Bees use anthropogenic habitats despite strong natural habitat preferences

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Abstract

Aim: Habitat loss and alteration are widely considered one of the main drivers of current pollinator diversity loss. Yet little is known about habitat importance and preferences for major groups of pollinators, although this information is crucial to anticipate and mitigate the current decline of their populations. We aim to rank and assess the importance of different habitats for bees, to determine the preference for and avoidance of particular habitat types by different bees and to quantify the diversity of bees within and among habitats.

Location: North-eastern USA.

Time period: The sampling was done over 15 years (2001–2015).

Major taxa studied: Apoidea.

Methods: We used an unprecedented extensive dataset of >15,000 bee specimens, comprising more than 400 species collected across north-east USA. We extracted habitat information from the sample points and used network analyses, null models comparisons and beta-diversity analysis to assess habitat importance, habitat preference, use and diversity.

Results: We found that natural habitats sustain higher bee diversity and a different set of species than agricultural and urban areas. Although many bee species used human-altered habitats, most species exhibited strong preferences for forested habitats and only a few preferred altered habitats over more natural habitats. In contrast to previous studies, landscape composition only had moderate buffer effects on diversity loss. The loss of biodiversity in human-altered environments could have been higher but it was partially compensated by the presence of human commensals and exotic species.

Main conclusions: Although human-altered environments may harbour a substantial number of species, our work suggests that preserving natural areas is still essential to guarantee the conservation of bee biodiversity.

Keywords
habitat importance, habitat preference, habitat use, landscape, pollinators, urban
1 | INTRODUCTION

Plant pollinators are considered to be of conservation concern worldwide (Goulson, Nicholls, Botías, & Rotheray, 2015). In Europe, for example, 9.1% are threatened of bees assessed by the IUCN are threatened and 5.2% are considered Near Threatened. (Nieto et al., 2014), and in North America, there is evidence that the populations of many bee species have drastically declined in the last decades (Bartomeus et al., 2013; Cameron et al., 2011). While the current loss of pollinators may have a variety of causes, the conversion of natural habitats into urban and agricultural systems is widely thought to be one of the main drivers (Winfree, Bartomeus, & Cariveau, 2011). Currently, over 40% of Earth’s terrestrial surface has already been altered by humans (Ellis, Goldewijk, Siebert, Lightman, & Ramankutty, 2010) and the surface is expected to continue increasing in the next decades (Tilman et al., 2001). Given that more than 80% of plants are pollinated by animals (Ollerton, Winfree, & Tarrant, 2011), including 75% of crops species (Klein et al., 2007), the extinction of pollinator species is expected to have far-reaching impact on ecosystem functioning and human well-being.

Despite growing concern over the consequences of pollinators loss, it is currently uncertain how they are affected by changes in land use intensity. A major obstacle has been the paucity of large-scale datasets on species-habitat associations at large geographical scales. As a result, current knowledge on habitat importance for bees comes mainly from expert opinion and modelling efforts (Koh et al., 2016; Lonsdorf et al., 2009).

In the present study, we use an unusually large dataset from an extensive monitoring programme for the north-east and midwest United States to directly estimate habitat importance and species habitat preference across the entire region. The dataset comprises 15,762 individual bees from 433 species recorded over 15 years, covering most of the habitats and species in the region. Based on this dataset, we first asked how bee communities differ in richness and composition within and among habitats at a regional scale. Although previous work has established that bee community richness and composition can strikingly differ between natural vegetation and altered habitats for particular regions (Brosi, Daily, & Ehrlich, 2007; Kleijn et al., 2015), ours is the most general and comprehensive assessment to date. We investigated habitat importance for bees using tools derived from network theory, which allow us to describe the complex web of habitat-species interactions. As pollinators are mobile species and the surrounding landscape often determines the presence of a species in the focal habitat (Kremen, Williams, & Thorp, 2002), we also investigated the effect of the surrounding landscape in determining bee responses beyond the habitat where each bee was observed.

The assessment of relative habitat importance can provide general insights into species sensitivity to environmental change. However, the presence of a species in a particular habitat does not necessarily indicate that the species is performing well in that habitat, but may reflect that this is the only habitat available. So to better assess species sensitivities to habitat alteration, it is necessary to assess specific habitat preferences. Preference is defined as the tendency of a species to be associated with certain environments more than expected by chance (Rice, 1984). Therefore, a second goal of our study was to investigate such species-habitat associations. We used null models to assess habitat preference and avoidance for 45 bee species with a sufficiently large sample of occurrences (species with ≥100 independent records). We then characterized their sensitivity to human-altered habitats by estimating the extent to which the species occurs in highly altered environments or, instead, use multiple habitats that buffer them against destruction of their preferred habitat.

