

Forest bees are replaced in agricultural and urban landscapes by native species with different phenologies and life-history traits

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Abstract

Anthropogenic landscapes are associated with biodiversity loss and large shifts in species composition and traits. These changes predict the identities of winners and losers of future global change, and also reveal which environmental variables drive a taxon's response to land use change. We explored how the biodiversity of native bee species changes across forested, agricultural, and urban landscapes. We collected bee community data from 36 sites across a 75,000 km² region, and analyzed bee abundance, species richness, composition, and life-history traits. Season-long bee abundance and richness were not detectably different between natural and anthropogenic landscapes, but community phenologies differed strongly, with an early spring peak followed by decline in forests, and a more extended summer season in agricultural and urban habitats. Bee community composition differed significantly between all three land use types, as did phylogenetic composition. Anthropogenic land use had negative effects on the persistence of several life-history strategies, including early spring flight season and brood parasitism, which may indicate adaptation to conditions in forest habitat. Overall, anthropogenic communities are not diminished subsets of contemporary natural communities. Rather, forest species do not persist in anthropogenic habitats, but are replaced by different native species and phylogenetic lineages preadapted to open habitats. Characterizing compositional and functional differences is crucial for understanding land use as a global change driver across large regional scales.

KEYWORDS

Apoidea, fourth-corner, global change, land use, phenology, pollinator, richness, traits

1 | INTRODUCTION

How many species persist in human-altered landscapes, and how do they differ from species dependent on declining reserves of wild habitat? Given the importance of these questions, it is surprising how poorly the answers are known (McGill, Dornelas, Gotelli, & Magurran, 2015). The effects of anthropogenic land use on site-level abundance and species richness are negative on average, but highly variable because some species tolerate or even prefer the altered environmental conditions in anthropogenic

habitats, thus partly compensating for loss of sensitive species (Dornelas et al., 2014; Newbold et al., 2015). When land use change drives high levels of species replacement, abundance and richness are not necessarily lost, but are redistributed across space, time, and species groups defined by phylogeny or life histories (Frishkoff, Karp, Gonigle, Hadly, & Daily, 2014; Garnier et al., 2007; Mayfield & Daily, 2005; Mayfield et al., 2013; Tabarelli, Peres, & Melo, 2012). Characterizing these ecological transitions helps researchers understand how land use change drives species loss and replacement (McGill, Enquist, Weiher, & Westoby, 2006),

and may predict the winners and losers of future global change (McKinney & Lockwood, 1999).

Different land use types can have divergent effects on community composition, suggesting that each presents different challenges and opportunities for species (Baldock et al., 2015; Jauker, Diekötter, Schwarzbach, & Wolters, 2009; Walker, Grimm, Briggs, Gries, & Dugan, 2009). We focus on agriculture, which covers 38% of the world's terrestrial surface, and urban land use, which covers a smaller 9.6% of total land area but is projected to rapidly increase in coming decades (Center for International Earth Science Information Network, 2013; Seto, Güneralp, & Hutyra, 2012). Conversion to both agricultural and urban land use involve direct replacement of natural vegetation by crops, ornamental plants or concrete, which generates a large compositional shift in associated plant and animal communities (Mayfield, Boni, Daily, & Ackerly, 2005; Mayfield et al., 2013; Tabarelli et al., 2012). In forest ecosystems, which cover 31% of terrestrial surface (World Bank Data, 2015), an additional mediator of these compositional shifts may be the dramatic changes in the magnitude and timing of light availability caused by removal of the tree canopy (Harrison & Winfree, 2015; Marks, 1983).

