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RESEARCH ARTICLE

Anthropogenic landscapes support fewer rare bee species

Tina Harrison (iD) · **Jason Gibbs** · **Rachael Winfree**

Abstract

Context The response of rare species to human land use is poorly known because rarity is difficult to study; however, it is also important because rare species compose most of biodiversity, and are disproportionately vulnerable. Regional bee pollinator faunas have not been assessed for rarity outside of Europe. Therefore, we do not know to what extent anthropogenic landscapes support rare North American bee biodiversity.

Objectives We ask how richness and abundance of bee species respond to land use, within quartiles of species defined by their numerical, phenological, and geographical rarity.

Methods We conducted a field study to sample bee communities in forested, agricultural, and urban landscapes replicated across a large spatial extent of the northeastern United States. We used large independent data sets to classify observed bee species according to three forms of rarity: their numerical rarity (low regional frequency in a museum-based data set), phenological rarity (short flight season length) and geographical rarity (small range size).

Results For all three forms of rarity, we found half as many rare bee species in agricultural landscapes compared to forest. We found half as many phenologically rare species in urban landscapes. Bees that had both shorter flight seasons and smaller range sizes were between one-third and one-half as rich in both types of anthropogenic landscapes, regardless of regional frequency.

Conclusions Although a minority of rare bee species were found in anthropogenic landscapes, our overall conclusion is that the native vegetation of our region, forest, is critical for supporting rare bee biodiversity.

Keywords Rarity · Commonness · Pollinator · Land use · Urban · Phenology · Apoidea

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Introduction

Human land use is currently the largest driver of global species loss (Pereira et al. 2010) and of local change in ecological communities (Newbold et al. 2015). Since land use change occurs at landscape scales, species loss and gain from local communities will ultimately

determine the future composition and diversity of global biodiversity (Villéger et al. 2011). In this context, the responses of rare species are particularly important, first because rare species compose most of biodiversity (Preston 1948; Gaston 1996), and second because rare species have greater risk of decline and extinction (Cardillo et al. 2008). Unfortunately, rare species are difficult to detect in community samples, and many remain undescribed (Coddington et al. 2009; Cardoso et al. 2011). These issues lead to large gaps in our understanding of how biodiversity responds to human land use (Pimm et al. 2014).

Although rarity is most often measured as population abundance (at local scales) or incidence (at larger scales), rarity has many other dimensions including range size and habitat specialization (Rabinowitz 1981). Different forms of rarity are controlled by different processes at different spatial and temporal scales; for example, local dominance may be associated with a close match between a species' traits and the immediate environment (Umaña et al. 2015), while range sizes are influenced by large-scale biogeography and evolution (Gaston 1996). Furthermore, different dimensions of rarity are associated with different vulnerability to ecological change. For example, small range size but not low local abundance is associated higher extinction rates in fossil species (Harnik et al. 2012), and bird species with large range sizes have increased over the past decade while species with high local abundances have declined (Godet et al. 2015). Interactions between two or more forms of rarity can also be important in predicting species' vulnerability. For example, beetle species with low abundances were sensitive to forest fragmentation, but only if they were also ecologically specialized (Davies et al. 2004). Therefore, it is important to consider different dimensions of rarity, including their synergisms, when asking how rare species respond to land use.

Insects account for most of the species on earth, and are diverse and abundant in most habitats, making them well-suited to questions requiring large data sets such as those related to rarity. In this study, we focus on bees, which in addition to being highly diverse, belong to one of most important functional groups on the planet, because almost 90% of plant species rely on animal pollinators like bees for sexual reproduction (Ollerton et al. 2011). It is largely unknown, however, whether bee communities in anthropogenic landscapes are dominated by common weedy species or include rarer species (Winfree et al. 2011; Cariveau and Winfree 2015). Two persistent research challenges have slowed our ability to understand how rare pollinators respond to anthropogenic land use. First, it is difficult to acquire reliable habitat association data for bees, which are highly mobile and may use multiple habitats based on spatial and temporal patterns of resources (Westrich 1996). The near proximity of alternative or complementary habitats may affect our perception of how bees respond to a focal land cover type (Kremen et al. 2007). Second, only a few regions worldwide have evaluated native bee species for relative rarity, due to a failure to invest in taxonomy and regional-scale distributional data for highly diverse species pools.