Although human-induced changes in the habitat are generally perceived to have a negative impact on pollinator species (Winfree et al., 2011), they can also offer ecological opportunities to some species (Moleson, Ascher, & Langellotto, 2008; McFrederick & LeBuhn 2006). Pollinators are highly mobile animals, and some are capable of using multiple habitat types (Kremen et al., 2002). For example, some bee species nest in forested habitats while foraging in agricultural habitats (Klein, Steffan-Dewenter, & Tscharntke, 2003), and some even use highly transformed environments such as those altered by urbanization and intensive agriculture (Baldock et al., 2015; Saure, 1996). If human-altered habitats create new opportunities for some pollinators, this may reduce the impact of habitat loss and alteration on pollinator communities and associated ecosystem services (Kremen et al., 2002). Our final goal was to assess the extent to which human-altered habitats provide opportunities for native and exotic species.

2 | METHODS

2.1 | Sampling design

Bees were intensively sampled from 2000 to 2015 by USGS Native Bee Inventory and Monitoring Laboratory, their collaborators, and volunteers using pan traps (~75%) and hand netting (~25%) (Westphal et al., 2008). As the sampling was designed to maximize the study area to accurately cover all the main habitats of the region, a different location was selected for each sampling point. However, care was taken to cover the entire phenology and to avoid biases in the use of monitoring techniques among habitats (Supporting Information Figure S1, Table S1). Although sampling was carried out over a larger region, we restricted our analyses to samples taken from the area with the highest sampling effort, covering latitude 35.01 S to 42.79 N and longitude −87.54 W to −69.97 E (Figure 1).

After capture, the coordinates of the collection site were recorded using GPS and the specimen was identified to the species level by expert taxonomists. Unidentified individuals or extremely rare species (i.e., those collected only once) were removed from the dataset. Some species that were particularly difficult to separate
taxonomically were pooled together for the analysis (see Table 2). Overall, we retained 291,195 individuals, which represent a 68% of the original data. To ensure the independence of the collection events, we excluded from analysis specimens belonging to the same species when collected at the same locality during the same day. After this last filtering, the final dataset comprised 15,762 individuals from 433 species collected from 1,452 different sites, all of which were used in subsequent analysis. All specimens were vouchered at USGS Native Bee Inventory and Monitoring Laboratory.

For each georeferenced sampling site, we extracted habitat information using the National Land Cover Database (NLCD) raster layer (Homer et al., 2015) with the R packages raster, rgdal and stringr (Bivand, Keitt et al., 2018; Bivand, Lewin-Koh et al., 2018; Hijmans, 2015). The 14 habitats considered in this study are described in Table 1, and the number of sampling points for each habitat is described in Supporting Information Table S1. We extracted the habitat type from the focal point based on the precise coordinates. To take into account the surrounding landscape, we also extracted the habitat composition in a buffer of 1,000 m radius around each focal point; 1,000 m is the maximum distance that most bees under 4 mm of intertegular span can forage (Greenleaf, Williams, Winfree, & Kremen, 2007). While our dataset spans 15 different years, information on land cover was only available for 2001, 2006 and 2011. To account for this, bees sampled before 2005 were assigned to habitats based on information from the 2001 layer (28% of our data), those sampled between 2006 and 2010 were assigned to the 2006 layer (42%) and for the rest (2011–2015) we used the 2011 layer (29%). The ninety eight per cent of the sites sampled maintained their land use classification along the three raster layers used. Field notes were taken during the sampling, and most of them matched with the NLCD raster layer, but there were too many note categories and only 51% of the data collected had field notes. To estimate availability of each habitat in our study region, we divided all the pixels of the habitat by the total pixels of the entire study area (Supporting Information Figure S2).

