Bee (Hymenoptera: Apoidea: Anthophila) functional traits in relation to sampling methodology in a restored tallgrass prairie

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Abstract

Analysis of functional trait composition can provide insights into effects of habitat alteration on ecological functioning of particular taxa. However, assessments of functional trait composition may be affected by the sampling methodology used. We assessed functional trait composition of bees (Hymenoptera: Apoidea: Anthophila) collected using 4 sampling methods (elevated bowl traps, ground-level bowl traps, Malaise traps, and vane traps). Functional diversity, as measured by functional dispersion (mean distance between individual species and the community centroid in multidimensional trait space), did not vary among sampling methods. Fourth corner analysis revealed statistically greater representation of solitary species and above-ground nesting species than expected in ground-level bowl traps. Polylecty was strongly associated with Malaise traps. Body length was negatively associated with Malaise traps and positively associated with vane traps. Our results suggest that sampling of bee functional traits can be method-dependent, and this should be considered in assessments of functional trait composition.

Key Words: functional composition; lecty; trait diversity; trap bias

Resumen

El análisis de la composición del rasgo funcional puede proporcionar información sobre los efectos de la alteración del hábitat en el funcionamiento ecológico de ciertos taxones. Sin embargo, la evaluación de la composición del rasgo funcional puede verse afectado por la metodología de muestreo utilizado. Evaluamos la composición del rasgo funcional de las abejas (Hymenoptera: Apoidea: Anthophila) recolectadas utilizando 4 métodos de muestreo (trampas de cubetas elevadas, trampas de cubetas a nivel del suelo, trampas Malaise, y trampas en forma de una veleta). La diversidad funcional, medida por la dispersión funcional (distancia media entre las especies individuales y el centroide de la comunidad en el espacio de rasgo multidimensional), no varió entre los métodos de muestreo. El análisis de cuarto esquinas reveló una representación estadísticamente mayor de especies solitarias y especies de anidación sobre el suelo de lo esperado en trampas de cuencas a nivel del suelo. La polilectia fue fuertemente asociada con las trampas Malaise. La longitud del cuerpo se asoció negativamente con las trampas Malaise y se asoció positivamente con las trampas en forma de una veleta. Nuestros resultados sugieren que el muestreo de los rasgos funcionales de las abejas puede ser dependiente del método, y esto se debe considerar en las evaluaciones de la composición del rasgo funcional.

Palabras Clave: composición funcional; lectia; diversidad de rasgos; sesgo de trampa

Functional traits are characteristics of individuals that affect fitness, and can determine species persistence and contribution to ecosystem functioning, the processes that sustain ecosystems (Violle et al. 2007). Species diversity does not directly determine ecosystem functioning, but rather indirectly determines functioning through the cumulative contributions of traits present in these species (Cadotte et al. 2011). Loss of biodiversity may result in decline of ecological functioning (Hooper et al. 2012), particularly if these losses are concentrated in particular functional groups with similar ecological niches (Flynn et al. 2009). Whereas identification of important functional traits has progressed most rapidly for plants (Díaz et al. 2007), trait analyses also have played important roles in studies of certain animal taxa, including hover flies (Schweiger et al. 2007), ground beetles (Barber et al. 2017), birds (Newbold et al. 2013), fish (Pont et al. 2006), and bees (Moretti et al. 2009; Williams et al. 2010; Forrest et al. 2015; Blitzer et al. 2016; Bartomeus et al. 2018).

Bees play an ecologically essential role as pollinators, and functional diversity may increase the proportion of flowers pollinated, seed set, and other measures of pollination success. For instance, Blitzer et al. (2016) showed that bee functional group diversity (based on nesting habits, sociality, and body size) was associated with increased seed set, and decreased pollen limitation in commercial apple farms. Several studies also have suggested that bee species composition and associated functional traits respond to habitat alteration. Forrest et al. (2015) showed that farmland supports lower bee functional diversity than do natural habitats, and Moretti et al. (2009) found that bee functional composition shifted in response to fire in temperate forest. Functional traits have been shown to be useful as predictors of bee species responses to a variety of habitat alterations (Williams et al. 2010), although bee traits were weak and inconsistent predictors of response to variation in land use practices in 49 sites across 3 crop systems (watermelon, cranberry, and blueberry) in New Jersey and eastern Pennsylvania, USA (Bartomeus et al. 2018).

