

Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient

RALPH GRUNDEL,^{1,3} ROBERT P. JEAN,² KRYSALYNN J. FROHNAPPLE,¹ GARY A. GLOWACKI,^{1,4} PETER E. SCOTT,²
AND NOEL B. PAVLOVIC¹

¹U.S. Geological Survey, Great Lakes Science Center, 1100 North Mineral Springs Road, Porter, Indiana 46304 USA

²Department of Biology, Indiana State University, Terre Haute, Indiana 47809 USA

Abstract. Given bees' central effect on vegetation communities, it is important to understand how and why bee distributions vary across ecological gradients. We examined how plant community composition, plant diversity, nesting suitability, canopy cover, land use, and fire history affected bee distribution across an open-forest gradient in northwest Indiana, USA, a gradient similar to the historic Midwest United States landscape mosaic. When considered with the other predictors, plant community composition was not a significant predictor of bee community composition. Bee abundance was negatively related to canopy cover and positively to recent fire frequency, bee richness was positively related to plant richness and abundance of potential nesting resources, and bee community composition was significantly related to plant richness, soil characteristics potentially related to nesting suitability, and canopy cover. Thus, bee abundance was predicted by a different set of environmental characteristics than was bee species richness, and bee community composition was predicted, in large part, by a combination of the significant predictors of bee abundance and richness. Differences in bee community composition along the woody vegetation gradient were correlated with relative abundance of oligolectic, or diet specialist, bees. Because oligolectes were rarer than diet generalists and were associated with open habitats, their populations may be especially affected by degradation of open habitats.

More habitat-specialist bees were documented for open and forest/scrub habitats than for savanna/woodland habitats, consistent with bees responding to habitats of intermediate woody vegetation density, such as savannas, as ecotones rather than as distinct habitat types. Similarity of bee community composition, similarity of bee abundance, and similarity of bee richness between sites were not significantly related to proximity of sites to each other. Nestedness analysis indicated that species composition in species-poor sites was not merely a subset of species composition at richer sites. The lack of significant proximity or nestedness effects suggests that factors at a small spatial scale strongly influence bees' use of sites. The findings indicate that patterns of plant diversity, nesting resource availability, recent fire, and habitat shading, present at the scale of a few hundred meters, are key determinants of bee community patterns in the mosaic open-savanna-forest landscape.

Key words: *bee abundance; bee diversity; fire; habitat specialists; Indiana Dunes; land use; nestedness; nesting resources; oak savanna; oligolectic; plant richness; species density.*

INTRODUCTION

Examining differences in community composition across biotic and abiotic gradients is a basic approach to understanding forces shaping animal community composition. For bees, such studies are not yet common (Goulson et al. 2008), especially studies that evaluate the relative effect of different environmental gradients on bee community composition (Williams et al. 2001, Potts et al. 2003b, Brosi et al. 2007, Schaffers et al. 2008). This is an important deficiency because of the central

ecosystem function bees have as pollinators, because of concern over possible declines in bee populations, because of uncertainties concerning the role of land use change on bee populations, and because of the possible need to supplement pollination of agricultural crops done by commercial bee colonies with increased pollination by native bees (National Research Council 2007).

Many factors can affect bee distribution. Pollen and nectar rewards attract bees to sites (Potts et al. 2004, Larsson and Franzen 2007). Disturbance, in the form of fire (Potts et al. 2003a, Campbell et al. 2007), agricultural development (Williams and Kremen 2007), and residential development and deforestation (Russell et al. 2005, Winfree et al. 2007) can affect bee community composition, as can habitat structure by changing availability of nesting resources (Potts et al. 2005, Cane et al. 2007) and by modifying the thermoregulatory environment

Manuscript received 29 September 2008; revised 21 October 2009; accepted 9 November 2009. Corresponding Editor (ad hoc): J. A. Powell.

³ E-mail: rgrundel@usgs.gov

⁴ Present address: Lake County Forest Preserves, 32492 North Almond Road, Grayslake, Illinois 60030 USA.

(Cane and Tepedino 2001). As we seek to quantify the status of pollinators worldwide (National Research Council 2007), we will benefit from understanding the relative strength of these factors in making landscapes suitable for robust native bee communities. This is important because, despite advances in quantifying pollinator status (Biesmeijer et al. 2006), it is not yet clear how pervasive pollinator declines might be and what might cause declines to occur at one location while robust populations persist at another (Ghazoul 2005, Steffan-Dewenter et al. 2005).

To gain perspective on factors influencing bee distribution, we evaluated the relative importance of floral and nesting resources, habitat structure, land use, and fire history on the abundance, diversity, and composition of the upland bee community in northwest Indiana, USA. Northwest Indiana, though changed by more than a century of widespread industrial, agricultural, and residential development, still retains remnants of an historic landscape of diverse habitats including the 6000-ha Indiana Dunes National Lakeshore, one of the floristically richest national parks in the United States (Pavlovic and Bowles 1996) and the site of seminal studies on ecological succession and the niche (Cowles 1899, Shelford 1913). Historically, much of the Midwest United States could be viewed as an ecological transition zone between grassland dominated biomes to the west and forested biomes to the east (Anderson and Bowles 1999). Today, the grassland-to-forest gradient persists in northwest Indiana natural areas not only because of northwest Indiana's placement in this transition zone (Cowles 1899, Cole 2001), but also due to alterations in the structure of savannas and grasslands related to human disturbances ranging from soil disruption (Wilcox et al. 2005) to fire suppression. Fire regulation by humans has decreased fire frequency compared to historic norms at many northwest Indiana locations, causing replacement of open grasslands, forblands, and savannas with woodlands and forests (Henderson and Long 1984, Cole and Taylor 1995). The resulting landscape today represents a mosaic of habitats ranging from open grasslands and forblands to black oak (*Quercus velutina*) savannas to forests (Grundel and Pavlovic 2007). A recent global survey suggested that temperate grasslands and savannas might be the most threatened major terrestrial biome worldwide (Hoekstra et al. 2005) and that the status of this biome in central North America might be especially poor in global perspective (Nuzzo 1986). Because of this decline, and subsequent interest in savanna restoration, we also examine whether bees experience savannas as a distinct habitat type or more as an ecotone between open and forested habitats.

METHODS

Study area

To understand bee community variation across a range of habitat, landscape, and fire regimes, we

surveyed bees at 25 sites along an open-forest gradient in northwest Indiana. Study sites were situated from 0.8 to 80 km inland from the southern shore of Lake Michigan, averaged 1.8 ± 3.4 km (mean \pm SD; range 0.08–16.9 km) between nearest neighbor sites, and were located at Indiana Dunes National Lakeshore (41°38' N, 87°09' W; $n = 17$ sites; 6000 ha total park area), Tefft Savanna Nature Preserve and Jasper-Pulaski Fish and Wildlife Area (41°10' N, 86°58' W; $n = 7$ sites; 3250 ha), and Hoosier Prairie Nature Preserve (41°31' N, 87°27' W; $n = 1$ site; 225 ha) (Grundel and Pavlovic 2007, Haney et al. 2008). Based on average densiometer-measured canopy cover percent and shrub density across sites, we classified sites as open (<20% canopy cover), savanna (20–50%), woodland (50–90%), scrub (>1000 woody stems 2.5–10 cm diameter at breast height [dbh]/ha), or forest (>90% canopy cover and >300 woody stems >10 cm dbh/ha) (Grundel and Pavlovic 2007). Five replicates of each habitat type were represented within the 25 sites. Within each site, bees were surveyed along a single 270-m transect by netting and along the central 160 m of the transect by capturing in colored pan traps (Roulston et al. 2007). For pan trapping, we placed out nine triplets of 178-mL plastic bowls at each site, with one bowl of the triplet painted fluorescent blue, one fluorescent yellow, and one left as the original white. Bees landing in the bowls drowned in soapy water filling the bowls. Along the transect, bowl triplets were separated by 20 m and, within a triplet, bowls were separated by 5 m. During a survey day, bowls were left out for a mean duration of 303 ± 28 minutes between 09:30 to 14:30. For netting surveys, we slowly walked the transect line, examining nearby plants for bees and capturing any bees observed during an average of 88 ± 28 minutes per survey. At each site, bowl surveys were carried out approximately once every 25 days from 30 May to 17 September 2003 and from 14 April to 8 July 2004, for a total of seven surveys. At each site, netting was also carried out approximately once every 25 days from 14 April 2004 to 9 September 2004, again for seven cycles. The first three netting cycles were carried out concurrently with bowl surveys.