We analysed the possible spatial autocorrelation in sampling events using Moran’s Index and a multivariate homogeneity of groups dispersions analysis using the package ape (Paradis & Schliep, 2018) and vegan (Oksanen et al., 2018). First, we tested autocorrelation for each habitat and we found that the autocorrelation values were very low (ranging from observed I values of 0.01–0.16). Second, we compared the dispersions of the habitat sampling points across habitats to assess the potential differences in the clustering of the sampled points in different habitats. Most of the habitats did

**FIGURE 1** Map of the sampling area. It covers the area from 35.01 S to 42.79 N and −87.54 W to −69.97 E, north-east USA. This area was selected as it represents a large but homogeneous region.
not present different dispersions and show the same distribution of distances to the centroid (Supporting Information Figure S5). Hence, and as our analysis are pooled by habitat type, we did not further correct for spatial autocorrelation, but acknowledge that the results are driven by the habitat configuration of the region and cannot be extrapolated to other regions.

2.2 Data analysis

2.2.1 Habitat importance

We evaluated the importance of different habitats for bee species using the number of species detected in each habitat (i.e., species richness). Although species richness is a widely used index of habitat importance (Chao & Jost, 2012), it treats all species as ecologically equivalent, which may not be justified for conservation purposes. For instance, a habitat may have high species richness but primarily sustain common species that are widely present elsewhere, whereas another habitat with equal or lower species richness could mostly support rare species that are highly dependent on this particular habitat. To tackle this limitation, we also evaluated the importance of different habitats by means of a metric of habitat strength.

Habitat strength was calculated using a metric derived from network analysis. The strength of a node (i.e., a single element from a network, in this case the focal habitat) in a bipartite interaction network of species per habitats is defined as the sum of the dependencies of nodes corresponding to the other level in the bipartite network (in this case, the bee pollinator species) linked to that

| TABLE 1 | Description of the habitats used to assess importance, use and preference for bee pollinator species, as they are defined and contained in the National Land Cover Database 2011, which is a modified version of the Anderson Land Cover Classification System (Anderson, Hardy, & Roach, 1976) |
|---|---|
| **Habitat** | **Description** |
| Barren land | Areas of bedrock, desert pavement, scarp, talus, slabs, volcanic material, glacial debris, sand dunes, strip mines, gravel pits and other accumulations of earthen material. Generally, vegetation accounts for less than 15% of total cover |
| Coastal | Areas next to open water, generally with less than 25% cover of vegetation or soil |
| Cultivated crops | Areas used for the production of annual crops, such as corn, soybeans, vegetables, tobacco, and cotton, and also perennial woody crops such as orchards and vineyards. Crop vegetation accounts for greater than 20% of total vegetation. This class also includes all land being actively tilled |
| Deciduous forest | Areas dominated by trees generally >5 m tall, and >20% of total vegetation cover. More than 75% of the tree species shed foliage simultaneously in response to seasonal change |
| Developed: low intensity | Areas with a mixture of constructed materials and vegetation. Impervious surfaces account for 20%–49% of total cover. These areas most commonly include single-family housing units |
| Developed: medium intensity | Areas with a mixture of constructed materials and vegetation. Impervious surfaces account for 50%–79% of the total cover. These areas most commonly include single-family housing units |
| Developed: high intensity | Highly developed areas where people reside or work in high numbers. Examples include apartment complexes, row houses and commercial/industrial. Impervious surfaces account for 80%–100% of the total cover |
| Developed: open space | Areas with a mixture of some constructed materials, but mostly vegetation in the form of lawn grasses. Impervious surfaces account for <20% of total cover. These areas most commonly include large lot single-family housing units, parks, golf courses and vegetation planted in developed settings for recreation, erosion control or aesthetic purposes |
| Emergent herbaceous wetlands | Areas where perennial herbaceous vegetation accounts for >80% of vegetative cover and the soil or substrate is periodically saturated with or covered with water |
| Evergreen forest | Areas dominated by trees generally >5 m tall, and >20% of total vegetation cover. More than 75% of the tree species maintain their leaves all year. Canopy is never without green foliage |
| Herbaceous/hay/pasture | Areas of grasses, legumes or grass–legume mixtures planted for livestock grazing or the production of seed or hay crops, typically on a perennial cycle, also containing areas dominated by graminoid herbaceous vegetation. Pasture/hay vegetation accounts for >20% of total vegetation |
| Mixed forest | Areas dominated by trees generally >5 m tall, and >20% of total vegetation cover. Neither deciduous nor evergreen species are >75% of total tree cover |
| Shrub/scrub | Areas dominated by shrubs <5 m tall with shrub canopy typically >20% of total vegetation. This class includes true shrubs, young trees in an early successional stage or trees stunted from environmental conditions |
| Woody wetlands | Areas where forest or shrub–land vegetation accounts for >20% of vegetative cover and the soil or substrate is periodically saturated with or covered with water |