The goal of this study is to determine if anthropogenic landscapes retain diversity of relatively rare bee species, using three complementary definitions of rarity. To observe bee communities that are truly associated with a single land use type, we designed a field study with sampling sites located in continuous landscapes (at a 1.5 km scale) of forest, agriculture, and urban land cover. Additionally, in order to have greater inference across the bee species in our study region, we replicated sampling sites across a large spatial extent (> 300 km). Defining species rarity within community samples produces dependence between species' relative abundances and the particular distribution of habitats included in the sampling design; therefore, we used independent, large data sets to conduct the first quantitative assessment of rarity for a regional assemblage of North American bee species. Specifically, we assess the bee species of our region according to three forms of relative rarity: (1) numerical rarity (low regional frequency), (2) phenological rarity (short flight season length), and (3) geographic rarity (small range size). We then ask how richness and abundance of rare bee species respond to land use both considering each rarity dimension alone, and considering rarity classes defined by the intersection of the three dimensions. As far as we know, our work represents the most comprehensive, large-scale evaluation of how relatively rare bee species respond to human land use.

Methods

Field study: sampling bee communities from forested and anthropogenic landscapes

Our study region covers a 75,000 km^2 extent of the northeastern U.S. (Fig. 1a) and crosses four ecoregions characterized by different dominant forest types: Atlantic Coastal Pine Barrens, Northern Piedmont, Ridge and Valley, and Northern Allegheny Plateau (Omernik 1987). Contemporary land use composition of the three states included in our study region (New Jersey, Pennsylvania and New York) is 53% forest, 21% agriculture, and 11% urban land use (Nickerson et al. 2011). All forests in our study region are under some regime of human disturbance and management; however, they represent a current baseline for natural
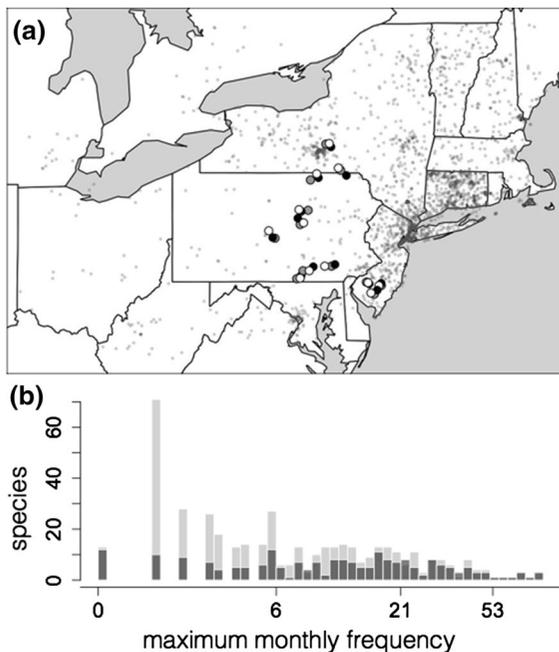

Fig. 1 **a** Geographic distribution of 12,003 museum specimen records (small points) used to assess rarity for bees in the northeastern USA. In order to associate bee rarity with different land cover types, we collected intensive community samples from 36 sites in forested (large black points), agricultural (gray) and urban (white) landscapes. **b** Frequency distribution of the maximum monthly abundances of 443 species in the museum data set used to define species rarity classes (light gray bars). Dark bars identify the subset of 226 species observed in our field study, which we classified into rarity categories based on the 25th, 50th, and 75th percentiles (x-axes values mark percentile boundaries)

habitat in contrast to intensive human activity that shapes "anthropogenic" (agriculture and urban) landscapes. To achieve a statistically replicated sample of urban landscapes, we chose twelve towns distributed throughout our study region having populations ranging from 5000 to 50,000. We then selected one forested site and one agricultural site within 4–25 km of each town. This spatial blocking ensures that landscape type is not correlated with other large regional gradients. Bees are mobile animals that 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 our study design was positioning sites so that they were surrounded by > 80% of the appropriate land cover type (forest, agriculture or urban) within a 1500 m radius (USGS 2006 National Land Cover Database, 30 m resolution). 1500 m is further than the regular flight distance of most bees in our region (Greenleaf et al. 2007; Zurbuchen et al. 2010), which makes it likely that bees we collected at a site are associated with a site's land use type. Our selection of towns and paired agricultural and forested sites was strongly constrained by the requirement for continuous landscapes, since landscapes in our study region are typically fragmented and complex at this scale.

