

BIOTIC HOMOGENIZATION OF BEE COMMUNITIES
ACROSS SPATIAL SCALES

by

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ABSTRACT OF THE DISSERTATION

Biotic homogenization of bee communities across spatial scales

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Human land use has variable effects on ecological communities at local and landscape scales, but these effects cumulate in clear trends of species loss and decline at larger continental scales. Linking changes in biodiversity across scales is therefore a major research challenge for global change ecologists. In a worst-case scenario known as biotic homogenization, anthropogenic changes such as land use drive the replacement of sensitive endemic species by widespread, disturbance-adapted species, leading to potentially little change in species diversity at small scales, but driving loss of diversity at larger scales as historically distinct communities become compositionally similar. This dissertation explores the role of land use in driving biotic homogenization and other forms of biodiversity change across spatial scales, using bee pollinators collected from a large-scale study design including forest, agriculture, and urban landscapes replicated across four distinct vegetation zones of the northeastern U.S. I used this dataset to ask (1) Do anthropogenic landscapes alter alpha diversity and composition of bee communities, and (2) Are anthropogenic landscapes homogenizing bee communities across regional spatial scales? I used a literature review focused specifically on the role of urban land

use, to ask (3) how do urban drivers affect the interactions between plants and pollinators, including bees? Relative to natural forest habitat, bee communities in agriculture and urban landscapes were less diverse, had fewer rare species, and were dominated by species with long flight seasons and social behavior. These changes in species composition did not result in detectable homogenization of species composition across anthropogenic versus natural landscapes. However, bee communities in anthropogenic landscapes were more closely related to one another, both within and across sites, indicating that land use is associated with a loss of phylogenetic diversity at small and large spatial scales. The literature review identified habitat fragmentation, invasive species, urban warming, and pollution as key drivers of change in bee communities and plant-pollinator interactions in urban landscapes. Overall, negative effects of land use on bee biodiversity were subtle and often masked by more dramatic changes in bee community composition. This indicates both current resiliency and a potential for large-scale biodiversity loss and decline in the context of continued land use change.

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Included in the thesis is a published review paper, which is my original work and is co-authored by R.W. in an advisory role.

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INTRODUCTION

Anthropogenic change is driving loss of sensitive species around the world (Pimm *et al.*, 2014). At the same time, other species have increased in abundance and expanded their ranges (Lockwood *et al.*, 2006). Loser species are often rare or endemic, while supplanting winner species tend to be cosmopolitan, common, and having generalized habitat requirements and ecological roles. The biotic homogenization hypothesis states that as anthropogenic change drives the replacement of narrowly distributed loser species by widespread winners, originally distinct regional species assemblages come to share an increasingly large proportion of their species (McKinney & Lockwood, 1999).

Anthropogenic change can also drive the loss of a wide range of life histories and specialized ecological traits, and millions of years of evolutionary history represented by loser species (Vamosi & Wilson, 2008; Davey *et al.*, 2012). Winner-loser replacement and biotic homogenization can therefore be measured as changes in species, trait, or phylogenetic composition and diversity, each providing a different perspective on the patterns and potential mechanisms of anthropogenic impacts on biodiversity (Winter *et al.*, 2009; Baiser & Lockwood, 2011).

Most studies testing the biotic homogenization hypothesis have identified winner species as non-native invaders, and losers as species that are extirpated from a biogeographic region over historical time scales that integrate the effects of many different anthropogenic changes. Currently, land use change is the leading driving of species loss

and extinction (Pereira *et al.*, 2010). Isolating the role of land use in winner-loser replacement and biotic homogenization is therefore a key challenge for understanding how anthropogenic change alters biodiversity. Land use change acts at a landscape scale, creating patchworks of natural and transformed habitat (Tschardt *et al.*, 2012). Therefore, biogeographic methods such as regional species lists are of little use, particularly for diverse taxa such as insects whose habitat preferences aren't known *a priori*. Furthermore, temporal data sets that can be used to isolate the effects of land use change are rare or non-existent for most taxa (Diniz-Filho *et al.*, 2010). Studying role of land use in biotic homogenization generally requires comparing local communities in space-for-time study designs, and accounting for species relative abundances which reflect success or failure in a local habitat (Shipley *et al.*, 2006).

My dissertation explores how land use affects community composition and biodiversity across spatial scales, using bee pollinators as a study taxon. Bees are diverse in terms of both species and life histories, and have a key ecosystem function as pollinators (Winfree *et al.*, 2011). They are also highly mobile and have short generation cycles, and therefore should efficiently sort among their preferred land use types without the extinction lags and other historical effects that may be present in longer-lived vertebrates and perennial plants (Helm *et al.*, 2006; Vellend *et al.*, 2007). Therefore, bees are well-suited for answering questions about the effects of land use at landscape and regional scales. Furthermore, because research on land use and biodiversity is dominated by studies of plants and vertebrates (Cardoso *et al.*, 2011), using an insect taxon addresses two current research gaps. First, we do not know habitat preferences for most insects; and second, we

do not know if insects that prefer anthropogenic habitat tend to be a subset of common, widespread species, or if they include more restricted species or rare species, or species of conservation concern (Winfree *et al.*, 2011; Cariveau & Winfree, 2015). Closing these research gaps is important for understanding how continued land use change and intensification will affect the biodiversity of insects, which comprise a vast proportion of total biodiversity (May, 1992).

To understand how land use affects biodiversity of bees from local to regional scales, I designed a large-scale study featuring 36 landscapes divided into forest, agriculture, and urban land use types replicated across a 75,000 km² expanse of the northeastern U.S that includes four different native forest types, or ecoregions (Omernik, 1987). Forest is the natural land cover type in this region and originally covered vast extents before European settlement (Lorimer & White, 2003). I used this data set to address two research goals corresponding to my first two dissertation chapters. First, I explored the ecological characteristics of bee communities in anthropogenic versus natural landscapes, to gain insight on how land use change might drive the winner-loser replacement process. Next, I asked if bee communities in anthropogenic landscapes were homogenized relative to bee communities in natural forest, at either a small within-ecoregion scale or a larger between-ecoregion scale. I also tested if any loss of compositional dissimilarity was driven by the replacement of narrowly distributed losers by widespread winners, as predicted by the biotic homogenization hypothesis.

Because of their importance for crop production, previous research on the impact of land use on bees and other pollinators has focused on agricultural study systems (Winfree *et al.*, 2011). Therefore, relatively little is known about how urban landscapes affect communities of bees and other pollinators, even though urban land use is the most rapidly growing form of anthropogenic land cover (Hernandez *et al.*, 2009; Seto *et al.*, 2012). In my final dissertation chapter, I used a literature review to ask how the specific environmental conditions in urban landscapes affect interactions between plants and pollinators, including bees. The mechanisms driving changes in pollinator composition or plant reproduction often act over very small scales; for example, the brief space in which an individual bee chooses one plant over another. However, these small-scale effects of urban drivers underpin the responses in species diversity and composition observed over much larger landscape and regional scales.

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CHAPTER I. FOREST IS IRREPLACEABLE FOR SUPPORTING BEE BIODIVERSITY

Abstract

Anthropogenic landscapes are associated with biodiversity loss and large shifts in species composition and traits for better-studied taxa such as plants and vertebrates. However, the response of a critically important functional group, bee pollinators, is still largely unknown. I collected bee community data from a regional-scale, spatially blocked study design to ask how agricultural and urban landscapes compare to forest in terms of bee abundance, species richness, and life history traits. I also provide the first assessment of the role of forested and anthropogenic habitats in supporting regionally rare bee species, using a large independent dataset to define species rarity *a priori*. I found reduced richness of rare species in anthropogenic landscapes, together with moderate loss of overall abundance and richness. Bee species traits differed by landscape type as well; forests supported many solitary and parasitic species with short flight seasons, whereas anthropogenic landscapes promoted bees with longer flight seasons and social behavior. My results suggest that large portions of regional bee biodiversity are dependent on forest, which has been largely overlooked as bee habitat by previous research and current bee conservation strategies.

Introduction

Wilderness is necessary for supporting natural levels of biodiversity (Gibson *et al.*, 2011). At the same time, vast extents of agriculture and other forms of anthropogenic land use are both inevitable and necessary for people, which means that conservation biologists must increasingly consider how different land use types may support biodiversity (Kremen, 2015). Given the importance of the question, it is surprising how poorly the answer is known (McGill *et al.*, 2015). The effects of land use on site-level abundance and species richness are negative on average, but are also highly variable and often weak or positive (Newbold *et al.*, 2015). An important reason is that many species tolerate or even prefer the altered environmental conditions in anthropogenic habitats, thus partly compensating for loss of sensitive species (Dornelas *et al.*, 2014). The resulting compositional shifts are often associated with strong shifts in community trait distributions, and in the distributions of abundance and richness across spatial and temporal scales (Mayfield & Daily, 2005; Garnier *et al.*, 2007; Tabarelli *et al.*, 2012). Land use may thus result in profound changes to ecosystem function (Tylianakis *et al.*, 2008) and regional biodiversity (Socolar *et al.*, 2015) that are not detectable in trends of local abundance and richness.

A major challenge in understanding the effects of land use on communities is that anthropogenic land use simultaneously imposes many environmental changes, which may have different directional effects in different natural habitat contexts (Groffman *et al.*, 2014). Changes to the temporal distribution of resources and environmental conditions in

anthropogenic habitats may be an important and overlooked filter of species across land use boundaries in a wide range of ecosystems (Kochmer & Handel, 1986; Harrison & Winfree, 2015). For example, in arid regions, irrigation in urban and agriculture landscapes alters the timing and duration of plant growth, as compared to native vegetation which is constrained by seasonal rainfall (Buyantuyev & Wu, 2012; Leong & Roderick, 2015). The extended growing season in irrigated landscapes likely explains the replacement of regional univoltine butterflies with cosmopolitan butterfly species capable of producing multiple generations per year (Blair & Launer, 1997). In temperature regions, forest canopy constrains many understory plants and associated animals to complete growth and reproduction in early spring (Motten, 1986). A major effect of urban and agriculture land use is the removal of forest canopy, which increases light availability throughout the year and encourages the growth of open-habitat meadow plants and their associated animals (Winfree *et al.*, 2007).

Animal pollinators are required for the reproduction of 90% of plant species, yet how pollinator communities change with land use is poorly known (Ollerton *et al.*, 2011). Syntheses show that while pollinator abundance and richness decreases in response to extreme loss of natural habitat, responses to more moderate habitat loss are mixed (Winfree *et al.*, 2009, 2011; Cariveau & Winfree, 2015). Strong patterns of compositional turnover between land use types suggest that abundance and richness patterns are stabilized by species that respond positively to land use change (e.g. Brosi *et al.*, 2007; Winfree *et al.*, 2007; Wray *et al.*, 2014). This may be especially true in systems where natural forest habitats are replaced by patchy open landscapes of farms and semi-natural

meadows, which are preferred habitat for many early-successional plant and associated animals including pollinators (Mayfield & Daily, 2005; Winfree *et al.*, 2011). However, there is little consensus on the identities and traits of pollinator species found in anthropogenic habitats, and on whether anthropogenic communities are dominated by common weedy species or include rare species of conservation concern (Winfree *et al.*, 2011; Cariveau & Winfree, 2015). Two research gaps have slowed our ability to understand this pattern. First, it is difficult to acquire reliable habitat association data for pollinators, which are highly mobile and may utilize multiple habitats in different times of the year or to acquire different resources (Westrich, 1996). The near proximity of alternative or complementary habitats may affect our perception of how abundance, composition and trait distributions respond to any one habitat category in the landscape (Kremen *et al.*, 2007). Second, the great majority of insect faunas including most pollinators have never been evaluated for rarity, due to challenging shortfalls in taxonomy and regional-scale distributional data for highly diverse species pools (Cardoso *et al.*, 2011; Fattorini *et al.*, 2013).

Here I present the first regional-scale, replicated assessment of native bee biodiversity found in natural and anthropogenic habitat types in the northeastern USA. My data set consists of >13,000 specimens representing 245 bee species, which I collected from 36 spatially independent sites located in forested, agricultural, and urban landscapes. In this paper, I explore how different aspects of composition change with land use in order to generate hypotheses about the ecologically relevant drivers of land use change and assess the conservation value of forest versus open anthropogenic landscapes. I first ask how

abundance, richness, and seasonal change in abundance and richness (community phenology) differ between forest and anthropogenic habitats. Second, I ask if forest and anthropogenic communities differ in trait composition and proportions of taxonomic families. Finally, I use a large independent museum dataset to conduct the first regional-scale assessment of rarity for North American bee species. I then apply the rarity classes to my data set to ask if forest, agriculture and urban land cover support different abundance and diversity of rare species. As far as I am aware, to date this represents the most comprehensive, large-scale evaluation of the response of rare bee species to human land use outside of Europe.

Methods

Study design

My study region covers 75,000 km² of the northeastern U.S. (Figure 1a, area within white rectangle) and is naturally dominated by temperate forests, including broadleaf lowland forests, mixed pine and broadleaf forests in hilly areas, and pine forest with oak understory in the pinelands of southern New Jersey (Omernik, 1987). Contemporary land use composition of the three states that include my study region (New Jersey, Pennsylvania and New York), is 53% forest, 21% agriculture, and 11% urban land use (Nickerson *et al.*, 2011). Agricultural landscapes typically included pasture, row crops (mainly corn and soybeans), forest fragments, and some exurban residential land use interspersed among fields. Agricultural land in the New Jersey pinelands is distinct in

being primarily used for fruit and vegetable crops. Urban landscapes in my study region range from the intensively urbanized areas of New York City and Philadelphia to large expanses of low-density single-unit housing interspersed with open lands.

To achieve a statistically replicated sample of urban land use, I chose twelve towns distributed throughout the study region with populations ranging from 5,000-50,000. I then selected one forest site and one agriculture site within 5-30 km of each town. This spatial blocking removes the need to consider spatial autocorrelation when analyzing effects of land cover on site-level variables. Bees are mobile animals and will forage in multiple available habitat types around their nest, which presents a challenge in determining bee habitat associations (Kremen *et al.*, 2007). Therefore, a key element of my study design was positioning sites so that they were surrounded by >80% forest, agriculture or urban land cover within a 1500 m radius. 1500 m is further than the regular flight distance of most bees in the region (Greenleaf *et al.*, 2007), which makes it likely that bees at the site are associated with the site's land use type.

Sampling bee communities

I sampled pollinator communities at all 36 sites throughout the 2013-2015 growing seasons, in multiple sampling rounds extending from April to early October. During each site visit I set twenty-four pan traps and two blue-vane traps for 24 hours. Both of these trap types attract bees with fluorescent colors that mimic flowers. Pan traps compete with nearby flowers for pollinators' attention, and additionally produce very low catch numbers when shaded by overhanging trees. To minimize these biases, traps at each site

were divided evenly among four strips of mowed open vegetation, such as roadsides, small parks, and vacant lots.

Independent assessment of bee species traits

I collected information on six species traits describing nesting habits, diet, body size and phenology for bees in the study region (Table S1; see also (Bartomeus *et al.*, 2013)). I selected these six traits because they describe major axes of a bee's life history and have low pairwise correlations (Table S2). I additionally searched published literature to add missing values for several species. I estimated bee body sizes by measuring the intertegular distance, the distance across a bee's thorax between the base of the wings (Cariveau *et al.*, 2016), for between 1 and 41 specimens of each species, and using a published equation to convert to dry body mass (Cane, 1987). To estimate flight season length, I used 58,833 records of specimens collected throughout the northeastern USA on known dates and subsequently identified to the species level (Table S3). I use the 10th and 90th percentiles of the collection dates to estimate emergence and senescence time for each species; the difference in dates yields the estimated length of the flight season in days.

Independent assessment of regional bee species rarity

Rarity is defined relatively among a pool of species; therefore it is sensitive to the spatial, and temporal, and taxonomic extent of the data set used (Fattorini *et al.*, 2013). For example, species classified as having low populations within a small geographic extent may be abundant and dominant elsewhere in their range (Leroy *et al.*, 2013).

Furthermore, differences among species in phenology, diet breadth and habitat preference alter detectability and interact with biases in collector behavior, potentially distorting species' observed relative frequencies. To solve these problems, I quantified bee species' rarity using a previously published data set compiled from museum specimens, which was spatiotemporally extensive, collected from diverse plants and habitats, taxonomically updated and carefully filtered to control for bias in collector effort (Figure 1a; (Bartomeus *et al.*, 2013)). I was concerned that species with short flight seasons would be more likely to appear rare regardless of true population size and regional prevalence; therefore, I used each species' maximum monthly number of specimens as a measure of its regional abundance. Thus, a species with 5 specimens in each of three months of the year will have the same rank as a species with 5 specimens in one month of the year (Figure S1). The final data set had 12,003 specimens of 443 species, which I used to defined four classes of rarity using quartiles (Figure 1b).

Analytical methods

All analyses were performed in R 3.2.4.

Abundance and richness. I compared abundance and richness of specimens collected at each site across land cover types, using generalized linear models with negative binomial error distributions (R package *lme4*; (Bates *et al.*, 2015)). I tested for an overall effect of land use by using chi-square test to compare the model deviance to the deviance of the reduced intercept-only model. Then, for the models that showed a significant effect of land use, I examined the model coefficients and 95% confidence intervals (calculated in

R package *sandwich*; (Zeileis, 2006)) to find how responses differed in anthropogenic versus forest landscapes.