*Herbaceous and hay/pasture are classified as two different habitats in NLCD. We merged them because herbaceous areas in our sampling region are always for livestock (Koh et al., 2016).*
The dependence of a bee pollinator on a given habitat is calculated as its proportional use of this habitat relative to the other habitats and ranges from zero to one. For example, if a species node has a dependence value near one on a habitat node, we conclude that species depends strictly on that habitat. However, if the dependence is close to zero, the species does not depend on that single habitat and instead, uses other habitats.

To calculate richness and strength for each habitat, we first rarified each habitat to equalize sampling effort to that of the least well-sampled habitat. To this purpose, we first calculated the coverage value (the percentage of the total species diversity) for each habitat and then rarified to the number of individuals necessary for equal coverage of all habitats (Hsieh, Ma, & Chao, 2016). We chose the common coverage value to be 0.60, because shrub/scrub was the less covered habitat (0.62 of coverage), meaning that 60% of species richness from each habitat was sampled to calculate richness and strength. Coverage was calculated using the "iNEXT" package (Hsieh et al., 2016). By using the same coverage for every habitat, we avoided that the most sampled habitats were over-represented. However, the total richness at the regional scale (i.e., gamma-diversity) is likely to depend on the area covered by each habitat, independent of the number of samples for each habitat, so we show the proportion of each land cover type (Supporting Information Figure S2) to aid interpretation of gamma-diversity values. However, species diversity did not increase with the total area of each habitat ($p = 0.56, R^2 = -0.052$). Although sampling date and trap/hours might also affect richness, this information was not available and hence we assume that these factors are not biasing the data.

Although the importance of a habitat can be characterized in terms of species richness and habitat strength, beta-diversity among and within habitats is fundamental to identify the habitats that are singular in species composition and to determine the degree of species turnover within habitats across space (Whittaker, 1960). Among-habitat beta-diversity was calculated using Sørensen beta-diversity dissimilarity index across all pairs of habitats (Sørensen, 1948). Habitats were then grouped according to their similarity using a hierarchical cluster analysis (Figure 2a). Within-habitat beta-diversity was calculated as the slope of the species–samples accumulation curves for each habitat (Figure 2b). This metric represents the rate at which new species appear within that habitat as sample size increases. The species–samples relationship was almost linear and hence we did not log-transformed the data (Baselga & Orme, 2012), although log-transforming the data using natural logarithms produced similar results.

As bees are mobile organisms that likely depend on adjacent habitats in the landscape, we repeated the above analyses at a landscape scale. We classified landscapes at a 1,000 m radius surrounding each sampling site into discrete groups using a $k$-mean algorithm. The total number of groups ($k$) was determined using "the
elbow method,” where $k$ is the number of clusters beyond which additional clusters no longer improve the model. In our analyses, $k$ was estimated as 20 (Supporting Information Figure S3) and hence 20 types of landscapes were defined. These 20 landscape categories range from mainly forested landscapes to more complex landscapes that include a mix of agricultural and forested areas (Supporting Information Table S2).

### 2.2.2 | Species habitat use and preference

Disentangling species habitat use and preference requires a large sample size for each species studied, thus we only used here species that had >100 independent collection events ($n = 45$ species). We considered that an habitat was used for a species when at least one individual of that species was sampled in that habitat. Although we cannot know if the species is nesting or foraging on the habitat where it was captured, we assume that the repeated capture of a species in the same habitat indicates that this is likely to happen. To normalize for differences in the number of species occurrences, we assessed habitat use on 100 rarefaction events for each species, that is performing 100 subsampling events of 100 occurrences, and extracting the mean number of habitats used by each species over 100 the subsample events.