We sampled pollinator communities at all 36 sites (3 land use types and 12 replicate triplets of sites) throughout each of the 2013–2015 growing seasons, for a total of 11 sampling rounds extending from April to early October. During each site visit, we set twenty-four pan traps and two blue-vane traps for 24 h. Both of these trap types attract bees with fluorescent colors that mimic flowers (Stephen and Rao 2005). Pan traps can compete with nearby flowers for pollinators' attention, and additionally can produce very low catch numbers when shaded by overhanging trees. To minimize these biases, we standardized the microhabitat in which pan traps were set to be mowed open vegetation in full sun, such as roadsides, small parks, and vacant lots. In addition, to make our data more robust to clustering in the spatial distribution of bees, each 'site' consisted of four mowed grass locations within 500 m of the center of the 1500 m radius landscape; we pooled data over these four samples within the site, because they are not independent.

We identified bee species based on published taxonomic revisions (Mitchell 1960; LaBerge 1961;

Mitchell 1962; LaBerge 1967; Ribble 1968; LaBerge 1971, 1973; LaBerge and Ribble 1975; LaBerge 1977; Bouseman and LaBerge 1979; LaBerge 1980, 1986; McGinley 1986; LaBerge 1987; Laverty and Harder 1988; LaBerge 1989; Coelho 2004; Gibbs 2011; Rehan and Sheffield 2011; Gibbs et al. 2013) and keys available online (Arduser 2016; Larkin et al. 2016). Bees in the genus *Nomada* were identified by Sam Droege (USGS Patuxent Wildlife Research Center, Beltsville, MD). We identified all specimens to species with the exception of three unresolved species groups (two in the genera *Nomada* and one in *Hylaeus*, with each group likely containing 2–5 species) that we retained in the data set and treated as species in analyses. We removed from analyses any species not native to the North American continent, since their distributions are likely affected by factors we are not investigating, such as the date and location of introductions (Lockwood et al. 2006).

Dimensions of bee species rarity

Numerical rarity

We measured numerical rarity as the number of collection events in which a species was detected, out of 12,003 collection events in a published, regional museum data set (Bartomeus et al. 2013). This data set includes 30,135 specimens of 443 bee species collected throughout the northeastern USA (Fig. 1b). These bees were collected from diverse plants, in diverse habitats and seasons, and by over 1,000 different data collectors. Prior to creating the database, all specimens were taxonomically updated and filtered to control for various potential biases (see details in Bartomeus et al. 2013).

The duration of bee species' flight seasons, or period in which active adults can be found, can be as short as 6 weeks or as long as 8 months. Thus, there is a bias towards classifying species with short flight seasons as numerically rare simply because there are fewer opportunities to collect them. Therefore, we instituted a further filter on the data to use each species' maximum monthly number of site records, as opposed to its annual total, as the measure of numerical rarity. For example, a species with 5 specimens in each of 3 months of the year will have the same rank as a species with 5 specimens in 1 month of the year. This method also makes our

measures of numerical and phenological rarity (described below) more independent.

Phenological rarity

Strong seasonality is a form of specialization, and is driven by the same trade-offs of efficiency and opportunity cost as spatial habitat specialization (Schoener 1974). Bees with short flight seasons, for example, can only forage on a small subset of plant species that bloom during that time. To estimate flight season length, we used 58,833 records of specimens of 379 species collected throughout the northeastern USA on known dates and subsequently identified to the species level (Table S1). We use the 10th and 90th percentiles of the collection dates to estimate emergence and senescence time for each species with at least 30 specimens (170 species). The difference in dates yields the estimated length of the flight season in days, our measure of phenological rarity.