Bees were identified to species, and their nesting habitat (soil, wood, open, or cavity nester or parasitic; see Plate 1), tongue length (short, long), sociality (social, solitary, parasitic), and degree of feeding specialization (oligolectic, polylectic) were determined from observations and published sources (Mitchell 1960, Michener 2000, Giles and Ascher 2006, National Research Council 2007). Oligolectic bees are specialist pollinators that collect pollen from only a few plant genera while polylectic species collect pollen from a wider variety of plant species (Cane and Sipes 2006). We used the published sources to obtain trait information at the lowest taxonomic level for which definitive information was available that could be applied to a given species. Most entries in the species by trait matrix were filled from those published sources and from field observa-

tions. Approximately 4% of the entries were still empty at this point. For these we assigned the trait based on the status of closely related species. Tongue lengths were assigned based on taxonomy, with Apidae and Megachilidae classified as long tongued and with Andrenidae, Colletidae, Halictidae, and Mellitidae classified as short tongued. Because honeybees (*Apis mellifera*) are often associated with commercial colonies, we eliminated them from most analyses.

Habitat assessment

At the 25 sites, we measured variables representing possible bee nesting resources, floral resources, habitat structure, and fire history, as well as landscape composition surrounding the site. Suitability for nesting can be related to soil and soil cover characteristics so we determined percent of organic content, sand, silt, and clay in the soil for a composite of 20 15 cm deep soil samples per site. Also, across six 0.05-ha plots surrounding each transect (mean distance from plot to transect centroid = 158 ± 108 m), we determined average percentage of bare ground, litter, and dead woody vegetation lying on the ground and number of small (2.5–10 cm dbh) and large (>10 cm dbh) dead and live woody stems present and we measured canopy cover. Methods in Grundel and Pavlovic (2007) describe how these variables were measured at these 25 sites. Dead woody vegetation can be an important bee nesting resource (Potts et al. 2005). Cover of dead woody vegetation lying on the ground and density of small and large dead stems were standardized by dividing by their respective maxima across all 25 sites. These three standardized measures were then averaged to yield an index of dead woody vegetation abundance. To assess possible effects of fire on bee communities, we used available fire maps to calculate fire frequencies within 50 m of each transect over 15 years and over two years prior to the start of the bee surveys.

To describe the community of plants in flower at the time of bee surveys, we counted stems bearing flowers for each plant species observed within a 5 m radius of the center of each of the nine triplets of bowls, during each netting or bowl survey. From those data, we calculated total number of plant species in flower, and total number of stems with open flowers (scaled to per ha), per transect on a given day. We then calculated the mean number of plant species in flower and number of stems with open flowers across all survey days for a site. We also partitioned the mean number of stems into percentage of stems that were from annual or perennial plants and native or nonnative plants (Swink and Wilhelm 1994, USDA NRCS 2007).

We used 30 m resolution data from the 2001 National Land Cover Database (NLCD) to calculate percentage of the landscape within 800 m of the transect line that was classified as agriculture (pasture, hay, cultivated crops mainly corn or soybeans) or that was under human development (all levels from open to high

intensity development) (database *available online*).⁵ Before calculations, NLCD data were verified and corrected by reference to local high-resolution aerial photographs (obtained from the National Park Service; data *available online*).⁶ We selected the surrounding distance of 800 m, in part, because greater distances would reach out to Lake Michigan at some of our sites, and, in part, because surrounding landscape composition within this distance has been shown to affect bee community composition (Steffan-Dewenter et al. 2002, Winfree et al. 2007, Ricketts et al. 2008).

Data analysis

To test for possible similarity of bee abundance, species richness, or community composition between sites, as a function of physical distance between sites, we used the Mantel test and Mantel's asymptotic approximation significance test (McCune and Mefford 2006). Differences in bee species richness and species density (Gotelli and Colwell 2001) across habitats were assessed by comparison of sample-based rarefaction curves (Colwell 2009), based on the 70 samples taken per habitat ([7 netting + 7 bowl samples per site] \times 5 replicate sites per habitat). Among the five habitats, we evaluated whether the number of species captured at a common number of individual bee captures (species richness) or at a common number of samples (species density) was significantly different between pairs of habitats using a *z*-test, as recommended by Schenker and Gentleman (2001). Since multiple *z* tests were carried out, *P* values were adjusted for multiple testing using the Benjamini-Hochberg procedure (Benjamini and Hochberg 1995, R Development Core Team 2009). Species density represents the number of species expected per sample. If we assume the sampling scheme collects bees from a similar area around each transect, species density will represent the number of species per unit area. Extrapolated estimates of the total number of bee species expected across the study sites, or within a site, were made using six nonparametric estimators (ACE, ICE, Chao1 and 2, and Jackknife1 and 2) (Colwell 2009) and using the individual bee as the sample unit. Selection, and presentation, of these six estimators, and use of the individual bee as the sample unit, followed recommendations of Hortal et al. (2006) who evaluated performance of many sample units and available estimators. Therefore, we present the average and range of the six estimates as indicators of the expected number of bee species.

Chao's abundance-based Sørensen similarity index was used to measure compositional similarity between sites (Colwell 2009). Nestedness analysis (Brualdi and Sanderson 1999, McCune and Mefford 2006) determined whether bee species present in less rich sites tended to be a subset of species present at richer sites. A

⁵ (http://www.mrlc.gov/mrlc2k_nlcd.asp)

⁶ (<http://www.indiana.edu/~gisdata/>)

measure of nestedness (N_a , using subscript a for the degree of nestedness of site-by-species incidence matrix \mathbf{A}) was calculated as was the probability that N_a deviated from random expectation (Jonsson 2001).

We used principal curves to ordinate sites by their bee composition (De'ath 1999, Walsh 2005). Principal curves are smooth one-dimensional curves that are fit to sites' locations in a multidimensional space defined by abundances of the different species occurring across the sites. Sites' locations on the principal curve represent their relative location on an underlying ecological gradient that helps determine the composition of the bee community. Bee counts used for the ordination were square root transformed, to decrease the relative emphasis on the most abundant species in the ordination, and were then standardized to a proportion of the site's (square-root transformed) count total so that species' relative abundances within a site were actually analyzed. We used regression analysis to evaluate the ability of several classes of variables to explain the underlying ecological gradient described by the principal curve analysis.