To compare how abundance and richness change throughout the growing season in forest and anthropogenic land use types, I fit numbers of specimens (or species) collected at each site on each sampling date, using two generalized mixed linear models of the form

$$land\ use + doy + doy^2 + land\ use:doy + land\ use:doy^2 + year + (1|site)$$

in which site is a random intercept effect, year is a fixed nuisance variable, and *doy* (Julian day-of-year) and *doy*² are orthogonal polynomial terms of first and second degree. Using the polynomial terms allowed me to fit hump-shaped responses in community metrics over time, which I expect since many bee species emerge in the spring, build abundances over time and collectively senesce towards the end of the year. I selected a negative binomial distribution for error in the bee abundance model, and a Poisson distribution for error in the richness model. I validated the models by visually inspecting for normal distribution of residuals and lack of trend or heteroscedasticity in plots of residuals over day of year, land use, and the fitted values. I additionally checked for multicollinearity as a Variance Inflation Factor exceeding a maximum recommended value of 5 (Zuur *et al.*, 2009). In order to understand the overall effects of different model terms, I conducted a log-likelihood comparison of each model in which I sequentially removed the second-order polynomial day-of-year term, the interaction between the first-

order day-of-year and land use terms, the first-order day-of-year term, the land use term, and the year term, and compared AIC values.

Traits and taxonomic families. I tested for different trait and family compositions across land use types using fourth corner tests (R package *ade4* (Dray & Dufour, 2007)). The fourth-corner test calculates the correlation between species' traits and the average environmental conditions of sites occupied by each species (i.e. the level of association of a species with each of the three categorical land use types), weighted by species' abundances (Dray & Legendre, 2008). I then tested the significance of the observed trait-environment correlations by randomizing land use type across replicate sites. This null model is sufficient to determine if different land use types have different trait compositions, which is my main question. However, randomly assigned null traits may produce similar trait-environment correlations that reflect other compositional differences between land use types, including differences in richness, species pool sizes and species abundances. In order to interpret my observed changes in trait composition as evidence for ecological links between land use and traits *per se*, I used a second null model randomizing trait states across species. I used 59,999 randomizations and only interpreted correlations between traits and land use types (or taxonomic families and land use types) if they were significant in both null model tests (Braak *et al.*, 2012).

In order to visualize trait composition, I calculated the community weighted mean (CWM) of each of the six trait values across species within each site. CWM is simply the mean of trait values across species weighted by the relative abundance of each species.

The patterns identified through fourth-corner testing were qualitatively the same as patterns identified by using an ANOVA F-statistic to summarize the response of CWM traits to land use type, and using combined site and species permutations for null significance testing (results not shown). To visualize family composition, I plotted the average proportional abundance of bee families across sites within each land use type.

Rare species. A land use type will have greater conservation value if it supports more rare species, either by having higher numbers of rare species in an average site (richness) or by having more total species pooled across sites. The total number of rare species supported by different land use types is a key question for conservation; however, we currently lack tests for comparing the total number of species between land use types (Socolar *et al.*, 2015), particularly when samples are sparse as is the case for rare species. Therefore, in this paper I focused on site-level richness of rare species. As a preliminary exploration, I also present and qualitatively compare the total numbers of rare and common species in each land use type.

To compare the richness of bees in each rarity class across land cover types, I fit generalized linear models with Poisson error distributions using the same techniques described above for analyses of overall abundance and richness. As for the traits analyses, I considered it likely that rarity groups could have higher richness in one land use due to chance drawing of species subsets, rather than to ecological links between rarity groups and land use. I used a simple randomization to test for this possibility for each rarity group in which the generalized linear models produced significant

relationships. Specifically, I calculated new richness values for each site from a random sample of species of the same size as the rarity group, and then recalculated model coefficients using these new values as the response variable. This resampling procedure is equivalent to permuting rarity group assignments across species. I iterated this process 999 times and constructed distributions of the resulting model coefficients describing the log ratio of species in anthropogenic habitat to species in forest. Finally, I checked that coefficients estimated from my actual data were larger or smaller than 95% of randomly generated coefficients (two-tailed test).

Results

Abundance and richness.

Land use had significant effects on per-site abundance ($p = 0.02$; log likelihood ratio test) and species richness ($p = 0.003$). Average site abundance in forest, agriculture and urban landscapes was estimated at 493.3, 300.4, and 348.7 specimens, with the difference between forest and agriculture being significantly different (odds ratio = 0.61, $p = 0.005$) and the difference between forest and urban barely significant (odds ratio = 0.71, $p=0.051$). Average site richness was estimated at 59.5, 44.4, and 48.5 species, with significant differences between both anthropogenic landscapes compared to forest (agriculture odds ratio = 0.75, $p = 0.0004$; urban odds ratio = 0.82, $p = 0.012$).

Forest and anthropogenic landscapes differed strongly in how abundance and richness changed within sites throughout the growing season. For abundance in forest, the coefficient on the first-order Julian day-of-year term (doy) was negative, while the coefficient on the second-order term (doy^2) was positive, indicating a convex polynomial relationship with Julian day-of-year (Table 1). The larger magnitude of the first-order coefficient compared to the second-order coefficient indicated an early peak in abundance. Correspondingly, the plotted relationship shows that abundance in forest peaked at the earliest sample dates in April - May, declined rapidly during early summer and remained low for the rest of the year (Figure 2). In both agriculture and urban habitat, coefficients on doy were positive, while coefficients on doy^2 were negative, and the difference in magnitudes between the two coefficients were relatively small, indicating a concave relationship with more centrally located peak. The plotted relationships for agriculture and urban landscapes show abundance increasing from spring to peak in mid-summer (July-August) before declining through late summer and fall. Richness followed the same temporal patterns as abundance (Table 1, Figure 2).

Traits and taxonomic families

Of the six life history traits I examined, three were significantly correlated with land use: sociality ($r = 1297$, $p = 0.0008$), nest construction ($r = 931$, $p = 0.005$), and flight season ($r = 3385$, $p = 0.00002$). Agriculture and urban communities tended to have high proportions of social, ground-nesting, and long flight season species, while forest communities had high proportions of solitary, cavity-nesting, and short flight season species (Figure 3, Table S5). Body size was significantly smaller in urban land use ($r = -$

0.29, $p = 0.01$). Proportions of oligolectic bees were too low and variable to detect significant trends; oligolectic bees comprised an average of 8% (and never more than 17%) in agricultural communities, versus less than 5% in most forest and urban communities.

Parasitism was not significantly correlated with land use; however, the community weighted means plot clearly showed that all agriculture and urban communities consistently had very low proportions of parasites (close to the 0% bound), while forest communities were almost 20% parasitic on average (Figure 3). I therefore conducted an additional fourth-corner test using Pearson's homogeneity of variance statistic (instead of the correlation), to confirm that the low incidence of parasitism in anthropogenic landscapes was more consistent than expected under the null (agriculture $X^2 = 0.06$, $p = 0.003$; urban $X^2 = 0.1$, $p = 0.04$).

Overall, family identity was correlated with land use ($p = 0.006$; Figure 3). Forest sites hosted roughly equal proportions of bees in the Andrenidae, Apidae, Halictidae, and Megachilidae (about 20% each of specimens in the average community). Relative to forest, agriculture sites had higher proportions of Halictidae (50%), while urban sites had reduced proportional abundance of all families except for Halictidae (60%). Only the link between Halictidae and urban land use was significantly different from null expectations (Figure 4, Table S5)

Rare species

Of the 443 species for which rarity was defined using the museum data set, I recaptured 38 species in the rarest frequency quartile, and 42, 62, and 86 species in the second, third, and fourth quartiles. Within each rarity class, forest had the largest total numbers of species within each land use type; this difference was most apparent in the second-quartile rarity class (Figure 5a). The number of species that occurred only in agriculture or urban habitat was fairly constant across rarity classes (from rarest to most common, 15, 9, 15 and 13; see the difference between gray and green points in Figure 5a); however, this necessarily represented a decreasing percentage of species found only in anthropogenic habitat (from rarest to most common groups; 39%, 21%, 24% and 15%).

Generalized linear models found significant decreases between richness in anthropogenic versus forest landscape for all but the rarest species group (Table 2, Figure 5b). However, only the decreases observed within the second quartile rarity group were significantly smaller than expected based on null models that randomize rarity across species ($p < 0.002$; 2-tailed test on 999 randomizations). The negative effects of anthropogenic land use on richness in the two more common species groups were not distinguishably different from effects of land use on richness within random species groups of the same total sizes.

Discussion

I found that eastern North American forests support highly abundant and diverse bee communities that are dominated by solitary spring ephemeral species and their associated brood parasites. These communities are being replaced in agricultural and urban landscapes by long flight-season, social species. These trait shifts are accompanied by changes in overall community phenology, from a narrowly peaked, springtime distribution of abundance and richness in forest communities, to a flatter distributions with a peak in mid-summer in agriculture and urban communities. Together, these changes in species traits and community phenology suggest that a major driver of ecological change between forest and open anthropogenic habitat is the removal of the summertime forest canopy, which imposes a strong temporal resource constraint on the growth and reproduction of understory herbs and associated pollinators (Motten, 1986; Ten Brink *et al.*, 2013). This result was foreshadowed by a recent study in a dry oak savannah system, which found longer and later periods of peak bee abundance in anthropogenic landscapes, likely driven by increased water availability due to irrigation of crops and gardens (Leong *et al.*, 2015). These findings in different ecosystems support the hypothesis that removing temporal constraints on resource availability is a general mechanism for how human land use affects pollinator communities in diverse environments (Mandelik *et al.*, 2012; Neil *et al.*, 2014; Harrison & Winfree, 2015; Leong *et al.*, 2015).

Historical context for bee phenology

Forest is the dominant natural habitat in the northeastern United States, and covered most of the landscape before the expansion of European settlements (Rudel *et al.*, 2005). What then are the origins of the open-habitat associate species, the great majority of which are native to the northeastern region? Many species that colonize contemporary anthropogenic open habitat may have evolved as forest gap and meadow specialists before finding themselves pre-adapted to the early-successional conditions common in anthropogenic habitats (Klemm, 1996). Other species are distributed throughout the North American continent and originally evolved in other biogeographic regions that are naturally open; for example the squash specialist *Peponapis pruinosa*, which evolved in the southeastern US and Mexico but is now common in northeastern agricultural landscapes due to widespread cultivation of its preferred host plant (Cane *et al.*, 2016).

Trait composition

The altered community composition and trait prevalence that I found in disturbed landscapes may well be driven by phenological changes. Many species of forest bees have short and early flight seasons that match the availability of spring forest flowers (Ginsberg, 1983), and some of these bee species are specialized on spring ephemeral flowers such as *Claytonia*, *Viola*, and *Erythronium* (Fowler, 2016). In contrast, the bees I sampled in agriculture and especially urban habitat tended to have longer flight seasons; these included high abundances of many social and thus multivoltine halictids such as *Lasioglossum pilosum* and *Halictus ligatus*. Agricultural landscapes contained

occasionally high abundances of *Melissodes* and *Peponapis* species that specialize on summer-blooming agricultural plants, sunflowers (*Helianthus*) and squash (*Pepo*).

The success of brood parasites in forest habitat may also be linked to the springtime phenology of forest understory, since the synchronous emergence and reproductive activity of host species in highly seasonal habitats appears to be a condition in promoting evolution and persistence of parasitic life histories in bees and other hymenopterans (Weislo, 1981). Parasitic species are a natural part of bee communities, represent a large portion of regional and global bee biodiversity (Litman *et al.*, 2013), and may be effective pollinators because they do not hoard pollen. The loss of parasitic taxa in anthropogenic habitats therefore represents an important loss for regional bee biodiversity.

Rare bees

I found some evidence that forest is particularly important for supporting regionally rare bee species, compared to anthropogenic habitat. First, I found that forest supported higher abundance, and the numbers of both rare and common species tended to be correspondingly higher. This suggests that rare species were more detectable in forest habitat due to higher overall population abundances, which is an important way for a habitat to contribute to rare species biodiversity. Second, I found that forest had significantly higher numbers of an intermediately rare species category than could be explained by the overall richness and abundance differences between land use types. As far as I am aware, this is the first evidence that land use change negatively affects a suite

of regionally rare bee species in North America, and the first such study anywhere focusing on forest-open habitat transitions. Previous studies have shown effects of land use on single declining species (Wray & Elle, 2014), or have been conducted in European countries where natural habitat is mostly open due to long history of human land use (Baldock *et al.*, 2015; Scheper *et al.*, 2015).

At the same time, I cannot rule out the possibility that agriculture and urban habitat also support large proportions of regionally rare species. Although I recaptured 38 of the rarest species identified in the regional dataset, these species were distributed thinly across the 36 sites, producing statistically indistinguishable richnesses of 2-3 species per site in each of the three land use types. Furthermore, almost half of these rarest species were collected only from agriculture or urban sites. As for common species, it is likely that rare species include both forest-associated and open-habitat associated species. In other taxa, open anthropogenic habitat support many rare species, especially in regions that have historically lost large amounts of forest habitat (Foster & Motzkin, 2003).

My definition of species rarity as incidence in a regional museum dataset integrates across different forms of rarity, including range size, population number or local dominance, and specialization on narrow range of habitats or resources (Rabinowitz, 1981). Species will be included in my definition of rarity for a number of different reasons. Flower specialists, habitat specialists, and bees that have short flight seasons may appear rare if their preferred plants, habitats, or seasons are poorly sampled. Parasitic bee species may appear rare if they visit flowers less frequently (since females

do not need to provision nests). And finally, some species may be at their range edge in the region, and appear rare despite being common elsewhere. These are all valid reasons to be rare within an area of interest, and furthermore, they are often highly correlated, so regional incidence is an appropriate proxy (Hercos *et al.*, 2013). Distinguishing among different forms of rarity is an important goal for future research, especially if they are associated with different vulnerability to global change (Harnik *et al.*, 2012); however this will require overcoming several shortfalls in the available data on bee species ranges, habitat preferences and local abundances across large geographic extents (Cardoso *et al.*, 2011).

Conclusions for biodiversity conservation

My results show that land use change has negative effects on species diversity, rare species, and the persistence of life history strategies that indicate adaptation to the conditions in forest, the dominant native habitat for the northeastern US. My findings contrast with most previous studies that have found higher total bee abundance in anthropogenic habitats compared to natural forest habitats worldwide (Winfree *et al.*, 2011). The importance of forest as habitat for a highly productive and functionally distinct community of native bees may have been overlooked for three reasons. First, the forest bee community needs to be sampled very early in the year (April – early May). Second, the importance of bees as crop pollinators has focused the great bulk of pollinator research on open agricultural habitats. Third, there exists a European research bias where much natural habitat is open due to a long history of intensive deforestation and grazing (Rudel *et al.*, 2005; Baldock *et al.*, 2015; De Palma *et al.*, 2015). Because of

the distinct habitat and temporal niche occupied by forest bee communities, it is likely that this group requires specialized attention currently lacking in pollinator restoration efforts, which typically involve planting summer-blooming meadow flowers in agricultural landscapes (Vilsack & McCarthy, 2015; Hicks *et al.*, 2016). Plans that aim to conserve wild native bees in northeastern North America, and probably in other temperate forest regions, should incorporate efforts to protect forest habitat and prevent or reverse forest degradation that reduces native spring-blooming understory plants.

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Tables and Figures

Table 1. Coefficients from generalized linear mixed models testing how anthropogenic and forest landscapes differ in how abundance and richness changes throughout season within sites (site is included models as a fixed effect). All coefficients on day-of-year variables (doy and doy^2) in agriculture and urban are significantly different from forest; however the model intercepts, which correspond to log average abundance or richness throughout the year, do not differ between anthropogenic and forest landscapes.

Model	Land use	Equation
Abundance	Forest	$2.85 (0.13) - 16.6 (1.47) doy + 7.6 (1.49) doy^2$
	Agriculture	$2.8 (0.15) + 11.9 (2.09) doy - 16.1 (2.05) doy^2$
	Urban	$3.0 (0.15) + 16.6 (2.09) doy - 12.9 (2.06) doy^2$
Richness	Forest	$2.0 (0.07) - 11.7 (0.62) doy + 1.4 (0.57) doy^2$
	Agriculture	$2.0 (0.09) + 8.8 (0.88) doy - 6.6 (0.80) doy^2$
	Urban	$2.1 (0.09) + 12.3 (0.84) doy - 5.5 (0.78) doy^2$

Table 2. Exponentiated coefficients from generalized linear models showing the effects of land use on species richness within four species rarity groups. Models with significant overall effect of land use on group richness are highlighted in gray. Since forest was used as the model intercept, the coefficient values are the expected species counts for a typical forest site. For the anthropogenic land uses, coefficient values are the odds ratios between species counts in a typical agriculture or urban site versus a typical forest site. Therefore, coefficients less than 1 indicate an expectation for fewer species in a particular rarity group, as compared to forest.