We defined habitat preferences as the nonrandom association of a species with certain habitats. Therefore, a species was considered to exhibit habitat preference if it was sampled in a habitat more frequently than expected by chance. Species preferences can be confounded with species distributions if their geographical range only covers some of all available habitats. For example, species distributed only in the northern part of the sampling area may appear to prefer evergreen forests simply because this habitat is more common there. However, this limitation was negligible in our study because the geographical range of the almost all species studied covered the entire study area (Supporting Information Table S4, Bartomeus et al., 2013; Schuh, Hewson-Smith, & Ascher, 2010), implying that all sites could have been potentially occupied by any species if habitat choice was completely random. We compared a habitat–species matrix (i.e., the “observed” matrix) to 1,000 null matrices (i.e., the “null” matrices). These null matrices were created by means of the function “nullmodel” contained in the “bipartite” package (Dormann, Frund, Bluthgen, & Gruber, 2009). This function generates random bipartite tables maintaining the sum of rows and columns using Patefield’s (Patefield, 2012) algorithm, so the proportional abundance of species and habitats is maintained, but their associations are re-shuffled. We considered that a species exhibited preference for a particular habitat if it was more abundant than the 0.95 quantile of expected abundances, whereas species less abundant than the 0.05 quantile were considered to avoid that habitat (Sol, González-Lagos,)

![Figure 3](image-url) Importance of each analysed habitat. We defined importance as a function of both strength and richness. Both metrics are correlated, but give different information (see text for details). Each point represents the mean of 100 rarefied strength and richness values for each habitat. Bars are the standard deviation across 100 runs for both strength and richness. (a) Shows habitat importance results considering only the habitat where bees were found. While human modified habitats are less important than the natural habitats, they still sustain a substantial amount of pollinator species. (b) Shows habitat importance considering landscape composition where species were collected. Similar landscapes were grouped by colour; detailed composition of each landscape can be found in Supporting Information Table S2.
### TABLE 2  
Species habitat preference or avoidance. The first column indicates the number of rarefied habitats used for each species listed, the other three columns show for every habitat (see Figure 4 for habitat grouping) the habitat preference (>0.95, marked in blue) or avoidance (>0.05, marked in red), calculated as the probability of having a higher or lower observed abundance than expected under the null model.

| Species                        | Habitats used | Pasture and crops | Forests | Urban |
|--------------------------------|---------------|-------------------|---------|-------|
| Agapostemon virescens          | 12.47         | 0.66              | 0.1     | 0.89  |
| Andrena carlini                | 11.38         | 0.43              | 0.78    | 0.01  |
| Andrena cressonii              | 12.41         | 0.53              | 0.61    | 0.02  |
| Andrena erigeniae              | 11.43         | 0.1               | 1       | 0.01  |
| Andrena nasonii                | 12.32         | 0.09              | 0.99    | 0.03  |
| Andrena perplexa               | 10.82         | 0.94              | 0.51    | 0.01  |
| Andrena violae                 | 11.85         | 0.39              | 0.92    | 0.01  |
| Apis mellifera                 | 12.46         | 0.5               | 0.61    | 0.69  |
| Augochlora pura                | 11.34         | 0.29              | 0.96    | 0.21  |
| Augochlorella aurata           | 12.3          | 0.05              | 0.75    | 0.5   |
| Bombus bimaculatus             | 12.04         | 0.05              | 0.99    | 0.04  |
| Bombus fervidus                | 12.93         | 0.87              | 0.03    | 0.73  |
| Bombus griseocollis            | 12.28         | 0.19              | 0.43    | 0.82  |
| Calliopsis andreniformis       | 12.68         | 0.76              | 0.14    | 1     |
| Ceratina calcarata/dupla/mikmaq | 12.53         | 0.53              | 0.24    | 0.27  |
| Ceratina strenua                | 12.06         | 0.99              | 0.02    | 0.73  |
| Halictus confusus              | 12.2          | 0.52              | 0.6     | 0.99  |
| Halictus ligatus/poeyi         | 12.42         | 0.09              | 0.26    | 0.95  |
| Halictus rubicundus            | 11.64         | 0.78              | 0.18    | 0.67  |
| Hylaex affinis/modestus        | 12.38         | 0.3               | 0.95    | 0.41  |
| Lasioglossum bruneri           | 11.81         | 0.87              | 0       | 0.96  |
| Lasioglossum callidum          | 12.35         | 0.99              | 0.01    | 0.11  |
| Lasioglossum coriaceum         | 12.52         | 0                 | 1       | 0.02  |
| Lasioglossum cressonii         | 11.9          | 0.01              | 1       | 0.04  |
| Lasioglossum hitchensi         | 12.13         | 0.88              | 0.17    | 0.55  |
| Lasioglossum illinoense        | 11.59         | 0.79              | 0.77    | 0.89  |
| Lasioglossum imitatum          | 12.18         | 0.11              | 0.99    | 0.9   |
| Lasioglossum near_admirandum   | 11.29         | 0.85              | 0.44    | 0.83  |
| Lasioglossum oblongum          | 12.33         | 0.34              | 0.01    | 0.15  |
| Lasioglossum pectorale         | 11.59         | 0.58              | 0.11    | 0.15  |
| Lasioglossum pilosum           | 12.59         | 0.79              | 0       | 0.99  |
| Lasioglossum tegulare          | 12.51         | 0.76              | 0.01    | 0.25  |
| Lasioglossum versatum          | 11.96         | 0.5               | 0.7     | 0.25  |
| Megachile brevis               | 12            | 0.89              | 0.01    | 0.63  |
| Megachile mendica              | 11.9          | 0.08              | 0.34    | 0.81  |
| Melissodes bimaculatus         | 11.94         | 1                 | 0       | 0.84  |
| Nomada bidentate_group         | 12.52         | 0.42              | 0.98    | 0.02  |
| Nomada pygmaea                 | 11.65         | 0.21              | 0.96    | 0     |
| Osmia atriventris              | 10.27         | 0.18              | 0.98    | 0     |
| Osmia bucephala                | 11.94         | 0.29              | 1       | 0.11  |
| Osmia georgica                 | 12.93         | 0.22              | 0.95    | 0.12  |
| Osmia pumila                   | 12.45         | 0.19              | 0.97    | 0.02  |
| Osmia taurus                   | 11.64         | 0.57              | 0.59    | 0.01  |
TABLE 2 (Continued)