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A variety of sampling methods are available for assessing bee assemblages, including bowl traps (sometimes called "pan traps"), Malaise traps, and vane traps. Bowl traps used in bee sampling are usually plastic bowls, with blue, white, and yellow colors typically used. Bowl traps are generally placed on the ground in insect surveys, but are sometimes elevated to match surrounding vegetation (Leong & Thorp 1999; Hopwood 2008; Tuell & Isaacs 2009; Droege et al. 2010; Geroff et al. 2014; Shapiro et al. 2014). Both Malaise traps (Townes 1972; Bartholomew & Prowell 2005; Ngo et al. 2013; Geroff et al. 2014; McCravy et al. 2016; McCravy & Ruholl 2017) and vane traps (Stephen & Rao 2005; Kimoto et al. 2012; Geroff et al. 2014; Buchanan et al. 2017; McCravy & Ruholl 2017) are flight interception traps that also have been used effectively in collecting bees. There is evidence that elevated and ground-level bowl traps, Malaise traps, and vane traps vary in the abundance and species composition of bees collected (Geroff et al. 2014; Joshi et al. 2015). Because species richness and diversity are major foci in assessments of bee conservation status, it is important that such methodological variation be recognized. However, as with more traditional measures such as species richness and diversity, particular sampling methodologies may produce biased estimates of functional trait composition of bee communities as well. For instance, Gonzalez et al. (2016) found that bowl trap height can produce biased estimates of bee body size in unmanaged grass and wild carrot-dominated areas in northwestern Turkey, and bee body size and proportions of oligolectic and parasitic species varied with the sampling method in northwestern USA bunchgrass and forb-dominated prairie (Rhoades et al. 2017). There is evidence that eusocial bees are more attracted to blue and white bowl traps, whereas non-eusocial bees are more attracted to yellow (Sircom et al. 2018). In the desert southwestern USA, native bee species associated with creosote bush, *Larrea tridentata* (DC) Coville (Zygophyllaceae), were poorly represented in bowl traps compared to aerial netting (Cane et al. 2000). In Michigan and Pennsylvania, USA, apple and sour cherry orchards, blue vane traps collected an assemblage of largely non-crop visiting bees that was different from that collected via aerial netting on crop flowers (Gibbs et al. 2017b).

In this study, we compare the performance of 4 bee-sampling methods (elevated bowl traps, ground-level bowl traps, Malaise traps, and vane traps) with respect to 4 functional traits: body length (as a measure of body size), lecty, sociality, and nest location. Body size and lecty are associated with dispersal capabilities and foraging behavior in bees (Greenleaf et al. 2007), and these traits have been used to assess responses of bees to habitat changes. Nest location is also habitat-dependent and thus can be affected by habitat disturbance. Information on potential sampling bias associated with these traits could be important when considering the experimental design of studies aiming to assess bee communities using these functional traits.

Materials and Methods

This study was done in an approximately 12 ha restored tallgrass prairie at the Alice L. Kibbe Field Station (40.3660°N, 91.4070°W), Western Illinois University in Hancock County, Illinois, USA. As part of an assessment of bee sampling methods by Geroff et al. (2014), bees were collected from 9:00 AM to 6:00 PM on 6 d (based on weather conditions) during each of the 4 sampling periods in 2010: early Jun, mid-Jul, late Aug, and late Sep-early Oct. Four sampling methods were employed: bowl traps (elevated 1 m using wooden posts), bowl traps (ground level), Malaise traps, and vane traps. Bowl traps were 354 mL colored plastic bowls (Hallmark, Kansas City, Missouri, USA). Malaise traps were standard Townes-style (Sante Traps, Lexington, Kentucky, USA). Vane traps (SpringStar, Inc., Woodinville, Washington, USA) were suspended from shepherd hooks with the top of the collection jar 1 m above the ground. Traps were deployed in a transect of 20 plots, with 5 plots per trap type. Each plot consisted of 3 elevated bowl traps (1 each of blue, white, and yellow), or 3 ground-level bowl traps (1 each of blue, white, and yellow), or 1 Malaise trap, or 4 vane traps (2 each of blue and yellow). Within plots with multiple traps, traps were located 5 m apart, and plots were separated by 25 m. Trap types were randomly assigned to plots, and trap color positions were randomly assigned within plots. Geroff et al. (2014) provided further details on the study site and design.

