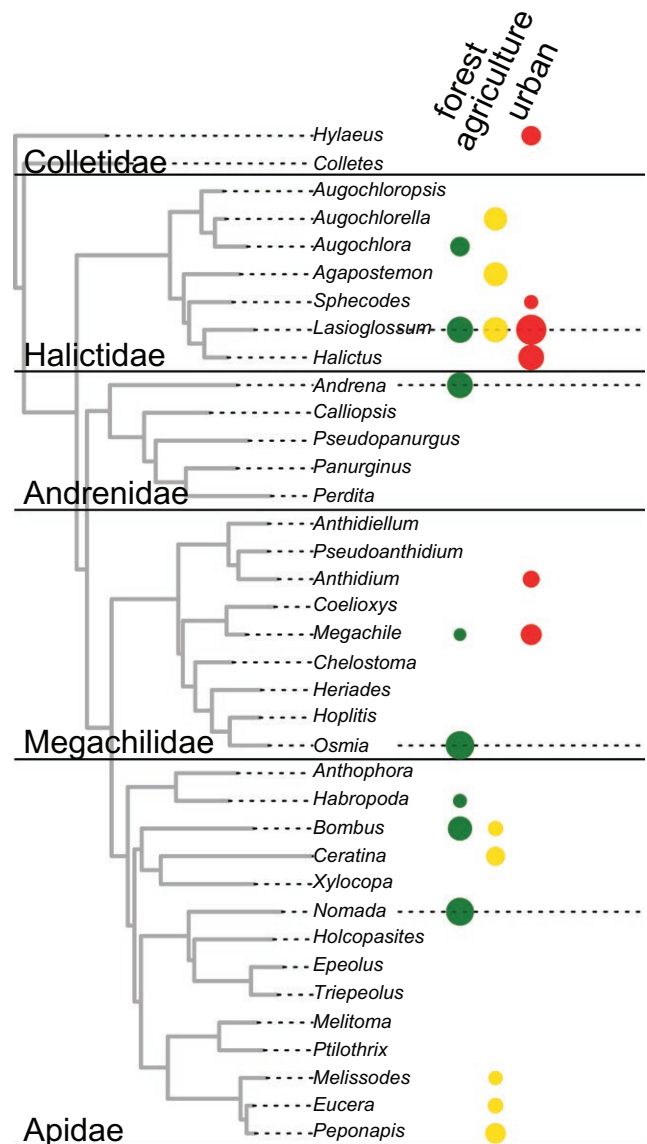


FIGURE 3 The unrooted phylogenetic tree of bee genera used in this study. The tree was created using sparse sequence data from multiple loci; the placement of Andrenidae relative to other bee families is uncertain (Hedtke et al. 2011). Repeating the analysis on two trees with alternative placements of Andrenidae did not qualitatively change our results. Colored circles are sized by the numbers of species in each genus associated with forested (green), agricultural (yellow) or urban (red) land use types

the forested sites, species composition became more dissimilar with increasing geographic distance. This confirms that there was greater potential for biotic homogenization at the regional, as compared with the landscape, scale. However, bee communities in agricultural and urban sites also diverged as geographic distance increased, suggesting that the natural distance-decay relationship that underpins regional species diversity is maintained across the anthropogenic landscapes in our study region. Winners of land use change tend to have high occupancy rates due to small body size, high dispersal

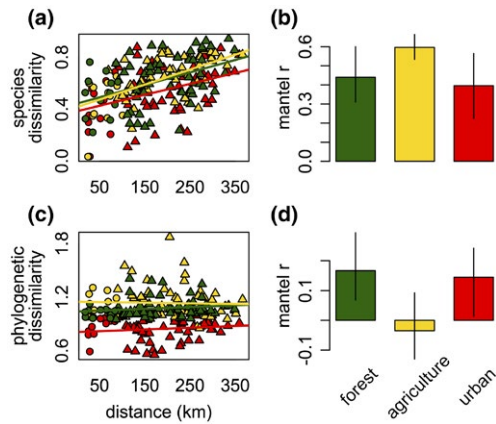


FIGURE 4 (a) Relationship between bee species dissimilarity (Morisita–Horn index) and geographic distance between pairs of forest (green), agricultural (yellow) and urban (red) sites. Pairs of sites are drawn either from within the same ecoregion (circles) or from different ecoregions (triangles). (b) Correlation coefficients between species dissimilarity and geographic distance for each land use type, with 95% confidence intervals calculated using a bootstrapped Mantel test. (c) Relationship between bee phylogenetic dissimilarity (mean relatedness index) and geographic distance between pairs of forest, agricultural and urban sites. (d) Correlation coefficients between phylogenetic dissimilarity and geographic distance for each land use type

ability, dietary generalism, and large range sizes (Horner-Devine, Daily, Ehrlich, & Boggs, 2003; Mayfield, Boni, Daily, & Ackerly, 2005; Ranganathan, Daniels, Chandran, Ehrlich, & Daily, 2008), leading to the expectation that compositional turnover driven by land use change should be accompanied by loss of beta diversity across a range of spatial scales (Tabarelli et al., 2012). Our study provides contrasting evidence that winning clades may be represented by rich native species pools that maintain beta diversity at not only the landscape but also the regional scale.