| Species         | Habitats used | Pasture and crops | Forests | Urban |
|-----------------|---------------|-------------------|---------|-------|
| *Ptilothrix bombiformis* | 11.53         | 0.78              | 0       | 0.99  |
| *Xylocopa virginica*    | 11.65         | 0.28              | 0.6     | 0.79  |

*This group of species was merged because they are morphologically similar and very difficult to separate by classic taxonomy. Note grouping can mask specific habitat preferences.

Moreira, Maspons, & Lapiedra, 2014). However, the degree of preference is better described as a continuum, and hence, we also describe it as effect sizes. Note that for parasitic species, like Nomada spp., habitat preferences should correspond to those of their hosts. Preferences calculated for groups of species may mask each species preferences if they are not specialist. Thus, our results for these groups must be interpreted carefully.

For the sake of clarity, we present in the results section habitat preferences grouped by three main habitat types: (a) urban: developed, high intensity and medium intensity; (b) crops and semi-natural areas: cultivated crops, herbaceous/hay/pasture, developed, low intensity and open space; and (c) forested: deciduous forest, evergreen forest and mixed forest, see Figure 2 for details.

3 | RESULTS

3.1 | Habitat importance

Our estimates of species richness and strength for each habitat were positively correlated (Figure 3, Supporting Information Table S3). However, the strength values allowed us to further differentiate the importance of habitats with similar richness values. For example, except for evergreen forest, which was the habitat with the greatest rarefied species richness (107.7), all rarefied richness values for the three other forested habitats were very similar (range = 91.0–91.2 species). In contrast, the strength values for these habitats varied substantially, being lowest in mixed forest (22.46), intermediated in woody wetlands (24.56) and highest deciduous forest (25.80). This is because the strength value for a habitat does not only increase with species richness but also when the species are highly dependent on a particular habitat (Supporting Information Figure S4).

Human-altered habitats sustained a considerable fraction of the regional pool of bee species (see Figure 3 for exact numbers in each altered habitat), but they had lower species richness and strength than less altered and more natural habitats (Figure 3). However, their lower biodiversity was in part compensated by the presence of many nonindigenous species. From the nine exotic bee species we recorded, seven were collected in crops, pasture and semi-natural habitats (crops and semi-natural; Figure 2a). The beta-diversity within habitats, which describes the rate at which diversity increases when adding new sampling events, also differed across habitats (Figure 2b). The higher value was observed in evergreen forests, which may explain its high overall species richness; the lower value was instead found in deciduous forests, indicating a high resemblance in species composition across space.