Before analysis, males (10.1% of total captures) were excluded from the data set because of sex-related differences in body lengths, and because females are the primary foraging and nest-building sex. Three data matrices were constructed: (1) a main matrix, with bee species and their counts as columns, and plots as rows; (2) a second matrix, specifying a sampling method for each plot; and (3) a trait matrix, with traits as columns and bee species as rows. Four traits were used that reflect important aspects of bee ecology, behavior, and natural history, and for which information is widely available for most bee species in the literature: body length (a quantitative variable, expressed in mm), sociality (categorical: social or solitary), nest location (categorical: aboveground or belowground), and lecty (categorical: oligolectic or polylectic). Communal bees were classified as 'solitary,' so sociality is actually a measure of division of labor. Information on these traits was obtained from Mitchell (1960, 1962), LaBerge (1967, 1971, 1973, 1977, 1989), Bouseman and LaBerge (1979), Michener (2007), Gibbs (2010), and Gibbs et al. (2017a), or predicted based on phylogeny (Gibbs et al. 2012; Danforth et al. 2013). The mean value was used where a range was given for body length.

For each of the 4 sampling methods, functional dispersion, a measure of functional diversity, was calculated for each plot. Functional dispersion is the mean distance between individual species (weighted by relative abundances) and the community centroid in multidimensional trait space (Laliberté & Legendre 2010). Because the traits include categorical variables, the species X trait matrix was represented as a series of principal coordinate axes based on a Gower distance matrix, with correction for negative eigenvalues (Legendre & Anderson 1999). The Kruskal-Wallis test was performed to compare functional dispersion among sampling methods.

Fourth corner analysis was used to examine relationships between sampling methods and traits of the bee species collected. This analysis allows analysis of bivariate linear associations between quantitative and categorical species traits and explanatory variables (sampling method), based on the relative abundances of the species that link these traits and variables. For pairs of categorical variables, fourth corner analysis calculates a log-likelihood ratio *G*-test. For mixed pairs of categorical and quantitative variables, fourth corner analysis produces an *R*-value (equivalent to a correlation value) and *D*-value. The *D*-value is a measure of the degree of clustering of the quantitative variable within levels of the categorical variable (Peck 2016).

For fourth corner analysis, species with fewer than 3 non-zero cells were excluded to reduce sparsity, and values for each species were then relativized by the maximum value to reduce heterogeneity and the effect of dominant species. To eliminate decimal values for analysis of categorical variables, these values were then transformed via multiplication by 100 and rounded to the nearest whole number (Peck 2016). To test the null hypothesis that species were distributed according to preference for sampling method but independently of their traits, randomization by entire columns (species) was done (Dray & Legendre 2008), with the Benjamini and Hochberg (1995) *P*-adjustment for false discovery rate.

All analyses were done using PC-Ord, version 7 (MjM Software Design, Gleneden Beach, Oregon, USA; McCune & Mefford 2016), except for the Kruskal-Wallis test, which was done using Sigma Plot, version 13 (Systat Software, Inc., San Jose, California, USA).

Results

One hundred eleven bee species were collected during the study. See Geroff et al. (2014) for a complete list of species and abundances per sampling method. After exclusion of males, 99 species remained. Median functional dispersion was 0.906 for elevated bowl traps, 0.890 for ground-level bowl traps, 0.882 for Malaise traps, and 0.951 for vane traps. There was no significant difference in functional dispersion among the 4 methods ($H = 4.451$; df = 3; $P = 0.217$).

After exclusion of species with fewer than 3 non-zero cells, 58 species remained for fourth corner analysis. See Table 1 for a list of these species and their functional traits. Globally, there was a significant relationship between the sampling method and sociality ($G = 910.02$; $P = 0.038$). Among individual methods, there was a significant association between ground-level bowl traps and sociality (solitary: $P = 0.040$; social: $P = 0.043$), with greater representation of solitary bees (and lower representation of social bees) than expected (Table 2). This result was driven to a great extent by the relatively low incidence of social *Lasioglossum* (Hymenoptera: Halictidae) in ground-level bowl traps. Of 15 species of social *Lasioglossum*, only 6 (40%) were represented in ground-level bowl traps, vs. 15 in elevated bowl traps, 15 in Malaise traps, and 10 (66.7%) in vane traps. *Bombus* (Hymenoptera: Apidae) also were poorly represented in ground-level bowl traps. Of the 4 species of *Bombus* combined, ground-level bowl traps accounted for only 3 of 35 trap plot occurrences (*Bombus griseocollis* [DeGeer] in 2 ground-level bowl trap plots and *Bombus impatiens* Cresson in 1 ground-level bowl trap plot). Overall, 20 of 32 species (62.5%) collected in ground-level bowl traps were solitary, vs. 29 of 51 species (56.9%) in elevated bowl traps, 24 of 45 species (53.3%) in Malaise traps, and 23 of 41 species (56.1%) in vane traps.