We also used principal curves to ordinate sites by their composition of plant species in flower at the time of surveys. As with bees, counts of stems of plants in flower were square root transformed and then standardized to a proportion of each site's (square-root transformed) stem count total. The principal curve site scores calculated for the 25 sites were used as an independent variable in regressions examining potential predictors of bee richness, abundance, percent of oligolectic individuals, and bee community composition. Bee community composition was represented by the principal curve site scores. Therefore, for the regression analysis of factors affecting bee community composition, we were asking how well the ecological gradient that helped determine plant community composition was related to the ecological gradient that helped determine bee community composition.

We used the multiple response permutation procedure (MRPP), based on relative Sørensen distance, to test whether bee community species composition (counts square root transformed) differed significantly among habitats (McCune and Mefford 2006).

Bayesian model averaged (BMA) multiple regression models (Wintle et al. 2003, Raftery et al. 2009) were calculated to examine possible relationships between environmental variables as predictors and bee or plant community characteristics as responses. BMA averages parameter estimates from many potential regression models and thereby helps to account for uncertainties in model selection. Results from BMA are a series of expected values of regression coefficients and a posterior probability (%) that the predictor coefficient is not zero. Higher posterior probability values indicate variables that are more likely to be statistically significant predictors of the response. For predictors with posterior probability > 90%, we calculated regression coefficients

and, using hierarchical partitioning (Mac Nally 2002, Walsh and Mac Nally 2008), we calculated the amount of the dependent variable's variance that could be attributed independently to each predictor, as a means of ranking the relative importance of the predictors in explaining variation in the dependent variable.

Co-correspondence analysis is an ordination technique that allows a direct comparison of the community composition of two communities sampled at the same set of sites (ter Braak and Schaffers 2004, Simpson 2005). Predictive co-correspondence analysis was used to examine whether composition of the plant community (square-root transformed) significantly predicted composition of the bee community (square-root transformed). Cross-validated fits evaluated how well the matrix of sites by flowering plant abundances predicted the response matrix of sites by bee abundances. The cross-validated fits measured with co-correspondence analysis tend to be lower than other measures of fit and can even be highly negative (ter Braak and Schaffers 2004). However, fits greater than zero indicated prediction of the bee community by the plant community that was significantly better than chance. Co-correspondence analysis produces a number of ordination axes describing the predictor community (plants) and the response community (bees) and relates the two sets of ordination axes using partial least squares (PLS) regression (ter Braak and Schaffers 2004). We selected the number of axes that maximized the cross-validated fit.

Indicator species analysis (Dufrêne and Legendre 1997, McCune and Mefford 2006) evaluated the degree to which a bee species was regularly and exclusively observed in only one habitat type. Perfect indication of a species for a habitat (indicator value = 100) occurred if a species was observed in every site of a given habitat type and if the species was never observed in another habitat type. Lower indicator values (minimum = 0) signaled that the species was distributed across multiple habitats. Significance of the indicator value for the habitat with the highest indicator value was evaluated by a Monte Carlo test comparing the observed indicator value for a habitat type to indicator values calculated after randomly reassigning observed species abundances among sites.

Unless otherwise indicated, errors following mean values represent standard deviations (SD). For significant ($P < 0.05$) analysis of variance (ANOVA), differences among groups was evaluated using Tukey's B multiple comparisons test (SPSS 2004). As required, data were examined to determine if the assumption of homogeneity of variance was upheld and transformations applied as necessary if the assumption was violated.

RESULTS

Bee community and habitat characteristics

Habitats differed significantly (ANOVA, $P < 0.05$) in dead wood abundance, litter cover, richness of plants in

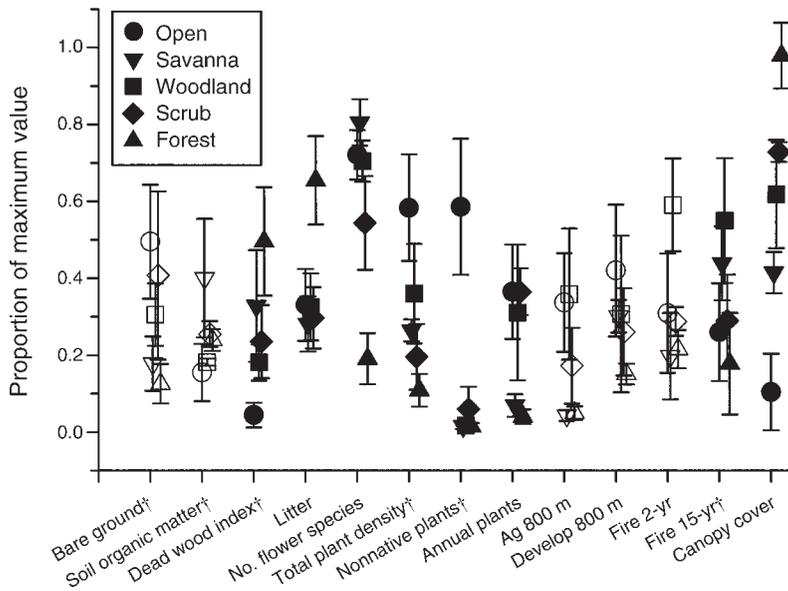


FIG. 1. Characteristics of 25 northwest Indiana, USA, sites at which bees were collected, displayed by habitat type. For each site, each variable was scaled by dividing by its maximum value among the 25 sites. Mean values of the scaled variables are shown by habitat type. Maximum and minimum observed raw (unscaled) values and units are listed in Table 1, as are *P* values for an ANOVA examining differences in values among the five habitats. Variables with solid symbols have significant differences ($P < 0.05$) among habitats. Daggers indicate that the scaled variable was square-root transformed for ANOVA. However, untransformed mean values are shown in the figure (\pm SE). The abbreviations Ag and Develop indicate the percentage of land that was agricultural or developed, respectively, within 800 m of site.

flower, which was significantly lower in forests than in any of the other habitats, density of plant stems bearing flowers, percentages of nonnative and annual plants, number of fires over prior 15 years, and percent canopy cover (Fig. 1, Table 1). Cover of bare ground, percentage of organic matter in the soil, percentage of land in agriculture, or percentage developed, within a radius of 800 m of the survey transect, and number of fires over the prior 2 years did not differ significantly among habitats.

We collected 4631 bees from at least 170 species and 35 genera (68% of individuals collected by bowls, 32% by netting), including 161 *A. mellifera* specimens that were removed from analyses, except as noted. Forty-six specimens were not identifiable to species and were omitted from species-based analyses. Based on the remaining 4585 bees, including *A. mellifera*, we estimated that 229 species (averaged across results from six non-parametric richness estimators, range 219–248) occurred across the 25 sites. This suggests that about 74% of existing species were captured. All six North American bee families were represented, Halictidae (63 species), Apidae (37), Megachilidae (31), Andrenidae (27), Colletidae (11), and Melittidae (1).

Phenological differences in bee abundance occurred across habitats. Most bees in forested sites were captured early in the spring, before tree leaf out, while bees were captured more evenly throughout the spring and summer in the other habitats (Fig. 2).

Nestedness of bee species among sites ($N_a = -0.66$) was not significant ($P = 0.25$). Of the five habitats, four differed significantly from the fifth, forest, in bee

composition and three of the habitats, open, savanna, and woodland, did not differ significantly from each other ($P_{adjusted} > 0.05$; Table 2).

Bee community compositional similarity between sites did not vary significantly as a function of physical distance between sites (standardized Mantel statistic $r = 0.10$, $P = 0.27$, based on relative Sørensen distance).

TABLE 1. Characteristics of 25 northwest Indiana, USA, sites at which bees were collected.

