

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.

The Grey Mite

The grey mite is a small arthropod, tiny, less than 1 mm (0.04 in) in length, and has a simple, unsegmented body plan. Its small size makes it easily overlooked; some species live in water, many live in soil as decomposers, others live on plants, sometimes creating galls, while others again are predators or parasites. The grey mite is a parasite and pest to several species of insects, but is best known as being lethal to crickets.

To address these research gaps, we collected a dataset of >13,000 specimens representing 245 mite 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. [23]

The Grasshopper

Grasshoppers are insects of the suborder Caelifera within the order Orthoptera, which includes crickets and their allies in the other suborder Ensifera. They are likely the oldest living group of chewing herbivorous insects, dating back to the early Triassic around 250 million years ago. Grasshoppers are typically ground-dwelling insects with powerful hind legs which enable them to escape from threats by leaping vigorously. They are hemimetabolous insects (they do not undergo complete metamorphosis) which hatch from an egg into a nymph or "hopper" which undergoes five moults, becoming more similar to the adult insect at each developmental stage. At high population densities and under certain environmental conditions, some grasshopper species can change colour and behaviour and form swarms. Under these circumstances they are known as locusts.

The thorax and abdomen are segmented and have a rigid cuticle made up of overlapping plates composed of chitin. The three fused thoracic segments bear three pairs of legs and two pairs of wings. The forewings, known as tegmina, are narrow and leathery while the hindwings are large and membranous, the veins providing strength. The legs are terminated by claws for gripping. The hind leg

is particularly powerful; the femur is robust and has several ridges where different surfaces join and the inner ridges bear stridulatory pegs in some species. The posterior edge of the tibia bears a double row of spines and there are a pair of articulated spurs near its lower end. The interior of the thorax houses the muscles that control the wings and legs.[1]

Ensifera, like this great green bush-cricket *Tettigonia viridissima*, somewhat resemble grasshoppers but have over 20 segments in their antennae and different ovipositors.

The abdomen has eleven segments, the first of which is fused to the thorax and contains the tympanal organ and hearing system. Segments two to eight are ring-shaped and joined by flexible membranes. Segments nine to eleven are reduced in size; segment nine bears a pair of cerci and segments ten and eleven house the reproductive organs. Female grasshoppers are normally larger than males, with short ovipositors.[1] The name of the suborder "Caelifera" comes from the Latin and means chisel-bearing, referring to the shape of the ovipositor.[2]

They 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).

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). porttitor. Donec laoreet nonummy augue. Suspendisse dui purus, scelerisque at, vulputate vitae, pretium mattis, nunc. Mauris eget neque at sem venenatis eleifend. Ut nonummy. Fusce aliquet pede non pede. Suspendisse dapibus lorem pellentesque

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METHOLOGICAL CONSIDERATIONS

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interdum wisi nibh nec nisl. Ut tincidunt volutpat urna. Mauris eleifend nulla eget mauris. Sed cursus quam id felis. Curabitur posuere quam vel nibh. Cras dapibus dapibus nisl.

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).

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).

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 (Lopez-Uribe, 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).

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