Rarity group	X ² p		Forest (Int.) p		Agriculture Coef p		Urban Coef p	
0-25%	1.98	.372	3.1	.0001	0.70	.168	0.81	.393
25-50%	26.5	.0001	7.4	.0001	0.40	.0001	0.52	.0003
50-75%	14.4	.0007	13.3	.0001	0.63	.0002	0.76	.020
75-100%	8.56	.014	32.5	.0001	0.89	.0097	0.80	.037

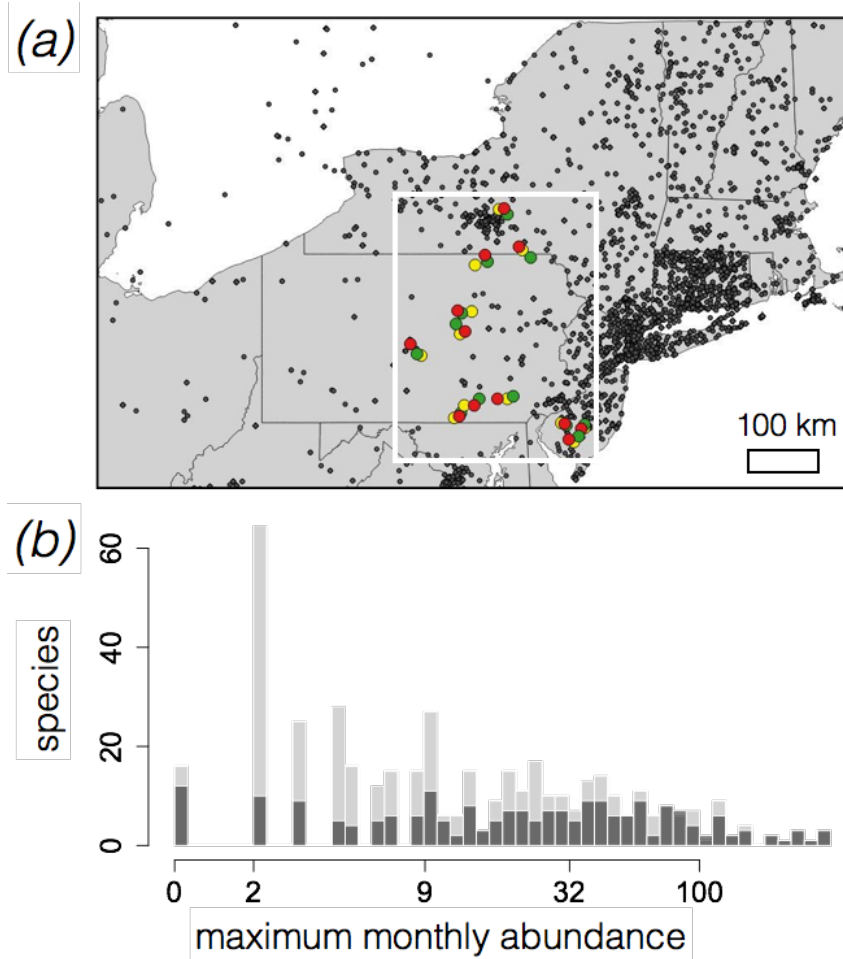


Figure 1. (a) Geographic distribution of 12,003 museum specimen records used to assess rarity for bees in the northeastern US (small dark points). In order to associate bee rarity with different habitat types, I collected intensive community samples from 36 sites in forest (green points), agricultural (yellow) and urban (red) landscapes. (b) Frequency distribution of the maximum monthly abundances of 443 species in the museum data set used to define species rarity classes based on the 25th, 50th, and 75th percentiles (light gray bars; x-axes values mark percentile boundaries). Dark bars identify the 228 native species observed in my community data set.

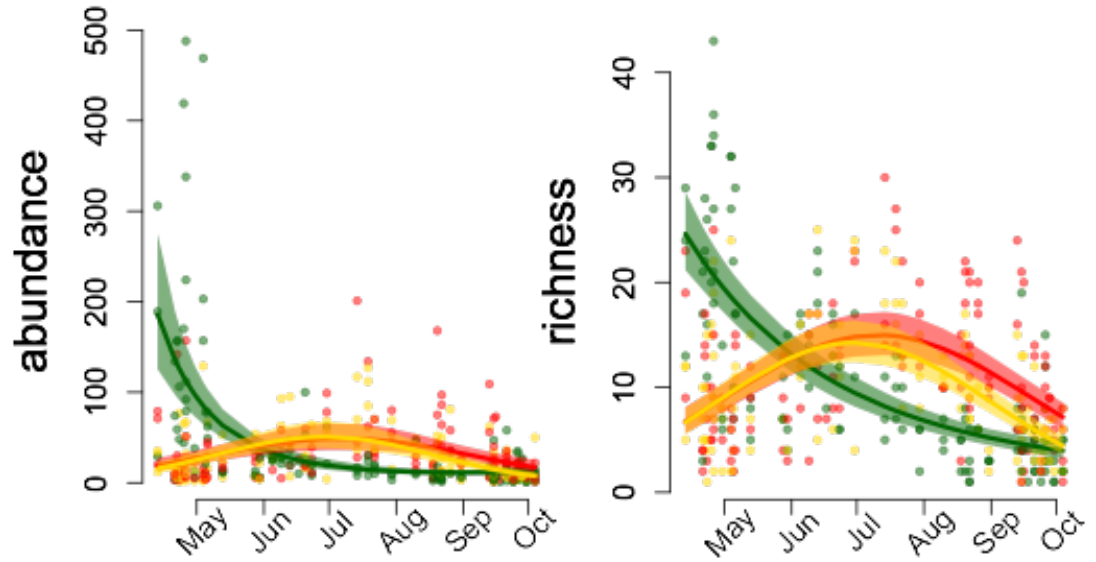


Figure 2. Abundance and species richness of bees change throughout the season differently within forest sites (green) versus within agriculture and urban sites (yellow and red). Each point represents one site-visit ($N = 36$ sites visited 11 times). Fitted model curves are surrounded by calculated 95% confidence intervals.

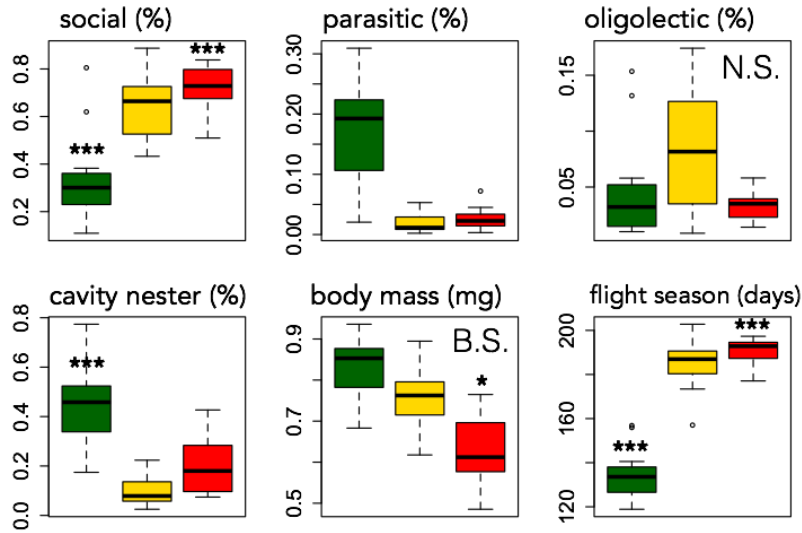


Figure 3. Community weighted mean (CWM) values of six traits for bee communities from forest (green), agriculture (yellow) and urban (red) land use. For continuous traits (phenology and body size), CWM represents the average trait value across species present at a site, weighted by species abundance. For the remaining four binary traits, CWM represents the proportion of individual bees at a site expressing one of the two possible trait states (social versus solitary, parasitic versus pollen-collecting, oligolectic versus polylectic, and cavity nester versus excavator). Asterisks indicates significant associations between a trait state and a land use type, as determined by fourth-corner tests. See text for the statistical interpretation of the parasite result.

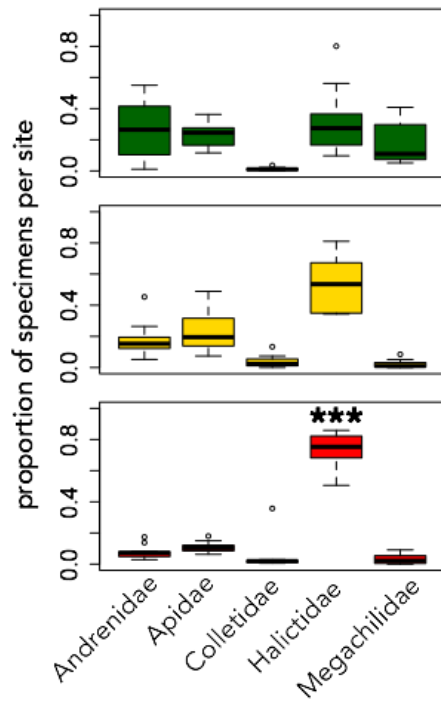


Figure 4. Composition of bee communities in forest, agriculture and urban habitats differ in the proportional abundance of taxonomic families. In permutational fourth-corner tests, only the association between Halictidae and urban landscapes was greater than expected by chance ($p = 0.0008$).

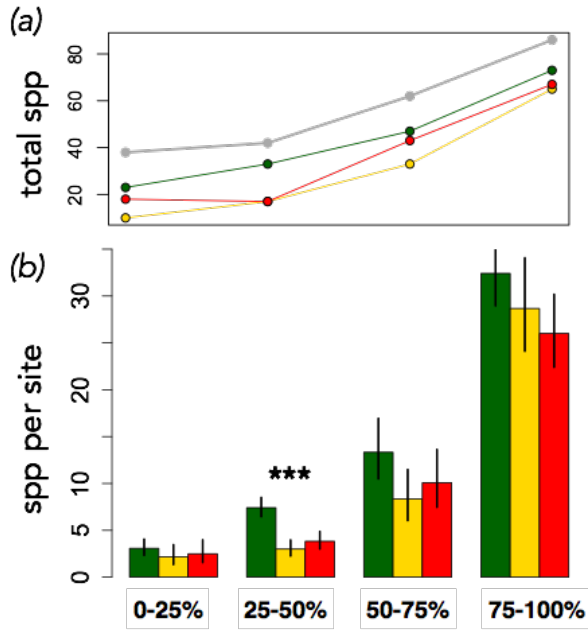


Figure 5. (a) Total numbers of species observed in four species rarity groups, for three land use types (forest - green; agriculture - yellow; urban - red) and for the total community data set (gray points). (b) Estimated richness (number of species per site) in forest, agriculture and urban landscapes, within four species rarity groups determined by species' occurrence in a large museum data set. Whiskers show 95% confidence intervals around richness estimates. Asterisks indicate significant differences between richness in anthropogenic versus forest landscape. Species' rarity is determined by species' occurrence quartiles in a large museum data set.

Supplementary Tables and Figures

Table S1. Species traits used in analysis. Parasitic species are obligate brood parasites that invade other species' nests and deposit offspring, which will then host brood's pollen stores (and sometimes the host brood). The "social" category includes 14 facultatively social species. Column "Values" shows the number of species in each binary trait state or the range of values and units for continuous traits. Column NA displays the percent of total specimens in the community belonging to species with missing values for a trait.

Trait	Values	NA
Parasitic	Yes (37); No (208)	0.0%
Sociality	Social (70); Solitary (169)	0.3%
Lecticity	Oligolectic (35); Polylectic (199)	0.1%
Nest construction	Excavator (152); Non-excavator (88)	0.6%
Body mass	Dry body mass (range 1 - 165 mg)	8.5%
Flight season length	Range of Julian day-of-year of capture (18 - 160 days)	2.2%

Table S2. Pearson's r correlations among the six bee traits. Flight season and sociality are correlated in most data sets because social species have multiple generations which requires a longer period of seasonal activity.

	Social	Parasitic	Specialist	Excavator	Body mass
Parasite	-0.26				
Specialist	-0.27	-0.14			
Excavator	-0.29	0.50	-0.15		
Body mass	-0.18	-0.15	0.13	0.33	
Flight season	0.61	-0.24	-0.34	-0.21	-0.11

Table S3. Studies used to calculate bee phenology were chosen because their sampling effort was distributed across a broad seasonal range and included multiple plant species. All data sets were collected, curated and identified to species level by same professional taxonomists in the Winfree lab, except for Droege *et al.* which was collected and identified by Sam Droege and associates at the United States Geological Survey - Patuxent Wildlife Research Center.

Citation	Study description	Years	Spatial extent	Specimens	Species	Locations
[1]	museum dataset, rarefied to remove sampling bias among species	1970 - 2011	NJ, NY and PA	9760	335	552
Cariveau et al. <i>unpublished</i>	pollinator restoration plantings in meadow/old field habitat	2011 – 2014	NJ	9275	149	29
[2]	pollinator restoration planting experiment	2010 - 2013	NJ	8286	84	1
[3]	deciduous forest fragments in urban and agricultural matrix	2006 - 2007	NJ	4322	113	20
Droege et al. <i>unpublished</i>	USGS bee monitoring	1992 – 2011	NJ, NY and PA	3500	142	112
[4]	pine barrens forest fragments in urban and agricultural matrix	2003	NJ	2557	133	44

Totals 42552 379 783

- [1] Bartomeus, I., Ascher, J.S., Gibbs, J., Danforth, B.N., Wagner, D.L., Hedtkke, S.M. & Winfree, R. (2013) Historical changes in northeastern US bee pollinators related to shared ecological traits. *Proceedings of the National Academy of Sciences*, **110**.
- [2] MacLeod, M., *MA Genung, J Ascher, R Winfree. Measuring partner choice in plant–pollinator networks: Using null models to separate rewiring and fidelity from chance. *Ecology* (accepted).
- [3] Winfree, R., Fox, J.W., Williams, N.M., Reilly, J.R. & Cariveau, D.P. (2015) Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters*, **18**, 626–635.
- [4] Winfree, R., Griswold, T. & Kremen, C. (2007) Effect of human disturbance on bee communities in a forested ecosystem. *Conservation Biology*, **21**, 213–23.

Table S4. AIC model selection results used to determine the overall importance of different terms in the full models predicting bee abundance and richness in different land use types and seasons. Significant chi-square values are bolded.

predictor variables included in model	df	Chi-squared values	
		abundance	richness
year + site	2	719.6	104.2
lu + year + site	2	4.9	2.4
lu + DOY + year + site	1	2533.2	218.2
lu + DOY + lu:DOY + year + site	2	2956.1	296.1
lu + DOY + DOY ² + lu:DOY + lu:DOY ² + year + site	3	8580.7	670.9

Table S5. Fourth-corner statistics (correlation estimate, standard deviation and p-value) for association between trait states and land use type, or between taxonomic family and land use type. Significant negative associations are highlighted in blue; positive associations in red.

		r	SD	p	
Social	fo	-0.43	-2.94	0.00134	***
	ag	0.09	0.74	0.50158	
	ur	0.36	2.95	0.0009	***
Parasites	fo	0.26	1.90	0.05366	
	ag	-0.14	-1.39	0.14092	
	ur	-0.14	-1.19	0.2441	
Oligolects	fo	-0.03	-0.24	0.81816	
	ag	0.11	1.24	0.22276	
	ur	-0.07	-0.56	0.60152	
Non excavators	fo	0.39	2.71	0.00362	***
	ag	-0.21	-1.53	0.10222	
	ur	-0.21	-1.59	0.08642	
Body mass	fo	0.22	1.54	0.12708	
	ag	0.06	0.67	0.51194	
	ur	-0.29	-2.38	0.01128	*
Flight season	fo	-0.63	-4.24	0.00002	***
	ag	0.27	1.81	0.05872	
	ur	0.40	2.65	0.00218	***
Andrenidae	fo	1053	-0.34	0.75342	
	ag	485	-0.65	0.52938	
	ur	216	-1.45	0.1361	
Apidae	fo	1075	0.58	0.5928	
	ag	609	0.06	0.95716	
	ur	326	-1.05	0.30476	
Colletidae	fo	36	-0.86	0.28062	
	ag	113	0.31	0.8685	
	ur	148	-0.07	0.96936	
Halictidae	fo	1027	-0.97	0.35786	
	ag	1564	-0.50	0.62868	
	ur	2486	3.15	0.00078	****
Megachilidae	fo	902	0.73	0.48798	
	ag	46	-1.47	0.1107	
	ur	88	-1.26	0.19586	

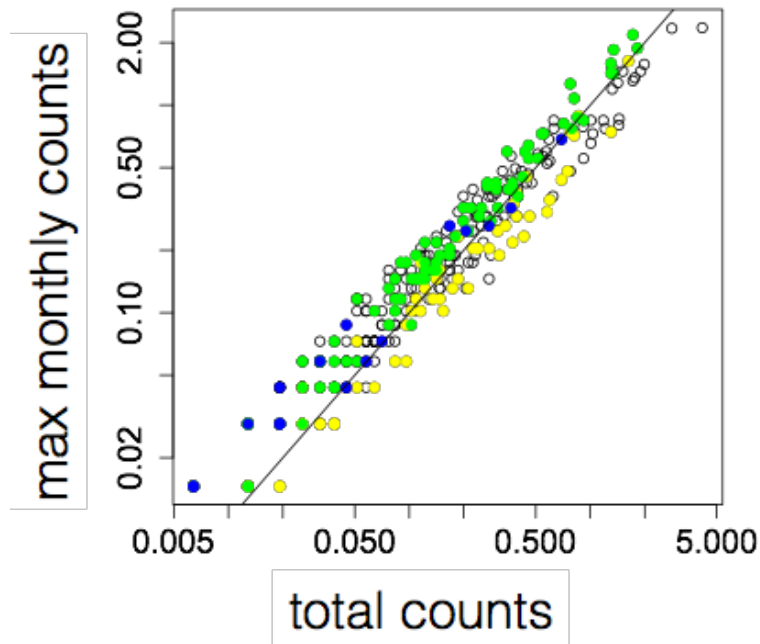


Figure S1. I defined bee rarity using occurrences of species in a regional museum data set. Instead of using the total number of specimens for each species in the dataset (“total counts”), I used the maximum number of specimens found within one month of the year (potentially including many years; “max monthly counts”). The axes are scaled by total counts across species and log-transformed to aid visualization. Species’ points lie close to the 1:1 line, indicating that the two methods produce similar results. However, two genera characterized by short flight seasons, *Andrena* and *Osmia* (green and blue points), consistently fall above the 1:1 line, indicating that the maximum monthly counts does appear to somewhat correct for rarity due to short flight season lengths. Similarly, *Lasioglossum* (yellow points) includes many long flight season, social species, and their numeric dominance has generally been downweighted (yellow points below the 1:1 line). I conclude that using maximum monthly counts is helpful for correcting for phenological effects on perception of species’ rarity.