Animal pollinators are required for the reproduction of nearly 90% of flowering plant species, yet how pollinator communities change with land use is poorly known (Ollerton, Winfree, & Tarrant, 2011). Syntheses show that while pollinator abundance and richness decrease in response to extreme loss of natural habitat, responses to more moderate habitat loss are mixed (Cariveau & Winfree, 2015; Winfree, Aguilar, & Vázquez, 2009; Winfree, Bartomeus, & Cariveau, 2011). 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, Daily, & Ehrlich, 2007; Winfree, Griswold, & Kremen, 2007; Wray, Neame, & Elle, 2014). However, there is little consensus on the identities and traits of pollinator species found in anthropogenic habitats. For example, different studies have concluded that large- and small-bodied pollinators are more sensitive to agricultural intensification (Benjamin, Reilly, & Winfree, 2014; De Palma et al., 2015; Rader, Bartomeus, Tylianakis, & Laliberté, 2014). One reason for lack of consistency is that many studies sample sites in complex landscapes, where mobile insect pollinators captured in one habitat may be associates of a different, near-by habitat. Another is that species-environment or trait-environment relationships may be locally variable, so that traits associated with anthropogenic land use in one locality are associated with a different land use in another (De Palma et al., 2016).

To address these research gaps, we collected a dataset of >13,000 specimens representing 245 bee species, from forested, agricultural, and urban landscapes distributed throughout 75,000 km² of the northeastern United States. We first ask how abundance, species richness and community composition differ between forested and anthropogenic (agricultural and urban) landscapes. We then determine whether forested and anthropogenic habitats are associated with different bee species traits. To identify which trait-land use associations are more likely to be robust to

different regional species pools, we use a novel test that combines the fourth-corner trait-environment correlation with a phylogenetically informed, permutational null model.

2 | MATERIALS AND METHODS

2.1 | Field study design and sampling

Our study region 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). Agricultural landscapes typically included pasture, row crops (mainly corn and soybeans), small 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, including perennial crops such as blueberry. We selected our 36 study sites as follows (Fig. S1a). To achieve a statistically replicated sample of urban land use, we chose 12 towns distributed throughout our study region (25–360 km apart) with populations ranging from 5,000 to 50,000. We then selected one forest site and one agriculture site within 5–30 km of each town. This spatial blocking minimizes spatial autocorrelation when analyzing effects of land cover on site-level variables. Bees are mobile animals and 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% forest, agriculture or urban land cover according to site type within a 1,500 m radius; this is further than the regular flight distance of most bees in our region (Greenleaf, Williams, Winfree, & Kremen, 2007), which makes it likely that bees at the site are associated with the site's land use type. Site selection was not random but was strongly constrained by the requirements of the study design, as most landscapes in our region are fragmented and heterogeneous in land cover types at the scale of a 1,500 m radius. In order to ensure representation of the different forest types in our study region, we also stratified site selection within four major forest types in our region: Atlantic Coastal Pine Barrens, Northern Piedmont, Ridge and Valley, and Northern Allegheny Plateau (Omernik, 1987).

To sample pollinator communities at each site, we chose four mowed, grassy, sunny locations, where we placed arrays of six pan traps ($6 \times 4 = 24$ total traps per site visit), in alternating colors of fluorescent blue, fluorescent yellow and white (Westphal & Bommarco, 2008; Fig. S1b-e). Two of the four arrays also included a blue-vane trap (manufactured by Springstar), which may be more efficient at trapping fast-flying or large-bodied bees. We left traps to collect bees for 24 hr. We visited all 36 sites throughout the growing season in each of 3 years (2013–2015), in 3–5 sampling rounds per year for a total of 11 rounds extending from April to early October.

Bee specimens are fully curated and currently stored at Rutgers University. We identified bee species based on published taxonomic revisions (Bouseman & LaBerge, 1979; Coelho, 2004; Gibbs, 2011;

Gibbs, Packer, Dumesh, & Danforth, 2013; LaBerge, 1961, 1967, 1971, 1973, 1977, 1980, 1986, 1987, 1989; LaBerge & Ribble, 1975; Laverty & Harder, 1988; McGinley, 1986; Mitchell, 1960, 1962; Rehan & Sheffield, 2011; Ribble, 1968) and keys available online (Arduser, 2016; Larkin, Andrus, & Droege, 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 poorly resolved species groups (two in the genus *Nomada* and one in *Hylaeus*, with each group likely containing 2–5 species) that we retained in the dataset and hereafter refer to as 'species'. The European honeybee, *Apis mellifera*, is a managed species in our region and occurs infrequently in our samples, and therefore was not included in any analysis.