The results at the landscape level highly resembled those at the habitat level. Landscapes dominated by forests had the highest species richness and strength (Figure 2b, groups 14, 4, 10, 12, 13), even when mixed with crops (groups 5, 9, 17). Coastal areas (6) had also high levels of richness and strength, yet these values diminished again when the proportion of crops and/or pastures increased (1, 3). When crops were the dominant habitat (8), instead, the values of species richness and strength were significantly lower. Finally, urban landscapes (11, 19) had low importance than other habitats in terms of species richness, yet their strength values were unexpectedly high because of the presence of human commensals (Supporting Information Tables S2 and S3).

3.2 | Species habitat use and preference

Most species used a variety of habitats, but 33 out of 45 showed a strong preference for a single habitat (Supporting Information Table S3). After grouping habitats in three main categories (see justification in the methods), 23 out of 45 showed preferences for a single group: Fourteen species preferred natural forested habitats, six preferred urban habitats, and three preferred agricultural habitats (Table 2, Figure 4).

Species that exhibited a preference for forests also showed a tendency to avoid urban habitats. Thus, 13 of the 14 species that preferred forested habitats avoided urban habitats (Table 2). The only exception was Lasiglossum imitatum, which had a preference for forested habitats but also presented preference for urban habitats (Table 2). A certain degree of habitat specialization was also detected among urban dwellers (Table 2, Figure 4): seven out of 11 that preferred some type of urbanized environment avoided crops, pastures and forests (Supporting Information Table S3). From all studied species, the most generalist was the managed bee *Apis mellifera*, which exhibited no preference or avoidance for any habitat.

4 | DISCUSSION

Four main conclusions can be drawn from our comprehensive analysis of bee species across north-east USA. First, although no habitat...
appeared to be completely inhospitable to bees, many species showed a strong preference for natural habitats while consistently avoiding human-altered habitats. Second, the dominant habitat within the landscape was the strongest determinant of species diversity and, contrary to previous studies (Steffan-Dewenter & Tscharntke, 1999), landscape composition only had moderate buffer effects on diversity. Third, and as a consequence of the two previous findings, human-altered habitats supported significantly less diversity of species (and had less strength) than the surrounding natural environments. Fourth, the loss of biodiversity in human-altered environments could have been higher had not been partially compensated by the addition of human commensals and some exotic species.

Natural habitats were the most suitable for bees regarding both importance (richness and strength) and the number of species that preferred them. Evergreen forests in particular exhibited the highest habitat importance in the region, despite harbouring very few habitat specialists. These forests are widespread in the region and comprise flower rich areas like the coastal Pine Barrens that are fragmented and crossed by right of way infrastructures, which can increase their attractiveness for bees and help explain why they exhibited high spatial beta-diversity (Hill & Bartomeus, 2016). Unlike evergreen forests, bee communities associated with deciduous forests and other natural habitats had lower beta-diversity and lower overall species richness. However, they sustained a large number of habitat specialists, a possibility already advanced in previous studies (Burkle, Marlin, & Knight, 2013).

As specialized adaptations to particular habitats may limit the success of bee species in other habitats, it is unsurprising that the majority of forest specialist species avoid urban habitats and/or crops and pastures. It follows that many of these species may become extinct, at least locally, if forested habitats disappear from the landscape (Burkle et al., 2013).

Much of the current risk of species loss comes from the replacement of natural forests by crops and pastures, the most frequent alteration of natural habitats (Newbold et al., 2015). Crops and pastures exhibited a significantly low species richness and strength values compared to natural forests. Thus, while some species use crops and pastures opportunistically, seem to perform well in such habitats (see also Kleijn et al., 2015). Moreover, within-habitat beta-diversity for agricultural habitats was low, reinforcing the view that these habitats sustain a limited set of common habitat generalists. Cropping systems are however highly diverse, ranging from cereal monocultures to diverse flowering cropping systems (Donald, 2004), implying that the impact may vary depending on the intensity of the alterations. Although our dataset does not allow for finer scale analyses separating the effects of different crops, current evidence suggests that most modern crop managing practices (i.e., herbicide and insecticide application) are likely to negatively impact on bee populations (Goulson et al., 2015; Woodcock et al., 2016).

