
Effect of Human Disturbance on Bee Communities in a Forested Ecosystem

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Abstract: *It is important for conservation biologists to understand how well species persist in human-dominated ecosystems because protected areas constitute a small fraction of the Earth's surface and because anthropogenic habitats may offer more opportunities for conservation than has been previously thought. We investigated how an important functional group, pollinators (bees; Hymenoptera: Apiformes), are affected by human land use at the landscape and local scales in southern New Jersey (U.S.A.). We established 40 sites that differed in surrounding landscape cover or local habitat type and collected 2551 bees of 130 species. The natural habitat in this ecosystem is a forested, ericaceous heath. Bee abundance and species richness within forest habitat decreased, not increased, with increasing forest cover in the surrounding landscape. Similarly, bee abundance was greater in agricultural fields and suburban and urban developments than in extensive forests, and the same trend was found for species richness. Particular species groups that might be expected to show greater sensitivity to habitat loss, such as floral specialists and bees of small or large body size, did not show strong positive associations with forest habitat. Nevertheless, 18 of the 130 bee species studied were positively associated with extensive forest. One of these species is a narrow endemic that was last seen in 1939. Our results suggest that at least in this system, moderate anthropogenic land use may be compatible with the conservation of many, but not all, bee species.*

Keywords: agriculture, body size, *Colletes bradleyi*, forest fragmentation, heath, hymenoptera, pollinator conservation, suburbanization

Efecto de la Perturbación Humana sobre Comunidades de Abejas en un Ecosistema Boscoso

Resumen: *Es importante que los biólogos de la conservación entiendan como persisten las especies en ecosistemas dominados por humanos porque las áreas protegidas constituyen una pequeña fracción de la superficie terrestre y porque los hábitats antropogénicos pueden ofrecer mejores oportunidades de conservación que las previamente pensadas. Investigamos como un grupo funcional importante, polinizadores (abejas; Hymenoptera: Apiformes), es afectado por el uso de suelo por humanos a escala de paisaje y local en el sur de Nueva Jersey (E.U.A.). Establecimos 40 sitios que difirieron en la cobertura del paisaje circundante o en el hábitat local y recolectamos 2551 abejas de 130 especies. El hábitat natural en este ecosistema es un brezal ericáceo boscoso. La abundancia y riqueza de especies de abejas decreció dentro del hábitat boscoso, no incrementó con el incremento de cobertura forestal en el paisaje circundante. De manera similar, la abundancia de abejas fue mayor en los campos agrícolas y en desarrollos urbanos y suburbanos que en los bosques extensivos, y se encontró la misma tendencia para la riqueza de especies. Los grupos particulares de especies que se pudiera esperar mostraran mayor sensibilidad a la pérdida de hábitat, como los especialistas florales y abejas de tamaño corporal pequeño o grande, no presentaron asociaciones positivas con el hábitat boscoso. Sin embargo, 18 de las 130 especies de abejas estudiadas se asociaron positivamente con el bosque extensivo. Una de estas especies es una endémica que fue vista por última vez en 1939. Nuestros resultados sugieren que, por*

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lo menos en este sistema, el uso de suelo antropogénico moderado puede ser compatible con la conservación de muchas, pero no todas, las especies de abejas.

Palabras Clave: agricultura, brezal, *Colletes bradleyi*, conservación de polinizadores, fragmentación de bosques, himenoptera, suburbanización, tamaño corporal

Introduction

Recent work in conservation biology and landscape ecology explicitly investigates species' use of anthropogenic habitats, as opposed to assuming that these habitats form a "hostile sea," as does the traditional island-biogeography approach (Haila 2002). It is pragmatic for conservation planning to consider species' use of anthropogenic habitats for two reasons. First, more than 87% of the Earth's land surface is not currently protected (Groom et al. 2006), meaning that many species will have to survive in human-modified areas if they are to survive at all. Second, some anthropogenic habitats may support more species than has been previously assumed (Andrén 1992; Gascon et al. 1999; Driscoll 2005). For example, results from studies in a mosaic landscape of farms and forests in Costa Rica show that half or more of bird, mammal, moth, butterfly, and herbaceous and shrubby plant species commonly inhabit human-dominated habitats (e.g., Ricketts et al. 2001; Daily 2005; Mayfield & Daily 2005). In Britain many native species are typical of countryside habitats, and their population trends are associated with changes in farming practice rather than with the establishment of reserves (Krebs et al. 1999).

It is especially important to understand whether organisms that perform particularly important ecosystem functions persist in human-dominated ecosystems. Pollinators are one such group: most of the world's flowering plants require animal pollinators (Axelrod 1960; Ashman et al. 2004), and plant populations in human-dominated ecosystems will only maintain genetic diversity if pollinators are present and can move freely through anthropogenic habitats (Keller & Waller 2002). Pollinator conservation has attracted public attention recently because there is evidence that pollinators are declining in some parts of the world (Kearns et al. 1998; Kremen & Ricketts 2000).

Bees (Hymenoptera: Apiformes) are the main pollinators in most ecosystems (Nabhan & Buchmann 1997; Aizen & Feinsinger 2003). Conservation biologists are concerned about bees in Europe, where 37–52% of species are on the World Conservation Union Red List (Mohra et al. 2004). The status of the approximately 4000 bees native to North America is poorly known (Cane & Tepedino 2001). A recent series of papers reviewing the state of our knowledge about North American invertebrate pollinators concludes that we do not presently know the net effect of anthropogenic activities, which

may be detrimental to some bee species and beneficial to others (Cane & Tepedino 2001). Furthermore, high natural variability in bee populations (Williams et al. 2001) and difficulties with drawing inferences about pollinator populations via observations of pollination deficits in plants (Thomson 2001) make it challenging to rigorously demonstrate pollinator decline or the lack of it. Despite the importance of bees as pollinators and concerns about pollinator conservation, there is little scientific understanding of how the conversion of natural habitats to human use affects bees (Cane 2001). Replicated, landscape-scale studies have been conducted in relatively few ecosystems. Most, but not all, of the results show that bees are negatively affected by human land use (e.g., Aizen & Feinsinger 1994; Klein et al. 2002; Kremen et al. 2002; Steffan-Dewenter et al. 2002; Kremen et al. 2004; Tylianakis et al. 2005).

We studied how wild bee communities change across gradients of agricultural and suburban and urban development. Specifically, we asked (1) How do bee communities in forests, the natural habitat, change with decreasing proportion of forest in the surrounding landscape? (2) How do bee communities differ between three local habitat types: extensive forested heath, agricultural fields, and suburban and urban developments? Finally, because habitat specialization and body size may cause some species to be more extinction-prone than others (e.g., McKinney 1997), we asked, (3) Do species tied to particular floral or nesting resources and species of small or large body size show patterns that differ from the bee community as a whole?

