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Local landscapes and microhabitat characteristics are important determinants of urban–suburban forest bee communities

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Abstract. Despite their diversity and abundance, the importance of native, forest bee communities to pollination services and inherent biological diversity conservation is often overlooked. We studied forest bee communities in Delaware and Pennsylvania, USA, to better understand how forest bee community structure varies with changing land use and microhabitat quality among small, urban and suburban forest fragments in the mid-Atlantic United States. Our hypotheses were that (1) microhabitat quality would affect relative abundance of bee taxa, (2) surrounding landscape composition would drive local patch colonization–extinction dynamics, and (3) forest patch size would not affect community structure and composition. We found a lack of spatial autocorrelation among forest patches, indicating the importance of individual fragments in the autonomous generation and/or maintenance of bee communities. Community analyses revealed the importance of both landscape context and microhabitat quality in defining forest bee communities. By partitioning beta diversity into its constituent components, we also found that landscape composition drove changes in the relative abundance of taxa, while both landscape and microhabitat characteristics significantly influenced species turnover. Neither landscape composition nor quality of the microhabitat influenced initial site occupancy or colonization–extinction dynamics. Bisected by highways, suburban neighborhoods, agricultural lands, and urban development, many urban and suburban forest patches in the eastern United States are similar in composition to our study sites. As many native forest bees have limited capacity for long-range movement between forest patches, these remaining forest fragments are critical to the conservation of unique and speciose forest bee communities.

Key words: Anthophila; bees; beta diversity; community; occupancy; urban ecosystem.

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Introduction

Bees (Anthophila) are a diverse and cosmopolitan group of hymenopteran insects with approximately 3500 species in North America, most of which are solitary species (Triplehorn and Johnson 2005). Native, solitary bees not only provide significant pollination services for economically important agricultural crops (Winfree et al. 2008, Julier and Roulston 2009) but are also essential for the successful reproduction and dispersal of many native plants across the landscape. Monolectic and oligolectic bees, those that only utilize a single plant species or several closely related genera, can be sensitive to reductions in host plant diversity or availability, particularly

if floral resources have limited distributions. On the other hand, changes to the overall composition of the bee community could result in pollen limitation and reduced fecundity of plants that rely on certain bee taxa for transporting pollen (Menz et al. 2011). Speciose native bee communities have been shown to improve pollination and reproduction of plants in both natural and agricultural habitats (Winfree et al. 2007, Hoehn et al. 2008). With continuing dramatic declines in honey bee populations in the United States (Kulhanek et al. 2017), research focusing on the health and significant role of native bees as pollinators for the preservation of native flora is an increasingly important conservation issue to be addressed.

Past research related to non-honey bee contributions toward agricultural crop pollination has shown that native bees are most often found closer to forest edges, even while foraging (Gathmann et al. 1994, Bailey et al. 2014). In fragmented landscapes, patches of suitable forested habitat provide critical refugia for native bee populations that significantly support crop and native plant pollination, particularly as these sites provide necessary foraging sources as well as nesting substrate and materials (Potts et al. 2005, Steffan-Dewenter and Schiele 2008, Ballare et al. 2019). Such fragmented forest patches can contain undisturbed soils for nesting and a high floral diversity that can support speciose communities better adapted to anthropogenic landscapes (Breeze et al. 2011, Harrison et al. 2017, Proesmans et al. 2019). Forest patches remaining in the developed eastern United States, interspersed with urban–suburban development and agricultural lands, are often considered of poor quality in reference to the conservation of larger taxa. Nevertheless, natural forested areas within fragmented mosaics of developed and/or agricultural lands are believed to be critical for the conservation of native bee communities that thrive in anthropogenic landscapes (Harrison et al. 2017, Proesmans et al. 2019).

Small, urban–suburban forest patches may effectively provide bee habitat despite unsuitable surrounding landscapes and the effects of environmental stressors; however, sustained preservation of such natural islands can be uncertain or tenuous. Remaining forests are often subject to further fragmentation and habitat loss due to encroaching human development and disturbance, which can affect both native bee abundance and species richness across the landscape (Winfree et al. 2009, Boscolo et al. 2017). Forest habitat loss and fragmentation disrupts pollinator–plant interactions through reduced metapopulation habitat connectivity and resulting changes in site-specific habitat quality (Rathcke and Jules 1993, Kremen et al. 2007). Smaller, native bee species may experience greater negative effects from increased isolation due to reduced dispersal abilities when compared to larger taxa or the more mobile European honey bee (Winfree et al. 2007, Storck-Tonon and Peres 2017). Although a moderate level of habitat disturbance can prove beneficial to bee diversity and abundance (Potts et al. 2003, Winfree et al. 2007), increased levels of human development and division of extant habitat can cause barriers to immigration as well as changes in community structure (Steffan-Dewenter 2003, Bommarco et al. 2010). The composition of natural vegetation in the surrounding landscape significantly influences native pollinator communities (Steffan-Dewenter et al. 2002, Cândido et al. 2018, Proesmans et al. 2019), supporting the notion that plant diversity is critical throughout a landscape. Landscape composition and inter-patch migration barriers strongly influence the ability of species to disperse, colonize new habitats, and occupy forest patches: For species with distinctly delimited habitats and an unsuitable matrix, as is commonly found with remnant forests in urban–suburban areas, community structure and inter-patch differences may largely be driven by metapopulation dynamics (Ewers and Didham 2006, Wray et al. 2014).

The structure of local bee communities is also spatially dependent upon local floral resources (Wray et al. 2014, Rhoades et al. 2018) as well as available nesting substrates and materials (Wray and Elle 2015), while overall abundance has shown positive correlations with habitat size, connectivity, and composition of the local landscape (Brosi et al. 2008, Proesmans et al. 2019). Population density similarly increases with connectivity across the landscape (Steffan-Dewenter 2003), depending on the suitability of the forest patches to host bee taxa. Bee abundance is also positively correlated with proximity to forest edge (Bailey et al. 2014). Bee species richness

generally increases with habitat area (Steffan-Dewenter 2003) and is inversely related to habitat size and habitat interior-to-edge ratio (Brosi et al. 2008). Spatiotemporal variation in community structure is dependent upon differences in natural history requirements across taxa as well as environmental covariates that may differentially affect species and populations (Everaars et al. 2018). Smaller, cavity-nesting bees may preferentially use smaller, disturbed forests, whereas larger, ground-nesting bees may be more commonly observed in larger and less-disturbed habitats (Wray et al. 2014).