2.2 | Independent assessment of bee species traits

We collected information on six species traits describing nesting habits, diet breadth, body size and phenology for bees in our study region (Table S1; see also Bartomeus et al., 2013). We selected these six traits because they describe major axes of a bee's life history and have low pairwise correlations (Table S2). The three nesting habit traits were social vs. solitary, parasitic vs. nest building, and nesting in soil burrows vs. in plant stems, wood, or cavities. For diet breadth, we scored bees as oligolectic if females are known to collect pollen from within a single plant family. We 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). We estimated flight season peak, the time of year when most adults are actively foraging, as the median collection date for each species with at least 30 records in an independent dataset of 58,833 bee specimens collected throughout the northeastern United States (Table S3).

2.3 | Analytical methods

All analyses were performed in R 3.2.4 (R Core Team, 2016).

2.3.1 | Abundance and richness

Before conducting any data analysis, we knew that abundance and richness of bee community samples would depend on the interaction between land use and season, because the pattern was obvious during data collection. This interaction could bias estimates of abundance and richness based on aggregating samples across season. Therefore, we analyzed abundance and richness at the sample level, using generalized linear mixed models (GLMMs) to separate the effects of land use (varying across sites), season (varying across samples within sites), and the land use \times season interaction. A significant effect of land use would indicate that land use types differ in the abundance or richness of community samples averaged across the growing season. Specifically, we fit numbers of specimens (or

species) collected at each site on each sampling date, using two GLMMs of the form

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

where 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 allows us to fit hump-shaped responses in community metrics over time, which we expect as many bee species emerge in the spring, build abundances over time and collectively senesce toward the end of the year. We used R package *lme4* to fit all models (Bates, Maechler, Bolker, & Walker, 2015), and R package *sandwich* to construct 95% confidence intervals around estimated model coefficients (Zeileis, 2006). We selected a negative binomial distribution for error in the bee abundance model, and a Poisson distribution for error in the richness model. We validated models by visually inspecting for normal distribution of residuals and lack of trend or heteroskedasticity in plots of residuals over day-of-year, land use, and the fitted values. We additionally checked for multicollinearity as a variance inflation factor exceeding a maximum recommended value of 5 (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). In order to understand the overall effects of different model terms, we conducted a log-likelihood comparison of each model in which we sequentially removed doy^2 , land use:doy, doy, land use, and year. We then used chi-square tests to compare the deviance between each of the five models and the preceding reduced model.

2.3.2 | Community composition

Measures of composition and traits in ecological communities can either ignore or include information about species' abundances. Ignoring species abundances allows community metrics to be influenced by many rare species, which are poorly sampled in community data and generally add more noise than information about community-environment associations. In contrast, more abundant species are sampled enough to accurately reflect their habitat preferences, and are more likely to display traits associated with optimal performance in a preferred habitat (Muscarella & Uriarte, 2016; Umana, Zhang, Cao, Lin, & Swenson, 2015). We therefore weight all measures of community composition and traits by species' abundances.

We calculated species composition dissimilarity among pairs of sites using the Morisita–Horn index, which is sensitive to turnover and richness differences of more abundant species and performs well according to a number of ecologically meaningful criteria (Barwell et al., 2015). To calculate phylogenetic composition dissimilarity, we used a previously published genus-level bee phylogeny calculated from multiple protein-coding nuclear DNA sequences stored on GenBank (Hedtke, Patiny, & Danforth, 2013). We first transformed the phylogenetic tree into a species-by-species matrix of pairwise branch distances between tips, and 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*). As we used a genus-level

phylogeny, specimens of the same genus have a phylogenetic distance of 0. To test if land use is correlated with species or phylogenetic composition, we used two permutational analyses of variance using the composition 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). We conducted post hoc pairwise contrast analyses among all three combinations of land use types (forest–agriculture, forest–urban, and agriculture–urban). To visualize the results of all the tests of community composition, we created two nonmetric multidimensional scaling (NMDS) plots showing community distances among sites, based on species or phylogenetic dissimilarity. Finally, to help interpret both composition results, we plotted the species scores from the species composition NMDS ordination and highlighted the five most speciose genera.