There was a significant global relationship between sampling method and nest location ($G = 1144.21$; $P = 0.039$). A significant association between ground-level bowl traps and nest location was found (belowground: $P = 0.024$; aboveground: $P = 0.024$), with greater representation of above-ground nesting species (and lower representation of below-ground species) than expected (Table 3). Again, *Lasioglossum* and *Bombus* were important drivers of this pattern. Only 6 of 15 below-ground nesting *Lasioglossum* were represented in ground-level bowl traps. Only 1 of these 6 species was solitary, indicating substantial overlap of results for nest location and sociality. Likewise, the below-ground nesting *Bombus* were poorly represented in ground-level bowl traps as described above. *Melissodes* (Hymenoptera: Apidae) also contributed to the significant result for ground-level bowl traps, as well as the relatively low *P*-values for Malaise traps. All 5 *Melissodes* (all solitary below-ground nesters) were absent from ground-level bowl traps and Malaise traps, but all were present in elevated bowl traps, as well as vane traps. Overall, 13 of 32 species (40.6%) collected in ground-level bowl traps were above-ground nesters, vs. 15 of 51 species (29.4%) in elevated bowl traps, 17 of 45 species (37.8%) in Malaise traps, and 13 of 41 species (31.7%) in vane traps.

There was a significant global relationship between sampling method and lecty ($G = 1076.62$; $P = 0.029$). There was a significant association between Malaise traps and lecty (polylectic: $P = 0.024$; oligolectic: $P = 0.024$), with greater representation of polylectic species (and lower representation of oligolectic species) than expected (Table 4). All 3 oligolectic *Melissodes*, as well as *Peponapis pruinosa* (Say) and *Svastra obliqua* (Say) (both Hymenoptera: Apidae), were absent from Malaise traps, but present in 2 of the 3 other trap types. Overall, 1 of 45 species (2.2%) collected in Malaise traps were oligolectic, vs. 2 of 32 species (6.3%) in ground-level bowl traps, 6 of 51 species (11.8%) in elevated bowl traps, and 5 of 41 species (12.2%) in vane traps.

Globally, there was a significant association between sampling method and body length ($F = 986.85$; $P = 0.001$), with significant clustering within Malaise trap ($D = 0.206$; $P < 0.001$), i.e., low variation of data points around the mean. Malaise traps showed a significant negative association ($R = -0.290$; $P < 0.001$), and vane traps a significant positive association ($R = 0.306$, $P < 0.001$) with body length, i.e., relative to the other sampling methods, body length of collected bees is less for Malaise traps and greater for vane traps. *Bombus* were relatively poorly represented in Malaise traps. *Bombus auricomus* (Robertson) was absent from Malaise traps but appeared in 6 other trap plots, whereas *Bombus bimaculatus* Cresson appeared in 1 Malaise trap of 5 total plots, *B. griseocollis* in 3 Malaise traps of 14 total plots, and *B. impatiens* in 2 Malaise traps of 10 total plots. Eucerine bees (*Eucera hamata* (Bradley), *Melissodes* spp., *P. pruinosa*, and *S. obliqua*) also were absent from Malaise trap collections. *Eucera hamata* (Bradley) (Hymenoptera: Apidae) was collected in all 3 of the other trap types. All 5 species of *Melissodes* were collected exclusively in elevated bowl traps and vane traps, as was *P. pruinosa*, whereas *S. obliqua* were collected only in elevated and ground-level bowl traps. On the other hand, *Bombus* were well represented in vane traps, as were the eucerines with the exception of *S. obliqua*. Among the 4 species of *Bombus* combined, vane traps accounted for 16 of 35 trap plot occurrences, and among the 5 species of *Melissodes*, 15 of 26 trap plot occurrences. Among the very short-bodied (< 5 mm) species *Hylaeus mesillae* (Cockerell), *Lasioglossum illinoense* (Robertson), *Lasioglossum imitatum* (Smith), and *Lasioglossum weemsi* (Mitchell) (all Hymenoptera: Apidae), vane traps accounted for only 3 of 24 trap plot occurrences.