While the importance of the ecosystem services provided by native bee species is well established, the significant role that small urban–suburban forests play in the conservation of bee populations and species diversity is less understood. Considering continued declines in managed bee populations and the reliance of many native plants on bees for pollination, this study provides a timely look into the multi-scale factors that affect the conservation of native bee species in populous, human-dominated landscapes. Our main objectives in this study were to better understand the importance of both surrounding land use and microhabitat quality on urban and suburban forest bee communities and how communities vary among small forest patches within an urban–suburban landscape. We hypothesized that (1) microhabitat characteristics describing nesting substrate suitability, such as volume of coarse woody debris, soil pH, and stem density, would drive changes to relative abundance of taxa within a forest patch, while (2) landscape-level traits, including land cover estimates and local stream density, would more strongly influence colonization–extinction dynamics of taxa as they disperse across a fragmented landscape. We also hypothesized that (3) individual forested habitat area would not affect overall bee community structure at higher taxonomic resolutions, given the resilient nature of such communities in small urban forests.

Methods

We sampled bee communities in 14 individual forest patches in and around Newark, Delaware, and one site each in Hockessin, Delaware, and Landenberg, Pennsylvania (Fig. 1). Forest patches were selected to represent a range of sizes (4.618–163.557 ha; $\bar{x}$ = 56.590 ha; SE = 15.702) and were located 0.630–19.620 km apart ($\bar{x}$ = 6.559 km; SE = 0.542 km) in areas protected from development and management (Appendix S1: Fig. S1). Forests consisted of relatively recent secondary growth, with mostly overstory *Quercus* spp. and *Liquidambar sytraciflua*, with *Carya* spp., *Acer* spp., and *Liriodendron tulipifera*. The understory was comprised of mostly *Viburnum* spp., *Vitis* spp., *Toxicodendron radicans*, and non-native species such as *Rosa multiflora* and *Lonicera japonica*. Forest site age since full canopy closure ranged from 24 to 119 yr with a mean age of 76.083 yr. Forest patches were subdivided into systematic 25 × 25 m grids, upon which we randomly selected five grid intersections for sampling plot locations. At each of the 70 plots, we deployed a pollinator trap array between mid-March and July in both 2013 and 2014. Each array consisted of three 3.5-oz plastic bowls painted either yellow, white, or blue, each containing propylene glycol, bleach, and dish soap to preserve samples and reduce surface tension (Droege et al. 2010). We began operating traps in mid-March, depending on the phenological condition of resident angiosperm species in each forest patch. We collected traps in each forest patch in two-week intervals and maintained their operation until canopy closure and collections of Hymenoptera ceased. Upon trap collection every two weeks, we discarded other invertebrates and transferred all Hymenoptera to centrifuge tubes with 70% ethanol for species identification. We stored all captured hymenopteran insects in centrifuge tubes at −80°C and then rinsed, dried, and pinned collected specimens before species identification. The authors, in collaboration with S. Droege (USGS Patuxent Wildlife Research Center), identified species based on Michener et al. (1994) and Michener (2000). Voucher specimens for most species were kept for a reference collection in the University of Delaware's Department of Entomology and Wildlife Ecology.

Given the importance of available nesting substrate for solitary bee taxa, we collected microhabitat covariate data for sampled forest patches in 2011 (Table 1). We measured woody plant stem density (stems/m^2) throughout a 2.5-m^2 circular area surrounding plot centers. To measure forest understory structure, we placed a 2.5-m