While the conversion of natural habitats to cities is not so widespread as the replacement by crops and pastures (Newbold et al., 2015), such conversion is considered the most drastic alteration of natural ecosystems. In line with previous studies (Chapin, 1997; Sol et al., 2014), urbanized habitats harboured substantially fewer species than the surrounding natural habitats. The persistence of bee populations in urban habitats may be limited by resource availability. Food resources are often dominated by exotic or ornamental species (Ellis, Antill, & Kreft, 2012), which few bee species are able to exploit (Bartomeus, Fründ, & Williams, 2016). However, urban habitats also offer resource opportunities for some species. For example, *Ptilothrix bombiformis* specializes in exploiting plants from the *Hibiscus* genus, a popular ornamental plant. New opportunities may also emerge for some bees that are able to use pre-existing cavities or holes in of human-made constructions (Cane, Griswold, & Parker, 2007). As natural enemies are often scarcer in cities (Sorace & Gustin, 2009), these human commensals may proliferate despite their little opportunity to adapt to the new environments. Likewise, we show that nonindigenous species mostly proliferate in urbanized environments, being most of the exotic bees collected only in urban areas. Although the presence of human commensals and nonindigenous species importantly contributed to increase species richness in urbanized environments, their diversity was low and hence did not fully compensate for the loss of diversity associated with urban avoiders (see also Sol, Bartomeus, González-Lagos, & Pavoine, 2017).

Past work suggests that while undisturbed habitats are essential to preserve biodiversity, habitats that have experienced low

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**FIGURE 4** The distribution of species habitat preferences (See also Supporting Information Table S4). Red bars are the number of species avoiding that habitat, and blue bars are the number of species preferring that habitat. Urban habitats have both avoiders (14 of 45) and exploiters (6 of 45). Forests also have avoiders (10 of 45) but have a higher proportion of exploiters (14 of 45). Crops and pasture are more equally distributed, with few species preferring or avoiding them.
intensity alterations may still help buffer against extreme diversity loss (Frishkoff et al., 2014; Sol et al., 2017). Our results provide some support to this view, showing that species loss was not as accentuated in moderately altered habitats (Table 2). For example, large gardens within cities provide diverse food resources for pollinators, harbouring a higher bee diversity and abundance than city centres. As example, in Berlin, half of the total German bee fauna was recorded inside the city (Saure, 1996) and in San Francisco, USA, higher mean abundances of Bombus spp. were found in urban gardens compared with natural parks beyond the city boundaries (McFrederick & LeBühn, 2006). Likewise, some flowering crop fields provide good foraging opportunities for generalist bee species (Magrach et al., 2018), despite low plant diversity and short bloom periods (Donald, 2004).

Although the analyses of single focal habitats are essential to establish habitat importance and assess the sensitivity of species to habitat alterations, species diversity typically depends on the mosaic of habitats present in a region (Steffan-Dewenter & Tscharntke, 1999). We expected that species able to use multiple habitats would be less vulnerable to habitat modification than species with specific habitat requirements. However, at the landscape level, our results show that the dominant habitat within the landscape was the strongest determinant of species diversity and that more complex landscapes only had intermediate diversity levels. This is exemplified by the finding that forested habitats intermixed with human-altered habitats had lower species diversity than fully forested habitats.

Altogether, our results provide clear evidence that the loss and alteration of natural habitats caused by human activities lead to many “losers” and a few “winners.” Albeit the specific bee–habitat associations vary as a function of the intensity of the alterations and may change in other geographical regions, the observed diversity loss associated with land use changes might be general (Palma et al., 2017). Admittedly, our estimations of species sensitivity to habitat alterations are conservative, as these analyses were restricted to common species and hence some habitat specialists may have been missed. However, the analyses using the strength index, which did include rare species, consistently showed that the species dependency on a given habitat decreased with the degree of habitat modification. Although the loss of bee diversity may be in part compensated by the colonization of native opportunists and exotic species, their diversity is insufficient to replace the species that are lost by land use changes. Moreover, the new species may differ from those they replace in functional traits (see Bartomeus et al., 2013; Kitahara & Fujii, 1994; Scheper et al., 2014; Sol et al., 2014), and hence, there is little guarantee that they may play similar roles in the ecosystem (Bartomeus, Cariveau, Harrison, & Winfree, 2017). Thus, preserving natural habitats may provide the most effective strategy to guarantee in the long term the ecosystem functions and services provided by bee biodiversity.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA ACCESSIBILITY

The data used for this research will be archived in dryad/figshare upon acceptance. Code used to reproduce the analysis can be consulted at GitHub https://github.com/MiguelAngelCollado/habpref.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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