Range size

The most extensive and reliable source for geographic ranges of North American bees is the American Museum of Natural History (New York, USA) database of bee species presence within political units (states and provinces), drawn from the literature and from museum collections, and published online (Discover Life AMNH_BEES database; Ascher 2006–2017). To estimate range size, we downloaded species' state records from the contiguous USA and large neighboring regions of Canada and Mexico, and then computed the area of the minimum bounding polygon containing the records for each species (Fig. S1). This measure of range size assumes that ranges are continuous, and is minimally influenced by variable sampling effort within the range.

Analysis

To determine how rare (and common) bee species were distributed across land use types, we compared the richness of bees within rarity quartiles across forested, agricultural and urban landscapes. We analyzed each quartile within each form of rarity separately using generalized linear models with Poisson error distributions (three rarity measures x four rarity quartiles = 12 glm tests). Because richness can be

strongly dependent on the number of individuals observed (Gotelli and Colwell 2001), we checked that our main results were not driven by abundance using a rarefaction analysis (Appendix 2 in Supplementary material). Abundance is a critical component of biodiversity response to anthropogenic change (Hull et al. 2015); therefore, we repeated all tests using number of individuals within rarity classes, in this case using negative binomial error distributions.

To find how responses differed in anthropogenic versus forested landscapes, we calculated p values and 95% confidence intervals around model coefficients using an estimator robust to heteroscedasticity (R package *sandwich*; Zeileis 2006). All analyses were performed in R 3.3.2; Poisson models for richness were performed using R package *lme4* (Bates et al. 2015), and negative binomial models for abundance were performed using R package *MASS* (Venables and Ripley 2002). To check the assumption of distributions for all generalized linear models, we used Chi square tests to assess if the residual deviance was similar to the residual degrees of freedom. We additionally checked for assumption of spatial independence among sites using Moran's *I* test for spatial autocorrelation in the residuals of models of species richness in the three land use types.

To explore how simultaneous rarity in more than one dimension affects species' response to land use, we used the approach introduced in Rabinowitz (1981). We first categorized bee species as rare or common using the median values of numerical, range, and phenological rarity. We then combined these measures into eight classes of rarity, in which one class was rare in all dimensions (less than median frequency, flight season, and range size), one class was common in all dimensions (greater than median frequency, flight season length, and range size), and the remainder of the eight classes were rare in some dimensions but common in others. We used medians because dividing the data in quartiles produces $4^3 = 64$ rarity classes, each represented by 2 or 3 species. To compare the richness of bees in each rarity class across land cover types, we fit generalized linear models with Poisson error distributions (8 glm tests). As for the analyses of single rarity classes, we also repeated all tests using number of individuals (abundance) instead of number of species (richness) within rarity classes.

Interpreting response to land use within different rarity groups, as tested by the generalized linear models described above, assumes that observed responses result from ecologically meaningful similarities among species within a particular rarity group. However, the species we observed are a sample from a larger, hypothetical pool of species that comprises the group. The observed sample of species may be too few or too variable in their response to land use to adequately represent the group. Furthermore, response to land use within one group may simply reflect trends in richness or abundance present in the whole community, in which case we should avoid attributing the response to group membership per se. To test the hypothesis that observed responses to land use are linked to particular rarity groups, we subjected all glm model results to a second significance test in which we randomized species' assignments to rarity groups, recalculated site richness and abundance, and then compared the observed glm model coefficients to the distribution of glm model coefficients calculated from the null species groups. To assign significance to richness or abundance differences within a particular rarity group, the observed coefficients must be more extreme than 95% of the coefficients calculated from random subsets of species drawn from the total community (two-tailed test). This approach is derived from species randomizations used to test species-environment relationships (Dray and Legendre 2008). We used 59,999 randomizations per test and only interpreted a response to land use as significant when both the glm test and its associated species randomization test were significant at alpha = 0.05 (ter Braak et al. 2012). Because of the requirement for joint significance under two independent tests, this two-step significance testing procedure is more conservative than a single glm test of richness differences among landscape types.

Results

We captured 12,635 specimens of 226 native species in our field study. This represents approximately 45% of the native species that are known to occur in the states of New York, New Jersey and Pennsylvania (Ascher 2006–2017). Of the species observed in our field data set, 213 (94%) were also observed in the museum data set. We assigned zero to the remaining

13 species' abundances, putting them in the rarest quartile together with species having fewer than six records in the filtered museum data set. Because our method for calculating phenological breadth required records of 30 or more specimens per species, we were able to assign flight season length to 170 (75%) of species observed in our field data set; the remaining 56 species were not analyzed with respect to phenological rarity. Range size data was available for all 226 species.