Characteristic	Maximum	Minimum	<i>P</i>
Bare ground (%)	23	0	0.38
Soil organic matter (%)	6.6	0.3	0.14
Dead wood index	0.7	0	0.02
Litter (%)	82	0	0.04
Number of flower species	10.6	0.5	0.001
Total plant density (stems/ha)	13 293	222	0.01
Nonnative plants (%)	29	0	0.001
Annual plants (%)	77	0	0.04
Ag 800 m (%)†	32	0	0.29
Develop 800 m (%)†	60	3.3	0.51
Fire 2-yr (number of fires/2 yr)	2	0	0.24
Fire 15-yr (number of fires/15 yr)	7.9	0.02	0.04
Canopy cover (%)	100	0.05	<0.001

Notes: Values are maximum and minimum observed raw (unscaled) values for characteristics shown in Fig. 1. Also shown are *P* values for an ANOVA examining differences in values among the five habitats shown in Fig. 1 (open, savanna, woodland, scrub, and forest).

† Percentage of land that was agricultural (Ag) or developed (Develop) within 800 m of the site.

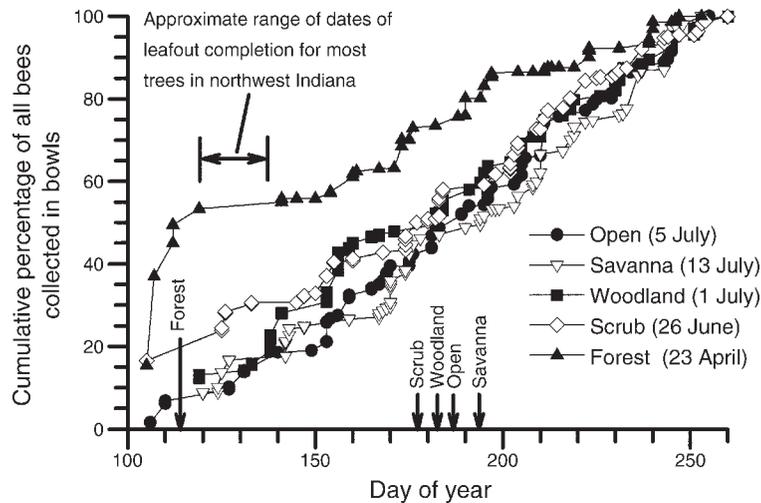


FIG. 2. Cumulative percentage of all bees collected in bowls, within a habitat type, as a function of day of the year (1 January = 1) in northwest Indiana. Arrows indicate the date at which 50% of all bees within a habitat type had been collected. Corresponding calendar dates are indicated in the key to symbols. The two-sided arrow indicates the approximate date range by which most trees typically have leafed out in northwest Indiana.

Chao's abundance-based Sørensen index of similarity between sites was not significantly correlated (Pearson correlation, $P > 0.05$) with distance between sites, even if compared pairs of sites were limited to those separated by <20 , <10 , <5 , or <1 km. Similarity between sites in number of bee species captured per site, and in total number of bees captured per site, also did not vary significantly as a function of distance between sites (standardized Mantel $r = 0.07$, $P = 0.42$ for number of bee species and $r = 0.02$, $P = 0.78$ for number of bees).

The five habitats differed significantly in number of bees captured per site (Fig. 3a) (ANOVA, $F_{4,20} = 7.8$, $P = 0.0006$), did not differ significantly in number of species captured per site (ANOVA, $F_{4,20} = 1.6$, $P = 0.22$; Fig. 3b, hatched bars), but did differ significantly in species captured per daily sample at a site (ANOVA, $F_{4,345} = 9.9$, $P < 0.0001$; Fig. 3b, gray bars, numbers shown in figure multiplied by 10). Total number of species captured increased from forest ($n = 60$ species) to scrub (81) to woodland (84) to savanna (92) to open (99). However, when rarefaction curves were compared across habitats, at a common number of bees caught ($n = 350$ bees per site), the number of species expected per individual caught was not significantly different among habitats (z test, Fig. 3c). Species density, or species per sample, however, was significantly lower in forests than in other habitats (at $n = 70$ samples per habitat; Fig. 3d). Based on samples from bowls only, the mean values of Chao's abundance-based Sørensen similarity index among samples within a habitat type ($n = 35$ samples per habitat) were significantly different among habitat types (ANOVA, arcsine-square-root transformed, $F_{4,2970} = 87.7$, $P < 0.001$), with the lowest similarity occurring among forest samples (Fig. 3e).

The percentage of soil nesting bees captured in open habitats ($80\% \pm 5\%$) was significantly higher (ANOVA,

$F_{4,20} = 5.2$, $P = 0.005$) than in all other habitats except woodlands (Fig. 3f). The percentage of soil nesting bees at a site was significantly negatively correlated ($r = -0.44$, $P = 0.03$) with the percentage of organic matter in the soil, but was not significantly correlated with percentage of silt ($r = 0.02$, $P = 0.91$), clay ($r = 0.004$, $P = 0.99$), or sand ($r = -0.02$, $P = 0.94$) in the soil. Soil silt percentage among sites was the most variable soil component (coefficient of variation = 117%), while clay (86%) and organic (75%) were less, and sand was least (10%), with most sites being quite sandy ($90.8\% \pm 9.4\%$

TABLE 2. Significance of compositional differences in bee communities between habitat types, based on multiple response permutation procedure (MRPP) analysis from 25 northwest Indiana, USA, sites.

Habitat 1	Habitat 2	A^\dagger	P^\ddagger
Open	savanna	0.07	0.059
Open	woodland	0.05	0.117
Open	scrub	0.15	0.022
Open	forest	0.15	0.017
Savanna	woodland	0.01	0.343
Savanna	scrub	0.003	0.407
Savanna	forest	0.07	0.039
Woodland	scrub	0.05	0.041
Woodland	forest	0.15	0.013
Scrub	forest	0.09	0.013
Overall		0.12	0.00003

$^\dagger A$ is chance-corrected within-group agreement, a measure of effect size describing within-habitat homogeneity compared to random expectation (McCune and Mefford 2006). Increasing A corresponds to increasing similarity in bee composition among sites within a habitat compared to similarity expected after randomly assigning sites to habitats.

‡ Probability, adjusted for multiple comparisons (Benjamini and Hochberg 1995), that species composition differs between habitat pairs. $P < 0.05$ indicates that differences in bee community composition between habitats were statistically significant. The analysis is based on relative Sørensen distance measure and square-root transformed bee abundances.