Discussion

Results of this study suggest that overall trait diversity of bees (as measured by functional dispersion) in this restored tallgrass prairie habitat does not vary substantially with the sampling method. However, fourth corner analysis indicates that particular traits are strongly associated with individual sampling methods. In particular, ground-level bowl traps, probably the most commonly used bee trapping method, were significantly associated with relatively high representation of solitary bees and above-ground nesting bees. Somewhat surprisingly, these patterns were driven largely by the absence of over half of *Lasioglossum* species from this trap type. *Lasioglossum* have been collected in great abundance in ground-level bowl traps in several studies (Toler et al. 2005; Wilson et al. 2008; Droege et al. 2010). Geroff et al. (2014) collected 189 *Lasioglossum* in ground-level bowl traps, but 167 (88.4%) of these were the very abundant *Lasioglossum versatum* (Robertson) that also was collected in large numbers (> 2,000) in Malaise traps and vane traps. The low incidence of *Bombus* in ground-level bowl traps is not surprising and has been noted by Roulston et al. (2007).

Gonzalez et al. (2016) found that bowl traps that were elevated 70 cm collected larger bees (based on intertegular distance) than did ground-level bowl traps, and Rhoades et al. (2017) found that ground-level bowl traps collected smaller bees (again based on intertegular distance) than did blue vane traps and net collecting (elevated bowl traps were not used in the study). We found no evidence of an effect of bowl trap height on collected bee body size (based on body length).

Malaise traps were significantly associated with polylecty and were negatively associated with body length, whereas vane traps were posi-

Table 1. Traits of bee species collected using 4 sampling methods (elevated bowl traps, ground-level bowl traps, Malaise traps, and vane traps) in a west-central Illinois restored tallgrass prairie. See Gibbs et al. (2017a) for citations for species traits.

Genus & species	Body length (mm)	Sociality	Nest location	Lecty
Agapostemon				
sericeus (Förster)	10.00	Solitary	Belowground	Polylectic
virescens (F.)	11.00	Solitary	Belowground	Polylectic
Andrena				
commoda Smith	11.00	Solitary	Belowground	Polylectic
cressonii Robertson	11.00	Solitary	Belowground	Polylectic
imitatrix Cresson	10.00	Solitary	Belowground	Polylectic
robertsonii Dalla Torre	9.00	Solitary	Belowground	Polylectic
wilkella (Kirby)	11.00	Solitary	Belowground	Oligolectic
Anthophora				
abrupta Say	14.50	Solitary	Belowground	Polylectic
terminalis Cresson	12.25	Solitary	Aboveground	Polylectic
Apis				
mellifera L.	12.00	Social	Aboveground	Polylectic
Augochlora				
pura (Say)	8.00	Solitary	Aboveground	Polylectic
Augochlorella				
aurata (Smith)	5.50	Social	Belowground	Polylectic
Augochloropsis				
metallica (F.)	9.00	Social	Belowground	Polylectic
Bombus				
auricomus (Robertson)	19.00	Social	Belowground	Polylectic
bimaculatus Cresson	13.50	Social	Belowground	Polylectic
griseocollis (DeGeer)	13.75	Social	Belowground	Polylectic
impatiens Cresson	12.25	Social	Belowground	Polylectic
Calliopsis				
andreniformis Smith	7.00	Solitary	Belowground	Polylectic
Ceratina				
calcarata Robertson	7.25	Solitary	Aboveground	Polylectic
dupla Say	7.00	Solitary	Aboveground	Polylectic
mikmaqi Rehan & Sheffield	7.00	Solitary	Aboveground	Polylectic
strenua Smith	5.75	Solitary	Aboveground	Polylectic
Eucera				
hamata (Bradley)	16.50	Solitary	Belowground	Polylectic
Halictus				
ligatus Say	9.00	Social	Belowground	Polylectic
Heriades				
carinata Cresson	7.00	Solitary	Aboveground	Polylectic
variolosa (Cresson)	6.00	Solitary	Aboveground	Polylectic
Hoplitis				
pilosifrons (Cresson)	7.50	Solitary	Aboveground	Polylectic
producta (Cresson)	8.00	Solitary	Aboveground	Polylectic
spoliata (Provancher)	11.00	Solitary	Aboveground	Polylectic
Hylaeus				
affinis (Smith)	5.50	Solitary	Aboveground	Polylectic
mesillae (Cockerell)	4.25	Solitary	Aboveground	Polylectic
Lasioglossum				
birkmanni (Crawford)	6.00	Solitary	Belowground	Polylectic
cattellae (Ellis)	5.34	Social	Belowground	Polylectic
cinctipes (Provancher)	8.00	Social	Belowground	Polylectic
coeruleum (Robertson)	6.18	Social	Aboveground	Polylectic
coriaceum (Smith)	9.00	Solitary	Belowground	Polylectic
cressonii (Robertson)	6.00	Social	Aboveground	Polylectic
fuscipenne (Smith)	9.00	Solitary	Belowground	Polylectic
hitchensi Gibbs	5.19	Social	Belowground	Polylectic
illinoense (Robertson)	4.70	Social	Belowground	Polylectic
imitatum (Smith)	4.18	Social	Belowground	Polylectic
obscurum (Robertson)	5.37	Social	Belowground	Polylectic
oceanicum (Cockerell)	6.72	Social	Belowground	Polylectic
smilacinae (Robertson)	6.60	Social	Belowground	Polylectic