CHAPTER II. LAND USE CHANGE CREATES WINNERS AND LOSERS BUT NOT SPECIES HOMOGENIZATION IN BEE COMMUNITIES

Abstract

Land use change produces changes in ecological communities that cannot be detected by analyzing species diversity alone. In particular, the biotic homogenization hypothesis states 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 large spatial scales and at multiple levels of ecological organization. I 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. I particularly aim to understand the role of individual winner and loser species in creating overall beta diversity patterns. I sampled bee communities from replicated sites in forest, agriculture and urban land use types within a large spatial extent spanning four distinct ecoregions. I compared community composition and pairwise compositional dissimilarity within and between ecoregions, using both species and phylogenetic dissimilarity indices. I used a jack-knife method to isolate the contributions of individual species to overall beta diversity patterns. I found large differences in species and phylogenetic composition between forest and anthropogenic land use types. Additionally, anthropogenic land use was associated with strong phylogenetic homogenization, at both within- and between- ecoregion scales. Inspecting the contributions of individual species revealed that winners had both

homogenizing and differentiating effects within anthropogenic land use types. Urban and agriculture land use produce shifts in bee composition and loss of phylogenetic beta diversity across a large regional extent. Measuring multiple community responses, and in particular tracking identities of winner and loser species, are important tools for detecting biotic homogenization caused by land-use driven changes in species composition.

Introduction

The conversion of natural habitats to agriculture and urban land 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 current knowledge is based on studies of local species richness, or alpha diversity (McGill et al., 2015). However, species richness does not capture two major responses that provide critical insight into how land use change affects biodiversity. First, land use change is associated with change in community composition, in which the loss of species sensitive to land use change, or “losers”, is compensated for by positive responses of “winner” species. At local scales, the process of winners replacing losers tends to buffer against richness declines (Supp & Ernest, 2014), or produces highly variable richness trends (Dornelas et al., 2014). Second, land use change is associated with changes in species similarity among communities (beta diversity). Beta diversity is a critical counterpart to alpha diversity for assessing how land use affects diversity at the large regional scales relevant for preserving species (Socolar et al., 2015).

Biotic homogenization is a hypothesized worst-case scenario in which a few widespread, disturbance-adapted winner species replace many sensitive, endemic loser species, thus driving beta diversity loss among historically distinct communities (McKinney & Lockwood, 1999). Biotic homogenization has profound effects on ecosystem properties and biodiversity (Olden, 2006). Winners may represent small non-random subsets of species traits and phylogenetic lineages (Clavel et al., 2011; McGill et al., 2015), which may result in loss of ecosystem functioning (Gagic et al., 2015; Wolf & Zavaleta, 2015) and of evolutionary diversity (Winter et al., 2009). Loss of beta diversity can result in regional biodiversity loss, even in cases where local richness has increased (Smart et al., 2006). At present, however, the biotic homogenization hypothesis is a broadly defined verbal concept, and researchers have employed a wide range of approaches for testing it, thereby producing many interesting cases but few generalizable conclusions (Olden, 2006).

The existence of winners and losers in response to land use change does not necessarily result in beta diversity loss (Figure 1a), and beta diversity has other drivers not directly related to the existence of winners and losers (Figure 1b; Burkle et al., 2015). Therefore, testing the biotic homogenization hypothesis requires first testing if winners are replacing losers, and second, testing if the distribution of winners relative to losers is driving beta diversity loss. The early biotic homogenization literature achieved this by defining winners as invasive species and comparing community similarity before and after their introduction (Marchetti et al., 2006), and key insights have been made by recent papers

following in this tradition (Harris et al., 2011; Villéger et al., 2011; Baiser et al., 2012; Toussaint et al., 2016). However, the winners in a land use change scenario are commonly native species from local and regional species pools (Tabarelli et al., 2012; McCune & Vellend, 2013; La Sorte et al., 2014). Identifying winners and losers of land use change is challenging for diverse taxa with poorly known habitat preferences, such as insect pollinators (Winfree et al., 2011). This may explain why, despite its critical importance to predicting global biodiversity loss, very few studies have explicitly assessed the role of winner and loser species in beta diversity loss associated with land use change (McCune & Vellend, 2013).

Change in beta diversity associated with land use must be defined against a baseline of natural heterogeneity. Since natural communities tend to be less similar when compared across increasing geographic and environmental distance (Soininen et al., 2007), there is more scope for detecting biotic homogenization when data are collected across larger scales. In contrast, when land use gradients are studied at smaller scales, patterns of compositional change can be complex and produce both homogenization and differentiation (Figure 2). Surprisingly few studies have tested for biotic homogenization in response to land use change at multiple spatial scales, despite long-standing calls to do so (Olden & Poff, 2003). Biotic homogenization in response to land use change can occur at both small and large (regional) scales, when there are widespread winner species with high dispersal abilities (Tabarelli et al., 2012; Solar et al., 2015). Differentiation could likewise occur at large scales, for example if human land use has divergent effects in different places (Laurance et al., 2007), or if beta diversity increases due to dispersal

limitation caused by habitat fragmentation (Arroyo-Rodríguez et al., 2013).

Differentiation also occurs at small scales when intensive land use strongly reduces local abundance and richness, causing species identity of the remaining individuals to vary stochastically across sites (Karp et al., 2012).

Biotic homogenization is most frequently measured using species as units, in which case it is known as taxonomic or species homogenization (Olden & Rooney, 2006). In this analysis each species is allowed to contribute equally to compositional difference between two sites, so that a pair of closely related and ecologically similar species represents the same diversity as two species from divergent clades with different ecological roles. Phylogenetic homogenization can reveal homogenizing effects of land use that might be obscured by using taxonomic measures alone (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 may capture similar patterns to trait homogenization, since species traits tend to be phylogenetically correlated (Webb et al., 2002; Winter et al., 2009). Furthermore, phylogenetic homogenization implies human-driven loss of evolutionary diversity, which is a primary conservation concern (Vamosi & Wilson, 2008; Frishkoff *et al.*, 2014).

Here I ask if land use change is associated with biotic homogenization at two ecologically meaningful spatial scales, by comparing community composition and compositional heterogeneity (beta diversity) of bee pollinators between baseline forested sites and the

two major anthropogenic land use types, agricultural and urban. To explore the role of winner-loser species replacement in beta diversity change, I examined how the distributions of individual winner and loser species contributed to differences in compositional heterogeneity between natural and anthropogenic land cover types. My study taxon was wild bees, which are both diverse, with over 500 species in the region, and essential to ecosystem function as the main pollinators of flowering plants (Ollerton et al., 2011). Because non-native bees constitute a small minority of the fauna (8% of specimens collected; Figure S1), my study design largely isolates land use change as the driver of biotic homogenization, as opposed to the better studied driver of species invasion. I established a replicated, nested study design for sampling bee communities in three land use types within four northeastern USA ecoregions, thus covering a spatial extent of roughly 75,000 km², and resampled the same 36 sites for three years. I ask three questions:

- (1) Is land use type associated with consistent differences in community composition, indicating winners and losers resulting from land use change?
- (2) Does beta diversity (compositional dissimilarity between sites) differ by land use type?
- (3) How important are winner and loser species in driving biotic homogenization?

For each question I distinguish between the smaller within-ecoregion scale and the larger between-ecoregion scale, and between the units of species versus phylogenetic distance.

Methods

Study design

I designed a regional-scale study containing 36 sites divided among three land use types (forest, urban and agriculture) and spatially grouped in twelve blocks (Figure 3). The sites were located in four different ecoregions, as defined by USGS Level III classification, which is based on geology, climate and vegetation (Omernik, 1987). The ecoregions are, from southeast to north, Atlantic Coastal Pine Barrens, Northern Piedmont, Ridge and Valley, and Northern Allegheny Plateau. I quantified agriculture, urban, and forest land cover in ArcGIS using the USGS 2006 National Land Cover Database (30 meter resolution), and selected sites for which one of these three land cover types constituted $\geq 80\%$ of the surrounding land cover at a 1500 m radius. This design makes it likely that the bees I 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 1500 m from their nests (Greenleaf et al., 2007).

Data collection

I 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, I 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, and therefore flowers in the immediate vicinity of my traps could bias my collection rates either positively or negatively, I standardized this variable by placing all of the pan traps

in patches of mowed grass (100 - 5000 m², or 10 - 100 m wide when using a linear patch such as 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 100 - 500 m apart, which is too close to be independent; rather I pooled specimens from each site.

I sampled bee communities in spring, summer and fall, conducting one complete sampling round of all sites in 2-4 weeks depending on weather conditions. During spring rounds, I 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 I randomized ecoregion order, but modified this order as necessary to meet my weather conditions for data collection (sunny to partly cloudy, high temperature > 18°C, wind < 20 km per hour). In each sampling round, I set up traps at all 9 sites (36 sampling locations) in an ecoregion in one 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 hours, thereby capturing the full range of pollinator diurnal activity. At each of the four sampling locations within a site, I set a line of 6 pan traps spaced 1.5 meters apart, alternating white, blue, and yellow, and filled with soapy water (1 tsp blue Dawn dish soap dissolved in 1 gallon water). Additionally, I haphazardly chose 2 of the 4 of the sampling locations within each site at which to set up a blue vane trap (Springstar).

When collecting specimens, I 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 all specimens at Rutgers University. JG determined species identifications, except for genus *Nomada* which were determined by Sam Droege at the USGS Patuxent Wildlife Research Center. I had specimens from three unresolved species groups (bidentate *Nomada* species, *Nomada sayi-illinoense*, and *Hylaeus affinis-modestus*), which I treat as species in analysis. Other unresolved species represented 1% of specimens and were removed from analysis. Honey bees (*Apis mellifera*) are a managed species in the region and I therefore removed them from analyses as well (honey bees constituted < 5% of specimens).

No species-level phylogenies are available for the bee species of the study region. I therefore used a previously published genus-level bee phylogeny calculated from multiple protein-coding nuclear DNA sequences stored on GenBank (Hedtke et al., 2013; Figure S2). I replaced genus branch tips with species polytomies of very short branch lengths.

Analytical Methods

I repeated all main analyses on two different site-by-site dissimilarity matrixes describing differences in communities' abundance-weighted species and phylogenetic composition. Abundance weighting puts focus on species that can be clearly identified as winners (anthropogenic associates) and losers (forest associates); I do not have the statistical power to infer the winner or loser status of rare species and therefore give them minimal opportunity to influence the results. I calculated species composition dissimilarity using the Morisita index, which detects turnover and richness differences of abundant species

between site pairs and performs well according to a number of criteria (Barwell et al., 2015). Morisita ignores both singletons (species represented by one specimen from one site) and doubletons. For phylogenetic composition dissimilarity, I first transformed the phylogenetic tree into a species-by-species matrix of pairwise branch distances between tips. I then calculated mean phylogenetic distance between the specimens of each pair of communities, effectively measuring the overall phylogenetic relatedness between two communities (R package picante). Because I am using a genus-level phylogeny, specimens of the same genus have a phylogenetic distance of 0. Therefore, the lowest values for mean phylogenetic distance between two sites will result from either shared abundant species, or unshared abundant species from the same genus.

I used a mantel test to assess Spearman's rank correlation between the species and phylogenetic dissimilarity matrixes, to determine how much novel information each community measure is capturing. If the matrixes are highly correlated and the results are concordant for species and phylogenetic-based analyses, I will not know which compositional aspect is most responsible for the overall pattern.

Is land use type associated with consistent differences in community composition, indicating winners and losers resulting from land use change? To test if land use is correlated with species or phylogenetic composition, I used two permutational analyses of variance using the site-site dissimilarity matrices as response variables (PERMANOVA; Anderson 2001). When used to analyze balanced study designs, PERMANOVA accurately detects differences in community composition among groups

of sites (Anderson & Walsh, 2013). I included ecoregion as a term in the model in order to establish that my study design captures species turnover at the between-ecoregion spatial scale. I additionally included the land use-ecoregion interaction term, in order to determine if winner and loser species are the same across ecoregions. To assess differences among factor levels, I conducted post-hoc contrast tests, choosing forest as the intercept against which to measure the effects of agriculture and urban land use. To find out how communities within a land use type differ across ecoregions, I chose the northern-most ecoregion (Figure 3) as the intercept against which to measure the effect of ecoregion on forest, urban, or agriculture community composition. Lastly, to visualize the results of all the tests of community composition, I created two non-metric multidimensional scaling plots showing community distances among sites, based on species or phylogenetic dissimilarity.

Does beta diversity (compositional dissimilarity between sites) differ by land use type, either within or across ecoregions? I define beta diversity using pairwise dissimilarity, and consider the land use type with the smaller mean pairwise dissimilarity (MPD) as being more compositionally homogeneous (Anderson et al., 2011). I prefer MPD as a measure of beta diversity because it is possible to use sites as statistical replicates. Furthermore, MPD is robust to the number of sampling sites, which can have a strong and unpredictable effect on multiple-site dissimilarity indexes or 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 $MPD = 0.5$ (mean proportion of unshared to total species). However, 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 (Socolar et al., 2015).

To check that the MPD analyses are not masking important differences in regional species pool sizes among the land use types, I present both total richness and effective species diversity (exponentiated Shannon diversity index) for each land use type as a preliminary analysis. Additionally, because strong richness differences between land use types could theoretically drive both composition and beta diversity results, I calculated effective species diversities (exponential Shannon diversity index) for all sites, and compared means among land use types using ANOVA.

If biotic homogenization is occurring within ecoregions, I expect that the mean dissimilarity calculated between pairs of sites in the same ecoregion is higher in forest than in urban or agricultural land use types. If biotic homogenization is occurring across regions (at a larger spatial scale), then I expect that the mean dissimilarity calculated between pairs of sites in different ecoregions to be higher in forest than in urban or agricultural land use types. Because pair-wise dissimilarities between all sites are not independent, I bootstrapped by randomly drawing subsets of dissimilarities such that

each site is only represented by one dissimilarity value per draw. For each draw, I calculate mean dissimilarity for forest, agriculture and urban pairs, and then use the results from 9999 such draws to calculate a bootstrapped mean and 95% confidence intervals. I interpret non-overlapping confidence intervals to indicate significant difference in mean pairwise dissimilarity between two land use types. These statistical methods are modified from a similar previously published analysis (Karp et al. 2012).

How important are winner and loser species in driving biotic homogenization? I define winners as species that are associated with anthropogenic land use, while losers are associated with forest. In order to classify bee species as winners and losers, I used a multinomial approach that tests if each species is significantly at least two-thirds more abundant in one land use relative to another (Chazdon et al., 2011; function “clamtest” in *vegan*). This test additionally includes a p-value adjustment to account for multiple comparisons. Species that are categorized as neither winners nor losers are either equally common in both forest and anthropogenic land use (habitat generalists), or are too rare for any difference to be detectable. I distinguished these groups from one another by applying post-hoc a simple rule, in which the abundances of the rarest significant associate is taken as the threshold abundance needed to detect a significant association for that land use type (Chazdon et al., 2011). I assume that unclassified species with abundances greater than this threshold are neither winners nor losers, but are indifferent land use change.

To assess the contribution of each species to compositional heterogeneity within a land cover type, I used a *jackknife* approach. I calculated a species' contribution as the original MPD among sites, less the MPD among sites calculated after removing the focal species. Species that have a homogenizing effect within a land cover therefore have a strong negative score, since the original MPD is lower than the MPD calculated without the species. Conversely, species that have a differentiating effect within a land cover have a strong positive score. I plotted species scores from urban and agriculture land cover against their scores from forest, and visually assessed the position of winner, loser, and generalist species. The contribution of a species to difference in compositional heterogeneity between forest and anthropogenic land cover types – that is, its potential contribution to biotic homogenization – is indicated by the distance of the species from the one-to-one line.

Results

In 3 years of sampling I collected 13,398 specimens of 248 species. Forest had the highest total number of species (186), followed by urban (163) and agriculture (136); however, forest and agriculture had similar numbers of effective species (46 and 45), and urban had the lowest (35). At the site level, mean effective species diversity was very similar (25, 22 and 21) and statistically indistinguishable among all three land use types; however, phylogenetic diversity was lower in urban sites than forest (Figure S3). The correlation between species and phylogenetic dissimilarity matrixes was significant but

low, indicating low redundancy between the two response variables (Spearman rank correlation $r = 0.44$, $p < 0.001$).