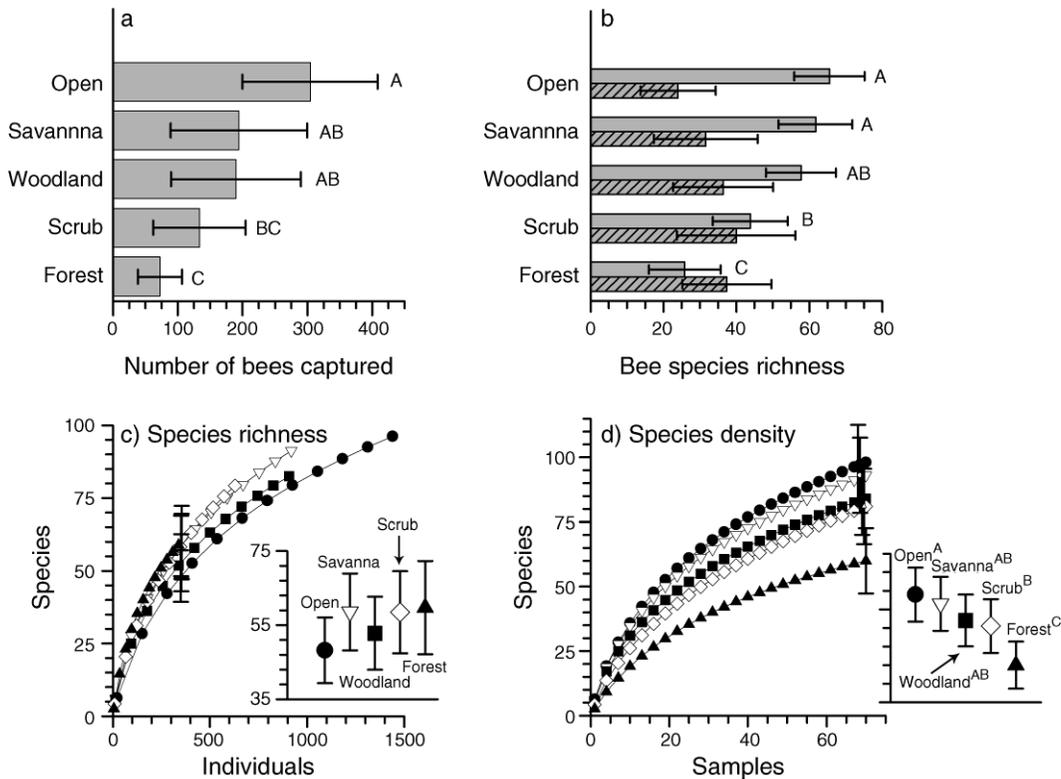


FIG. 3. Bees captured in northwest Indiana, as a function of habitat type. (a) Total number of bees captured per site; (b) total number of bee species captured per site (hatched bars) and per sample (plain gray bar; values are $\times 10$). (c, d) Rarefaction curves (Gotelli and Colwell 2001) showing (c) species richness and (d) species density. (e) Mean values of Chao's abundance-based Sørensen similarity index for bees taken in bowl samples within a habitat. (f, g) Mean percentages of individuals per site that are (f) soil nesters and (g) solitary nesters; (h) mean percentage of all species per site that are oligolectic. Error bars are 95% confidence intervals in all panels. Habitats with the same letter next to error bars are not significantly different [$P > 0.05$; z test for panels (c) and (d), ANOVA with Tukey's B multiple comparisons test for all others]. No significant differences occurred in panel (b) for species per site or in panel (c). Untransformed data are shown, but multiple comparisons results for panels (a) and (h) are based on natural-log transformation, panel (f) on square-root reflex, and panel (e) on arcsine-square-root transformations. In panels (c) and (d) the number of species per habitat were compared, across habitats, at a common number of individuals [$n = 350$ in panel (c)] and samples [$n = 70$ in panel (d)]. Insets in panels (c) and (d) show expanded views of habitats' 95% confidence intervals at 350 individuals in panel (c) and at 70 samples in panel (d) with significant differences based on z -test. In insets, x -axes are arbitrary.

by weight). The percentage of solitary nesters among all bee specimens differed significantly among habitats (ANOVA, $F_{4,20} = 4.7$, $P = 0.008$) with the lowest mean percentage of solitary nesters occurring in open habitat and the highest in scrub (Fig. 3g). Open sites also had the highest mean percentage of social nesters ($77\% \pm 5\%$, ANOVA, $F_{4,20} = 5.5$, $P = 0.004$) and lowest mean percentage of wood nesters ($10\% \pm 3\%$, ANOVA, $F_{4,20} = 3.4$, $P = 0.03$) of any of the habitat types.

Of the 170 species identified (including *A. mellifera*), 49 (29%) were singletons (captured only once) and 20 (12%) were doubletons (captured twice). Fifty percent of oligolectic species were singletons compared to 25% of polylectic species, a significant difference ($\chi^2 = 7.2$, $df = 1$, $P = 0.007$). The number of individuals caught per oligolectic species present at a site (3.1 ± 3.3) was also significantly lower than per polylectic species (5.6 ± 2.2 ; paired $t = -3.5$, $P = 0.002$, $n = 21$ sites with oligolectic species).

The percentage of oligolectic species at a site was significantly positively correlated with abundance of native ($r = 0.45$, $P = 0.02$, $n = 25$) and perennial plants ($r = 0.42$, $P = 0.04$) but not with abundance of nonnative ($r = 0.27$, $P = 0.20$) or annual plants ($r = 0.29$, $P = 0.16$). However, when examined in the context of other environmental predictors, sites' plant richness was not a significant predictor of the percentage of oligolectic individuals among the specimens captured at a site (Table 3). Instead, increasing percentage of oligolectic individuals at a site was best predicted by increasing percent of developed land in the surrounding matrix, 2-year fire frequency, litter cover, and by decreasing canopy cover. Percentage of developed land accounted for the most variation in the percentage of oligolectic individuals at a site. The most commonly captured oligolectes were *Perdita gerhardi*, *P. swenki*, and *P. bequaerti* (Andrenidae). During netting surveys, these species were captured on *Monarda punctata*

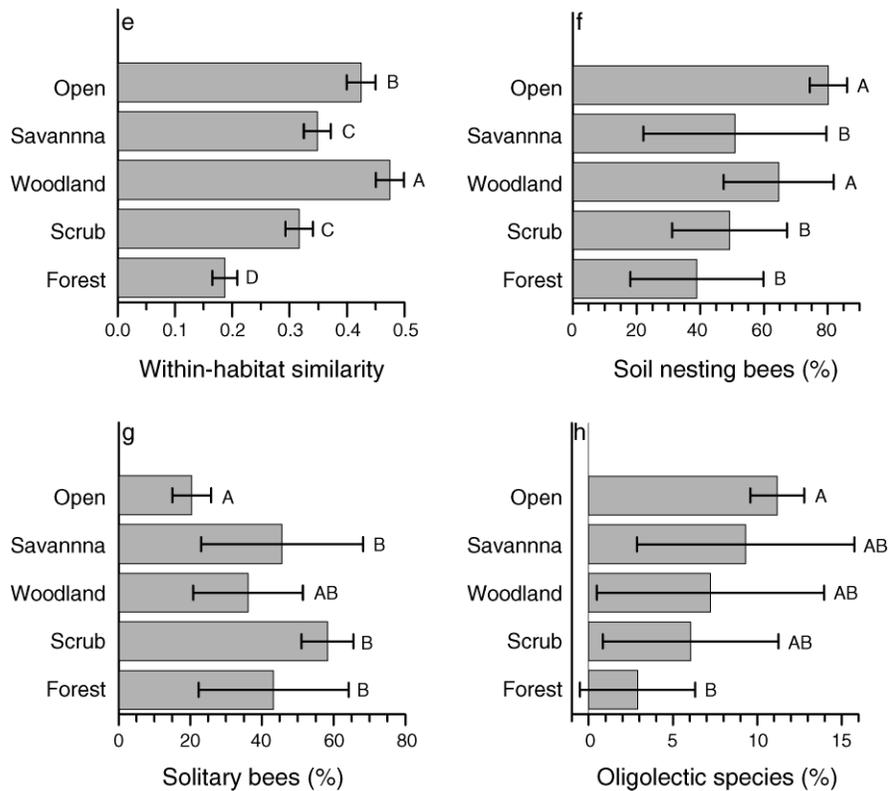


FIG. 3. Continued.