2.3.3 | Species traits

We tested for different trait 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 our three categorical land use types), weighting by species' abundances (Dray & Legendre, 2008). We 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 our 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 and abundance, species pool sizes, and patterns of beta diversity. In order to interpret our observed changes in trait composition as evidence for ecological links between land use and traits per se, we used a second null model randomizing trait states across species. To control for autocorrelation in trait states among closely related species (Webb, Ackerly, McPeck, & Donoghue, 2002), we constrained species randomizations so that trait values were more likely to be exchanged between more closely related species (Harmon & Glor, 2010; Lapointe & Garland, 2001). Using this null model in context of fourth-corner analysis has been recently suggested (ter Braak, Peres-Neto, & Dray, 2017), but to our knowledge has not yet been implemented. To calculate transition probabilities in the permutations, we used a species-by-species phylogenetic distance matrix based on the published genus-level bee phylogeny (Hedtke et al., 2013). The phylogenetic permutation method requires setting a parameter k ranging from 1 to ∞ , where it converges with the standard, phylogenetically uninformed species permutation model. We use $k = 1$ for the most conservative (constrained) null. We used 9,999 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 (ter Braak, Cormont,

& Dray, 2012). We used a parallel analysis to analyze the relationships between taxonomic groups (genera and families) and land use.

In order to visualize trait composition, we calculated the community weighted mean (CWM) of each of our 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, and is closely related to fourth-corner analysis (Peres-Neto, Dray, & ter Braak, 2016).

3 | RESULTS

3.1 | Abundance and richness

We did not detect differences in the abundance and richness of bee community samples among different land use types, when averaging across time-of-year (Tables 1 and S4). However, forested 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 (doy²) was positive, indicating a convex polynomial relationship with Julian day-of-year (Table 1). 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 1a). In both agriculture and urban habitat, coefficients on doy were positive, while coefficients on doy² were negative, indicating a concave relationship. The plotted relationships for agriculture and urban landscapes show abundance increase 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 1b).

3.2 | Community composition

Land use was associated with variation in species composition ($F_{2,33} = 7.3$, $p = .001$; Figure 2a) and phylogenetic composition

TABLE 1 Coefficients (and SE) from generalized linear mixed models testing if anthropogenic and forested landscapes differ in how abundance and richness changes throughout season within.

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

Site is included in all models as a random effect. All coefficients on day-of-year variables (orthogonal polynomials doy and doy²) in agriculture and urban are significantly different from forest. Model intercepts, which correspond to log average abundance or richness of samples within each land use across time, do not differ between anthropogenic and forest landscapes.

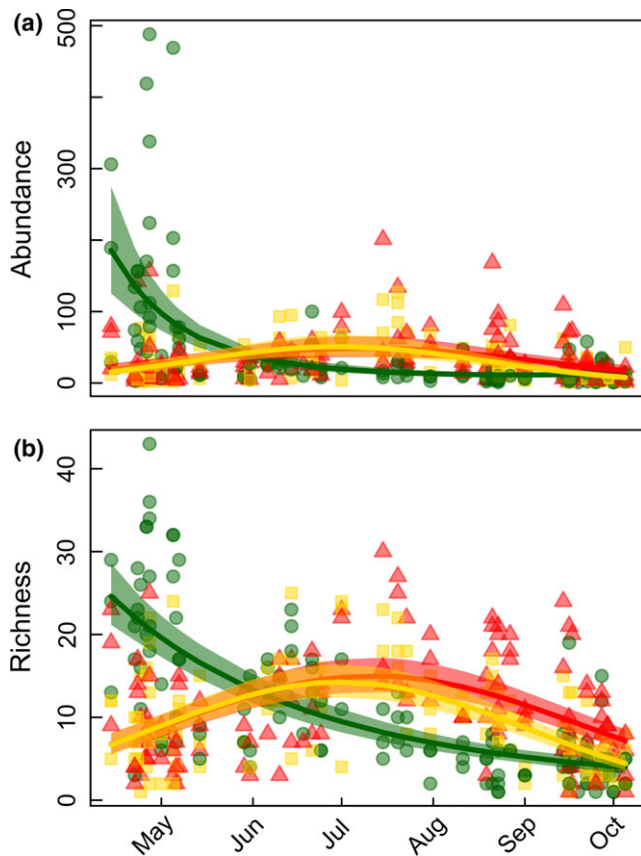


FIGURE 1 Abundance (a) and species richness (b) of bees change throughout the season differently within forest sites (green circles) vs. within agriculture and urban sites (yellow squares and red triangles). Each point represents one site visit ($N = 36$ sites visited 11 times). Fitted model curves are surrounded by calculated 95% CI [Colour figure can be viewed at wileyonlinelibrary.com]