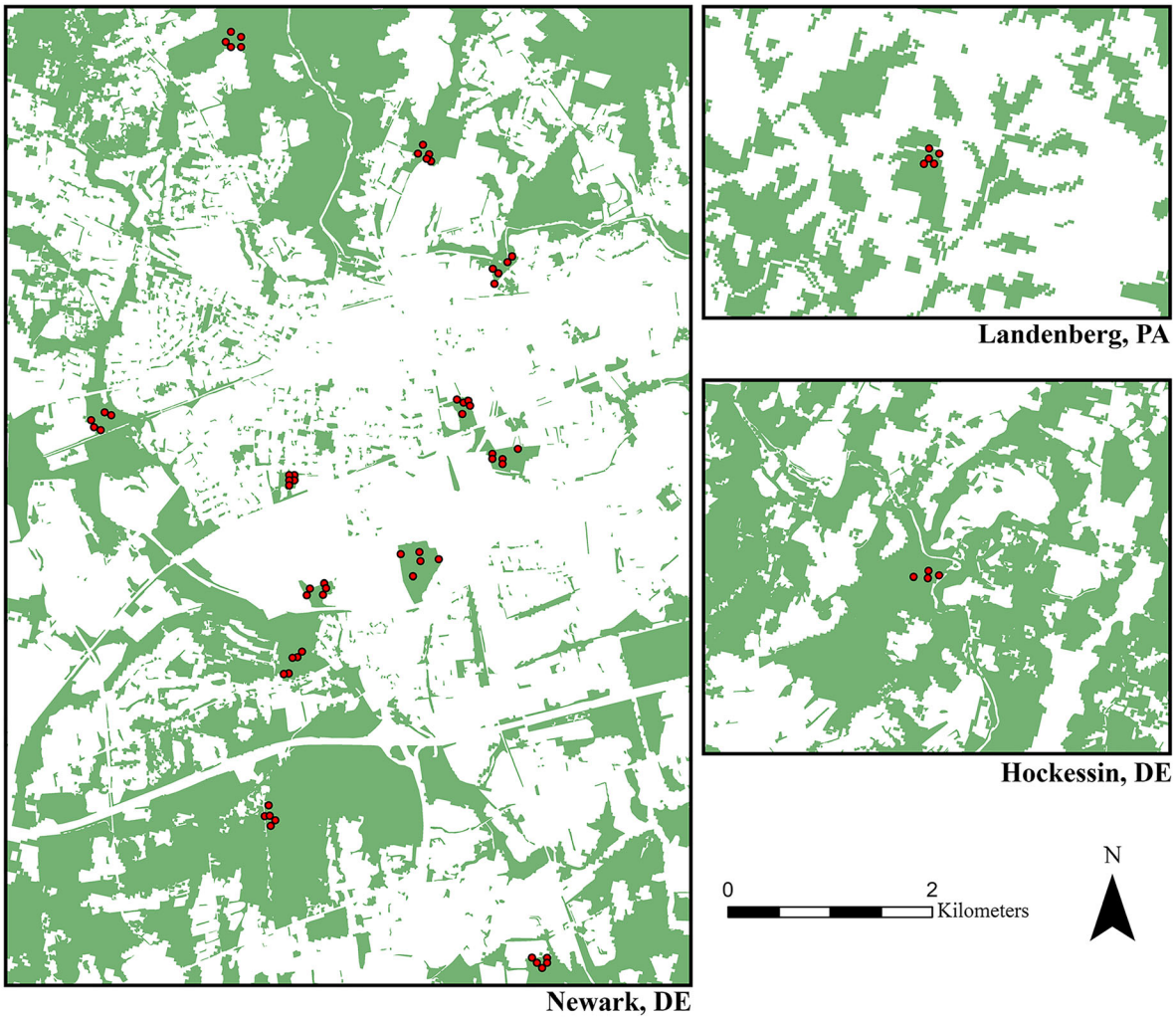

Fig. 1. Contextual map illustrating forested land cover surrounding sampling locations in Delaware and Pennsylvania.

vegetative profile board in the center of each plot and estimated the percent of the board obscured by vegetation at a distance of 15 m. These estimates were made facing the board from the north, south, east, and west, and we averaged estimates to obtain a single value per plot. We measured patch-level soil pH from 10 randomly selected points within each forest patch. We measured leaf litter volume by collecting all leaf litter within 0.5-m^2 rectangular plots centered on each point and allowed litter to dry in Berlese funnels before measuring the dry volume (L). Centered at each trap array, we measured the length and diameter of all fallen dead trees and branches within a 10 m radius to calculate volume of coarse woody debris per m^3. All plot-specific covariates, including leaf litter volume, vegetative structure, volume of coarse woody debris, and stem density, were averaged to obtain patch-level values. Beyond microhabitat covariates, land cover composition has also proven important in defining native bee community composition. To define landscape-level traits of forest patches in our study area, we used 2009 land cover data from the National Land Cover Database (Fry et al. 2011) to calculate percent cover of forest, agriculture, human development, and impervious surfaces, as well as density of freshwater

Table 1. Environmental and landscape covariates collected at sampling sites across the study area in Delaware and Pennsylvania, USA.

Covariates	Mean ± SE	Range
Percent understory vegetative structure	30.15 ± 2.16	11.00–53.5
Forest patch size (ha)	56.59 ± 15.70	4.62–163.56
Soil pH	4.90 ± 0.10	4.02–6.00
Leaf litter volume (L)	5.18 ± 0.30	1.95–7.40
Native plant stem density (stems/m^2)	7.96 ± 1.03	0.80–23.00
Total woody plant stem density (stems/m^2)	18.80 ± 3.91	1.80–85.40
Percent forested land cover in 1000 m radius buffer	29.65 ± 5.79	3.96–65.30
Percent agricultural land cover in 1000 m radius buffer	13.01 ± 3.15	1.30–42.20
Percent impervious land cover in 1000 m radius buffer	24.10 ± 3.85	2.13–47.12
Percent developed land cover in 1000 m radius buffer	54.43 ± 7.63	11.86–89.86
Stream density in 1000 m radius buffer (km/km^2)	1.35 ± 0.23	0.22–3.53
Mean temperature of sampling period (°C)	15.88 ± 1.55	4.60–25.42
Growing degree-day of sample collection	240.34 ± 78.87	0.00–1433.10
Available host *Andrena* spp. in sampling period	2.33 ± 0.22	0.49–3.54

Note: Environmental data were collected in 2011 and landscape variables derived from analysis of 2009 land cover data.

streams (km/km^2) within a 1000-m buffer around each forest patch. While many small bee species travel <1000 m, this spatial configuration accounts for the foraging distance of many bee taxa and constitutes an approximate minimum distance between forest patch centers within our study area (Greenleaf et al. 2007, Carper et al. 2014). Finally, we determined mean temperature (°C) during each trapping event and calculated growing degree-days on day of sample collection.

All data manipulation and statistical analyses were performed in Program R 3.5.1 (R Core Team 2018). To examine overall bee community structure and the variables that may influence the relative taxonomic composition, we first separated trap data into five prevalent taxa: Andrenidae, Halictidae, Megachilidae, and Apidae (excluding *Nomada* spp.), with the fifth group consisting of *Nomada* spp. The *Nomada* species were treated separately from other apid bees due to their kleptoparasitic behavior which greatly differs from con-familial species. We additionally collected five species of kleptoparasitic *Sphecodes*; however, these are parasites of con-familial species, so their response to microsite conditions and local land cover should be consistent with other members of the Halictidae. Therefore, the *Sphecodes* spp were included with all Halictidae and not treated separately in analyses. We used the mean raw abundance of each taxon within the five plots in a forest site and across trapping events during the study period. We calculated ecological dissimilarity of our community data using the Bray-Curtis index prior to assessing spatial autocorrelation among sampled plots. Despite the semi-metric nature of Bray-Curtis dissimilarity matrices as compared to the Euclidean distance of Hellinger-transformed data, both are similarly robust in ordination analyses (Legendre and Gallagher 2001). Given the insignificant results of a redundancy analysis of community dissimilarity data and geographic distances, we did not need to linearly detrend data in order to obtain second-order stationarity: This step ensures that spatial variation can be consistently explained across the study area with a single spatial correlation function (Borcard et al. 2011). To test for pairwise spatial autocorrelation between forest patches, we performed a Mantel test and Mantel correlogram analysis using the vegan package (Oksanen et al. 2017) and determined whether any correlations existed between our community data and pairwise geographic distance between plots. We used Sturges' rule to determine distance classes in Mantel correlogram analysis (Borcard et al. 2011). For further examination into potential spatial autocorrelation, we additionally used distance-based Moran's eigenvector maps and a redundancy analysis to test for significance of eigenvectors in explaining variation within our data (Borcard et al. 2004, Borcard and Legendre 2012).