(Lamiaceae), and *Solidago* spp., *Helianthus* spp. and *Coreopsis* spp. in the Asteraceae.

Indicator value (IV) scores were calculated based on three sets of habitats (open, savanna plus woodland, and scrub plus forest). Among species with at least 10 captures (57 of 170 species, including *A. mellifera*), we found 15 significant ($P < 0.05$) indicator species, eight with highest IV scores for open, five for scrub/forest, and two for savanna/woodland. Species that were significant indicators of a habitat included *P. gerhardi* (IV = 79), *Lasioglossum pilosum* (78), *A. mellifera* (72), *Hoplitis pilosifrons* (66), *L. vierecki* (62), *Hylaeus mesillae* (57), *L. ellisiae* (49), *Osmia michiganensis* (39) for open habitats, *L. foveolatum* (57), *Megachile addenda* (55) for savanna/woodland habitats, and *Andrena carlini* (60), *L. macoupinense* (57), *L. coeruleum* (57), *Nomada maculata* (55), and *Andrena vicina* (51) for scrub/forest habitats.

Predictors of bee abundance, richness, and community composition

Significant predictors of bee abundance differed from significant predictors of bee richness (Table 3). Canopy cover and 2-year fire frequency had the highest posterior probabilities (>90%) of being significant predictors of bee abundance with canopy cover accounting for more variance in bee abundance. Amount of dead woody vegetation and species richness of plants in flower best

predicted bee richness with dead woody vegetation accounting for more of the bee richness variance. Total flowering stems was not a significant predictor of overall bee abundance. Human disturbance, in the form of agricultural or urban development occurring with 800 m of sites, was not a significant predictor of bee abundance or richness.

Bee species density and fire frequency over 15 years, but not bee species richness, were significant positive predictors of plant species richness with bee species density accounting for the more of the variance in plant richness (Table 3).

Principal curve ordination of the bee community accounted for 50% of the species variation among sites. Mean ordination scores for savanna sites (0.29 ± 0.17) were intermediate to open sites (0.09 ± 0.16) and forest (0.88 ± 0.17). With respect to categories of bees, the ordination scores were most highly correlated with percentages of soil nesters ($r = -0.69$, $P = 0.0001$), oligolectic/polylectic bees ($r = -0.65$, $P = 0.0005$ for oligolectic), wood nesters ($r = 0.62$, $P = 0.001$), social species ($r = -0.52$, $P = 0.008$), and solitary nesters ($r = 0.49$, $P = 0.013$). Correlations with proportion of parasitic species, open, and cavity nesters, and short/long tongued species were not significant ($P > 0.05$).

Co-correspondence analysis indicated that the community of plants in flower (cross-validated fit = 0.7%, two significant axes) was a significant solo predictor of

TABLE 3. Ability of nesting and plant resources, landscape matrix, fire frequency, and habitat structure to predict bee community richness, abundance, and composition, percentage of oligolectic individuals in the captured sample, and flowering plant richness at 25 northwest Indiana, USA, sites.

Predictor	Bee		
	Richness	Abundance	Community composition
Intercept	100 (0 ± 0.12)	100 (0 ± 0.14)	100 (0 ± 0.05)
Nesting resources			
Bare ground†	55	2	8
Soil organic matter†	5	26	100 (0.40 ± 0.05) (0.16)
Dead woody vegetation†	100 (0.79 ± 0.15) (0.54)	16	45
Litter	8	3	54
Plant community			
Flowering plant richness	92 (0.20 ± 0.18) (0.04)	18	100 (−0.70 ± 0.06) (0.52)
Total flowering stems†	4	4	6
Nonnative plants†,‡	52	37	12
Annual plants‡	17	25	31
Plant composition§	10	12	56
Landscape			
Agriculture within 800 m	16	16	8
Development within 800 m	7	3	24
Fire frequency			
2-year	12	94 (0.37 ± 0.17) (0.13)	81
15-year†	18	6	21
Habitat structure			
Canopy cover	74	100 (−0.67 ± 0.14) (0.40)	100 (0.29 ± 0.06) (0.27)
Bee diversity			
Species richness	na	na	na
Species density	na	na	na
Model fit#	0.58	0.53	0.94
Model fit probability	3×10^{-5}	9×10^{-5}	2×10^{-13}

Notes: Table entries are the posterior probability percentages that the predictor is in the model. For predictors with posterior probability percentage >90%, the value in the first parentheses after the posterior probability percentage is the expected standardized regression coefficient (±SD) from BMA multiple regression analysis, followed, in the second parentheses, by the amount of variance in the dependent variable independently accounted for by the predictor, based on hierarchical partitioning. Bee richness was determined by averaging richness estimates from six nonparametric estimators (ACE, ICE, Chao1, Chao2, Jackknife1, Jackknife2) taken at a sample size of 40 individuals at each site, equal to the smallest sample size among the sites. Bee abundance is the number of bees captured at a site. Bee community composition is site scores based on bee community composition (counts for each bee species were square-root transformed and converted to percentage of site totals) from principal curve ordination. Percentage oligolectic is the percentage of oligolectic individuals among all individuals captured at a site. Flowering plant richness is the number of plant species observed in flower during bee surveys at a site; na, not applicable.

† Predictors are square-root transformed.

‡ Percentage of stems.

§ Site scores based on plant community composition (stem counts for each plant species in flower were square-root transformed and converted to percentage of site totals) from principal curve ordination.

Bee species richness determined from rarefaction curves at a common number of individuals per site ($n = 40$) and density at a common number of samples per site ($n = 14$).

R^2 (adjusted) for multiple regression including only predictors with posterior probability percentage >90%.

bee community composition. Principal curve ordination of the community of plants in flower accounted for 65% of the species variation among sites. However, these plant ordination scores were not a significant predictor (posterior probability = 56%) of the bee community ordination scores when considered in conjunction with other possible predictors. Rather, flowering plant richness, canopy cover, and organic content of soil were significant predictors (posterior probability > 90%) of the bee ordination scores, with plant richness accounting for more of the variance in the bee ordination scores (Table 3). Because ordination scores accounted for 50% of bee compositional variation across sites and these three predictors, plant richness, canopy cover, and soil

organic content, accounted for 94% of the variation in the ordination scores, together these three predictors accounted for about 47% of the compositional variation of the bee community.

DISCUSSION

Different suites of environmental characteristics are associated with different aspects of bee distribution in northwest Indiana. Bee richness is positively associated with plant richness and likely nesting resources, bee abundance is negatively associated with canopy cover and positively with recent fire frequency, and bee community composition is associated with plant richness, canopy cover, and soil characteristics that likely

TABLE 3. Extended.

Percentage oligolectic	Flowering plant richness
100 (0 ± 0.12)	100 (0 ± 0.10)
5	21
8	7
9	66
100 (0.53 ± 0.15) (0.06)	39
7	na
12	na
5	10
15	4
35	10
38	77
100 (0.62 ± 0.13) (0.29)	70
100 (0.58 ± 0.14) (0.12)	79
5	100 (0.26 ± 0.21) (0.18)
100 (-0.52 ± 0.14) (0.19)	40
na	66
na	100 (0.54 ± 0.17) (0.29)
0.66	0.47
3×10^{-5}	4×10^{-4}

affect nesting suitability. Therefore, maintenance of a diverse and abundant bee fauna requires consideration of a suite of local and landscape characteristics and management actions (Kremen et al. 2007).