Methods

Study System and Design

Our study system was the 438,210-ha New Jersey Pinelands Biosphere Reserve in southern New Jersey (U.S.A.). The native vegetation in this ecosystem is a pine-oak heath characterized by sandy soil and an open canopy of pitch pine (*Pinus rigida* P. Mill.) and oak (*Quercus*) above an ericaceous shrub layer. Most ericaceous species are obligatorily pollinated by bees (East 1940), and sandy soil provides a good substrate for ground-nesting bees. We used a combination of geographic information systems (GIS) and on-the-ground site visits to select 40 study sites. All sites were situated within the same ecoregion

(Atlantic Coastal Pine Barrens; Ricketts et al. 1999) and shared a similar elevation (0–63 m), geologic history, and soil type (the outer coastal plain; 1999 Geologic Map of New Jersey, New Jersey Department of Environmental Protection Geological Survey).

We investigated the landscape-scale and the local-scale effects of human land use. To investigate landscape-scale effects we used a subset of 28 sites that were matched for local habitat variables: upland oak-pine-heath habitat type, approximately 85% cover by three dominant bee-pollinated plant species (*Gaylussacia baccata* [Wangenh.] K. Koch, *Gaylussacia frondosa* [L.] Torr., and *Vaccinium pallidum* Ait.), fire history (for most sites >3 years since controlled fire and >10 years since wildfire), and light penetration through the canopy (which was uncorrelated with forest cover in the surrounding landscape, Spearman's $\rho = -0.20$, $p > 0.30$). To account for the fact that there can be edge effects in forest fragments but not continuous forest (Harrison & Bruna 1999), we situated all sites, including those in extensive forest, along habitat edges.

The 28 sites varied in surrounding land cover from 25% to 99% natural habitat (forest) at a 1600 m radius (as used for our analyses; see below). Half of these sites had >82% forest cover in the surrounding landscape, and we refer to these sites as extensive forest. The other 14 sites, although situated in forest habitat, were all within tens of meters of human land use and had 25–70% natural land cover in the surrounding landscape. We refer to these sites as fragmented forest. Few of the fragmented forest sites were situated in discrete fragments because in this system the patches of remaining forest are irregularly shaped and often interconnected by narrow extensions of natural habitat such as hedgerows or riparian vegetation. Therefore in our analyses we did not consider fragment size or dispersion as separate variables. We analyzed landscape cover as the proportion of natural habitat (forest) at various radii surrounding each site (see below). Proportional area is strongly, positively correlated with other area-based indices of habitat proximity (Winfree et al. 2005).

To investigate local-scale effects we contrasted the 14 extensive forest sites, which were surrounded by >82% forest cover, with 12 sites set in the human land use types themselves, 5 in agricultural fields and 7 in suburban or urban areas (which contained a combination of low- and high-density development). We positioned these 12 sites haphazardly within the largest continuous blocks of agriculture or suburban and urban development in our study system, without trying to control local habitat variables because local habitat was the variable of interest.

For purposes of spatial independence all sites were at least 1.4 km apart (median intersite distance 18.8 km; maximum 48.7 km), and sites of a given type were dispersed throughout the study area (Fig. 1). We assessed the degree of spatial autocorrelation with Mantel tests.

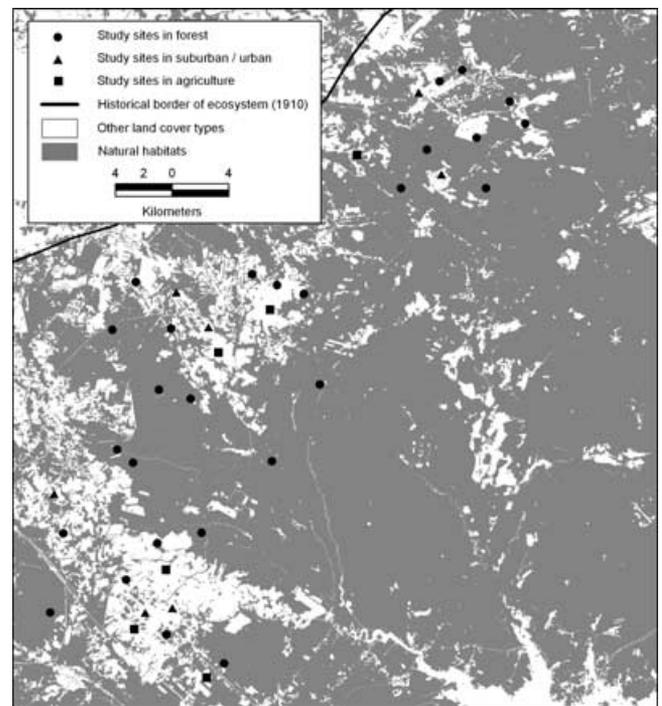


Figure 1. Geographic information systems map of the study area in New Jersey (eastern U.S.A.), with the location of study sites indicated by points.

Data Collection

At each of the 40 sites we collected data within one 110 × 10 m transect. We sampled bee diversity and flower abundance four times at each site during the peak season of bee activity in our area (14 April 2003–14 August 2003). We used standardized active (hand netting) and passive (pan trapping) collecting methods to survey bees. To adequately sample species with different diurnal patterns, hand netting was done for two 30-minute periods, one between 0900 and 1200 hours and the other between 1200 and 1500 hours. To control collector bias, each site was netted by each of three collectors. Our pan traps were 178-mL plastic bowls (Solo brand, Kernersville, North Carolina) in white, fluorescent blue, and fluorescent yellow. Four pan traps of each color were placed at 10-m intervals along each transect between 700 and 900 hours and collected between 1500 and 1700 hours, for a total of 8 hours trapping time per day. Data were only collected on sunny or partly cloudy days. To assess floral abundance during each collection period, we counted all open flowers in 1.6-m³ quadrats placed every 5 m for a total of 46 quadrats per site; cubic quadrats were used to sufficiently measure flowering shrubs. We sampled sites in roughly the same order during each of the four monthly collection periods. Within each sampling day, we randomized site-collection order (i.e., time of day at which we visited the site).

We collected data on all unmanaged bees in our study area. We did not collect data on the managed, non-native honeybee (*Apis mellifera*) because the abundance of this species primarily reflects placement of managed hives, rather than ecological variables (Steffan-Dewenter et al. 2002; Kremen et al. 2004).