We also used Bray-Curtis dissimilarities for community analyses of trap data, focusing only

on traps that produced successful captures during the length of operation. For analysis in community models, we transformed quantitative landscape and habitat variables into four-factor categorical predictors based on quantiles of the raw data. We then used betadisper and ANOVA.betadisper functions in vegan to ensure multivariate homogeneity of variance of community data across categorical variables (Anderson et al. 2006, Oksanen et al. 2017). To test for effects of habitat and landscape context on bee community structure, we performed permutational multivariate analysis of variance (MANOVA) with the adonis2 function in the package vegan, and assessed the marginal effects of each variable after 20,000 permutations (McArdle and Anderson 2001, Oksanen et al. 2017, Appendix S2: Figs. S1, S2). We employed a successive, iterative process to test for significant predictor variables in permutational MANOVA models, adding variables individually and comparing *F* statistics. The explanatory variable with the greatest *F* statistic was retained in the model, and each remaining individual variable was again added to assess fit. We continued adding new covariates to permutational MANOVA models until no additional covariates were significant at $\alpha = 0.10$. As limitations may exist with such iterative procedures for producing full regression models, we used this variable selection for guidance, but additionally explored the significance of other variables to ensure there did not exist a model with better fit (Mundry and Nunn 2009). To assess the relative contributions of beta diversity among plots, we also used the betapart package to partition Bray-Curtis dissimilarity into its additive components: species loss/gain and species replacement/turnover (Baselga 2013). We then applied the best-fit permutational MANOVA models to dissimilarity matrices of both Bray-Curtis components to test for relative significance.

In addition to community analyses, we also examined habitat occupancy and detectability of dominant families throughout the study area through the use of dynamic occupancy models (MacKenzie et al. 2003). These models estimate parameters associated with a metapopulation, including whether a species occupies a certain habitat patch as well as the ability of the species to colonize new patches. Dynamic occupancy models also allow for the incorporation of data from multiple years and can account for imperfect detection, an important facet when considering seasonal species such as native bees. To assess how landscape composition and microhabitat characteristics affect habitat colonization, local extinction, site occupancy, and detection probability of forest bees, we specifically applied multi-season colonization–extinction occupancy models to bee capture data using function colext in package unmarked (Fiske and Chandler 2011). For analysis, we again classified bees into the five groups identified for family-level analyses and transformed abundance data into binomial presence–absence during trap collection periods. Significant seasonal variability in the abundance of taxa between trap collection periods, as would be expected in ephemeral taxa such as forest bees, precluded the successful use of multinomial hierarchical models or generalized linear mixed models with abundance data. Initial occupancy covariates included land cover characteristics within 1000 m radius, soil pH, leaf litter volume, native plant stem density, and total woody plant stem density. Land cover characteristics and overall forest patch size were included as both colonization and extinction covariates, and we used mean temperature during trapping period and growing degree-day on trap collection for detection covariates. We also included a polynomial variable for mean temperature to account for potential reduced activity at the end of the flowering season. We included the abundance of andrenid bees as a detection covariate for *Nomada* spp, as these are kleptoparasitic species that mostly utilize Andrenidae. We employed a variable selection process similar to that which was used for permutational models. We compared separate models with each variable added individually, kept the model with the lowest AIC value provided by the modsel function in package unmarked, and then continued to assess additional variables until the most parsimonious model did not include any additional variables. To ensure we did not fail to identify a better-fit model, we continued to build and test models with resulting ΔAIC values up to 2.00. This variable selection was repeated for the four parameters. We conducted parametric bootstrapping goodness-of-fit tests with 1000 simulations and $\alpha = 0.1$ to determine adequacy of model fit.

Results

We operated bowl trap arrays between 77 and 88 consecutive days in 2013 and between 76 and 83 d in 2014. We captured 2865 individual bees, representing 15 genera and 102 species (Appendix S3: Table S1). Bees in the Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae were represented in the study area; however, only two colletid bees were captured, so this family was excluded from community analyses. Within the Andrenidae, *Andrena erigeniae*, *A. carlini*, and *A. violae* were most commonly collected, with remaining species comprising just over 26% of all captures. *Lasioglossum subviridatum* were most abundant within the Halictidae with 57% of all captures, and *Osmia pumila* and *O. taurus* were the most commonly captured species in the Megachilidae with 71% of captures in this family. Mantel analysis of community data and pairwise geographic distance indicated a lack of spatial autocorrelation among forest patches ($r = 0.0285$; $P = 0.4003$; Fig. 2). However, Mantel correlogram analysis revealed slightly positive spatial autocorrelation among forest patches within approximately 3000 m ($r = 0.1992$; Holm-corrected $P = 0.0709$), and negative correlation with patches greater than 10,000 m ($r = -0.3574$; Holm-corrected $P = 0.0034$). Spatial eigenvectors produced by distance-based Moran's eigenvector maps did not significantly explain variation in community data between forest patches ($F_{4,9} = 0.6085$; $P = 0.8010$). As distance-based Moran's eigenvector map tests did not indicate significant