Effects of habitat on bee distribution

How well does the composition of a plant community predict the composition of a bee community? Schaffers et al. (2008: Appendix E) noted that because bees are flower visitors, we might expect bee community composition to be more strongly related to plant community composition than would be true for many other arthropods. However, in a study of arthropod-plant relationships in the Netherlands, they found a lower fit between plant community composition and bee community composition than between plant community composition and composition of spider, grasshopper, beetle, planthopper, or hoverfly communities. Cross-validated fits, from the co-correspondence model between plant species and bee species, in their study (2.4%) and in our study (0.7%) were significant, similar, and low, suggesting a gross relationship between total bee and plant community compositions that is significant but relatively weak. When considered along with flowering plant richness, flower abundance, nesting resources, fire history, landscape context, and canopy cover, plant community composition, represented by

plant community ordination scores, was not a significant predictor of bee abundance, bee richness, or bee community composition, with bee community composition represented by bee community ordination scores (Table 3). Together, these results suggest that plant community composition is a relatively weak predictor of bee community composition. Potential reasons for the lack of a stronger gross relationship between bee and plant communities include, first, that plant species retention in pollination networks can be relatively tolerant to loss of pollinators, due to pollination redundancy (Mommott et al. 2004). Second, limited subsets of plants may be required to retain specialist bee species (Goulson et al. 2005). Finally, plant species differ in quality as pollen or nectar resources (Potts et al. 2003b). In northwest Indiana, flower abundance was not a significant predictor of bee abundance, as was also observed in Wyoming short grass prairies (Tepedino and Stanton 1981), suggesting unequal importance of different plants as foraging resources. These three trends indicate that a given plant species is often linked to many bee species, that specialized plant-bee linkages are often uncommon, diffusing the ability of specific plants to predict the presence of specific bees, and that plant species are not visited in proportion to their abundance. Together these trends weaken the ability of the overall plant community to predict the overall bee community.

Canopy cover was a correlate of several aspects of bee distribution. We documented a moderately rich bee community (cf. Williams et al. 2001) with at least 170 observed and 229 estimated bee species, similar to the 169 species collected in a 1930–1931 survey of natural areas within 120 km of Chicago, including surveys in the Indiana Dunes (Pearson 1933). The number of bees collected declined with increasing canopy cover among sites, as also occurred in southern U.S. forests (Campbell et al. 2007) and in the New Jersey Pinelands (Winfrey et al. 2007). Nonetheless, significant differences in species richness (species recorded at a common number of bees collected) were not observed among the canopy cover-defined habitats. Species density (species recorded at a common number of samples collected), however, declined with increased canopy cover (Fig. 3d). This, in part, reflects decreasing bee abundance per sample with increasing canopy cover. Because there are more individuals caught per sample in more open habitats, there are likely to be more species present in a sample from a more open habitat, even if the overall number of species is similar across habitats (Fig. 3b, c). Additionally, species turnover in time, and intra-habitat structural variability, contribute to these patterns in bee abundance and species density. For example, bee collections among northwest Indiana forest sites were significantly less similar across time and space (Fig. 3e) than were samples collected in other habitats, likely related to differences in bee use of forests at different stages of tree leafout (Fig. 2). Greater dissimilarity among forest samples suggests that greater

bee compositional changes in space and time in forests than in open habitats may contribute to similar species richness in open and forest habitats over time, even though species density is greater in open habitats.

About 11% of bee species visiting open sites were oligoleges compared to 2% of forest bee species, indicating that open habitat bee species were more likely to have relatively narrow diets, which characterizes oligoleges, than were forest bee species. Differences in distribution of oligolectic bees were important to differences in bee communities along the woody vegetation gradient because compositional separation of sites was relatively highly correlated with percentage of oligolectic bees. As in other published bee surveys (Williams et al. 2001), many species were infrequently captured: 29% of species were captured only once. The percentage of oligolectic species captured only once was considerably higher than the percentage of polylectic bee species captured only once, and the number of individuals captured per oligolectic species was significantly lower than for polylectic species, indicating that oligolectic bees were often rarer than polylectic bees. Thus, oligolectic species were more likely to find their forage plants in open areas than in forests, contributing to observed differences in bee community composition along the woody vegetation gradient. That oligoleges were often rarer than polylectic species is consistent with the finding that rare bumble bee species (*Bombus* spp.) tend to have narrower diet breadth than more abundant bumble bees (Goulson and Darvill 2004).

Although oligolectic species were more likely to be found in open areas (Fig. 3h), and the percentage of oligolectic individuals among bees collected at a site declined with increased canopy cover (Table 3), flowering plant richness, which was highest in savannas and open areas (Fig. 1, Table 1), was not a significant predictor of oligolectic percentage. Oligolege percentage increased, however, as nearby land cover in residential and industrial land use increased. Native plants, including *Monarda punctata* and several plant species in the Asteraceae that were preferred by common oligoleges in this study, are associated with disturbed sandy soils (Swink and Wilhelm 1994) that often occur in residential areas in sandy, northwest Indiana. Recent fire was also a positive predictor of percentage of oligolectic individuals captured at a site (Table 3), also suggesting a possible positive link between disturbance and relative oligolege abundance or a negative link between fire and relative polylectic bee abundance. Being floral specialists, it might be expected that oligoleges would be particularly sensitive to loss of native habitats and, indeed, the percentage of oligolectic individuals was positively correlated with percentage of native flowering plant stems among all plant stems in flower. However, the observed positive relationship between oligolectic percentage and amount of surrounding developed land suggests that some oligoleges can benefit, relative to polylectic species, from aspects of

land development, such as the presence of disturbance dependent plants, or at least not be as negatively affected by land development. Positive relationships between human development of landscapes and abundance of particular bee taxa have been observed in temperate and tropical landscapes (Carvell 2002, Klein et al. 2002, Russell et al. 2005). Oligoleges were not significantly more abundant in native pine-oak heath than in areas of human development in southern New Jersey (Winfree et al. 2007), again emphasizing that even bees dependent on a few plant species are often retained in developed areas.

Potts et al. (2003b) and Schaffers et al. (2008: Appendix E) suggested that bees often move transiently over large areas, potentially resulting in weakened linkages between bee communities and local plant and nesting resources. However, in northwest Indiana much of the variation (about 47%) in bee community composition across sites was explainable by environmental conditions within ~150 m of the bee survey transects, specifically by soil organic matter, canopy cover, and flowering plant richness near the transect. Distance between sites was not a significant predictor of how similar sites were in bee composition, abundance, or richness, as Winfree et al. (2007) also observed for richness and abundance of pine barren bees in southern New Jersey. Wilson et al. (2009) found low bee community similarity between closely situated plots in Utah. Potts et al. (2003b), on the other hand, did find a significant negative relationship between bee community similarity and intersite distance in northern Israel. Bee assemblages were not compositionally nested across northwest Indiana sites, suggesting that species composition of less rich sites was not merely a subset of species occurring at richer sites. The lack of significant proximity or nestedness effects, plus the adequate prediction of bee community structure by conditions within 150 m of survey routes, is consistent with bee community composition being significantly shaped by factors acting at a spatial scale of a few hundred meters, even if movement patterns or rarity of many bee species might weaken the link between local resources and bee populations.