Species and phylogenetic composition both significantly differed by land use, although land use explained a much greater percent variation in species composition (40% vs. 14%; Table 3, first row of upper level). Contrast analysis showed that both species and phylogenetic composition differed between forest and each of the two anthropogenic land use types (Table 3, first two rows of lower level). Species composition differed significantly by ecoregion and by the land use-ecoregion interaction. The contrast analysis showed that both species and phylogenetic composition in forests differed between ecoregions, confirming that the spatial scale of the design was large enough to capture the increased potential for biotic homogenization at the larger scale. Species composition in agriculture and urban land use also differed between ecoregions, but phylogenetic composition did not, indicating that abundant species in anthropogenic land use are phylogenetically similar across different ecoregions (Table 3, lower level).

The relative effect sizes of land use and ecoregion on composition can be determined by comparing the mean squared errors of the PERMANOVA terms (Anderson et al. 2001). For both compositional measures, the effect of land use was several times greater than the effect of ecoregion: approximately 4x for species composition ($MSE_{lu} = 2$ versus $MSE_{eco} = 0.5$) and 2x for phylogenetic composition ($MSE_{lu} = 0.16$ versus $MSE_{eco} = 0.7$). Differences among land use types are clearly visible in the NMDS ordinations (Figure 4).

I found that differences in mean pairwise species dissimilarity between land use types were neither large nor significant, either within or between ecoregions (Figure 5, top row). However, I found strong homogenization results for mean pairwise phylogenetic dissimilarity, which was clearly lower in both agriculture and urban land use compared forest at both spatial scales (Figure 5, bottom row). Furthermore, MPD was lower in urban relative to agriculture. These results are also apparent in the narrow dispersions among agriculture and urban sites in the NMDS ordination of phylogenetic composition (Figure 4).

My analysis of species' preference for forest versus agriculture found 23 equivalently abundant species, 25 forest associates, 26 agriculture associates, and 143 species too rare to detect differences. The analysis of species' preference for forest versus urban found 23 equivalently abundant species, 27 forest associates, 22 agriculture associates, and 159 species too rare to detect differences. Inspecting the positions of winner and loser species on the bee phylogenetic tree revealed that winner and loser species were represented broadly across the genera-level phylogenetic tree, but losers (forest associates) were particularly rich in three genera from three different families, including *Andrena* and two genera with no winner species (*Osmia* and *Nomada*). Winners (anthropogenic associates) were noticeably richer in a single super-abundant genus, *Lasioglossum* (Halictidae; Figure S2).

Winner and loser species each contribute to homogenization and differentiation in all three land use types (Figure 6). Rare and generalist species were for the most part not

important in generating beta diversity patterns. Most species that had strong homogenizing effects in a land use within an ecoregion, also had strong homogenizing effects in that land use across ecoregions (compare Figure 6.a with 6.b, and Figure 6.c with 6.d). Likewise, species with a differentiating effect at one scale generally had a differentiating effect at the other scale. I found only one example of a species with strong and opposite effects at the two spatial scales: *Lasioglossum illinoense*, which homogenized urban sites at the within-ecoregion scale (Figure 6.c) but strongly differentiated urban sites at the between-ecoregion scale (Figure 6.d).

Discussion

I found strong winner-loser turnover across land use types, but it did not lead to species homogenization. Land use was associated with a strong pattern of winner-loser replacement, as indicated by both species-specific associations with different land use types and large shifts in community composition. In fact, the effect of land use on species composition was about four times larger than the effect of ecoregion, although the ecoregions span 370 kilometers and include distinctive vegetation zones. At the same time, I found no corresponding patterns of species homogenization or differentiation among land use types. This finding highlights the importance of separately evaluating the processes of winner-loser replacement and beta diversity change in studies of biotic homogenization.

There were consistent winners in anthropogenic land use types, but they had both homogenizing and differentiating effects. Jack-knife analysis showed that winner species differentiate pairs of anthropogenic sites about as often as they homogenize them. At the same time, ‘loser’ species typical of forested sites homogenize these sites about as often as they differentiate them. Non-native species are known to have both homogenizing and differentiating effects on recipient communities (e.g. Marchetti *et al.*, 2006); for example, more recent introductions tend to be differentiating within their new range (Harris *et al.*, 2011). To my knowledge, only one other study has separated differentiating and homogenizing effects of individual winners of land use change; they found that winners were homogenizing communities across the 330 km² study extent (McCune & Vellend, 2013). There is an expectation that winners of land use change should be generally homogenizing, since traits that confer advantage in disturbed habitat, such as small body size, high dispersal ability, and dietary generalism, also tend to confer a high occupancy rate among suitable sites (Tabarelli *et al.*, 2012). My results instead show that winners include both widespread and patchily distributed species, reinforcing the conclusion that winner-loser turnover should not be equated with biotic homogenization.

In contrast to the equivocal results with respect to species homogenization, I found strong phylogenetic homogenization of anthropogenic communities relative to forest, both within and between ecoregions. Furthermore, phylogenetic homogenization was significantly greater in urban land use compared to agriculture, and was additionally accompanied by a loss of phylogenetic alpha diversity. I conclude that land use drives phylogenetic homogenization in my system by filtering diverse, abundant and spatially

variable loser taxa (e.g. *Nomada*), while simultaneously promoting dominance within a phylogenetically narrow range of dominant winners (especially *Lasioglossum* and other halictids). The species-level analyses indicate that these phylogenetically narrow winner taxa are represented by equally diverse, abundant and spatially variable species.

Phylogenetic measures may be generally more sensitive when analyzing communities comprised of ecologically distinct clades of many ecologically similar species. It is also likely that analysis of phylogenetic homogenization has a sampling advantage over analysis of species homogenization that makes it more likely to detect responses. For example, it might be 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.

Surprisingly, and despite a study design that explicitly contrasted spatial scales over a 75,000 km² region, I found no distinguishable differences in results between two spatial scales. I expected that forest, the baseline habitat type, would have higher compositional heterogeneity at larger spatial scales and thus increase my chance of finding stronger homogenization at larger, between-ecoregion spatial scales. I confirmed that my study design does capture greater natural compositional dissimilarity at the larger spatial scale by showing that, in forest, species and phylogenetic composition are somewhat different among different ecoregions, as I expect them to be due to variation in soil, climate, and vegetation. Nevertheless, I observed similarly strong homogenization patterns at the within-ecoregion scale as for the larger between-ecoregion scale. I suggests that relative abundances of the four large genera of forest associates tend to be variable across forests sites within an ecoregion for any number of reasons, environmental and otherwise, and

thus contribute to high phylogenetic dissimilarity among forest sites regardless of spatial scale. At the same time, relative abundances of anthropogenic winners are mostly restricted to vary within a single family (Halictidae), thereby contributing to low phylogenetic dissimilarity among anthropogenic sites regardless of spatial scale.

I can draw conclusions from my study about the likely consequences of land use change for bee biodiversity. Forests in the region, and 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, before being observed in my study.

However, I believe that using current forest communities, in addition to being the 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 *et al.*, 2012) and regionally. My results show that urban land use is associated with strong phylogenetic homogenization relative to both forest and agriculture (Figure 5), suggesting that further urbanization may result in loss of both biodiversity and evolutionary history at multiple spatial scales (Winter *et al.*, 2009).

Summary and conclusions

My results highlight the importance of looking beyond species diversity and species-based analyses when investigating anthropogenic impacts on communities. First, the loss of forest-associated species from agriculture and urban land use was compensated for by an equivalently diverse, abundant and largely native suite of winner species, so that the

impact of land use was invisible from the point of overall species alpha diversity (McGill *et al.*, 2015). Second, individual winners had both homogenizing and differentiating effects within anthropogenic land use, leading to no detectable differences in species beta diversity among land use types. Accounting for phylogenetic relatedness among species was necessary to reveal a strong biotic homogenization pattern, in which agriculture and particularly urban land use are associated with strong loss of phylogenetic diversity and dissimilarity across both spatial scales of my large regional study design. I suggest that a focus on the identities and ecological characteristics of winner and loser species is a productive approach for understanding biotic homogenization associated with land use change.

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Tables and Figures

Table 1. PERMANOVA R^2 values showing the proportion of variation in species and phylogeny-composition explained by land use (lu), ecoregions (eco) and the interaction. Significance levels are indicated with asterisks for significant results ($p < 0.001$, ***; $p < 0.01$, **; $p < 0.05$, *). Results for the overall model are above the double line; results for the post-hoc contrasts are below the double line. For each of the models, the remaining R^2 is assigned to the residuals.

			Species		phylogeny	
	term	d.f.	F values	R^2	F values	R^2
Overall effect of factors	lu	2	17.8	0.40***	2.9	0.14***
	eco	3	4.7	0.16***	1.3	0.10
	lu:eco	6	2.6	0.17***	1.1	0.16
	residual	24		0.27		0.60
Land use contrasts	fo.vs.ag	1	20.6	0.23***	3.1	0.08***
	fo.vs.ur	1	15.1	0.17***	2.6	0.07***
Ecoregion within land use	eco.in.fo	3	3.2	0.11***	1.4	0.11*
	eco.in.ag	3	3.9	0.13***	1.1	0.08
	eco.in.ur	3	2.9	0.09**	0.8	0.06
	residual	24		0.27		0.60

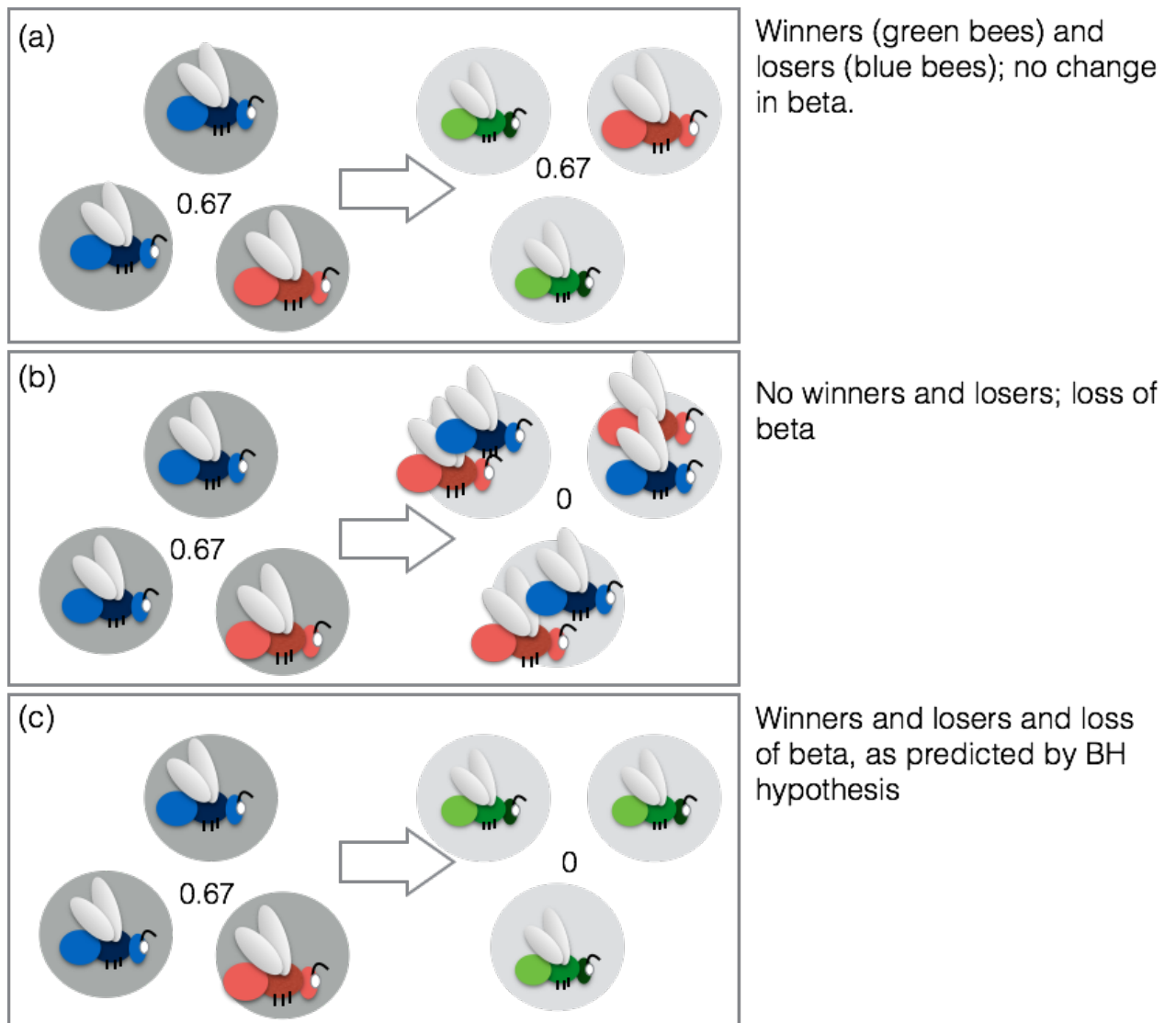


Figure 1. Land use change, represented by the transition from dark grey to light gray, can produce winner and losers species leading to compositional change (top panel) or alter beta diversity among sites (middle panel), but these two responses are not necessarily linked and may occur independently from one another. Biotic homogenization is the process of winners and losers occurring simultaneously with loss of beta diversity (bottom panel).

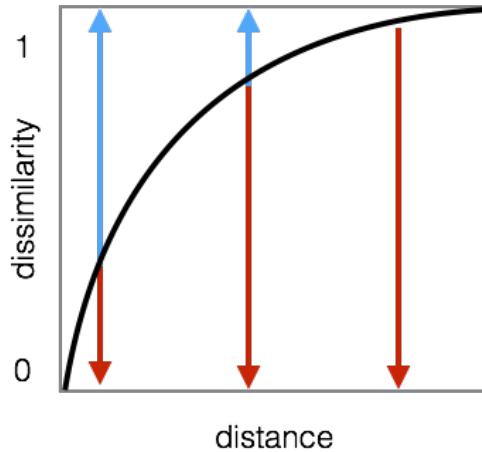


Figure 2. The distance-decay curve in community similarity (black line) is one of few general rules in ecology. It generates the expectation that there will be a greater scope for loss of dissimilarity (i.e. loss of beta diversity) at larger spatial extent (red arrows). Conversely, there is greater scope for increase in dissimilarity (i.e. gain in beta diversity) at smaller spatial scales (blue arrows). Homogenization appears to be more frequently detected at larger spatial scales when driven by invasion (Olden 2006, Quian & Ricklefs 2006, Villegger et al. 2011; but see Cassey et al. 2007), and the same pattern may hold for land use change (Karp et al., 2012).

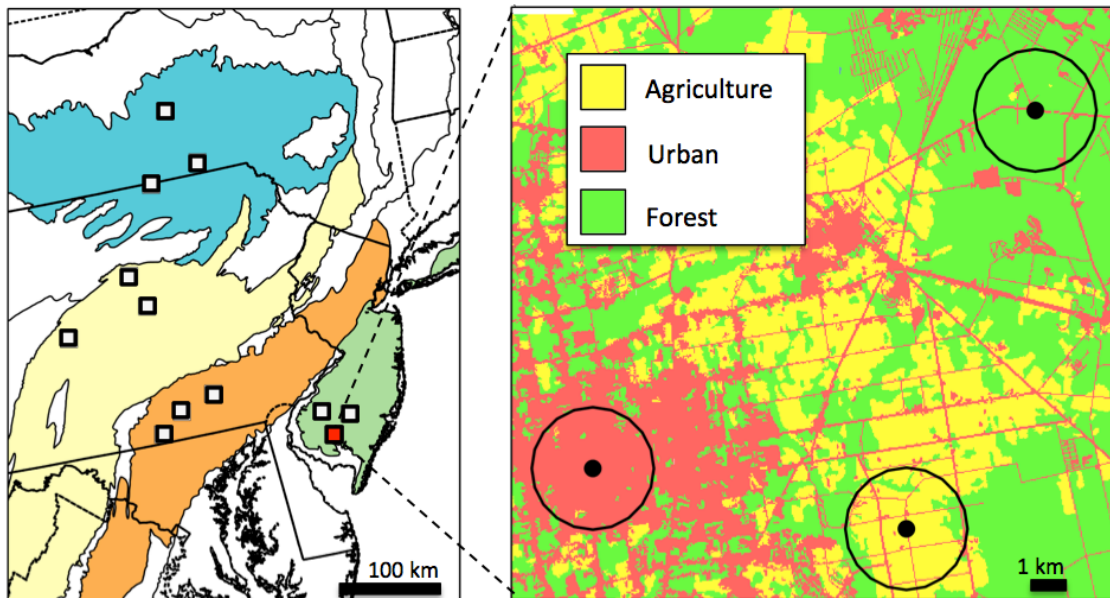


Figure. 3 (a) The 36 study sites are located in 12 sampling blocks divided among 4 ecoregions in New York, Pennsylvania and New Jersey (blue, Northern Allegheny Plateau; yellow, Ridge and Valley; orange, Northern Piedmont; green, Atlantic Coastal Pine Barrens). One sampling block (marked red) is blown up in (b) to show that each block consists of an agricultural site, and urban site and a forest site, defined by a 1500 m radius. Forest sites are located in either mature deciduous or mixed deciduous and soft woods. Urban sites are centered on towns or small cities with populations ranging from 5,000-50,000. Agricultural landscapes include pasture and row crops, as well as exurban residential land use interspersed among fields.