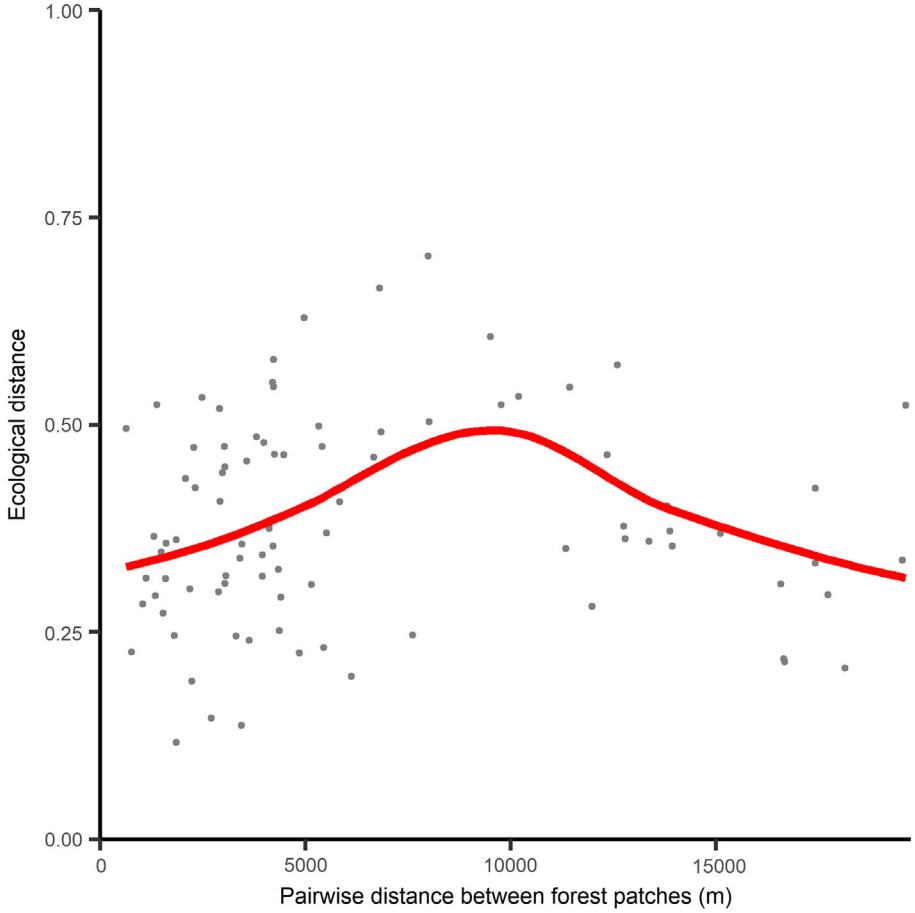

Fig. 2. Comparison of geographic and ecological distance between possible forest bee sampling patches with locally weighted smoothed trend line.

spatial autocorrelation, these eigenvectors were not included in community models.

Taxonomic groups displayed varying responses to microhabitat and land cover covariates (Appendix S4: Fig. S1) and across our study area (Appendix S1: Fig. S2). Exploratory permutational MANOVA produced two best-fit explanatory models for bowl trap data. The model that explained the greatest amount of variation seen in the bee community ($R^2 = 0.9111$) contained microhabitat characteristics including our measure of coarse woody debris ($F_{3,4} = 4.6124$; $P = 0.0034$) and understory vegetative structure ($F_{3,4} = 3.5898$; $P = 0.0130$), as well as the percentage of surrounding impervious surface land cover ($F_{3,4} = 2.4701$; $P = 0.0560$; Fig. 3a). The second-most powerful model ($R^2 = 0.7578$) included landscape-scale characteristics: stream density ($F_{3,7} = 3.5785$; $P = 0.0032$) and percentage of surrounding agricultural cropland ($F_{3,7} = 3.7457$; $P = 0.0026$; Fig. 3b). Partitioning of Bray-Curtis dissimilarity between pairwise forest patch comparisons showed that changes in abundance exhibited greater influence than species turnover in determining overall beta diversity (Fig. 4). Microhabitat characteristics exhibited a stronger influence in determining species turnover or replacement ($R^2 = 0.9358$), while the prevalence of surrounding agricultural cropland drove observed changes in the abundance gradient ($F_{3,7} = 10.8630$; $P = 0.0072$; Table 2).

Site occupancy, colonization, and extinction of our taxa were not significantly correlated with land cover or environmental factors in our occupancy models (Table 3). Detection probability was inversely related to growing degree-days for Andrenidae ($z = -6.65$; $P < 0.001$), Apidae ($z = -4.558$; $P < 0.001$), Megachilidae ($z = -5.78$; $P < 0.001$), and *Nomada* spp ($z = -6.65$; $P < 0.001$; Figs. 5a–d). The detection probability for the Halictidae exhibited a quadratic relationship: Temperature during the capture period positively increased detection ($z = 46.1$; $P < 0.001$) and probability of detection was negatively related to the quadratic temperature term ($z = -74.8$; $P < 0.001$; Fig. 5e).

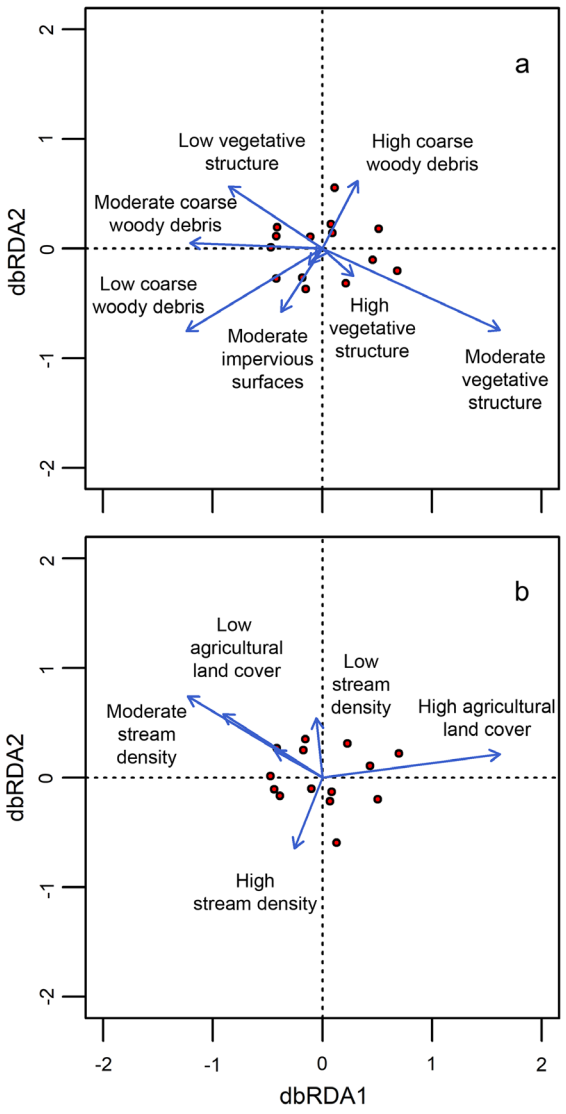

Fig. 3. Results of best-fit models in distance-based redundancy analyses for forest bee trap samples: (a) best-fit model including volume of coarse woody debris, understory vegetative structure, and surrounding impervious surface land cover, and (b) model including local stream density and surrounding agricultural land cover.