Based on the 170 species for which we defined all three types of rarity, regional frequency was weakly correlated with phenology ($r = 0.34$) and range ($r = 0.41$) (Fig. S2). Range and phenology were not correlated ($r = 0.03$). Only six species occurred jointly in the lowest quartiles of all three measures (out of 60, 54 and 43 species respectively). This demonstrates that our three forms of rarity are not simply proxies for one another.

For all three forms of rarity, the rarest quartile of species had lower richness in anthropogenic landscapes compared to forest (Fig. 2, left-most panels). The richness difference between agricultural and forested landscapes was significant for all three forms of rarity. However, the richness difference between urban and forested landscapes was only significant when considering phenological rarity (Table 1). The two next rarest quartiles tended to also have lower richness in anthropogenic versus forested landscapes, but the differences were not significantly greater than expected in random subsets of species (Table S2). For the most common quartile of all three forms of rarity, estimated richness at an average site was very similar across land use types (Fig. 2, right-most panels).

Classifying species using all three forms of rarity simultaneously produced results suggesting some interactions among the forms of rarity. Bees with both short flight seasons and small ranges were significantly less rich in both agriculture and urban landscapes compared to forest, regardless of their numerical rarity (Fig. 3, panels d, h). The remaining rarity classes did not have detectably different richness in anthropogenic and forested landscapes. Although the average richness tended to be higher in forest, these differences were not significantly greater than those expected in random subsets of species (Table 2). The exception was bees with low regional frequency, long flight seasons, and small ranges, which were
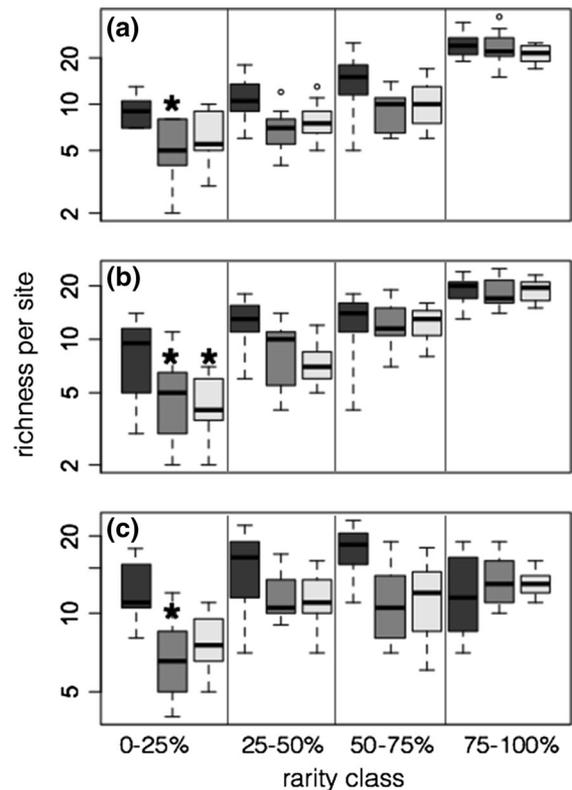

Fig. 2 Number of species per site (richness) in forested (dark gray), agricultural (medium gray) and urban (light gray) landscapes, within quartiles of three aspects of species' rarity: **a** frequency in a regional museum data set; **b** phenological breadth; **c** geographic range size. Asterisks indicate significant differences between richness in anthropogenic versus forested landscapes, determined using a two-step significance testing

significantly richer in urban sites compared to forest sites (Fig. 3g).