GIS Analyses

For the landscape-scale questions, we used GIS to calculate the proportion of various land use types in the landscape surrounding each site. We first mapped the center of each collection transect with a Trimble Geo-Explorer Global Positioning System (GPS; Trimble Navigation, Sunnyvale, CA, California) corrected to ± 10 -m accuracy with GPS Pathfinder Office (version 2.9, Touch Vision, Cypress, California). The GIS land-cover data were provided by the New Jersey State Department of Environmental Protection. Land-cover data were based on aerial photographs taken in 1995–1997 at a 1-m resolution and subsequently classified to 53 land-cover types at a resolution of between 0.004 and 0.4 ha. The land-cover data met national map accuracy standards at scale 1:24,000. We further updated all habitat classifications within a 1000 m radius of the study sites with aerial photographs taken in 2002.

We grouped the 53 land-cover types into the four broad categories of interest: forest, agricultural, and low- and high-density development (collectively, suburban and urban). In creating the “forest” category we first considered three natural habitat types (upland forest, wetland forest, and open natural habitats) separately, but these did not have statistically distinguishable effects on either bee abundance or species richness. We therefore combined these habitat types into forest. (Although open natural habitats are not forest, these habitats constituted <4% of the area analyzed, and we used the term *forest* for simplicity). In creating the agriculture category, it was necessary to combine various types of agriculture, including row crops, orchards, hay fields, and pastures, because types were not separated in the original GIS data. We were, however, able to separate low-density development (<35% impervious cover) from high-density development (>35% impervious cover) because these distinctions were made in the original GIS data. The proportion of forest, agriculture, low-density development, and high-density development around each site at various radii was then calculated using buffers in ArcGIS 9.0 (Environmental Systems Research Institute, Redlands, California).

Preliminary Statistical Analyses

Covariates associated with each of the eight data-collection dates at each site (temperature, wind speed, cloud cover, and floral abundance) were not significant in preliminary multiple regression analyses. We therefore

summed season-long bee abundance and species richness across all collection events for each site.

Two of our study sites had been burned within the past 2 years and therefore did not meet the study criteria in terms of fire history, but both were similar to other sites in terms of both bee abundance and species richness and were therefore included in subsequent analyses.

Before beginning analyses we used Mantel tests to check for spatial autocorrelation among sites for bee abundance and species number (R-*Package*; <http://www.bio.umontreal.ca/Casgrain/en/labo/R/v4/index.html>) but found none (all $p \geq 0.14$).

To identify the scale at which surrounding land cover had the most explanatory power, we used simple linear regression of aggregate bee abundance and species richness against the proportion of forest cover surrounding study sites at radii of 400, 800, 1200, 1600, 2000, 2400, and 2800 m. We then compared the resulting r^2 values (Holland et al. 2004). Results for abundance and species richness were highly significant at all scales >400 m and had the greatest r^2 values at 1600 m. We therefore used land cover at a 1600 m radius for the 28 study sites in all subsequent analyses. We repeated the above investigation across scales for the additional analyses done for bees of different body size classes (small, medium, and large bees; see below) because bees of different body size might be expected to respond to the surrounding landscape at different scales (e.g., Roland & Taylor 1997).

Statistical Analyses

LANDSCAPE-SCALE EFFECTS

To assess associations between forest cover in the surrounding landscape (1600 m radius) and bee abundance and species richness within forest habitat, we used the 28 sites matched for local habitat type in ordinary least-squares regression (JMP version 5.1, SAS Institute, Cary, North Carolina). Bee abundance was \log_{10} transformed to achieve homoscedasticity of residuals. To investigate the relative effects of agriculture, low-density development, and high-density development in the surrounding landscape, we used multiple regression with the proportion of each habitat type in the surrounding landscape as independent variables and bee abundance or species richness as the dependent variable. We left forest habitat out of the regression as a reference category to avoid problems of multicollinearity. Species composition was compared across all 40 sites with nonmetric multidimensional scaling.

LOCAL-SCALE EFFECTS

We compared bee abundance, species richness, and community composition among three local habitat types: extensive forest (14 sites), agricultural (5 sites), and

suburban and urban (7 sites). Abundance was compared with Wilcoxon tests (JMP version 5.1, SAS Institute). For species richness, we used accumulation curves (EstimateS, version 7.5.0; Colwell et al. 2004) to allow for comparison between habitat types that had unequal sampling effort. We calculated species-richness curves on the basis of total species and only species unique to a given habitat type.

SPECIES COMPOSITION AND ANALYSES BY SPECIES GROUP

We repeated the above-mentioned landscape- and local-scale analyses for groups of species that may be particularly sensitive to habitat loss: floral specialists, species that require wood for nesting, and bees of different body sizes. Information on floral and nesting specialization was compiled from the published literature and based on extensive examination of museum specimens and field experience (J. Ascher & T.G., unpublished data). We defined bees as floral specialists (oligolectic) if they collect pollen from only one plant family or, more often, one to a few plant genera. A problem with the definition of specialization, including oligolecty, is that it is sensitive to sampling effort. For our purposes, however, the important point is that the determination of oligolecty should not be biased with regard to the habitat type where the bee species was collected. We defined wood-nesting bees as those species obligatorily nesting in rotting wood or that use cavities in wood or twigs (but not those nesting in pithy stems). To analyze species by body size, we measured intertegular span for each species in our study and estimated dry body mass based on a known relationship between intertegular span and body mass (Cane 1987). We then divided the range of \log_2 dry body masses into three equal intervals: small (≤ 4 mg), medium (4–16 mg), and large (> 16 mg).

We used nonmetric multidimensional scaling (NMS; PC-ORD version 4, MjM Software, Glendeden Beach, Oregon) to visualize the dissimilarity among sites in terms of their bee species composition. Nonmetric multidimensional scaling is a method for graphically representing pairwise dissimilarity values between sites in a reduced number of dimensions. It first calculates all pairwise distances between sites with an ecological measure of species composition. It then positions the sites graphically in two or more dimensions so as to maximize the rank correlation between the pairwise intersite distances calculated by the ecological measure and the pairwise intersite distances in the graphical ordination (McCune & Grace 2002; Quinn & Keough 2002). As measures of ecological distance, we used the Bray–Curtis/Sorensen measure, which considers the absolute abundance of each species at each site, and the relative Sorensen measure, which considers only the relative or proportional abundance of each species at each site. With the relative Sorensen measure, sites with similar community structure but different overall abundances are considered similar.