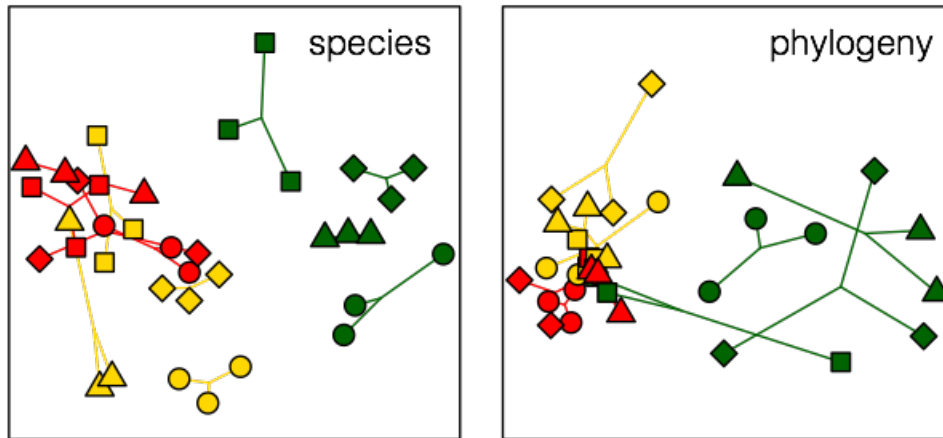


Figure 4. Comparing composition of bee communities in forest, agriculture and urban land use types. Colors indicate land use (dark green for forest, yellow for agriculture, red for urban), while different shapes indicate the four different ecoregions. These NMDS plots represent the multivariate data with fairly low stress (species composition stress = 0.14; trait composition stress = 0.09; phylogenetic composition stress = 0.13). Lines to centroids represent the within-ecoregion dissimilarity analyzed in Figure 5. Significance of the groupings is analyzed with PERMANOVA and discussed in results section.

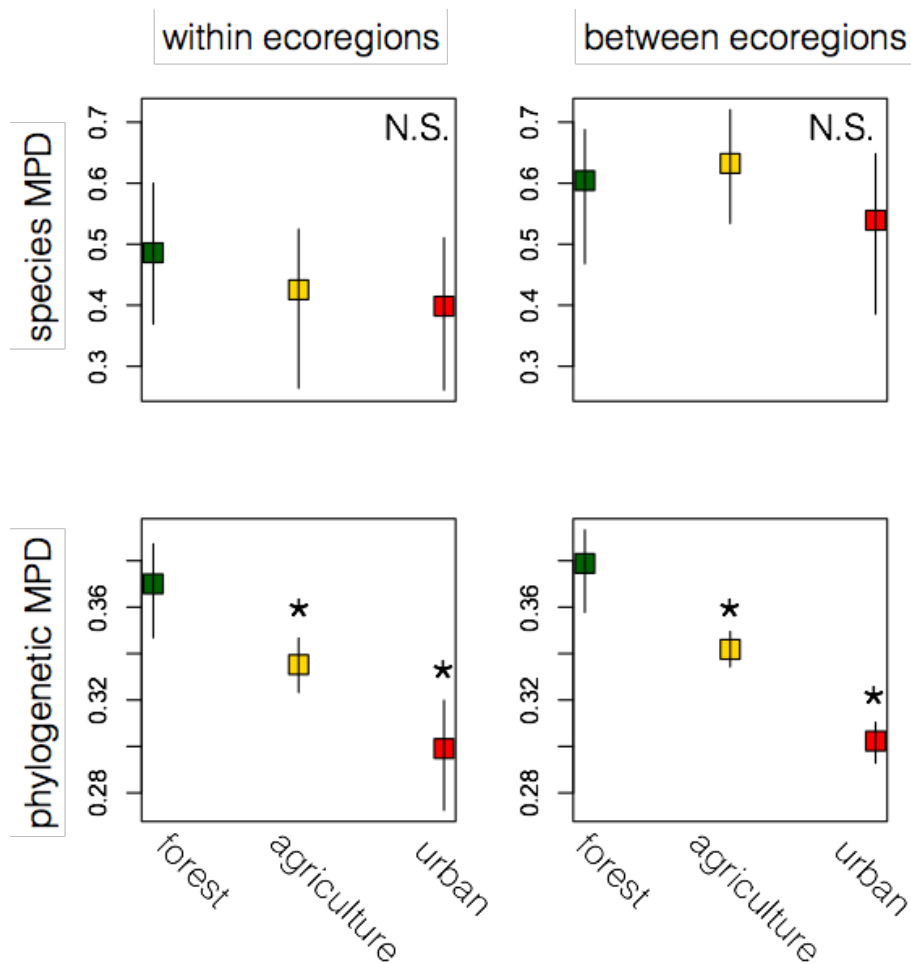


Figure 5. Mean pairwise community dissimilarity between sites within an ecoregion (left column) and dissimilarity between sites from different ecoregions (right column). Large squares indicate the means of the bootstrapped mean dissimilarities, while line segments indicate confidence intervals that span 95% of the iteratively bootstrapped means. Non-overlapping confidence intervals indicates significant difference between two land use types; asterisks indicate significant difference between an anthropogenic land use and forest. Species mean dissimilarity is not detectably different across land use types at either spatial scale. Phylogenetic dissimilarity is lower among agriculture and urban bee communities compared to forest at both spatial scales.

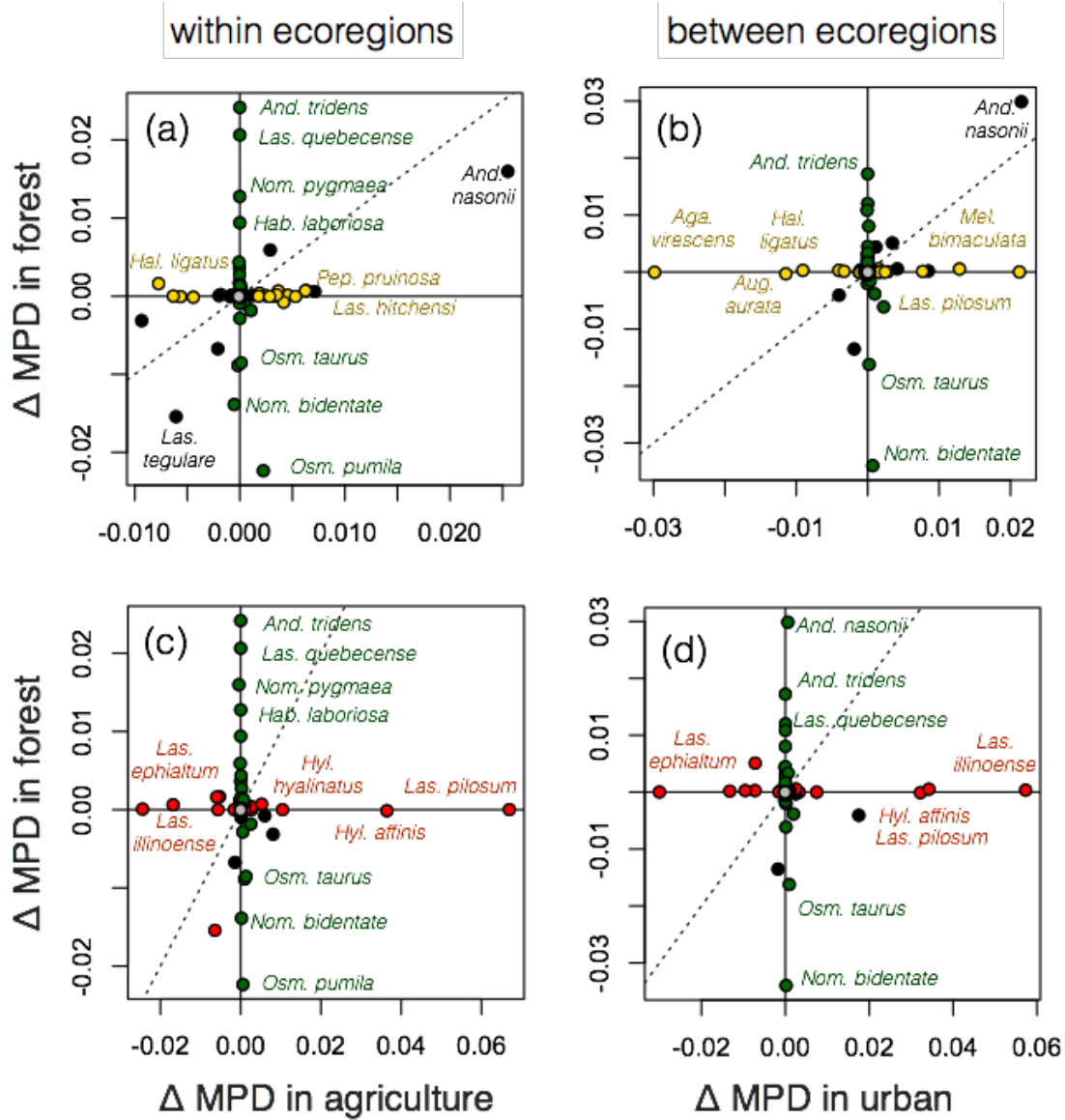


Figure 6. The contribution of each species to mean pairwise dissimilarity among sites in a land use (MPD) can be assessed using a jackknife approach, in which MPD within and between ecoregions is calculated with and without the focal species. The difference indicates whether a species has a homogenizing effect within a land use ($MPD_{\text{original}} - MPD_{\text{jackknife}} = \Delta MPD < 0$) or a differentiating effect ($\Delta MPD > 0$). For example, *Andrena tridens* has a strong differentiating effect in forest, both within ecoregions (a) and

between ecoregions (b). Additionally, species' contributions to differences in MPD between land use types can be assessed by calculating the difference between its contribution to MPD within each group of sites ($\Delta \text{MPD}_{\text{forest}} - \Delta \text{MPD}_{\text{anthropogenic}}$; or the amount of displacement of species from the 1:1 line. For example, *Andrena nasonii* is strongly differentiating at both spatial scales in forest and in agriculture (a, b), but its proximity to the 1:1 line indicates that it is not important in differentiating forest sites relative to agricultural sites.

Supplementary Tables and Figures

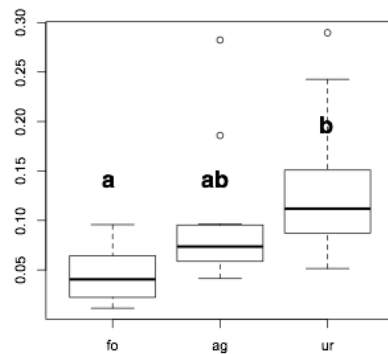


Figure S1. Across all land use types, 8.7% of individuals belonged to non-native species. An ANOVA indicated that proportion of non-native bees varied by land use type, but not by ecoregion ($F = 6.98$, $df = 2$, $p = 0.004$). A post-hoc Tukey Highly Significant Difference test indicated that urban land use had higher proportion of non-native bees than forest, with agriculture being intermediate. This pattern also held when using absolute abundances.

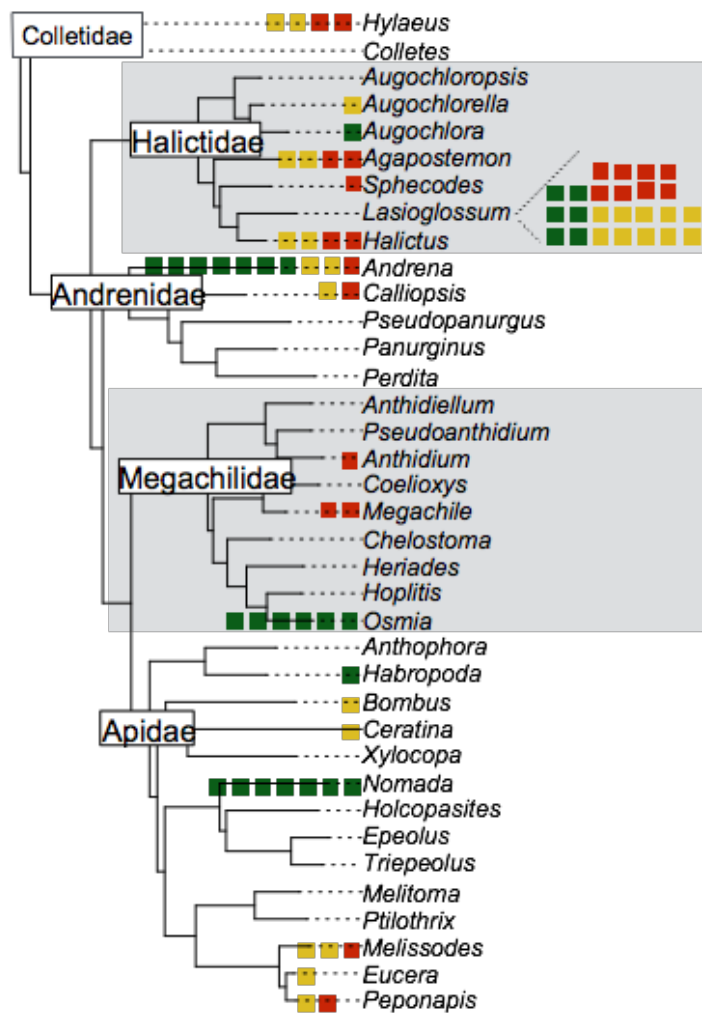


Figure S2. The unrooted phylogenetic tree of bee genera used in this study. The tree was created using sparse sequence data from multiple loci; the placement of Andrenidae relative to other bee families is uncertain (Hedtke et al. 2011). Repeating the analysis on two trees with alternative placements of Andrenidae did not qualitatively change my results, other than reducing the p-value for the overall effect of ecoregion on phylogenetic composition to significant levels. Colored squares represent species in a genera identified as associated with forest (green), agriculture (yellow) or urban (red).

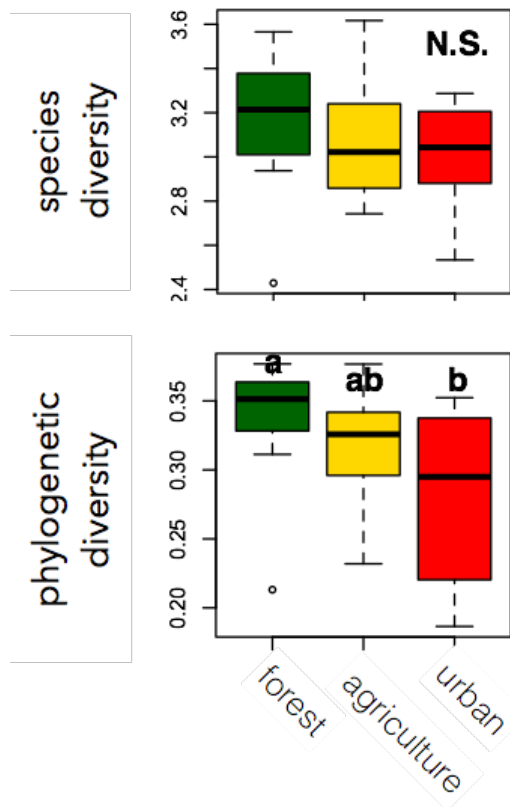


Figure S3. To help interpret beta diversity results, I also compared site-level diversities of bee communities among forest, agriculture and urban land covers. Letters indicate significance levels in post-hoc Tukey Highly Significant Difference tests. Effective species number (exponentiated Shannon diversity index) did not differ across land use types. Abundance-weighted phylogenetic diversity was lower in urban than forest land use, with agriculture being intermediate.

CHAPTER III. URBAN DRIVERS OF PLANT-POLLINATOR INTERACTIONS

Abstract

Plant-pollinator interactions are affected by global change, with largely negative impacts on pollination and plant reproduction. Urban areas provide a unique and productive study system for understanding the impacts of many global change drivers on plant-pollinator interactions. I review the mechanistic pathways through which urban drivers alter plant-pollinator interactions. The literature on urban drivers of plant-pollinator interactions is small but growing, and has already produced exciting insights about how population processes or pollinator behavior interact with landscape urban drivers to affect pollination outcomes. Habitat loss and fragmentation can change flower visitation rates and pollination success through changes in pollinator foraging behavior, or through population-level effects on pollinators. Urban environments, where impermeable surface provides an inhospitable matrix, may allow researchers to identify habitat fragments versus matrix more clearly than for many other environments. Recent studies have found that non-native plants are not differently preferred by pollinators relative to native plants, therefore removing the basis for expecting pollinator-mediated competition between native and non-native plants in urban habitats. However, non-native species together with managed vegetation may have powerful effects in urban habitats via changes in community-level plant phenology and consequent changes in pollinator phenology. The current level of climate warming has not caused plants and pollinators to become

detectably temporally separated, although at the same time, diversity among species' phenological responses could buffer plant-pollinator interactions from climate variation. Due to the urban warming effect, cities provide a promising system for better understanding warming effects on plant-pollinator interactions. Environmental contaminants such as soil nitrogen and heavy metal pollution have been examined with respect to plant-pollinator interactions in small-scale, mechanistic studies. The extent to which environmental contaminants drive plant-pollinator interactions in actual urban landscapes is currently unknown. Important study gaps to fill include understanding of the consequences of plant and pollinator trait filtering on plant-pollinator interactions, and expanding the literature to include underrepresented biomes and pollinator taxa.