($F_{2,33} = 2.6$, $p = .001$; Figure 2b). Land use explained more variation in species composition ($R^2 = 0.31$) than phylogenetic composition ($R^2 = 0.13$), probably due to high dispersion among forest sites in the phylogenetic analysis (Figure 2b). Contrast analysis showed that both species and phylogenetic composition differed between all three pairs of land use types, although differences between forest and both anthropogenic land uses were greater than differences between agriculture and urban land use (Table 2). Urban habitats were dominated by bees in the family Halictidae (sweat bees; Table S5), particularly members of the genus *Lasioglossum* (Table S6; Fig. S2). Nonnative bees constitute a small minority of the fauna of all land use types (8% of specimens collected; Fig. S3).

3.3 | Species traits

We used the full dataset of 245 species to analyze associations between land use type and parasitism, and all 208 nonparasitic species for sociality, nest substrate, and oligolecty. Body size measurements were available for 172 species (92% of specimens) and estimates for flight season peak were available for 184 species (98% of specimens). Overall fourth-corner test statistics showed that four traits were significantly correlated with land use: sociality (Pseudo-

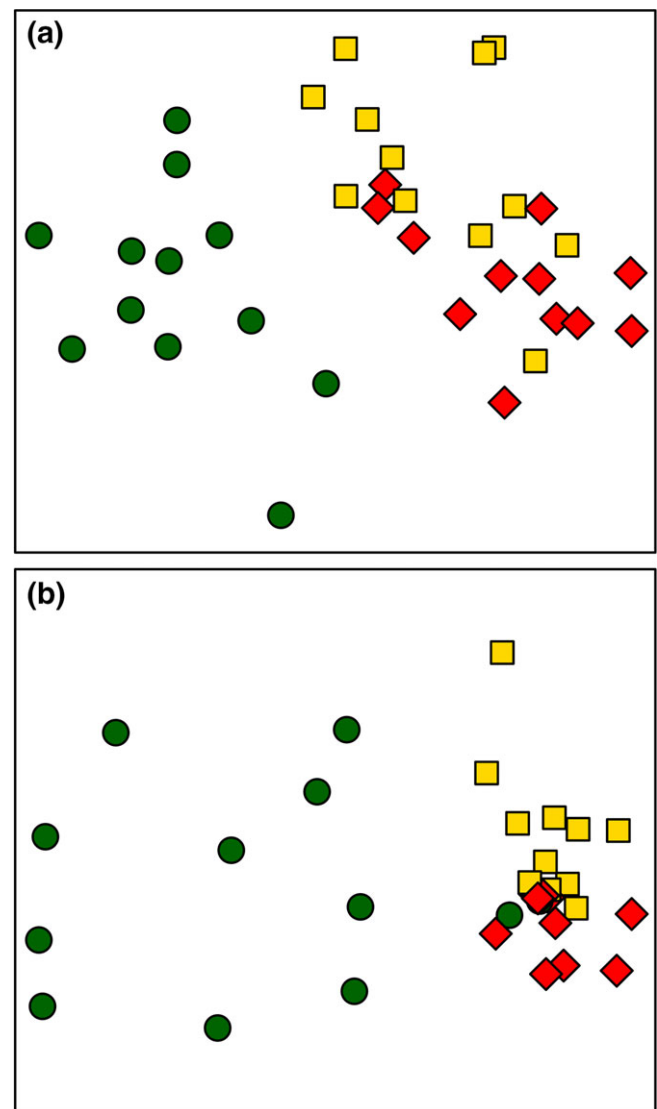


FIGURE 2 Comparing composition of bee communities in forest, agriculture and urban land use types, using measures of (a) dissimilarity in species' relative abundances and (b) average phylogenetic distance between individuals. Colors and shapes indicate land use (dark green circles—forest, yellow squares—agriculture, red triangles—urban). These NMDS plots represent the multivariate data with fairly low stress (species composition stress = 0.17; phylogenetic composition stress = 0.13). Compositional differences between land use types were significant (Table 2) [Colour figure can be viewed at wileyonlinelibrary.com]