Both measures have a robust monotonic relationship with true ecological distance when tested with simulated data (Faith et al. 1987); in these tests the relative Sorensen is equivalent to the relativized Manhattan.

We used two methods to identify the bee species positively associated with extensive forest. First, we used NMS to ordinate all 40 sites in terms of their bee-community composition and then visually identified the species associated with the forest sites. We used the Bray–Curtis dissimilarity measure because we wanted a species' absolute abundance at extensive forest sites to contribute to its identification as forest associated. Second, we used a G test with a Williams correction to identify the species that were significantly more abundant at extensive forest sites than would be expected by chance. We report species associated with forest at $p = 0.05$, despite the fact that we were doing multiple G tests (one for each species), because we wanted to be conservative (i.e., inclusive) in identifying forest-associated bees.

Finally, we used G tests to compare the frequency of floral and wood-nesting specialization among the forest specialist species with all other species.

Results

We collected 2551 bees of 130 species. (The abundance of each species in each habitat type is available; see Supplementary Material). With the exception of three naturalized exotic species (accounting for $< 0.5\%$ of individuals), all collected bees were native to our study area. All but four species (1% of individuals) are widespread across most of the eastern United States (Krombein et al. 1979). One species, *Colletes bradleyi*, is known from only two previous specimens, collected in the study area in 1923 and 1939, suggesting that *C. bradleyi* is a narrow endemic of pine-heath habitat in New Jersey.

Landscape-Scale Effects

Bee abundance and species richness within forest habitat decreased significantly with increasing forest cover in the surrounding landscape (Fig. 2; log abundance, $F_{1,26} = 12.0$, $r^2 = 0.32$, $p < 0.002$; species richness, $F_{1,26} = 21.2$, $r^2 = 0.45$, $p < 0.0001$). Agriculture was positively associated with bee abundance and species richness, and low-density housing was positively associated with species richness. High-density development did not show any significant associations (Table 1).

Local-Scale Effects

Compared with both extensive forest and suburban and urban developments, agricultural fields had the highest bee abundance ($\chi^2 = 14.4$, $df = 2$, $p = 0.008$; Wilcoxon test), species richness, and richness of unique species, although the results were not significant for species (based

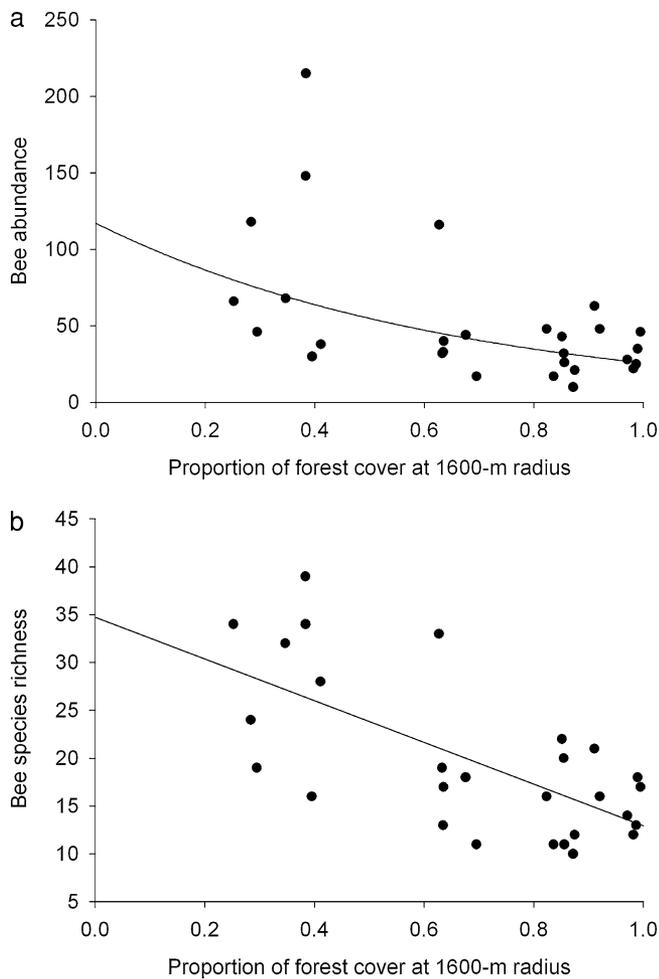


Figure 2. Single regression of (a) aggregate bee abundance against the proportion of forest cover in the surrounding landscape (dependent variable \log_{10} transformed for analysis and log fit is shown; $r^2 = 0.32$, $df = 27$, $p < 0.002$) and (b) observed bee species richness against the proportion of forest cover in the surrounding landscape ($r^2 = 0.45$, $df = 27$, $p < 0.0001$).

on nonoverlapping 95% CI; Fig. 3). Suburban and urban developments also had higher bee abundance ($\chi^2 = 6.44$, $df = 1$, $p = 0.01$; Wilcoxon test) and species richness than did extensive forest, although again the results were not significant for species (Fig. 3).

Species Composition and Analyses by Species Group

None of the extinction-prone species groups examined was positively and significantly associated with forest cover at the landscape scale (Table 2). At the local scale, the only significant positive association was for wood-nesting bees, which were significantly more abundant in extensive forest than in agricultural fields (but not suburban and urban areas, as determined by dropping categories from the Wilcoxon test; Table 3). Contrasts in

Table 1. Least squares multiple regression of log-aggregate bee abundance and observed bee species richness against surrounding landscape composition at a 1600-m radius.

Land-cover type	Coefficient	SE	t	p
Log abundance				
agriculture	0.80	0.28	2.82	0.009
low-density development	1.14	0.62	1.85	0.077
high-density development	-0.13	0.46	-0.28	0.779
Species richness				
agriculture	21.09	7.00	3.01	0.006
low-density development	46.84	15.35	3.05	0.006
high-density development	4.03	11.44	0.35	0.728

species richness across local habitat types were highly insignificant for all species groups, based on widely overlapping 95% CI, and are therefore not reported. Although no class of body size showed a positive association with forest cover, relationships did differ by body size. Small- and medium-sized bees showed the same patterns as did the