Table 1. (Continued) Traits of bee species collected using 4 sampling methods (elevated bowl traps, ground-level bowl traps, Malaise traps, and vane traps) in a west-central Illinois restored tallgrass prairie. See Gibbs et al. (2017a) for citations for species traits.

Genus & species	Body length (mm)	Sociality	Nest location	Lecty
subviridatum (Cockerell)	5.28	Social	Aboveground	Polylectic
timothyi Gibbs	6.10	Social	Belowground	Polylectic
truncatum (Robertson)	7.00	Social	Belowground	Polylectic
versatum (Robertson)	5.92	Social	Belowground	Polylectic
weemsi (Mitchell)	4.57	Social	Belowground	Polylectic
Megachile				
gemula Cresson	13.50	Solitary	Aboveground	Polylectic
mendica Cresson	12.00	Solitary	Aboveground	Polylectic
Melissodes				
agilis Cresson	12.75	Solitary	Belowground	Oligolectic
bimaculatus (Lepeletier)	14.00	Solitary	Belowground	Polylectic
comptoides Robertson	12.75	Solitary	Belowground	Polylectic
desponsus Smith	12.75	Solitary	Belowground	Oligolectic
trinodis Robertson	11.50	Solitary	Belowground	Oligolectic
Peponapis				
pruinosa (Say)	13.25	Solitary	Belowground	Oligolectic
Svastra				
obliqua (Say)	15.25	Solitary	Belowground	Oligolectic

Table 2. Numbers of social and solitary bees (unrelativized and relativized by the maximum) collected using 4 sampling methods in a west-central Illinois restored tallgrass prairie, with *P*-values. EBT: elevated bowl trap; GBT: ground-level bowl trap; MT: Malaise trap; VT: vane trap. Global *G*-value = 910.02; *P* = 0.038.

Trap type	Trait	# of Bees	Relativized # of bees	*P*-value
EBT	Social	453	22.22	0.450
EBT	Solitary	226	32.26	0.470
GBT	Social	248	6.32	0.043
GBT	Solitary	144	25.64	0.040
MT	Social	2,226	33.02	0.106
MT	Solitary	297	35.52	0.114
VT	Social	209	14.82	0.236
VT	Solitary	225	33.07	0.221

Table 4. Numbers of oligolectic and polylectic bees (unrelativized and relativized by the maximum) collected using 4 sampling methods in a west-central Illinois restored tallgrass prairie, with *P*-values. EBT: elevated bowl trap; GBT: ground-level bowl trap; MT: Malaise trap; VT: vane trap. Global *G*-value = 1,076.62; *P* = 0.029.