Discussion

Through this study, we discovered speciose bee communities throughout the forest fragments in our study area, independent of forest patch size. This supports the notion that, despite their size, small, urban forest patches remain critically important to the conservation of bee biodiversity, particularly in regions subject to anthropogenic development. Regarding habitat patch size, the literature shows variability in bee taxa response

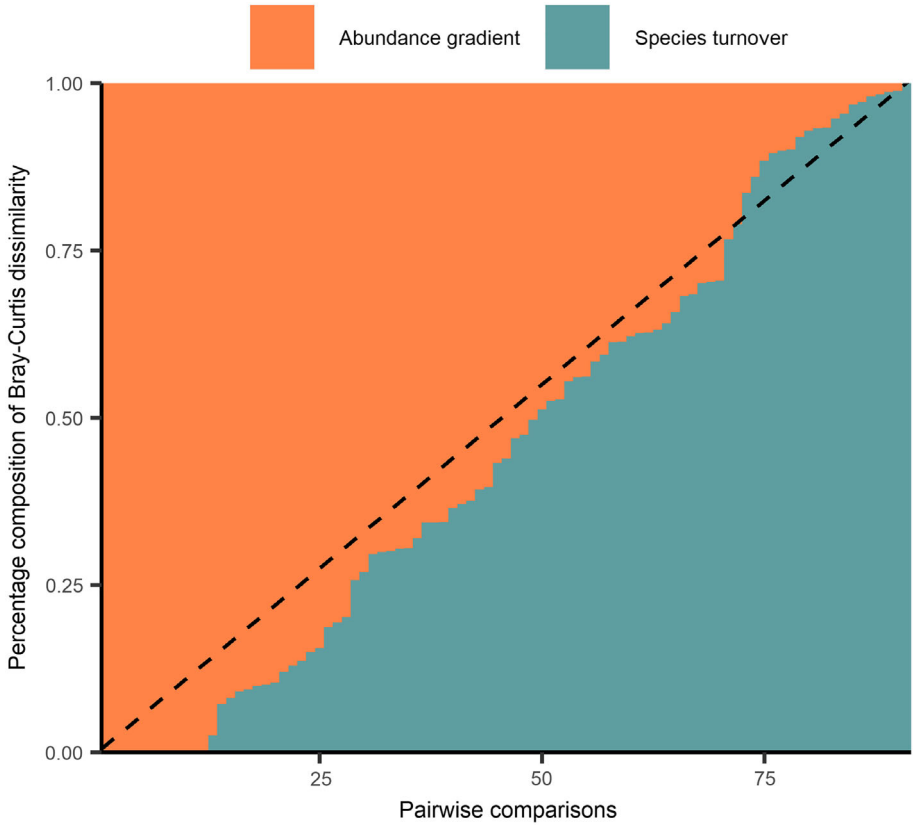

Fig. 4. Contribution of species turnover/replacement and changes to species relative abundance to overall ecological dissimilarity seen in sampled forest bee communities.

Table 2. Partitioned Bray-Curtis community dissimilarity and relationship with covariates in best-fit explanatory models for bowl trap data of forest bees.

			Bray-Curtis dissimilarity		Species turnover		Abundance gradient	
Models	Variables	df	*F*	*P*	*F*	*P*	*F*	*P*
Microhabitat	Coarse woody debris	3,4	4.612	**0.0034**	12.222	**0.0273**	2.681	0.1759
Microhabitat	Vegetative structure	3,4	3.590	**0.0130**	5.698	**0.0641**	2.389	0.2027
Microhabitat	Impervious surfaces	3,4	2.470	**0.0560**	7.772	**0.0456**	0.132	0.9782
Landscape	Stream density	3,7	3.579	**0.0032**	5.156	**0.0525**	2.903	0.1164
Landscape	Agricultural land cover	3,7	3.746	**0.0026**	2.187	0.2144	10.863	**0.0072**

Note: Significant *P*-values at $\alpha = 0.1$ are in bold.

depending on individual bee size, ability to disperse, and feeding habits (Bommarco et al. 2010, Proesmans et al. 2019). Forest patches in our study area ranged from approximately 5–164 ha, yet our covariate of habitat patch size did not significantly predict bee community structure or individual family occupancy. Disparate, variably sized urban forests may support different communities when examined at the species level, but these habitats nonetheless provide foraging resources and nesting substrate for resilient and speciose bee communities. Past research into bee community composition similarly shows that anthropogenic landscapes do not affect bee

Table 3. Significance of covariates for occupancy, colonization, extinction, and detection probability in analysis of forest bee trap data.

Taxonomic Group	Occupancy	Colonization	Extinction	Detection Probability	ΔAIC
Andrenidae†	Null	Null	Null	Growing degree-days	0.000
	Null	Null	Stream density	Growing degree-days	1.896
	Soil pH	Null	Null	Growing degree-days	1.906
Apidae‡	Null	Developed land	Forest cover	Growing degree-days	0.000
	Null	Stream density	Forest cover	Growing degree-days	0.001
	Null	Patch size	Forest cover	Growing degree-days	0.029
Halictidae§	Null	Null	Stream density	Temperature + Temperature^2	0.000
	Null	Patch size	Null	Temperature + Temperature^2	0.720
	Null	Patch size	Impervious cover	Temperature + Temperature^2	2.030
Megachilidae¶	Null	Null	Developed land	Growing degree-days	0.000
	Stream density	Null	Developed land	Growing degree-days	1.837
	Native stems	Null	Developed land	Growing degree-days	1.875
Nomada spp.#	Null	Null	Null	Growing degree-days	0.000
	Null	Null	Developed land	Growing degree-days	1.972
	Null	Null	Forest cover	Growing degree-days	1.987

Notes: Top three best-fit family-level occupancy models are shown, as determined by AIC. Referenced *P*-values indicate the significance of variable in 1000 subsample bootstrap goodness-of-fit tests, with bold text indicating significance at $\alpha = 0.1$.