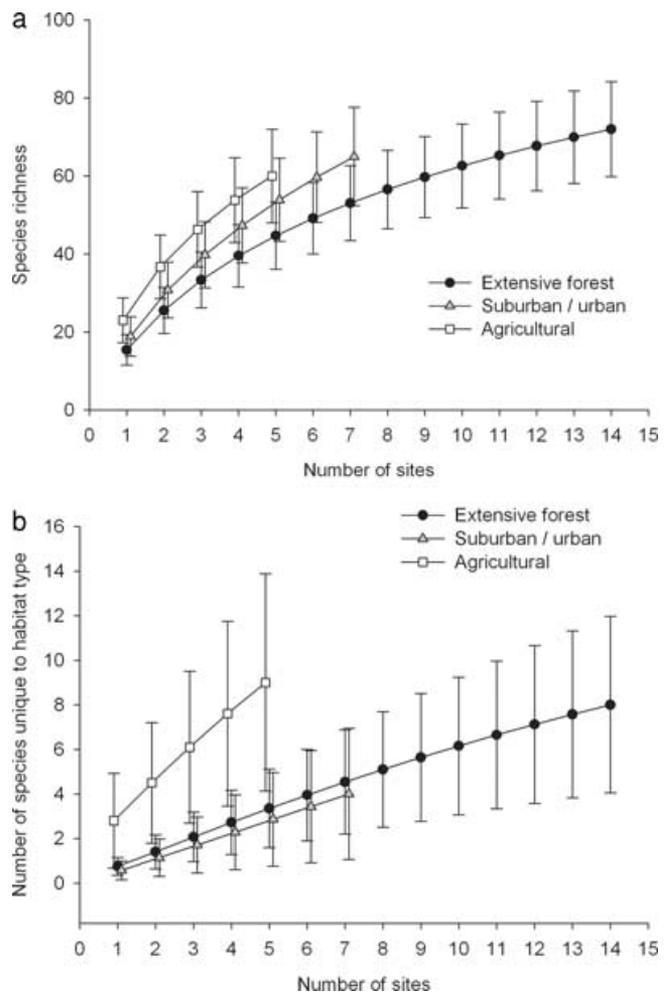


Figure 3. Species accumulation curves in extensive forest, agricultural fields, and suburban and urban developments: (a) species collected (mean \pm 95% CI) and (b) species collected that are unique to a given habitat type (mean \pm 95% CI).

Table 2. Results of regression analyses of bee abundance or log abundance and species richness against surrounding forest cover at a 1600-m radius for species groups predicted to be extinction prone.

Species group	Coefficient	SE	r ²	p
Abundance				
oligolectic	-0.88	3.70	0.00	0.81
wood nesting	-1.71	3.39	0.01	0.62
small body size	-1.11	0.29	0.37	<0.0006
medium body size*	-0.57	0.23	0.19	<0.02
large body size	-3.27	4.61	0.02	0.48
Species richness				
oligolectic	-1.05	0.86	0.05	0.24
wood nesting	-3.15	1.37	0.17	0.03
small body size	-8.32	1.90	0.42	0.0002
medium body size	-10.45	2.89	0.33	0.001
large body size	-3.05	1.81	0.10	0.10

*We did not have a prediction for medium-sized bees, but they are included for comparative purposes.

data set as a whole for both abundance and species richness at both the landscape and local scales. In contrast, large bees showed no significant association with surrounding land cover or across local habitat types (Tables 2 & 3). In analyses for bees of different body sizes, the directionality of the results did not vary across scales (radii) examined. The most explanatory scale in landscape-scale analyses for small and medium bees was 1600–2000 m radius, except for species richness of small bees, which was most explanatory at 400 m. For large bees, the explanatory value kept increasing with increasing radius up to the maximum of 2800 m, but even at the most significant scale, the relationship was weak ($r^2 = 0.13$). Results are reported at the 1600-m scale to allow consistency with other analyses (Table 2). Significance levels were only slightly different at the more-explanatory scales.

Ordination analysis showed that the extensive forest, fragmented forest, agricultural, and suburban and urban sites were clearly separable with both the Bray–Curtis measure (Fig. 4a) and the relative Sorensen (Fig. 4b). The reliability of a particular NMS ordination is summarized by three statistics. The match between the values of the ecological measure, and distances between sites in the ordination, is assessed using “stress,” which is inversely related to the fit of this relationship (McCune & Grace

2002). “Instability” is a measure of how much the stress value changes with subsequent runs of the algorithm; low instability values (approaching 10^{-4}) increase confidence in the reported stress value. The NMS selects the dimensionality of the final graphical solution such that adding further dimensions does not appreciably decrease the stress value. For the Bray–Curtis ordination (Fig. 4a), two dimensions were selected, the stress was 20.2, the instability was 0.001, and the cumulative proportion of variance explained by two axes was 0.70. For the relative Sorensen ordination three dimensions were selected (Fig. 4b shows the two axes explaining the most variance), the stress was 16.4, the instability was 0.0008, and the cumulative proportion of variance explained by three axes was 0.74.

On the basis of the ordination we identified 20 out of the total of 130 bee species that were positively associated with extensive forest (Fig. 4a). Two of these species (*Lasioglossum nymphale* and *Chelostoma philadelphii*), however, were equally or more common in fragmented forest and anthropogenic habitats as in extensive forest, so we did not include them in our final list. Presumably their proximity to extensive forest sites in the ordination resulted from the inaccuracies involved in reducing multivariate data to two dimensions. The *G* tests identified nine species as significantly associated with extensive forest. The *G* test cannot identify species unique to forest because the test cannot be performed when one category is zero. Therefore, we added to this list the eight species unique to extensive forest. Of the resulting total of 17 species, 16 were also selected as forest associated by the ordination. The species that was selected only by the *G* test, *Augochlorella aurata*, was very abundant in extensive forest but was also abundant in agricultural fields, and we did not consider it forest associated. Our final list of 18 forest-associated species (see Supplementary Material) included 16 species identified by both methods, plus an additional 2 species identified by NMS alone. They were probably not significant in the *G* test due to small sample sizes.

Compared with the other 112 species in the study, the 18 forest-associated species were no more likely to be oligolectic (*G* test; likelihood $\chi^2 = 0.30$, $p > 0.75$) or to require wood for nesting (*G* test; likelihood $\chi^2 = 0.21$, $p > 0.75$).

Table 3. Wilcoxon test analyses of bee abundance by local habitat type for species groups predicted to be extinction prone.

Species group	df	χ^2	p	Order of habitat type
Oligolectic	2	3.08	0.21	forest > agriculture > suburban/urban
Wood nesting	2	7.14	0.03	forest > suburban/urban > agriculture
Small body size	2	18.7	<0.0001	agriculture > suburban/urban > forest
Medium body size*	2	11.7	0.003	agriculture > suburban/urban > forest
Large body size	2	2.8	0.25	agriculture > suburban/urban > forest

*We did not have a prediction for medium-sized bees, but they are included for comparative purposes.