$F = 622.6$, $p = .041$), parasitism (Pseudo- $F = 709.5$, $p = .01$), nest substrate (Pseudo- $F = 789.5$, $p = .006$), and flight season (Pseudo- $F = 4783.9$, $p = .0001$). Agricultural communities tended to have low proportions of wood- and cavity-nesting species and low proportions of parasitic species, while forest communities had high proportions of wood- and cavity-nesting and high proportions of parasitic species (Table 3; Figure 3). Both agricultural and urban communities were dominated by late flight season species, while forest was dominated by early flight season species. Social species dominated anthropogenic and especially urban communities, but we could not detect a significant relationship between sociality and urban land use when

TABLE 2 Results from two pairwise contrast analyses showing differences in bee species and phylogenetic composition between all pairs of three land use types (forest, agriculture, and urban)

Contrast	Species			Phylogeny		
	F	R ²	p	F	R ²	p
Forest vs. Agriculture	11.1	0.34	.003	2.7	0.11	.003
Forest vs. Urban	14.8	0.40	.003	4.0	0.15	.003
Agriculture vs. Urban	5.0	0.19	.006	1.5	0.06	.006

p-values are Bonferroni-corrected for multiple comparisons, and are coincidentally the same for species and phylogenetic analyses.

TABLE 3 Fourth-corner statistics (correlation estimate, standard deviation and *p*-value) for association between trait states and land use type (forest, agriculture, urban) [Colour table can be viewed at wileyonlinelibrary.com]

	<i>r</i>	SD	<i>p</i>
Social			
Forest	-.29	0.35	.090
Agriculture	.06	0.27	.583
Urban	.24	0.32	.120
Parasites			
Forest	.31	0.35	.010
Agriculture	-.17	0.27	.035
Urban	-.17	0.31	.102
Oligoleges			
Forest	.02	0.35	.878
Agriculture	.06	0.28	.455
Urban	-.08	0.32	.684
Stem/wood/cavity nesters			
Forest	.33	0.35	.012
Agriculture	-.22	0.28	.011
Urban	-.13	0.32	.309
Log body mass			
Forest	.21	0.36	.339
Agriculture	.01	0.28	.827
Urban	-.24	0.33	.130
Peak flight season			
Forest	-.64	0.35	.0001
Agriculture	.29	0.28	.047
Urban	.42	0.32	.001

Significant negative associations are highlighted in blue; positive associations in red. Different traits are analyzed using different total numbers of species, as parasitic species are removed from analyses of sociality, lecty, and nesting substrate, and the continuous traits body mass and flight season have some missing values (Table S1).

applying the phylogenetic correction, probably because urban social species were represented by a phylogenetically narrow group (family Halictidae and especially *Lasioglossum*). We observed a nonsignificant trend toward smaller body size in urban land use (Pseudo-*F* = 414.9, *p* = .123; Figure 3). Proportions of oligolectic bees (bees that forage from a single plant family) were too low and variable to detect

significant trends (Pseudo-*F* = 42.3, *p* = .713); oligolectic bees comprised an average of 8% and never more than 17% of agricultural communities, vs. less than 5% of most forest and urban communities.