Our study contributes to evidence that land use drives large changes in species composition that are not necessarily accompanied by species homogenization (Norden et al., 2017). A previous analysis of our same data set found strong compositional differences among the three land use types, including clear shifts in trait distributions (Harrison, Gibbs, & Winfree, 2018) consistent with findings from other studies that winners tend to be characterized by small body size, high dispersal ability, dietary generalism, and large range sizes (Horner-Devine et al., 2003; Mayfield et al., 2005; Ranganathan et al., 2008). These common characteristics are also associated with high occupancy rates, motivating the hypothesis that compositional turnover driven by land use change should be accompanied by loss of beta diversity (Tabarelli et al., 2012). However, we find that all three land use types retained high levels of species turnover among sites, suggesting that anthropogenic communities include not only widespread but also patchily distributed species. Bees include many disturbance-associated species that appear to thrive in anthropogenic habitats (Matteson, Ascher, & Langellotto, 2008), and some species may currently rely on human activity to provide open habitat

in forested ecosystems (Hanula, Horn, & O'Brien, 2015; Winfree et al., 2011). We speculate that that bee communities in anthropogenic habitats are diverse enough in both species number and life histories to maintain levels of beta diversity indistinguishable from those observed in natural habitats, either through stochastic population variability or differential response of species to environmental variability across sites, such as soil types and available host plant species.

At both the landscape and the regional scale, we found strong phylogenetic (but not species) homogenization of bee communities in urban as compared with forested landscapes, and homogenization was additionally accompanied by a loss of phylogenetic alpha diversity. Phylogenetic homogenization occurs in our system when forest-associated taxa in multiple bee families (Andrenidae, Megachilidae and Apidae) are filtered out of anthropogenic landscapes, while a single family of winners is promoted to dominance in urban landscapes (the family Halictidae, and especially the genus *Lasioglossum*) (Harrison et al., 2018). These winners likely share characteristics that pre-adapt them to urban habitats, which may be analogous to formerly rare or ephemeral habitats in a region originally dominated by forest (Marks, 1983). Agricultural landscapes, on the other hand, were not homogenized relative to forested landscapes. Agricultural-associated species appear to maintain a more even abundance distribution across the deep nodes of bee phylogeny (Figure 3), suggesting that agriculture supports high levels of regional phylogenetic bee diversity. Agricultural landscapes have been shown to provide important habitat for open-habitat associated plants and animals (Foster & Motzkin, 2003; Marks, 1983), which are now threatened by agricultural intensification or conversion to other land use types (Storkey, Meyer, Still, & Leuschner, 2012). Our work is the first to explore phylogeny-based biotic homogenization in pollinator communities, but analogous losses of phylogenetic diversity with land use change has been found for birds (Frishkoff et al., 2014; Sol et al., 2017).

Our results show that the predictions of biotic homogenization can apply at the phylogenetic level, even in the absence of species-level homogenization. As has been proposed for trait homogenization (Baiser & Lockwood, 2011), we suggest that phylogenetic homogenization may occur in the absence of species homogenization when there are high levels of redundancy across the phylogenetic tree (i.e., deep nodes lead to highly diversified shallow tips). The taxonomic group associated with urban land use in our study system (family Halictidae and particularly genus *Lasioglossum*) has undergone a relatively recent and rapid radiation of diversity (Gibbs, Brady, Kanda, & Danforth, 2012). Thus, urban communities are consistently dominated by many closely related species that have variable occupancy rates and contribute to high beta diversity at the species level, but contribute to low phylogenetic beta diversity. In contrast, forest and agricultural communities vary in relative abundance across deep nodes of the phylogenetic tree, thus contributing to higher phylogenetic beta diversity. This structure has two consequences for interpreting our phylogenetic homogenization result. First, compared to species-based dissimilarity measures, abundance-weighted phylogenetic dissimilarity measures may be more robust to

incomplete sampling, as it is easy to miss a single shared species in one of two sites, but it would be highly unlikely to miss all species of a diverse genus from that site. Second, it is possible that using a phylogenetic tree with species-level resolution would produce different results if congeneric species of winner taxa tended to be more diverged in urban landscapes relative to forest. However, we believe that this is unlikely, as urban landscapes are dominated by a single genus characterized by relatively recent evolutionary diversification.