Introduction

Pollination is emerging as a model system for studying global change impacts on species interactions. The potential exists for integrating questions about global change with the physiological, behavioral and reproductive processes that characterize the plant-pollinator mutualism, because there is a large and long-standing literature on the mechanistic aspects of pollination. Research on urban drivers of plant-pollinator interactions is particularly promising because it could accomplish at least three important scientific goals. First, as a study system, urban environments provide spatial concentrations of major global change drivers, such as habitat loss and global warming, expressed at high local intensity and replicated across the world's biogeographic regions. As such, urban

ecosystems may be productively treated as natural experiments in which to understand global change processes. Second, urban land use is a driver of global change in its own right, and therefore studies on specific urban drivers or combinations of drivers are needed to predict the effects of future urban expansion, which is expected to increase globally by 185% between 2000 and 2030 (Seto *et al.*, 2012). Finally, urban plant-pollinator interactions provide pollination services to urban crops (Werrell *et al.*, 2009) and wild plants (Andrieu *et al.*, 2009). Understanding how urban drivers affect pollination services will be increasingly important for food production and biodiversity conservation goals as urban land use expands.

I identify four major categories of urban drivers shown to affect urban plant-pollinator interactions (Figure 1): habitat loss and fragmentation, the introduction of non-native species, urban warming, and environmental contaminants including nitrogen deposition and pollution. The first two have been relatively well studied in agricultural and natural systems, as demonstrated in recent reviews or meta-analyses of the effects of land use change and fragmentation on pollinators (Winfree *et al.*, 2011), on plant-pollinator interactions (Ferreira *et al.*, 2013) and on pollination (Aguilar *et al.*, 2006), and the effects of invasions on plant-pollinator interactions (Morales & Traveset, 2009). In order to avoid overlap with these previous reviews, I focus on studies that have at least some sites in urban habitat and emphasize the role of these drivers in a specifically urban context. While the effects of climate warming on plant-pollinator interactions have received much recent attention (Burkle & Alarcón, 2011), no studies have yet taken advantage of the opportunities created by urban warming for space-for-time substitution

climate studies. Finally, environmental drivers such as pollution have received little attention as drivers of plant-pollinator interactions in any landscape context, although they have been the subject of small-scale laboratory and field experiment studies. For this fourth section, I therefore synthesize smaller-scale studies to understand how these environmental drivers may operate at the landscape scales at which urbanization occurs. In order to focus on the four specific drivers, I avoid extensively citing a larger number of studies using urbanization gradient designs that fail to isolate any particular urban drivers.

The objective of this review is to trace potential pathways through which each specific urban driver may alter plant-pollinator interactions. Therefore I focus on the relatively small number of studies that measure interactions in a way that provides some mechanistic link between urban drivers and the mutualistic partner benefits (Figure 1). Urban drivers acting on various life history traits shape urban plant and animal communities, and thereby constrain potential interaction identities. For example, the introduction of non-native plants directly impacts composition of the urban plant community, which then affects plant-pollinator interactions via pollinator preferences or plant bloom time (Section 2: “Non-native and managed species”). Urban drivers can also directly affect the interaction rates of plants and animals that persist in the urban environment. For example, urban warming may alter their temporal overlap (Section 3: “Urban warming and climate change”), and environmental contaminants can interrupt attraction (Section 4: “Environmental contaminants”). Finally, once an interaction occurs, urban drivers can alter the mutualistic costs and rewards to one or both partners, which

may have population-level effects that lead to changes in the urban species community (Figure 1). For example, habitat fragmentation can promote transfer of pollen between closely related plants and result in low seed set or offspring vigor (Section 1: “Habitat loss and fragmentation”).

Habitat loss and fragmentation

The process of urbanization is characterized by spatially disjointed development of built-up areas, such that urban landscapes contain fragments of open space such as vacant lots, reserves, parks and gardens. Pollinator population and pollinator foraging dynamics are two mechanisms through which urban habitat loss and fragmentation might affect pollinators and subsequent pollination service to plants. Future studies of fragmentation as an explicitly urban driver may explain heterogeneous responses of pollinator life history traits such as body size to urbanization.

Habitat loss and fragmentation may alter pollinator visitation to plants by causing declines in pollinator populations and changes in pollinator community composition, as predicted by species-area relationships or pollinator resource requirements. These processes can affect pollination function, especially for plant species dependent upon a particular pollinator. For example, loss of a rare pollinator from small natural habitat fragments in an urban matrix led to pollen limitation in six dependent orchid species (Pauw, 2007). For plant species not dependent on a particular pollinator, the loss of

habitat-specific pollinators from small fragments may be offset by neutral or positive responses in other pollinator species. This was found in two studies in which smaller fragments lost some pollinator species while simultaneously receiving an influx of pollinator species associated with the surrounding matrix (Cane *et al.*, 2006; Winfree *et al.*, 2014), potentially buffering plant-pollinator interactions. A pollen limitation experiment done along a rural-to-urban gradient provided mixed support for this hypothesis, finding that small forest fragment size reduced pollinator flower visitation, species richness and pollination to one but not another woodland herb (Williams & Winfree, 2013).

Studies from urban areas have supported the prediction, based on optimal foraging theory, that pollinators will avoid traveling to smaller, more isolated resource patches, or will otherwise alter their visitation behavior in order to offset costs in time and energy (Pyke, 1980). These studies use one of two major methods: measuring pollinator visitation rates and behaviors at focal patches, or tracking pollinator movement between patches. Flower visitation rates and seed set both decreased in smaller plant populations for an unmanaged weed (*Crepis sancta*) growing in small-scale urban fragments (the small dirt patches surrounding street trees). Furthermore, selfing rates were higher in small fragmented urban populations than in large continuous rural populations (Cheptou & Avendaño, 2006). On the pollinator side, although visitation to urban fragment populations was lower, the time spent at each flower was longer, suggesting that pollinators were more fully exploiting each flower's resources to recoup energy spent flying longer distances (Andrieu *et al.*, 2009). Together, these papers demonstrate that

urban fragmentation can alter plant-pollinator interactions via pollinator behavioral responses to small-scale habitat fragmentation.

Pollen analogue methods such as fluorescent dye provide a way to determine whether habitat connectivity facilitates pollinator movement and thus functional connectivity between urban plant populations (see LaPoint *et al.* 2015 for definition of functional connectivity). A study of fluorescent dye movement among urban populations of a forest understory herb (*Primula elatior*) showed that habitat corridors increased pollinator movement between connected habitat fragments, thus mitigating the effects of fragmentation (Van Rossum & Triest, 2012). In contrast, almost no dye was detected in unconnected fragments. This result might suggest that the urban matrix is hostile to pollinator foraging movements and therefore pollen transfer; however, a parallel study in a meadow herb (*Centaurea jacea*) found that pollinators successfully transferred dye over 2 km through urban matrix habitat between parks (Van Rossum, 2010). A potential explanation for this difference is that urban habitats tend to be open or savannah-like rather than forested (Matteson, Grace, & Minor, 2013), so the perceived contrast between plant habitat fragment and urban matrix may be stronger for pollinators of *P. eliator*, a forest understory plant, than for pollinators of *C. jacea*, a meadow plant.

I identify three areas where future studies can improve our understanding of urban fragmentation as a driver of plant-pollinator interactions. First, while fragmentation of natural habitat is a necessary consequence of urbanization, the assumption that floral resources are more fragmented in urban habitats is rarely tested and may not hold true in

some types of urban land use or at some times of the year. One study found no difference in flower abundance or distribution between survey transects in urban parks versus residential neighborhoods (Matteson *et al.*, 2013). Second, because habitat associations are generally unknown for pollinators (Winfree *et al.*, 2011), pollinators can exhibit idiosyncratic responses to fragmentation when matrix habitat includes alternative foraging resources (e.g. Winfree *et al.* 2014). Because extensive areas of impermeable surface cover prevent most plant growth, urban areas have potential strength as fragmentation study systems, in that fragmentation may be defined commensurately across many plants and pollinators species.

Finally, the role of pollinator mobility in mediating the response of plant-pollinator interactions to urban fragmentation is unknown. Bee body size, which is directly related to foraging range (Greenleaf *et al.*, 2007), does not consistently respond to urban fragmentation, with some studies concluding that small-bodied bees are more sensitive (e.g. Cane *et al.* 2006) and other studies concluding that small-bodied bees respond positively to urbanization (e.g. Wray, Neame & Elle 2014). I expect that this variability reflects a trade-off between the ability to access widely distributed resources and the ability to thrive on locally low resources (Figure. 2). In the diagrammed example, a study comparing areas *a* and *b* would conclude that fragmentation is associated with high mobility, large body size, and connectivity among plant populations. On the other hand, a study comparing areas *a* and *c* would conclude that fragmentation is associated with low mobility, smaller body size, and isolation of plant populations. Understanding the importance of pollinator movement in acquiring necessary resources in different

landscapes is an important step in reconciling conflicting findings.

Non-native and managed species

Urban plant communities are characterized by high proportions of invasive and non-native species, many of which are also actively managed (e.g., in gardens; Pickett *et al.* 2011). Half of invasive urban plants with known introduction pathways have been deliberately introduced as ornamentals (La Sorte *et al.*, 2014). Managed or ornamental species may in some cases be native but are similarly subject to anthropogenic selection filters and intensively managed to produce novel communities, especially in affluent neighborhoods (Hope *et al.*, 2003). I first consider the effects of non-native and managed plant species on urban plant-pollinator interactions, and then discuss effects of non-native and managed pollinators.

Non-native and managed plants

Pollinator preference is an important mechanism for competitive effects of non-native plants on native neighboring plants. A meta-analysis found that non-native neighbors typically have negative effects on both visitation and reproductive success in focal native plants, particularly when the two plant species have phenotypically similar flowers (Morales & Traveset, 2009). However, there is likely a persistent study design issue in the selection of dominant, showy non-native plants that can be expected *a priori* to have strong effects. Recent studies conducted in urban settings have improved research design

by comparing pollinator visitation between multiple native and non-native plant species, while controlling for differences in plant species abundances. In New Jersey suburban habitat, pollinator interaction with non-native plants was dramatically higher than in natural forest, but in proportion to the higher abundance of non-native plants (Williams *et al.* 2011). A European study used experimental arrays of congeneric or con-familial native and non-native plants set in replicated rural, semi urban and urban landscape contexts. They found that while visitation to all plants decreased across the urban gradient, pollinators did not prefer non-native plants at any level of the treatment (Chrobock *et al.*, 2013). Similarly, native and wild-type plants sold as garden ornamentals did not consistently differ from cultivars and hybrids in attracting pollinators in a common garden experiment (Garbuzov & Ratnieks, 2014). These studies suggest that, in aggregate, pollinators do not perceive the non-native status of plants. This conclusion does not preclude the possibility that urban floras are more likely to include highly attractive or rewarding plants for other reasons, such as human preference for mass-flowering ornamentals, or for garden plants that attract charismatic animal pollinators such as butterflies and hummingbirds. Comparing the distributions of plant attractiveness to pollinators between urban and natural habitats would be an informative first step in asking whether pollinator preference is an important driver of urban plant-pollinator interactions.

The ability of pollinators to avail themselves of non-native and ornamental plants is likely an important condition for thriving in urban habitats. Specialist (oligolectic) pollinators are sometimes found to be absent or depleted in urban areas (Cane *et al.*,

2006; Matteson, 2008). However, there is no clear evidence that non-native plant invasion is a primary driver, as compared to other urban drivers of host plant decline, or other pollinator life history traits correlated with specialization. I suspect that the presence of preferred plant genera, families, or trait groups are more important to the persistence of specialist pollinators than are geographic origins of the plants.

High concentrations of non-native and managed plants in urban areas might have strong impacts on plant-pollinator interactions by altering seasonal availability of pollinator foraging resources. For several reasons, non-native plants might extend or shift community bloom phenology in urban relative to surrounding environments. First, the timing of bloom appears to be conserved by geographic origin, as demonstrated by a study of three Mediterranean-climate regions that found non-native plants may bloom later, earlier or in sync with native plants, but in all cases retained the basic phenology of their source region (Godoy *et al.*, 2009). Furthermore, a greenhouse study found that non-native cultivated species consistently germinate earlier than native plants, suggesting that human selection for convenient phenological qualities places a strong trait selection filter on many non-native plants before they are transported (Chrobok *et al.*, 2011). Similarly, ornamental plantings may be consciously designed to provide long-season bloom, either through selection of assemblages with complementary bloom periods or through selection or breeding of long-blooming plants (Garbuzov & Ratnieks, 2014). People also extend the growing season for flowering forbs in parks, gardens and lawns through management practices, in particular irrigation in arid environments and tree removal in temperate forested environments. Deforestation or tree thinning extends the duration of floral

resource availability by removing light limitation following early summer canopy closure (Winfree *et al.*, 2014). Finally, urban warming may shift or lengthen plant species' flowering phenology, discussed in further detail in the following section.

Several lines of evidence suggest that urban pollinator phenologies have changed to match those of non-native and managed urban vegetation. One way this could occur is through habitat filtering and, ultimately, selection against pollinator species adapted to the phenology of native plants. For example, bee species in natural desert habitats had short periods of activity matched with the timing of natural bloom, while irrigated gardens supported pollinator species with longer periods of activity that can take advantage of longer growing season unlimited by water (Gotlieb *et al.* 2011). Similarly, in a study of bees in oak-savannah fragments in different landscape contexts, bee species captured in forest-surrounded fragments had early flight seasons corresponding with the spring and early summer bloom period of native plants, while bee species captured in urban-surrounded fragments had late flight seasons, presumably sustained by late blooming plants in urban habitat (Wray *et al.*, 2014). Future research is needed to confirm the mechanistic links between temporal shifts in flower resources and shifts in community composition towards pollinators with longer or later flight seasons. Higher generalism of urban pollinators might be an important confounding factor, since specialization may constrain flight seasons to a temporally narrow subset of plant bloom periods. Pollinator specialization did not differ between urban and natural habitats in the two studies cited here (Gotlieb *et al.*, 2011; Wray *et al.*, 2014).

A second way pollinators, particularly social colony nesters, may adapt to different bloom phenology is by lengthening their flight season to match longer period of bloom. For example, during a mild winter in southern England, three colonies of *Bombus terrestris* collected large amounts of nectar and pollen from non-native ornamentals in an urban park (Stelzer *et al.*, 2010). Finally, across landscapes with urban and non-urban habitat types, pollinator species with longer flight seasons could respond to shifts in bloom phenology by foraging in different habitats depending on which offers the most resources at a given time. For example, seasonal changes in foraging activity between urban and rural habitats have been observed by decoding honey bee dances to determine worker flight directions and distances (Beekman & Ratnieks, 2000).

Non-native and managed pollinators

As for non-native plants, strong effects of non-native pollinators have been found in many research projects focusing on a few unusually dominant, invasive species, especially *Apis mellifera* and *Bombus terrestris*, both of which have been widely introduced for agricultural purposes. Managed *Apis* is emerging as an urban driver of plant-pollinator interactions because bee-keeping in cities is rising, even while the total number of managed and feral *Apis mellifera* colonies is falling in both the USA and Europe (Potts *et al.*, 2010). *Apis* has been shown to affect plant-pollinator interactions negatively as disease reservoirs for wild pollinators (Fürst *et al.*, 2014), but could potentially have positive effects through its role as a long-season supergeneralist that can rescue plants from other pollinator declines. Furthermore, managed pollinators are at least partly uncoupled from the positive feedbacks inherent to mutualisms; for example,

bee keepers supplement their bees' diets with sugar-water to tide them over periods of low bloom and replace failed hives. Therefore, managed *Apis* may buffer plant-pollinator networks from cascading extirpations, as has been hypothesized for managed plants (Keitt 2009). Given the recent increases in urban bee-keeping, and the variation among towns that do or do not allow it, there are opportunities for researchers to use urban areas as a system for studying the role of managed *Apis* in the environment.

Non-native, solitary insect pollinators have been little studied, yet they may be especially common in urban areas because of higher propagule pressure. A large-scale survey of urban bee communities found that 19% of the bee species in New York City were non-native species, which is surprisingly high compared to the 2% of the bee species in nearby rural New Jersey were non-native (Matteson, 2008). Furthermore, 90% of the urban non-native species were solitary (Matteson, 2008). Large cities may thus provide an opportunity for testing the effects of non-native pollinators as a global change driver, as opposed to effects driven by the few exceptionally invasive species. Further surveys are needed to determine the prevalence of non-native pollinators in other cities and global regions.

While non-native social pollinators may exert strong competitive effects on other bees by monopolizing floral resources (Winfree, 2010), concerns about non-native solitary pollinators center around their competition for nesting resources with ecologically similar native species. For example, *Megachile sculpturalis*, a recent introduction to North America, has been observed attacking and usurping nest tunnels excavated by the

similarly sized, native *Xylocopa virginica* (Roulston & Malfi, 2012). The effects of non-native solitary pollinators on urban plant-pollinator interactions are unknown, but I consider strong negative effects unlikely, due to the high generalism of plant-pollinator interactions (Memmott *et al.*, 2004).

Urban warming and climate change

Cities experience different climates from surrounding rural areas, and temperate cities in particular experience higher temperatures from surrounding environments (Pickett *et al.*, 2011). Urban warming may affect plant-pollinator interactions through community filtering mechanisms acting on species' physiological tolerances, through phenological shifts that may affect the ability of plants and pollinators to find one another in time. Despite the potential for urban warming studies to have broad relevance for climate change research, the use of urban study systems for testing temperature effects on plant-pollinator interactions is currently rare.