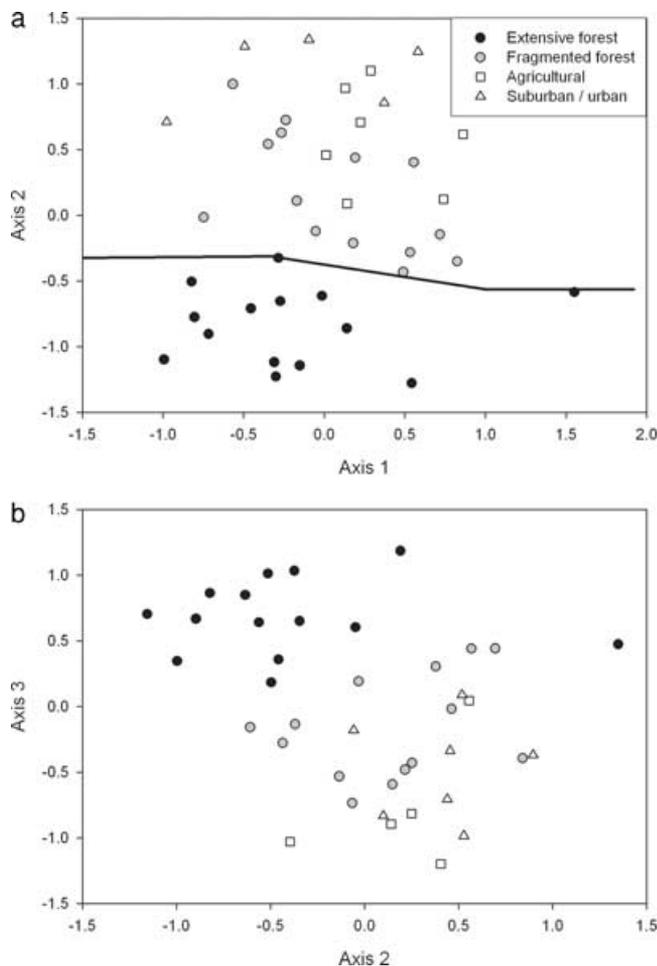


Figure 4. Nonmetric multidimensional scaling ordination of study sites according to bee species composition: (a) Bray-Curtis ordination, which separates sites according to both species composition and absolute abundance (when all 130 bee species were plotted on this same graph, the species falling below the black line were considered “forest associated”; see text for exceptions) and (b) relative Sorensen ordination, which separates sites according to proportional species composition only.

Discussion

Wild bee abundance and species richness were negatively, not positively, associated with the extent of forest cover in the surrounding landscape (Fig. 2). This effect was significant at all spatial scales we investigated, although it was strongest at a scale of a 1600 m radius, which is within the range of scales most explanatory in previous studies of wild bees' response to landscape cover (Steffan-Dewenter et al. 2001; Steffan-Dewenter et al. 2002; Kremen et al. 2004). Of the different types of human land use in the surrounding landscape, agriculture, and low-density development both had strong pos-

itive effects. A parallel result occurred in comparisons among local habitat types. Agricultural fields and suburban and urban developments supported a significantly greater abundance of bees than did extensive forest, and there was a similar but nonsignificant trend for species richness. In a pilot study done at 20 different study sites in 2002, we found broadly similar results: bee abundance and species richness were significantly greater in agricultural as opposed to natural or suburban habitats (R.W., unpublished data).

Species with particular traits, such as habitat specialization, limited mobility, or small or large body size, may be especially sensitive to habitat loss (McKinney 1997), and we therefore examined these species groups separately. In particular, floral and nest-site specialization correlates with extinction risk in invertebrates (Thomas & Morris 1995; Koh & Sodhi 2004), and large-bodied bees may be especially sensitive to habitat loss (Cane et al. 2006). Conversely, body size is positively associated with mobility in bees (Greenleaf 2005), which leads to the contrasting prediction that small-bodied bees, being less mobile, might be particularly sensitive to the loss of natural habitat. When we analyzed oligolectic bees and bees of different body size classes separately, however, we still found negative associations, although not always significant ones, with forest habitat at both the landscape and the local scales. For obligate wood nesters, we found a significant negative association at the landscape scale but a significant positive association at the local scale. This suggests that wood for nest sites is not limiting over the range of variation examined in the landscape-scale study (25–100% forest cover, with all local sites being situated in forest), but that it may become limiting once forests are removed completely.

Measures of species composition suggested that extensive forest contains some characteristic species and species found in deforested areas. Species accumulation curves indicated that extensive forest contained fewer unique species than agricultural fields, although the uncertainty on this analysis was large (Fig. 3b). Fragmented forest sites also had more unique species than extensive forest: 14 species were found exclusively in extensive forest (14 sites), compared with 44 species found exclusively in fragmented forest (14 sites). Nevertheless, ordination clearly separated the extensive forest bee communities from both the fragmented forest and the anthropogenic habitats, both in terms of absolute and relative abundance of each bee species (Fig. 4).

We expected bee abundance and species richness to be negatively associated with land use, as others have found (e.g., Aizen & Feinsinger 1994; Kremen et al. 2002; Kremen et al. 2004). There are several possible explanations for why our findings differed from our initial expectations. First, different bee species may occupy different successional stages in a disturbed landscape, making total species richness higher than in less-disturbed landscapes

(Chesson & Huntly 1997). Bee species richness may be maximized at an intermediate level of human disturbance, with negative effects only occurring when natural land cover falls below some threshold. In support of this idea we found a positive association with human disturbance in a system with a relatively high proportion (25–99%) of forest cover, whereas Steffan-Dewenter et al. (2002) found a negative association in a system where seminatural land cover ranged from <1% to 28%. Kremen et al. (2002, 2004), however, found negative effects of human land use across a gradient of 0–80% natural land cover.

Second, the type of ecosystem studied, and the floral resources available there, may determine how bees are affected by human land use. Kremen et al. (2002, 2004) worked in a Mediterranean ecosystem in California, which, along with the southwestern deserts, is the most species-rich region in North America for bees (Michener 1979). In contrast, forested eastern North America is thought to support roughly 4% as many bee species per unit area (Moldenke 1979). In the German landscapes studied by Steffan-Dewenter et al. (2002) the seminatural habitats assumed to be suitable for bees included grazed grasslands, orchards, and gardens, all of which would have been classified as agriculture or development in our study. These semi-natural habitats provide abundant floral resources. This contrasts with our forest-heath system, where bloom in the forest peaks in the spring and is limited from midsummer on. Even in the spring, however, forests had lower bee abundance than most other habitat types (R.W., unpublished data).