Trap type	Trait	# of bees	Relativized # of bees	*P*-value
EBT	Oligolectic	17	5.32	0.483
EBT	Polylectic	662	49.16	0.464
GBT	Oligolectic	3	2.08	0.429
GBT	Polylectic	389	29.88	0.385
MT	Oligolectic	19	1.58	0.024
MT	Polylectic	2,504	66.96	0.024
VT	Oligolectic	30	9.49	0.072
VT	Polylectic	404	38.40	0.077

tively associated with body length. Of the 4 sampling methods in this study, Malaise traps appear to be the least dependent on active color-based attraction of bees and may collect relatively fewer specialist bees that are attracted to particular flower colors. All 14 indicator species for Malaise traps in the study of Geroff et al. (2014) were polylectic. It is possible that larger bees, that are presumably stronger, more active fliers, are more adept at avoiding the Malaise traps altogether, or escaping from them before entering the collection container. The positive association of vane traps with body length was not surprising. Vane traps, particularly blue vane traps, are known to be especially effective in collecting larger bees, such as bumble bees and eucerine bees (Stephen & Rao 2005; Kimoto et al. 2012; Geroff et al. 2014; Buchanan et al. 2017; Gibbs et al. 2017b; McCravy & Ruholl 2017), particularly long-tongued bumble bees such as *B. auricomus* (Gibbs et al. 2017b). The light reflectance of blue vane traps may attract these bees by mimicking that of their preferred host plants (Joshi et al. 2015; Gibbs et al. 2017b).

Table 3. Numbers of aboveground and belowground-nesting bees (unrelativized and relativized by the maximum) collected using 4 sampling methods in a west-central Illinois restored tallgrass prairie, with *P*-values. EBT: elevated bowl trap; GBT: ground-level bowl trap; MT: Malaise trap; VT: vane trap. Global *G*-value = 1,144.21; *P* = 0.039.

Trap type	Trait	# of bees	Relativized # of bees	*P*-value
EBT	Aboveground	169	14.86	0.326
EBT	Belowground	510	39.62	0.308
GBT	Aboveground	141	19.36	0.024
GBT	Belowground	251	12.60	0.024
MT	Aboveground	304	28.57	0.078
MT	Belowground	2,219	39.97	0.086
VT	Aboveground	169	14.00	0.385
VT	Belowground	265	33.89	0.367

Analysis of functional traits is being increasingly used to evaluate effects of land-use changes on bee diversity and conservation. Our results provide additional evidence that functional traits represented in bee samples can vary depending on the sampling method used, and this should be considered in such studies. For instance, studies examining bee foraging ranges and effects of habitat fragmentation on bees should consider the potential body size biases associated with sampling methodology, because bee body size and foraging range are known to be associated (Greenleaf et al. 2007). The quality of these data is dependent on reliable sampling.

Because we have no independent estimate of the true number and species composition of bees in a community, we have no reference with which to compare sampling results (Colwell & Coddington 1994; Droege et al. 2010). Such independent data are needed badly, and can possibly be obtained through habitat manipulation studies and studies incorporating marking of individual bees (Droege et al. 2010). However, the variation in results of different sampling methods documented here and elsewhere suggests that a combination of sampling methods may provide a more complete picture of bee species and trait diversity. Incorporation of additional methods, particularly active netting (search-and-net, and sweep netting) would provide an additional dimension to the data (Cane et al. 2000; Grundel et al. 2011).

It also should be noted that functional traits can be difficult to measure and classify. Intraspecific body size measurements of worker bees can vary geographically (Skandalis et al. 2009), seasonally (Quezada-Euán et al. 2011), and individually over the course of their adult life (León-Contrera et al. 2006). Degrees of sociality range from that found in *Apis*, with thousands of workers per colony, to *Augochloropsis metallica* (F.) *fulgida* (Smith) (Hymenoptera: Halictidae), in which an excavated nest had 1 worker (Gibbs 2017). By manipulating food resources, *Ceratina calcarata* Robertson (Hymenoptera: Apidae) can produce a dwarf worker, and so is potentially social (Lawson et al. 2017). The concept of lecty also is fraught with complexity, and characterizations of lecty can involve fine-grained levels of classification (Cane & Sipes 2006). Further studies are needed to increase our knowledge of bee natural history, clarify the role of trait analysis in studies of bee/habitat relationships, and make informed decisions regarding the most effective methodological approaches to employ.

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