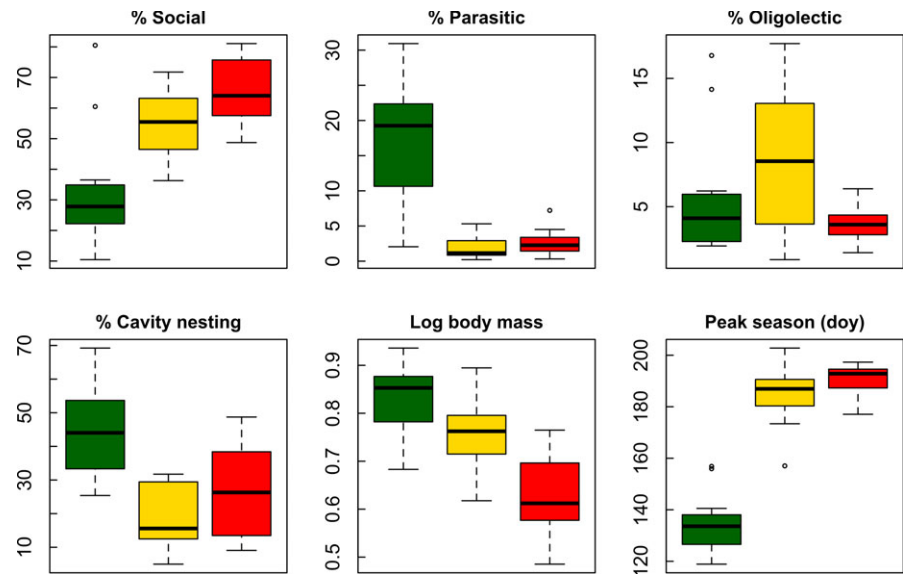
4 | DISCUSSION

Recent research in global change ecology questions to what extent anthropogenic land use causes loss of abundance and species richness, vs. replacement of original assemblages with differently adapted species (Dornelas et al., 2014; McGill et al., 2015; Newbold et al., 2015; Vellend et al., 2013). Here we explore this question for pollinators at large spatial scales for the first time. We did not detect a loss of bee abundance or species richness in anthropogenic landscapes, suggesting that there was a preexisting pool of native species that can use these habitats. In contrast, we found dramatic differences between natural and anthropogenic landscapes in community phenology, species and phylogenetic composition, and species traits. Specifically, the dominant species in the native forest landscapes are solitary spring-flying bees and their associated brood parasites. In agricultural and urban landscapes these species are replaced by late-season bees from different phylogenetic lineages.

We believe that the main driver of this pattern is the removal of a temporal constraint on resource availability, and propose that this could be a general driver of community change in anthropogenic landscapes (Harrison & Winfree, 2015). In our system, the transition from temperate forest to agricultural and urban land use results in expanding the period of high light availability from springtime to the entire growing season, thereby also expanding the period of floral resource availability for bees (Motten, 1986; Ten Brink, Hendriksma, & Bruun, 2013). Accordingly we found that bee abundance and richness were concentrated in springtime in forests (April and May), but evenly distributed throughout the growing season (April–September) in open anthropogenic landscapes. Analogously, in arid regions where native plant growth is constrained by seasonal rainfall, the growing season in agricultural and urban land use is extended by irrigating crops and ornamental plants (Buyantuyev & Wu, 2012; Leong & Roderick, 2015). In these systems, researchers have observed corresponding temporal changes in abundance and richness of associated insect communities (Gotlieb, Hollender, & Mandelik, 2011; Leong & Roderick, 2015; Neil, Wu, Bang, & Faeth, 2014).

Three mechanisms have been proposed for changes in community phenology between natural and anthropogenic habitats. Plasticity in species' phenology (Neil & Wu, 2006) and seasonal change in species' habitat use (Mandelik, Winfree, Neeson, & Kremen, 2012) both enable the same species to persist in phenologically altered environments. The third mechanism is replacement by species whose life histories better match the phenology of the anthropogenic habitat (Blair & Launer, 1997). The latter is most consistent with our results, as early-season, solitary forest species were replaced in anthropogenic land use by different, late-season species, including social species that require long growing seasons to produce multiple generations of workers. The loss of species with life-history traits

FIGURE 3 Community weighted mean (CWM) values of six traits for bee communities from forest (green), agriculture (yellow), and urban (red) land use ($n = 12$ sites each). For the four binary traits, CWM represents the proportion of individual bees at a site expressing one of the two possible trait states (social vs. solitary, parasitic vs. pollen-collecting, oligolectic vs. polylectic, and stem, wood or cavity-nesting vs. soil nesting). For the two continuous traits (peak flight season and log body mass), CWM represents the average trait value across species present at a site, weighted by species abundance [Colour figure can be viewed at wileyonlinelibrary.com]



adapted to native forest represents a loss for a regional bee biodiversity, despite the presence of a diverse pool of open-habitat species that buffer community richness and abundance at local sites.