† 1364 individuals in 39 species.
‡ 181 individuals in 8 species.
§ 526 individuals in 29 species.
¶ 320 individuals in 9 species.
# 445 individuals in 15 species.

species richness (Harrison et al. 2017), while species richness can remain constant from forest edge to the interior (Coswosk et al. 2018). Many urban forests, as was typically seen in our study area, have well-defined ecotones between adjacent habitat types: Such strongly contrasting habitat edges do not affect bee species diversity (Andrieu et al. 2018), further strengthening the implied conservation importance of small habitat patches.

As is expected given the local diversity of forest bees and the taxonomic resolution with which we analyzed the community, collected taxa responded differently to various environmental and landscape covariates (Appendix S4: Figs. S2–S6). Both of our best-fit community models included parameters of the surrounding landscape, with local stream density and surrounding agricultural and impervious surface land cover proving to be the strongest correlative factors (Appendix S1: Fig. S3). The importance of landscape composition surrounding habitat patches to community beta diversity in our study area is in line with past research on the effects of local landscapes on bee species richness and abundance (Gutiérrez-Chacón et al. 2018, Ballare et al. 2019). Many native forest bees are likely unable to cross the developed landscape matrix that exists between suitable forest patches in an urban–suburban environment (Ricketts 2001, Keilsohn et al. 2018). Within our study area, bee community structure was not spatially correlated at sites greater than 3 km apart, though when assessed at the individual trap array, positive spatial autocorrelation was only detected within 1562.722 m ($r = 0.104$; $P = 0.0013$). A lack of spatial correlation beyond 1500 m is consistent with past literature on the limited foraging ranges of many bee species (Greenleaf et al. 2007). More than half of captured bees were in the Andrenidae, a family comprised of small-bodied species with limited capacity for inter-patch movement: Andrenids are generally found foraging 50–75 m from available nesting substrate (Bailey et al. 2014). Similarly, the Halictidae also consists of smaller species that may be unable to move between patches separated by inhospitable matrix. *Bombus* spp. and other euglossine species in the Apidae, however, are much more robust fliers and can travel longer distances to find suitable habitat or food resources (Tonhasca et al. 2003, Leong et al. 2014). Though capable of traveling greater

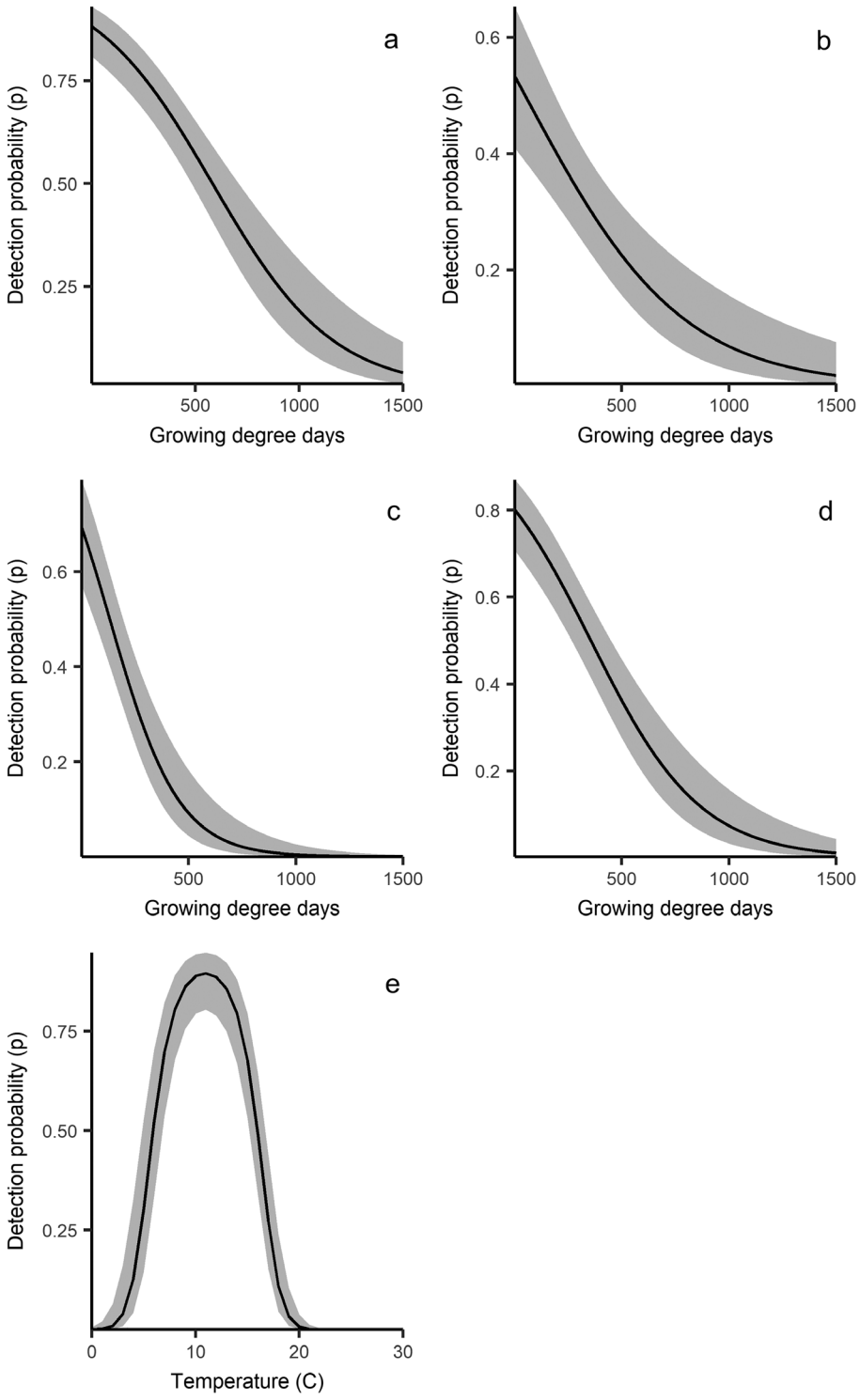

Fig. 5. Trends of detection probability across growing degree-days from occupancy models of (a) Andrenidae, (b) Apidae (excluding *Nomada* spp.), (c) Megachilidae, and (d) *Nomada* spp., and detection probability across temperature for (e) Halictidae.