Abundance patterns were more idiosyncratic, but broadly concurred with the richness-based results. When analyzing the three forms of rarity separately using quartiles, we tended to find fewer rare bee individuals in anthropogenic landscapes compared to forest, but this difference was only significant for phenologically rare bees in urban landscapes (Table S3, Fig. S3). Among the largest quartile of range sizes, we found many more bee individuals in both anthropogenic landscapes versus forest (Fig. S3c, right-most panel). When analyzing all three forms rarity together using medians, we found that bees defined by having short flight seasons and small ranges were less abundant in urban landscapes compared to forest, for both regionally frequent and infrequent

Table 1 We compared the number of rare species in forested landscapes with anthropogenic (agricultural and urban) landscapes (N = 12 per land cover type)

Form of rarity	Forest	Agriculture	p	Urban	p
Low frequency	8.1	**0.5 (0.39, 0.76)**	**0.03**	0.7 (0.49, 0.91)	0.23
Short flight season	7.5	**0.5 (0.34, 0.88)**	**0.05**	**0.5 (0.31, 0.69)**	**0.01**
Small range	11.4	**0.5 (0.38, 0.72)**	**0.02**	0.6 (0.46, 0.75)	0.08

"Rare species" are defined as those belonging to the lowest quartile of one of three forms of rarity (frequency in a regional museum data set, phenological breadth, and geographic range size). "Forest", used as the model intercept, shows the estimated number of rare bee species per forest site, while "Agriculture" and "Urban" show the ratio of bee richness per anthropogenic site relative to bee richness per forest site, together with 95% confidence intervals. Values less than one indicate lower richness in anthropogenic sites. For example, we observed an estimated 8.1 rare species per forest site, versus 0.5 × 8.1 = 4.05 rare species per agricultural site. For each model, we conducted a second significance test based on randomizing species across rarity categories, and chose the higher of the two p-values to interpret richness outcomes. Bolding highlights significant outcomes
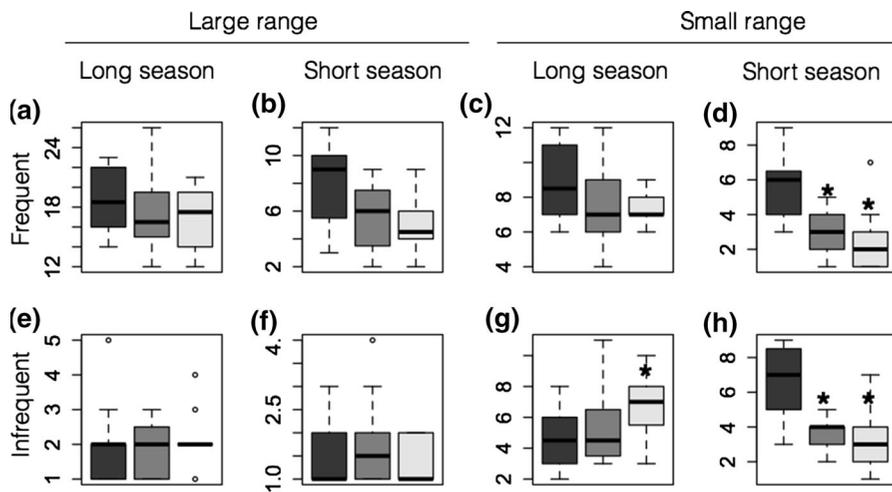

Fig. 3 Each panel shows bee species richness at sites characterized by either continuous forest (dark gray), agricultural (medium gray) or urban (light gray) land use. N = 12 sites per land use type. Different panels correspond to different groups of species defined by numerical rarity (frequent vs. infrequent in a regional data set), phenological rarity (long flight season vs. short flight season), and geographic rarity (large range size vs. small range size), using the median value to distinguish rare from common in each case. Each of 170 total species is represented in only one group. Species in panel (*a*) are common in every aspect, while species in panel (*h*) are rare in every aspect. Asterisks indicate significant differences between anthropogenic and forested landscapes, determined using a two-step significance testing

species (Table S4, Fig. S4d, h). We additionally found that bees with high regional frequency, large ranges, and short flight seasons were less abundant in urban landscapes (Fig. S4b).