Third, in forested regions many bees may have been originally associated with natural disturbances and may now be able to use areas disturbed by humans. Klemm (1996) argues that in central Europe, anthropogenic disturbance has replaced river floodplain disturbance in creating early successional habitats used by many bee species. Similar positive associations with human disturbance occur with bumble bees in grasslands (Carvell 2002) and stingless and solitary bees in tropical forests (Eltz et al. 2002; Klein et al. 2002). In a tropical study that included both bees and wasps, agricultural habitats had the greatest abundance of insects, but forests had slightly greater species richness (Tylianakis et al. 2005). In an agricultural landscape in Germany, bumble bees are positively associated with land cover by select blooming crops but not by seminatural habitat (Westphal et al. 2003). There is also increasing evidence that many bees respond positively to the disturbance caused by fire (Potts et al. 2003). This is relevant to our study because the forested heath habitat in our study system probably experienced more frequent, natural burning prior to fire suppression by humans (Windisch 1999). Therefore, it is possible that fire control in our system has decreased bee abundance and species richness within the extensive forested habitats below their historical levels. This possibility remains speculative, however, because our study was not designed to

investigate bees' response to fire history; rather, fire history was a variable we attempted to control.

In contrast to our overall results, 18 of the 130 bee species in our study were positively associated with extensive forest habitat (see Supplementary Material). The forest-associated bees were not more likely to be oligoleptic or to require wood for nesting compared with non-forest-associated species. Although only three of these species are oligoleges of ericaceous plants, roughly one-third use ericaceous plants frequently, which may explain their association with the heath habitat. For the other 112 bee species, our results provide grounds for cautious optimism about the persistence of the most important group of pollinators in at least one human-dominated ecosystem.

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Supplementary Material

The abundance of each species in each habitat type is available in conjunction with the on-line version of this article from <http://www.blackwellsynergy.com> (Appendix S1).

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Appendix S1: List of bee species collected, with their abundance by habitat type. The 18 species that were positively associated with extensive forest based on ordination analysis are indicated with an X. The 27 specimens that could not be identified to species are not listed here; these were used in analyses of abundance, but not analyses of species richness.

Family	Species	Extensive forest (14 sites)	Fragmented forest (14 sites)	Suburban and urban developments (7 sites)	Agricultural fields (5 sites)	Forest-associated?
Halictidae	<i>Agapostemon sericeus</i>	0	1	2	0	
Halictidae	<i>Agapostemon splendens</i>	3	1	1	6	
Halictidae	<i>Agapostemon texanus</i>	0	3	2	12	
Halictidae	<i>Agapostemon virescens</i>	0	54	26	57	
Andrenidae	<i>Andrena arabis</i>	0	0	0	1	
Andrenidae	<i>Andrena atlantica</i>	1	10	11	1	
Andrenidae	<i>Andrena banksi</i>	0	6	4	0	
Andrenidae	<i>Andrena barbara</i>	0	0	0	3	
Andrenidae	<i>Andrena barbilabris</i>	0	0	3	0	

Andrenidae	<i>Andrena bradleyi</i>	18	1	0	0	X
Andrenidae	<i>Andrena carlini</i>	3	5	1	5	
Andrenidae	<i>Andrena carolina</i>	5	11	1	0	
Andrenidae	<i>Andrena cornelli</i>	1	6	0	0	
Andrenidae	<i>Andrena cressonii</i>	1	1	0	2	
Andrenidae	<i>Andrena erigeniae</i>	0	1	0	0	
Andrenidae	<i>Andrena fenningeri</i>	1	1	0	0	
Andrenidae	<i>Andrena hilaris</i>	1	0	0	2	
Andrenidae	<i>Andrena imitatrix</i>	2	2	2	2	
Andrenidae	<i>Andrena krigiana</i>	0	0	1	0	
Andrenidae	<i>Andrena</i> <i>melanochroa</i>	0	6	0	0	
Andrenidae	<i>Andrena miserabilis</i>	3	5	2	6	
Andrenidae	<i>Andrena nasonii</i>	0	0	0	1	
Andrenidae	<i>Andrena perplexa</i>	0	0	1	2	
Andrenidae	<i>Andrena vicina</i>	7	12	2	0	
Andrenidae	<i>Andrena wilkella</i>	1	3	12	28	
Megachilidae	<i>Anthidiellum notatum</i> <i>notatum</i>	0	2	0	0	
Megachilidae	<i>Anthidium</i> <i>oblongatum</i>	0	1	0	0	
Halictidae	<i>Augochlora pura</i> <i>pura</i>	1	8	4	0	

Halictidae	<i>Augochlorella aurata</i>	65	4	1	34	
Halictidae	<i>Augochloropsis metallica</i>	2	0	0	0	X
Apidae	<i>Bombus bimaculatus</i>	16	10	4	5	
Apidae	<i>Bombus citrinus</i>	6	5	0	0	
Apidae	<i>Bombus fervidus</i>	0	0	0	13	
Apidae	<i>Bombus griseocollis</i>	1	3	2	6	
Apidae	<i>Bombus impatiens</i>	5	9	6	8	
Apidae	<i>Bombus perplexus</i>	3	8	1	1	
Apidae	<i>Bombus vagans</i>	5	12	1	0	
Andrenidae	<i>Calliopsis andreniformis</i>	5	54	6	2	
Apidae	<i>Ceratina calcarata / dupla</i>	8	56	18	61	
Apidae	<i>Ceratina strenua</i>	3	42	17	50	
Megachilidae	<i>Chelostoma philadelphi</i>	1	3	0	0	
Megachilidae	<i>Coelioxys immaculata</i>	0	2	0	0	
Megachilidae	<i>Coelioxys rufitarsis</i>	0	1	0	0	
Megachilidae	<i>Coelioxys sayi</i>	0	2	0	0	
Colletidae	<i>Colletes bradleyi</i>	1	0	0	0	X
Colletidae	<i>Colletes inaequalis</i>	15	2	1	1	X