Given that forest covered most of the landscape before the expansion of European settlements (Rudel et al., 2005), what are the origins of the native, late-season, open-habitat species? Some may have evolved as forest gap and riverine meadow specialists before finding themselves preadapted to the marginal or early-successional conditions common in anthropogenic habitats, as has been proposed for open-habitat species in previously forested regions of Europe (Klemm, 1996). Others may have evolved in biogeographic regions that are naturally open; for example, the squash specialist *Peponapis pruinosa* (Say) was originally restricted to southeastern United States and Mexico but is now common in northeastern agricultural landscapes due to widespread cultivation of its preferred host plant (López-Urbe, Cane, Minckley, & Danforth, 2016). Similar origin stories have been suggested for birds and plants that currently depend on anthropogenic open habitats in both temperate and tropical regions (Foster & Motzkin, 2003; Marks, 1983; Mayfield et al., 2005). The conservation value of native biodiversity associated with anthropogenic habitats is a matter of debate, with high value generally ascribed to species that are threatened and declining, unique to a small region, or perceived to be “natural” or what “should” occupy sites in the absence of (continued) anthropogenic pressure (McGill et al., 2015). In better-studied plant and bird taxa, the conservation value of open anthropogenic-associated assemblages is generally considered high in temperate regions with a long history of human land use, where baselines for “natural” biodiversity likely shifted long before the earliest reliable records (Foster & Motzkin, 2003; Storkey, Meyer, Still, & Leuschner, 2012). In contrast, in tropical forested regions, the open-habitat assemblages are considered to be early-successional, weedy species of low conservation value (Frishkoff et al., 2014; Tabarelli et al., 2012), probably because the relative value of primary forest is so high (Gibson et al., 2011).

Our results suggest several other relevant differences between forest and anthropogenic land use. Brood parasites, which comprise

20% of the world's bee species (Danforth, 2007), were abundant components of forest bee communities but almost absent from agricultural and urban land use. Global change often results in loss of secondary consumers (Voigt, Perner, & Hefin Jones, 2007), including parasites (Dunn, Harris, Colwell, Koh, & Sodhi, 2009; Sheffield, Pindar, Packer, & Kevan, 2013), and the resulting simplification of ecological networks can result in further biodiversity loss (Tylianakis, Didham, Bascompte, & Wardle, 2008). Wood, stem and cavity-nesting species were also reduced in anthropogenic habitat, possibly because the loss of trees reduces available nesting habitats. We observed a nonsignificant trend toward smaller body size in anthropogenic habitats, likely driven by bees from a typically small-bodied genus (*Lasioglossum*) that were particularly dominant in urban landscapes, and are known to persist in intensively anthropogenic habitats (Wheelock, Rey, & O'Neal, 2016). There was also a nonsignificant trend for agricultural communities to have higher abundances of specialist species, specifically of crop plants such as sunflowers (*Helianthus*) and squash (*Cucurbita*). Overall, we did not find notably different effects of agricultural and urban land use on community composition. Bee communities in agricultural and urban land use were compositionally different from one another, but they were both much more differentiated from forest communities. Forest, with its distinct spring bloom phenology, is probably so different from either anthropogenic land use type that differences between the two anthropogenic land use types are dwarfed.

Land use affects biodiversity across spatial and temporal scales that are much larger than most species composition datasets. This is a major challenge for studying land use as a global change driver (Gonzalez et al., 2016; Newbold et al., 2015). Understanding how a contemporary species pool is distributed between natural and anthropogenic land use types is achievable and provides insights into ecologically relevant aspects of land use (Mayfield et al., 2005). The contribution of this study is to show that forest and anthropogenic habitats support ecologically and evolutionarily distinct bee communities. This suggests that forest and anthropogenic habitats are

nonsubstitutable for a large subset of the regional bee species pool. Future scenarios of further land use conversion, degradation of forest habitat, or intensification in anthropogenic habitats may lead to loss of regional biodiversity.

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SUPPORTING INFORMATION

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