distances, anthropogenic barriers and disturbance may still limit the extent to which these taxa are able to travel between patches: Many urban and suburban forest patches in the mid-Atlantic United States are separated by intersecting roads, highways, and other anthropogenic impervious surfaces which have shown to lessen habitat connectivity and increase flight mortality for some Apidae species (Tonhasca et al. 2003, Keilsohn et al. 2018). Preserving not only remnant forest patches but also corridors for movement could greatly facilitate inter-patch connectivity for bees and other invertebrates, as bee density has been shown to increase with enhanced habitat connectivity in mosaicked landscapes (Steffan-Dewenter 2003). The lack of habitat connectivity and the extent of inhospitable matrix between habitat patches likely both contribute to the variation we see in bee communities across our study area.

In addition to the significance of local landscape composition in determining beta diversity, understory vegetative structure and the volume of available coarse woody debris were similarly important. The importance of these two factors is consistent with past literature that has documented the importance of specific characteristics of the nesting substrate for pith- and cavity-nesting species (Potts et al. 2005, Steffan-Dewenter and Schiele 2008, Ballare et al. 2019). Given the abundance of ground-nesting halictid and andrenid bees in our study area, a metric of available, bare ground for nesting would have likely been a significant covariate in community models and should be included in future research in this region (Ballare et al. 2019, Proesmans et al. 2019). We observed that differences in relative species abundance played more of a role in defining overall beta diversity than did species turnover/replacement, as would be expected when analyzing the community at a higher taxonomic resolution. Both our microhabitat and landscape covariates more strongly predicted the shifts in species turnover, while changes to various species' abundance were only related to agricultural land cover. Contrary to our hypothesis, microhabitat characteristics did not significantly explain changes in the abundance of bee taxa; however, the importance of nesting resources to local species abundance seems clear when viewing the relationships between captures of pith-nesting Apidae and understory vegetation (Appendix S4: Fig. S3) and cavity-nesting Megachilidae and coarse woody debris (Appendix S4: Fig. S5). This community attribute must be better explained by additional relevant factors not examined herein, potentially including individual plant species prevalence and availability of bare soil. Volume of coarse woody debris, understory vegetative structure, stream density, and surrounding impervious surface land cover were all considered significant in determining species turnover and replacement between patches, while surrounding agricultural land cover significantly predicted changes in abundance of taxa among patches. These findings corroborate recent, similar work that has shown the importance of both landscape composition and microhabitats to determining bee communities (Ballare et al. 2019, Proesmans et al. 2019).

While our landscape and habitat covariates affected forest bee community structure, neither of these factors influenced metapopulation dynamics in our occupancy models. Owing in part to the coarse nature of our environmental covariates, these microhabitat traits were not significant in predicting initial bee occupancy of a patch, colonization of new patches, or local extinctions within a patch. More spatially resolute, site-specific estimate of herbaceous and bare ground cover as well as present plant species would likely better predict initial bee occupancy. We expected colonization and extinction dynamics to be related to landscape composition, as the configuration of landscape elements in the surrounding matrix may block or facilitate the dispersal of bees between forest patches (Steffan-Dewenter 2003, Boscolo et al. 2017). The insignificant results of our occupancy models conflict with the lack of spatial autocorrelation detected across the study area, as our landscape covariates were not able to predict changes in colonization or extinction dynamics. This lack of significance likely resulted from analyzing the community at the family level when large differences in natural history may exist between taxa, or it could suggest that other factors may be more influential in affecting dispersal. Detection probability of all bee families was strongly correlated with temperature or growing degree-day, generally decreasing across the spring season. The downward trend in detection probability is to be expected given the seasonality of many ephemeral bee

species as they respond to early-emergent plant species such as spring beauty (*Claytonia virginica*). As their host plants senesce, adults die or estivate and are not as readily detected. Halictidae exhibited an increase in detection probability until mean temperatures reached above approximately 12°C, at which point the probability of detection decreased. These species are generalists: As spring ephemeral plants senesce and forest interiors contain fewer floral resources, these species could follow inflorescence availability outside of the forest interior.

Despite their small size, remnant urban forests contain unique assemblages of bees, different but no less rich than larger habitats or those in more forested landscapes (Harrison et al. 2017, Proesmans et al. 2019). Within our study area, we observed over 100 species among our plots, the smallest of which was <5 ha. Protection of these local forest patches is important for the subsequent conservation of unique forest bee communities, particularly as communities are defined at the forest patch level: Bee community structure, including taxonomic composition and relative abundance, was spatially independent among forest patches beyond 1500 m. As isolated forest patches maintain unique and speciose bee communities, these small, remaining urban forests retain significant conservation value, particularly as there are very few forest patches remaining in these areas. The conservation value held by these remnant patches does not, however, negate the importance of connectivity between patches among the unsuitable urban/suburban matrix (Ricketts 2001, Boscolo et al. 2017). Extant forests currently support speciose communities, but with continued anthropogenic development and other pressures, it is critical to facilitate species or population movement among patches and across the landscape. In addition to landscape-level factors that may be important to urban forest bee communities, conservation measures should also consider site-specific habitat quality, as community structure was also strongly influenced by traits including coarse woody debris and vegetative structure. As human development and urbanization is projected to continue throughout the United States, the importance of remnant forest conservation and the need for an increased understanding of forest bee ecology should remain a preeminent concern for ecologists.

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