Colletidae	<i>Colletes thoracicus</i>	3	4	3	0	
Colletidae	<i>Colletes validus</i>	16	4	0	0	X
Apidae	<i>Eucera hamata</i>	0	0	0	62	
Apidae	<i>Habropoda laboriosa</i>	50	14	4	0	X
Halictidae	<i>Halictus confusus</i>	0	20	19	11	
Halictidae	<i>Halictus ligatus</i>	1	43	19	86	
Halictidae	<i>Halictus parallelus</i>	0	1	0	1	
Halictidae	<i>Halictus rubicundus</i>	0	1	0	1	
Apidae	<i>Holcopasites calliopsidis</i>	0	1	0	1	
Megachilidae	<i>Hoplitis pilosifrons</i>	0	0	0	1	
Megachilidae	<i>Hoplitis producta producta</i>	0	1	1	2	
Megachilidae	<i>Hoplitis spoliata</i>	0	2	0	1	
Megachilidae	<i>Hoplitis truncata</i>	3	1	1	1	
Colletidae	<i>Hylaeus affinis</i>	0	4	1	0	
Colletidae	<i>Hylaeus modestus modestus</i>	0	3	0	0	
Colletidae	<i>Hylaeus sparsus</i>	0	0	1	0	
Halictidae	<i>Lasioglossum abanci</i>	1	1	0	0	
Halictidae	<i>Lasioglossum acuminatum</i>	2	1	0	0	X
Halictidae	<i>Lasioglossum</i>	7	22	33	18	

	<i>admirandum</i>				
Halictidae	<i>Lasioglossum bruneri</i>	5	14	8	0
Halictidae	<i>Lasioglossum</i>	0	2	0	0
	<i>coeruleum</i>				
Halictidae	<i>Lasioglossum</i>	0	1	0	2
	<i>coreopsis</i>				
Halictidae	<i>Lasioglossum</i>	0	3	0	0
	<i>coriaceum</i>				
Halictidae	<i>Lasioglossum</i>	1	6	0	0
	<i>cressonii</i>				
Halictidae	<i>Lasioglossum</i>	6	8	3	0
	<i>fuscipenne</i>				
Halictidae	<i>Lasioglossum</i>	1	97	5	0
	<i>illinoense</i>				
Halictidae	<i>Lasioglossum</i>	0	24	8	2
	<i>imitatum</i>				
Halictidae	<i>Lasioglossum</i>	1	3	1	0
	<i>laevissimum</i>				
Halictidae	<i>Lasioglossum</i>	3	6	11	6
	<i>leucozonium</i>				
Halictidae	<i>Lasioglossum</i>	1	1	0	0
	<i>macoupinense</i>				
Halictidae	<i>Lasioglossum</i>	2	0	2	1

	<i>nelumbonis</i>					
Halictidae	<i>Lasioglossum</i>	0	0	0	7	
	<i>nymphaearum</i>					
Halictidae	<i>Lasioglossum</i>	1	1	0	0	
	<i>nymphale</i>					
Halictidae	<i>Lasioglossum</i>	57	7	1	0	X
	<i>oblongum</i>					
Halictidae	<i>Lasioglossum</i>	0	4	0	0	
	<i>oenotherae</i>					
Halictidae	<i>Lasioglossum</i>	11	26	13	7	
	<i>pectorale</i>					
Halictidae	<i>Lasioglossum</i>	2	60	27	105	
	<i>pilosum</i>					
Halictidae	<i>Lasioglossum</i>	2	2	2	1	
	<i>rohweri</i>					
Halictidae	<i>Lasioglossum sopinci</i>	1	3	1	0	
Halictidae	<i>Lasioglossum</i>	6	62	33	17	
	<i>tegulare</i>					
Halictidae	<i>Lasioglossum</i>	0	2	6	3	
	<i>versatum</i>					
Halictidae	<i>Lasioglossum</i>	1	14	1	1	
	<i>vierecki</i>					
Halictidae	<i>Lasioglossum</i>	0	8	2	0	

<i>zephyrum</i>						
Megachilidae	<i>Megachile addenda</i>	0	4	0	0	
Megachilidae	<i>Megachile</i>	0	3	0	0	
<i>campanulae</i>						
Megachilidae	<i>Megachile exilis</i>	0	8	0	0	
Megachilidae	<i>Megachile mendica</i>	0	2	1	2	
Megachilidae	<i>Megachile rotundata</i>	0	2	2	5	
Megachilidae	<i>Megachile texana</i>	0	3	2	1	
Apidae	<i>Melissodes druriella</i>	0	0	0	1	
Apidae	<i>Nomada articulata</i>	0	3	2	5	
Apidae	<i>Nomada australis</i>	0	6	1	0	
Apidae	<i>Nomada bella</i>	1	0	0	0	X
Apidae	<i>Nomada cressonii</i>	0	3	0	0	
Apidae	<i>Nomada imbricata</i>	0	1	0	0	
Apidae	<i>Nomada lepida</i>	2	3	0	1	
Apidae	<i>Nomada luteola</i>	0	2	1	0	
Apidae	<i>Nomada luteoloides</i>	2	0	0	0	X
Apidae	<i>Nomada maculata</i>	10	11	0	0	
Apidae	<i>Nomada ovata</i>	2	4	0	0	
Apidae	<i>Nomada pygmaea</i>	1	7	0	4	
Apidae	<i>Nomada sayi</i>	1	0	0	0	X
Apidae	<i>Nomada valida</i>	6	0	1	0	X
Megachilidae	<i>Osmia atriventris</i>	2	8	1	7	

Megachilidae	<i>Osmia georgica</i>	1	3	0	0	
Megachilidae	<i>Osmia inspergens</i>	1	0	0	0	X
Megachilidae	<i>Osmia pumila</i>	14	45	1	6	
Megachilidae	<i>Osmia sandhouseae</i>	1	0	0	0	X
Megachilidae	<i>Osmia virga</i>	16	9	0	0	X
Andrenidae	<i>Panurginus potentillae</i>	0	16	0	1	
Apidae	<i>Peponapis pruinosa</i>	1	0	1	0	
Andrenidae	<i>Perdita bradleyi</i>	1	0	0	0	X
Andrenidae	<i>Perdita octomaculata</i>	0	0	0	1	
Apidae	<i>Ptilothrix bombiformis</i>	0	0	21	0	
Halictidae	<i>Sphecodes aroniae</i>	6	16	0	0	
Halictidae	<i>Sphecodes atlantis</i>	0	1	0	2	
Halictidae	<i>Sphecodes carolinus</i>	0	1	1	0	
Halictidae	<i>Sphecodes confertus</i>	10	0	1	0	X
Halictidae	<i>Sphecodes davisii</i>	0	1	0	0	
Halictidae	<i>Sphecodes johnsonii</i>	0	1	0	0	
Halictidae	<i>Sphecodes pimpinellae</i>	0	1	0	0	
Halictidae	<i>Sphecodes stygius</i>	3	0	0	1	X
Megachilidae	<i>Stelis labiata</i>	0	1	0	0	
Apidae	<i>Xylocopa virginica</i>	2	11	9	1	