Although native bee occurrence in agricultural fields is often influenced by the surrounding landscape (Kremen et al. 2002, Holzschuh et al. 2007, Ockinger and Smith 2007), the amount of farmland within 800 m of northwest Indiana natural area sites, conversely, did not significantly predict the composition, abundance, or diversity of bees in the natural areas, unlike the observed effect of industrial and residential development. In contrast to our findings, Winfree et al. (2007) documented significant positive effects of surrounding agricultural development on bee richness in the sandy, pine-oak New Jersey pine barrens ecosystem, an area similar to the Indiana Dunes in soil and woody vegetation structure. Such disparities between studies should not be surprising. For instance, agriculture



PLATE 1. *Trachusa zebrata* (Cresson, 1872) (family Megachilidae) is a sand-nesting bee species. A single individual was captured foraging on *Helianthus divaricatus* L. (woodland sunflower; family Asteraceae) at Indiana Dunes National Lakeshore during a study of bee distribution across a woody vegetation gradient in sandy habitats of northwest Indiana (USA). Photo credit: K. J. Frohnapple.

around the New Jersey pine barrens is dominated by bee pollinated crops, especially cranberries and blueberries (Sohl 2003), while corn and soybeans, typically self- or wind-pollinated, dominate northwest Indiana agriculture, even though corn and soybean fields often support weeds that flower prior to tilling and that can be productive pollen and nectar sources for native bees (Dailey and Scott 2006).

Cross-locale comparisons of factors affecting bee distribution are important for improving management for bee conservation but are not yet frequently available (Potts et al. 2003b). A broad comparison of habitat effects is possible, however, between results from this study and from a study of native bees of a north Israel pine woodland by Potts et al. (2003b). While bee abundance in northwest Indiana was most strongly related to canopy cover and recent fire history, in north Israel it was most strongly related to fire history, grazing intensity, and nesting resources. Bee richness was significantly related to plant richness and nesting resources in Indiana and in Israel to plant richness, especially richness of annuals, and fire history. Bee community composition was related to plant richness, soil characteristics, a potential measure of nesting suitability, and canopy cover in Indiana. In Israel, it was related to floral resources and fire history (Potts et al. 2003b), with bee richness peaking approximately two years after fires (Potts et al. 2003a), much as bee abundance in northwest Indiana was positively related to fire frequency over the prior two years (Table 3). Therefore, the arrays of factors predicting bee community characteristics in Israel and Indiana were similar though not identical. For instance, the Mediterranean

flora is often dominated by annuals (Potts et al. 2006) while the Midwest U.S. flora is dominated by perennials (Leach and Givnish 1999). This was reflected in a positive relationship between diversity of bees and annual plants in Israel and an increase in percentage of northwest Indiana oligolectic bee species with an increase in perennial plant abundance.

In both Israel and Indiana, potential nesting resources were important predictors of bee distribution. In Indiana open habitats, where dead wood was relatively sparse (Fig. 1, Table 1), the percentage of soil nesters was higher and the percentage of solitary nesters, which often nest in dead wood, and the percentage of wood nesters, were lower than in any of the other habitat types (Fig. 3). Soil organic content, potentially related to a site's nesting suitability, was a significant predictor of bee community composition and bee richness increased as availability of dead woody vegetation increased. Assuming that bees nesting in an area will frequently forage nearby, these results are consistent with findings that nesting resources are critical determinants of bee community composition, perhaps only exceeded by foraging resources in importance (Potts et al. 2005), and that soil composition and dead wood availability are among the chief factors determining a site's suitability for bee nesting (Vaughan and Black 2007).

Implications for bee, plant, and habitat conservation

Differences in the effects of canopy cover on bee abundance, bee species richness, and bee species density have implications for conservation of bee and plant communities and restoration of landscapes. Although areas may often be prioritized for conservation based on

species richness, or managed to increase species richness, as we have seen here species density often exhibits different patterns across environmental gradients than does species richness (cf. Fig. 3c, d) (Gotelli and Colwell 2001). Species density may be as important as species richness when setting goals for managing pollination networks. For example, increasing bee species density and increasing long term fire frequency, but not bee species richness, were significantly associated with increasing flowering plant richness.

The association observed in northwest Indiana among bee species rareness, narrow diet breadth, and use of plant rich areas by diet specialists (oligoleges) raises concern over a potential link between degradation of plant rich grasslands and savannas, such as has occurred with fire suppression in northwest Indiana (Cole and Taylor 1995), and decline of diet specialists, as has been observed with bumble bees following the loss of flower-rich grasslands in the UK (Goulson et al. 2005).

Savanna and grassland coverage has decreased almost to the point of complete loss across central North America over the past 200 years (Auclair 1976, Nuzzo 1986, Hoekstra et al. 2005). However, when considering the priority for savanna restoration in light of this decline, questions persist as to whether savannas are better considered to be distinct or ecotonal habitats (Temple 1998). The five northwest Indiana habitats were defined by a canopy cover based classification scheme often used to delimit habitats in the Midwest United States (Anderson et al. 1999). However, only two, or maybe three, habitat classes with significantly different bee composition existed (Table 2), with bee composition in forests being significantly different than in other habitats. Ecotonal habitats are characterized by high species diversity relative to the habitats to which they are considered ecotonal and with there being relatively few species that occur almost exclusively in the ecotone (Temple 1998). Across the same areas surveyed for bees, we previously found that savanna bird communities were relatively species rich, intermediate in composition between, and significantly different from, communities in open and forest habitats, and there were few savanna specialist birds (Grundel and Pavlovic 2007). Bees exhibited a similar pattern in that savanna sites had a relatively high estimated bee richness and density (Fig. 3b–d), ordination scores indicated that savanna bee communities were intermediate in composition between bee communities in open and forest habitats, although these compositional differences between habitats were not always significant (Table 2), and few habitat specialists were documented for savanna-woodland habitats. The results suggest that savannas, in comparison to other habitats along the ecological gradient, are not necessarily statistically distinct habitats in bird or bee composition but are species rich and thereby potentially important for conservation.

Pollinator limitation of plant seed production is well known (Aizen and Harder 2007) and the potential for a

pollinator crisis is evident (National Research Council 2007) but whether we are in the midst of, or will face, a global pollinator crisis for native and agricultural plants is being debated (Ghazoul 2007, Klein et al. 2008). Even at this stage of study, however, it is apparent that composition of bee communities and the services bees provide will be, in the words of Kremen et al. (2007), highly contextual. In northwest Indiana, the effects of temporal context on bee communities were seen in differences in bee phenology across habitats and by the significant effect of recent fires on bee abundance. The effects of spatial context were seen in the positive relationship between developed land in the matrix and presence of oligolectic bees in nearby natural areas, by a lack of effect of agricultural development in the matrix on bee community composition, and by the important effect of small scale habitat characteristics on bee community composition. The effects of environmental context were seen in the importance of floral and nesting resources and canopy cover in the determination of bee distribution. Evaluating the consistency of the effects of each of these contextual elements, plus the effects of dispersal and larger scale geographic trends on bee distribution (Kremen et al. 2007), requires comparative studies of bee communities in different ecosystems. Understanding these effects will provide insight into the likelihood of pollinator deficiencies, the mechanisms of pollinator declines, and improvements in management for sustaining pollinators.

ACKNOWLEDGMENTS

We thank Jason Gibbs for assistance in bee identification, Sam Droege for assistance in bee identification and for providing sample bowls, and Jean Adams for statistical advice. Support for this project was provided by the USGS Grasslands Research Funding Initiative and by the National Park Service Inventory and Monitoring Network. Research was conducted with permission and assistance of the National Park Service and the Indiana Department of Natural Resources, Division of Nature Preserves. This article is Contribution 1564 of the USGS Great Lakes Science Center.

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