We detected moderate overdispersion in two glm models comparing richness of bee species in different land use type, including for bees in the lowest flight season quartile (Table S5). Since re-running the models with quasi-Poisson error distributions produced the same results (not shown), and since the sandwich estimators we used are robust to some

overdispersion, we are confident in presenting the results from the original Poisson-distributed models. We did not detect overdispersion in models for richness within combined rarity classes (Table S6) or in any models of abundance (Tables S7, S8). We detected spatial autocorrelation in the residuals of five of the twelve models for richness in the rarest quartiles of species rarity (Table S9), which indicates that p-values for these models may be anticonservative; nevertheless, we did not detect effects of land use on richness within these rarity classes. We did not

Table 2 To explore how simultaneous rarity in more than one dimension affects species' response to land use, we compared the number of species in forested landscapes with anthropogenic (agricultural and urban) landscapes (N = 12 per land cover type), within eight groups of species defined by combinations of numerical rarity (infrequent in a regional data set), phenological rarity (short flight season), and geographic rarity (small range size)

	Low frequency	Short flight season	Small range	Forest	Agriculture	p	Urban	p
(a)				17.8	0.9 (0.78, 1.09)	0.34	0.9 (0.77, 1.04)	0.20
(b)		✔		7.0	0.6 (0.43, 0.97)	0.16	0.6 (0.4, 0.86)	0.11
(c)			✔	7.9	0.8 (0.65, 1.07)	0.42	0.8 (0.67, 0.96)	0.45
(d)		✔	✔	4.6	**0.4 (0.28, 0.69)**	**0.04**	**0.3 (0.16, 0.68)**	**0.01**
(e)	✔			1.0	0.9 (0.4, 2.12)	0.84	1.2 (0.55, 2.49)	0.69
(f)	✔	✔		0.5	1.5 (0.5, 4.51)	0.47	0.8 (0.28, 2.46)	0.74
(g)	✔		✔	3.7	1.2 (0.74, 1.81)	0.52	**1.6 (1.1, 2.23)**	**0.01**
(h)	✔	✔	✔	5.6	**0.5 (0.36, 0.64)**	**0.02**	**0.4 (0.24, 0.63)**	**0.00**

For each form of rarity, we used median values to divide species into "rare" and "common" categories. The first category (a) comprises species that were common in all three dimensions. "Forest", used as the models' intercepts, shows the estimated number of bee species per forest site, while "Agriculture" and "Urban" show the ratio of bee richness per anthropogenic site to bee richness per forest site, together with 95% confidence intervals derived from generalized linear models. Values less than one indicate lower richness in anthropogenic sites. For example, among species rare in all three dimensions (h) we observed an estimated 5.6 species per forest site, vs. half as many such species ($0.5 \times 5.6 = 2.8$) per agricultural site. For each model, we conducted a second significance test based on randomizing species across rarity categories, and chose the higher of the two p-values to interpret richness outcomes. Bolding highlights significant outcomes

observe spatial autocorrelation for the rarest quartiles, where the significant effects of land use were observed (Fig. 2).

Many of the differences in richness and abundance of species groups between land use types were significant according to the glms. However, because there are overall fewer total species in anthropogenic relative to forested landscapes sites, many apparent patterns (e.g., rarity class 25–50% in Fig. 2a) can be explained by overall trends in richness or abundance between landscape types. Requiring that relationships were simultaneously significant under both a glm and a randomization test ("two-step significance testing") exerted a strong filter on the number of significant results that we reported.

Discussion

We found fewer rare bee species in anthropogenic landscapes compared to the dominant native vegetation type, deciduous forest. This is the first evidence from North America that land use negatively affects rare bee species as a group. We know of only one other study that compares rarity of bees across different land use types (Baldock et al. 2015). The authors found equivalent numbers of rare species in natural and anthropogenic landscapes. However, natural habitats in their study region (Great Britain) have been subject to a long history of human land use and deforestation, such that many rare forest bee species may have been lost before they were recorded.

Our measures of numerical, phenological, and geographical rarity were uncorrelated, yet by each measure there were fewer rare bee species in anthropogenic landscapes. Studies of other taxa have also found negative effects of land use on one or another forms of rarity. For example, butterflies with only one generation per year are less likely to be successful in urban areas (Blair 2001), and small-range species were found to be more vulnerable to human land use in studies of plants (Mayfield and Daily 2005), butterflies (Horner-Devine et al. 2003), and fish (Scott 2006). A possible reason for rare species being more sensitive than common species to land use change is that species with large populations, broad habitat niches, and large geographic ranges must adapt to thrive in a wide variety of environmental conditions (or conversely, being so adapted allows a species to achieve commonness), and this flexibility gives common species a higher chance of successfully exploiting and

dominating novel anthropogenic habitats (McKinney and Lockwood 1999).