We can draw conclusions from our study about the likely consequences of land use for biodiversity of insect pollinators and likely other taxa as well. Forests in our region, as elsewhere, have undergone a long history of disturbance, transition and changes in extent (Rudel et al., 2005). Therefore, it is likely that the associated forest bee fauna also has undergone many community transitions, species losses and homogenization processes, even before being observed in our study. However, we believe that current forest communities, in addition to being our only available baseline, are also the correct baseline for understanding compositional effects of future land use conversions. Urbanization is the mostly likely future land use change, both globally (Seto, Güneralp, & Hutyra, 2012) and within our study region (Lawler et al., 2014). Our finding of phylogenetic homogenization of bee communities across urban landscapes suggests that further urbanization may result in loss of biodiversity and evolutionary history at multiple spatial scales.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA ACCESSIBILITY

The site-species matrix and analysis code are available upon request from the authors.

ORCID

Tina Harrison  <http://orcid.org/0000-0001-8735-0289>

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BIOSKETCHES

TINA HARRISON is a Postdoc in Ecology and Evolution in Rachael Winfree's laboratory at Rutgers University. Her research investigates how global change alters community composition and diversity at large spatial scales.

JASON GIBBS is an Assistant Professor in the Department of Entomology at the University of Manitoba. His research focuses on the biodiversity, phylogenetics and taxonomy of bees, and on their role as crop pollinators.

RACHAEL WINFREE is a Professor in the Department of Ecology, Evolution and Natural Resources at Rutgers University, New Brunswick. Her research investigates the relationships among global change, biodiversity, and ecosystem services, and in particular how pollinators and the pollination services they provide are affected by land use change.

SUPPORTING INFORMATION

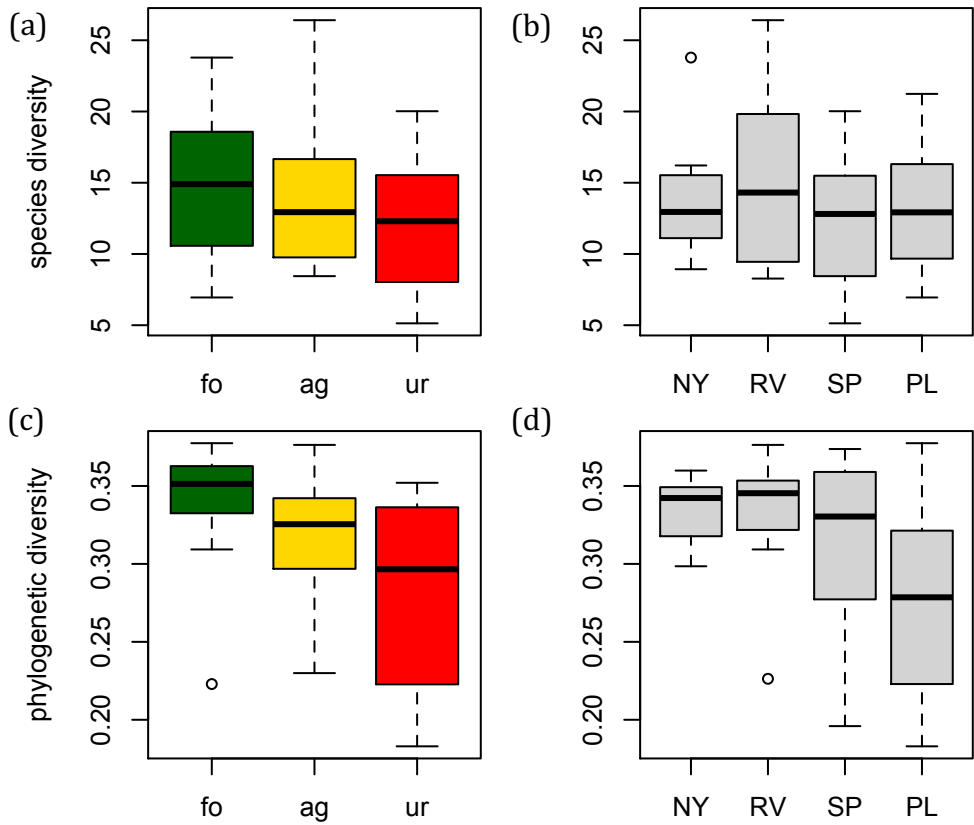
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1 **Appendices**

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5 Fig S1. (a) Alpha diversity, measured for species as inverse Simpson entropy (Jost 2007),

6 does not differ among land use types (forest, agriculture, and urban). (b) Species alpha

7 diversity does not differ among ecoregions. (c) Phylogenetic alpha diversity, measured as

8 mean phylogenetic dissimilarity among pairs of individual bees, is lower in urban sites

9 compared with forested sites. (d) Phylogenetic diversity was lower in the pinelands (PL)

10 than in upstate New York (NY) or Ridge and Valley in Pennsylvania (RV).

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