There is good evidence that warmer urban temperatures act as a direct filter on plant communities by selecting for thermophilic native plants and by enabling the establishment of non-native plants from warmer regions (Williams *et al.*, 2014). It is possible that urban warming similarly filter bee communities. In response to warm winter temperature treatments, spring-emerging bee species overwintering as adults lost more weight before emergence than summer-emerging bees overwintering as larva, likely

because of higher metabolic activity in response to warmth (Fründ *et al.*, 2013). Spring-emerging bees are negatively impacted by urbanization, although loss of habitat and spring foraging resources are currently considered the likely drivers (Matteson, 2008; Wray *et al.*, 2014). Further research is needed to determine what, if any, impact this physiological pathway has on urban pollinator communities and plant-pollinator interactions.

Recent studies of plant-pollinator interactions and climate warming are motivated by concerns that plant and pollinator phenology will respond to warming at different rates or to different phenological cues, and will therefore be temporally separated from one another. In aggregate, plants and pollinators respond similarly to climate warming (Bartomeus *et al.* 2011), thereby suggesting that warming will not driving mutualism collapse through plant-pollinator phenology mismatch. However, individual species may have variable phenological responses to climate warming, producing considerable shifts in species overlap and potential interaction partners, necessitating the development of novel interaction networks (CaraDonna *et al.*, 2014). Urban warming tends to advance plant flowering phenology, although species responses are heterogeneous and may be driven by correlated factors such as photoperiod, moisture and CO₂ concentrations (Neil & Wu, 2006). Future studies comparing temporal overlap between plants and pollinators occurring in both rural and urban habitats will provide information on whether urban warming, or other sources of intraspecific phenological variation, is causing synchronous shifts in plant and pollinator phenology or driving different patterns of association between plants and pollinators. Species found only in rural or urban habitats would be

unsuitable to include in such an analysis, since they would likely introduce large interspecific phenological variation due to other factors (as discussed in the previous section on non-native and ornamental plants).

Cities provide replicated natural experiments in which to test the effects of climate change on plant-pollinator interactions at large spatial scales. Co-varying climatic factors may be controlled experimentally, as done in a study of potted brittlebush (*Encelia farinosa*) that found urban-located plants bloomed later and longer than desert-located plants regardless of watering treatment (Neil *et al.*, 2014). Another approach is to use historical records to validate space-for-time substitution study designs for studying climate change. One such study combined herbarium records with contemporary surveys to determine that a plant-herbivore interaction responds positively to temperature increases occurring both between urban and rural habitats and over long-term climate trends within each habitat (Youngsteadt *et al.*, 2014). A potential third approach is to compare plant-pollinator responses to warming among urban areas experiencing different intensities of heat island effects. This study design has the advantage of partially controlling for other urban drivers, such as non-native and ornamental species, that likely have strong independent effects on phenological responses but are present in most urban areas. Finally, future research on urban climates as drivers of plant-pollinator interactions should take particular care to acknowledge temperate research bias, since urbanization may have different effects on tropical or arid climate variables. For example, in Phoenix in the arid southwestern United States, irrigation of ornamental plants causes cooler daytime temperatures through increased evaporation and transpiration, although

nighttime temperatures are warmer than in surrounding desert (Brazel *et al.*, 2000).

Environmental contaminants

Environmental contaminants are important ecological functions in urban landscapes (Pickett *et al.*, 2011), and have been the focus of a number of experimental studies of plant-pollinator interactions especially in laboratory settings. I discuss the effects of soil nitrogen deposition and soil pollution on plant-pollinator interactions in some depth, before briefly addressing contaminants that have been studied less often in the context of plant-pollinator interactions.

Nitrogen deposition

Urban soils are characterized by eutrophication caused primarily by atmospheric nitrogen compounds produced by industrial or transportation combustion and deposited in water and soil as nitrate (Pickett *et al.*, 2011). Plant species vary in their ability to take advantage of nitrogen additions, resulting in shifting competitive dynamics that can change relative abundances of pollinator host plants. For example, high levels of nitrogen addition reduced plant-pollinator interactions by shifting plant composition from flowering forbs to grasses, which do not interact with pollinators (Burkle & Irwin, 2010). Evidence for similar community filtering is found in northwestern European grasslands, where higher atmospheric nitrogen deposition is correlated with community shifts away from insect-pollinated forbs and towards grasses and other clonal and wind-pollinated

plants (Helsen *et al.*, 2013). In the case of urban grassland fragments, the nitrogen-mediated reduction in pollinator attractive plants may be mediated by compensating increases of urban-associated plants within either the natural fragments or the nearby urban matrix, since urban-associated plants also tend to prefer high-nutrient soil (Williams *et al.*, 2014).

Nitrogen deposition has been shown to alter plant-pollinator interactions through several non-filtering mechanisms, including plant reproductive investment and quality of mutualistic reward. For example, low levels of nitrogen addition increased forb growth and flower number, size and nectar production in two plant species, although these changes did not result in higher per-flower visitation (Burkle & Irwin, 2010). In another alpine system, adding both fertilizer and pollen to plants non-additively increased seed production, suggesting that nitrogen addition can increase per-visit effectiveness by removing bottom-up limitation on plant reproduction (Brookes *et al.*, 2008). From the pollinator perspective, increases in nectar and pollen quantity or quality could improve foraging efficiency and ultimately reproduction, as shown by an experiment in which female butterflies raised on poor larval diet produced more eggs when fed amino-acid fortified nectar as adults (Mevi-Schütz & Erhardt 2005). However, demonstrations of trophic transfer of nitrogen from soil to floral rewards to pollinators are currently rare and exhibit complex dynamics. For example, soil nitrogen additions did not change amino acid profiles in *Cucurbita* nectar, but did alter ratios of fructose to glucose sugars (Hoover *et al.*, 2012). Bumblebee workers (*Bombus terrestris*) consumed more of the altered nectar, but subsequently suffered reduced longevity. Furthermore, intraspecific

nitrogen addition effects tend to be highly context dependent, as demonstrated by different effects of nitrogen treatment levels (Burkle & Irwin 2010) or interactions between nitrogen treatments and pollen availability (Brookes *et al.*, 2008), pollinator larval nutrition (Mevi-Schütz & Erhardt 2005), and warming and CO₂ treatments (Hoover *et al.*, 2012). These context-dependent and non-additive effects highlight a need for future studies to consider interactive effects between nitrogen deposition and other urban drivers.

Soil pollution

Soil pollutants may affect plant-pollinator interactions through pollutant accumulate in plant nectar and pollen. Several studies have looked for effects on pollinator foraging choices in a laboratory setting. Adding nickel to nectar reduced *Bombus* visit duration in jewelweed (Meindl & Ashman, 2013). Other metal pollutants such as selenium were not shown to affect pollinator behavior at flowers (Hladun *et al.*, 2013), which may have negative effects on plant-pollinator interactions if metal toxicity reduces bee fitness or pollinator availability to plants.

A study in Europe tested landscape-scale effects of heavy metal pollution along long (~20 km) gradients surrounding industrial smelters. They found that soil pollution was correlated with high levels of cadmium, lead and zinc pollution in trap nest pollen stores, demonstrating that bees use contaminated plants in the field. Pollen pollution correlated with mortality before emergence. The diversity and abundance of bees using trap nests declined sharply at the most polluted site (Moroń *et al.*, 2012), suggesting either negative

long-term demographic effects or an ability of dispersing females to detect and avoid polluted habitat, as hinted in the previously discussed laboratory *Bombus* studies.

Other environmental contaminants

The effects of pesticides, air pollution, light pollution, and human noise and traffic have all received brief consideration as drivers of plant-pollinator interactions via pollinator behavior. Although pesticides are associated with agricultural land use, pesticides are applied regularly and at high concentrations in residential areas to maintain lawns and gardens. One study found that neonicotinoid lawn treatment negatively impacted bumblebee colonies but the effect was removed if flowers exposed to direct application were mowed directly after (Larson *et al.*, 2013). Common urban air pollutants such as diesel exhaust break down some floral volatiles in a laboratory setting, which reduces recognition by trained honey bees and may interfere with honey bees locating rewarding flowers by smell (Girling *et al.*, 2013). Nocturnal plant-pollinator interactions may also be sensitive to light pollution, which attract night-flying insect pollinators like moths (Fox, 2013). The effects of light on pollination by nocturnal vertebrates is unknown, but is likely affected by light avoidance behaviors, as demonstrated in seed-dispersing bats (Lewanzik & Voigt, 2014). Finally, human noise and traffic may impact plant-pollinator interactions by frightening animals. An unusual example is from Argentina, where European house sparrows (*Passer domesticus*) forage nectivoresly on South African ornamental aloe (*Aloe arborescens*). Sparrow visitation to aloe plants and movement between plant patches decreased on weekends, apparently in response to higher traffic and pedestrian activity (Leveau, 2008).

Future directions

Studies that explicitly attempt to link specific urban drivers with changes in community composition and consequences for partner reproduction or nutrition are needed to understand the roles of key plant-pollinator traits, such as phenology, body size and mutualist specialization. Thus far, studies have identified sensitive traits in plants or pollinators that don't have readily interpretable meaning vis-à-vis plant-pollinator interactions, such as nesting habitat and seed size (Hernandez *et al.*, 2009; Williams *et al.*, 2014). Even when relevant sensitive traits are identified, such as lower proportions of specialist pollinators in urban habitats (Hernandez *et al.*, 2009), few studies attempt to determine if partner species experience any consequences. Or, traits like pollinator body size may have demonstrated consequences for partner species (Geslin *et al.*, 2013), but researchers have yet to identify consistent responses to specific urban drivers.

Additionally, both the studies I review here and the literature overall are heavily biased towards insect and especially bee pollinators. Flies were rarely represented, despite evidence from agricultural and natural systems that flies are frequent flower visitors and passive pollen carriers (Winfree *et al.* 2011; Orford, Vaughan & Memmott 2015). Further research is needed to determine the extent to which the mechanistic pathways presented here function similarly in systems dominated by non-bee pollinators, for example in regions where vertebrate pollination is common.

As discussed in the urban climate section, the current literature on urban plant-pollinator interactions is heavily biased towards temperate cities in Europe and North America. Cities share many abiotic and biotic features, but vary widely in how those features differ from the regional natural habitats they are superimposed upon (Pickett *et al.*, 2011). Therefore, similar urban drivers may filter plant-pollinator traits differently in different biogeographic regions. I expect large collaborative studies that achieve replication at the level of cities will continue to contribute important insight on the role of regional context (e.g. La Sorte *et al.* 2014). Expanding current understanding to include cities in Africa and Asia is particularly important since these continents will experience the great majority of global urban expansion in coming decades (Seto *et al.*, 2012).

Finally, environmental heterogeneity exists within as well as between cities (Pickett *et al.*, 2011). For example, higher bee abundance was associated with urban areas of higher population density, likely mediated through higher abundance of flowers (Lowenstein *et al.*, 2014). Within urban areas, neighborhood income level is an important driver of plant community properties such as richness and proportion of non-native ornamentals (e.g. Hope *et al.* 2003), and I expect that these effects of socioeconomics extend to pollinators and plant-pollinator interactions, although this was unsupported by studies in New York City (Matteson *et al.*, 2013) and Chicago (Lowenstein *et al.*, 2014). Despite high within-urban heterogeneity, I expect that the broad drivers I discuss here are fairly universal to urban landscapes, and that the mechanisms documented in the literature can be expected to occur in many contexts albeit with widely differing strengths and outcomes. A key challenge is understanding the extent to which variation in surrounding

environmental variables such as soil moisture, species identity, management and landscape configuration, modify the effect of the main drivers identified in this review.

Conclusions

Many studies reviewed here demonstrate the benefits of urban environments as a study system for understanding the mechanistic effects of different global change drivers on plant-pollinator interactions. For example, urban habitat fragmentation has provided a tractable system in which to study pollinator foraging movement and behavior as mechanism for fragmentation effects on plant pollination and reproduction. Urban research has also contributed to understanding the role of pollinator foraging preference in plant-plant competition, by making use of the high concentration of non-native plants in urban environments. I expect that urban areas additionally provide a uniquely powerful system for researching effects of large community-level shifts in bloom phenology, driven by non-native plants and management practices such as selection of long-blooming cultivars and irrigation, as well as intra-specific phenology shifts driven by urban warming. Because large urban areas provide more extreme temperature conditions than can be observed in regional temperature trends across time, urban warming may provide a useful proxy system for studying the effects of climate warming on plant-pollinator interactions. Urban environments also provide gradients in many different environmental contaminants, such as soil nitrogen and heavy metal pollution, which are valuable for extending the results of small-scale mechanistic studies to landscape scales.

Future studies are needed to address knowledge gaps such as the role of traits in community filtering mechanisms, and to correct research biases towards temperate European-American regions and bee pollinators.

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Tables and Figures

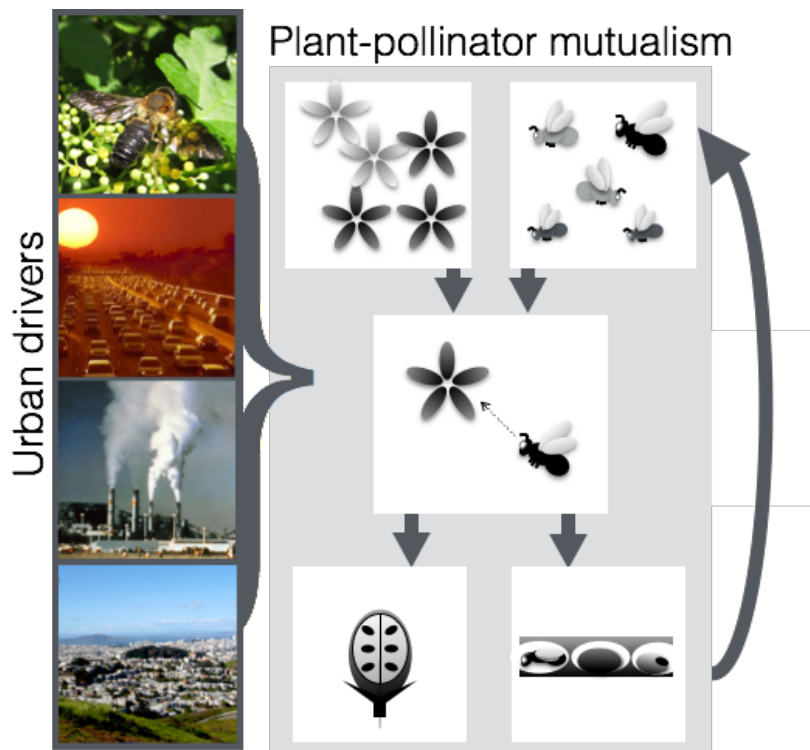


Figure 1. Fragmentation, non-native and managed species, urban warming, and environmental contaminants (left column) are specific urban drivers that directly affect plant-pollinator interactions at different stages of the plant-pollinator mutualism process (right column). Arrows indicate processes endogenous to the plant-pollinator mutualism, which includes a positive feedback loop between the rewards from individual interactions and plant and pollinator community structure (right). (1) Urban drivers filter plant and pollinator species by acting on life history traits unrelated to the pollination mutualism, such as soil preferences and nesting habitats. (2) Urban drivers simultaneously affect conditions for interaction between persisting plants and animals, which include spatial and temporal overlap and attraction between potential partners. (3) Once an interaction has occurred, urban drivers can affect the rewards received by plants or pollinators.

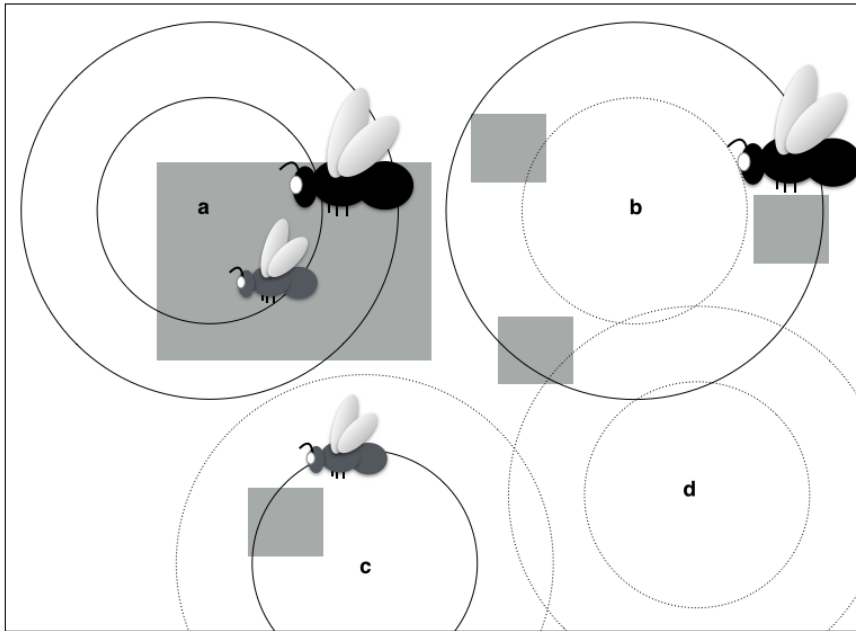


Figure 2. This diagram explores potential outcomes in the interaction between fragmentation of flowering plant habitat, pollinator nesting habitat, and the flight ranges of central-place foraging pollinators. Grey patches represent plant habitat fragments; letters show locations of pollinator nest sites in fragments or matrix, and circles show flight diameters of nesting female bees varying by body size. Dotted lines indicate flight ranges containing too few floral resources for successful pollinator nesting. At nest site a, both large and small pollinators persist; at nest site b, only the larger pollinator can access enough flowering plant habitat fragments; at nest site c, only the small pollinator can persist on the limited available resources; nest site d has too few resources for either pollinator.