An additional, system-specific explanation for our results is that bees with both short flight seasons and small range sizes (i.e., the right half of Fig. 3) are also likely to be associated with forested habitats. Short, univoltine flight seasons may be an important adaptation for exploiting the brief period of spring bloom in deciduous forest, before the canopy leafs out and shades the forest floor (Motten 1986). For bee species in our study region, small geographic ranges are more likely to coincide with the geographic extent of seasonal deciduous forest, whereas larger ranges extend into regions of North America characterized by extensive grass and shrub land. Because forest was the predominant land cover in eastern North America before European colonization (Rudel et al. 2005), it is possible that a disproportionate number of bee species restricted to this region—that is, species with small range sizes—have adapted to forest conditions. Conversely, the open, early successional habitats common in agricultural and urban landscapes likely benefit species with long flight seasons, because these habitats provide floral resources later in the year when resources are absent from forests (Winfree et al. 2007, 2011).

Two limitations affect our study's interpretation and inference space. First, in using quartiles and medians to define relative rarity amongst our observed species, we almost certainly classify many species as "rare" that would not be considered absolutely rare using complete species inventories and holistically applied criteria. Although absolute definitions of rarity are valuable for conservation work, they are often impractical for community-scale ecology. Researchers are unlikely to observe such rare species (Scheper et al. 2015), and holistic definitions (such as those used for Red List categories) tend to integrate across multiple forms of rarity so that the resulting collection of species may have little in common with one another (Collen et al. 2016). Second, in order to correctly replicate land use types at large landscape scales, our sampling design avoided many potentially important bee habitats, including complex, fragmented landscapes (Tscharntke et al. 2012) and habitats that occur only at finer spatial grains, such as bogs (Fowler 2016). For example, our results do not predict anything about the richness of rare bees in a small-scale patchwork of agriculture and forest, or an urban wetland. Because fine-scale habitats are relevant to smaller subsets of species and difficult to define consistently in different landscape contexts, our gross land cover categories are more appropriate for comparing the response of many species across large spatial scales.

Our data suggest that agricultural and urban landscapes also support large proportions of regionally rare species. In each rarity class, we observed some rare species at almost every anthropogenic site, and almost half of the rarest species were collected only from agricultural or urban sites (Table 3). Intriguingly, we found one rarity class (low-frequency, small-range species with long flight seasons) that was richer in urban sites than forested sites, despite overall lower richness in urban sites. Although the data are too sparse to analyze species individually, it appears that rare species include both forest-associated and open-habitat associated species. This concurs with previous

Table 3 Total numbers of bee species belonging to different rarity groups collected across 12 sites located in forested, agricultural, or urban landscapes

Quartile	Forest	Agriculture	Urban
Frequency			
1	40 (21)	22 (7)	28 (11)
2	42 (19)	24 (5)	31 (4)
3	41 (8)	32 (2)	39 (7)
4	51 (7)	46 (2)	47 (2)
Phenology			
1	32 (14)	22 (7)	20 (3)
2	32 (8)	23 (1)	30 (5)
3	34 (6)	32 (2)	32 (2)
4	40 (3)	36 (1)	38 (0)
Range			
1	43 (22)	22 (4)	26 (7)
2	47 (14)	33 (3)	35 (3)
3	42 (10)	30 (4)	38 (5)
4	36 (9)	34 (5)	39 (8)

Within a form of rarity (frequency, phenology, or range size), every bee species belongs to exactly one quartile, which are ranked from rarest (1) to most common (4). Parenthetical values indicate the numbers of species in the rarity group that were unique to a given land use type. Note that the rarest species groups are noticeably less species-rich in anthropogenic landscapes (agriculture and urban) compared to forest, while the commonest species groups have similar numbers of species across the land use types

findings that bee faunae in urban areas can be diverse (Matteson et al. 2008). Our results are also consistent with the hypothesis that many rare species depend on anthropogenic habitats that function as analogues for marginal or early-successional open natural habitats that are no longer available (Knapp et al. 2009; Hall et al. 2016). However, our results suggest that forest is still the most important habitat for supporting diversity of rarer bees in the northeastern USA, and that preventing forest loss and degradation is a priority for bee conservation.

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