Bee (Hymenoptera: Apoidea) diversity within apple orchards and old fields in the Annapolis Valley, Nova Scotia, Canada

Cory S. Sheffield,[1] Peter G. Kevan, Alana Pindar, Laurence Packer

Abstract—Bees are important within terrestrial ecosystems, providing pollination, which facilitates plant reproduction. Agricultural regions are large landscapes containing varying proportions of cropland, natural, and semi-natural habitats. Most bees are not restricted to any of these and move freely throughout, exploiting food and nesting resources in favourable locations. Many factors affect bee diversity, and knowledge of these is crucial for promoting healthy bee communities. The main objectives of this study were to compare diversity and guild structure of bee communities across a range of land disturbance levels within the Annapolis Valley, Nova Scotia, Canada, in habitats ranging from managed apple orchards to old fields. The two habitat extremes differed significantly; intensely managed orchards had significantly lower species richness (~50%) than observed/estimated in old fields, but orchards with intermediate levels of adjacent natural/semi-natural habitat showed affinities to either extreme depending on the metrics used for estimating species richness. Species assemblages in orchards had lower proportions of several guilds, particularly cavity-nesters, bumble bees, and cleptoparasites, than other habitats. These guilds accounted for over 30% of bees collected in old fields but only 3–10% in orchards, increasing with habitat complexity. The use of guilds for assessing the health of bee communities is discussed.

Résumé—Les abeilles jouent un rôle important dans les écosystèmes terrestres par la pollinisation qui facilite la reproduction des plantes. Les régions agricoles présentent de grands paysages contenant des proportions variables d'habitats agricoles, naturels et semi-naturels. Les abeilles ne sont pas restreintes à l'un ou l'autre de ces habitats et se déplacent librement dans tout l'espace pour y exploiter les ressources de nourriture et de nidification dans les sites favorables. Plusieurs facteurs affectent la diversité des abeilles et il est absolument nécessaire de les connaître si on veut favoriser des peuplements d'abeille en santé. L'objectif principal de notre étude est de comparer la diversité et la structure en guildes des peuplements d'abeilles le long d'un gradient de terres perturbées, allant de pommeraies aménagées à des champs abandonnés, au sein de la vallée d'Annapolis, Nouvelle-Écosse, Canada. Les deux habitats extrêmes diffèrent significativement: les pommeraies à aménagement intensif possèdent une richesse spécifique significativement plus basse (environ 50%) que celle observée/estimée dans les champs abandonnés; toutefois, les pommeraies à niveau intermédiaire d'aménagement montrent des affinités avec l'un ou l'autre des extrêmes selon la métrique utilisée pour estimer la richesse spécifique. Les peuplements des pommeraies contiennent des proportions plus basses de plusieurs guildes, en particulier d'abeilles nichant dans les cavités, de bourdons et de cleptoparasites que ceux des autres habitats. Ces guildes représentent 30% des abeilles récoltées dans les champs abandonnés, mais seulement 3–10% dans les pommeraies, pourcentage qui augmente avec la complexité de l'habitat. Nous discutons de l'utilisation des guildes pour évaluer la santé des peuplements d'abeilles.

Introduction

Bees are keystone components of most terrestrial ecosystems, pollinating plants in both natural and agricultural settings (Kevan *et al*. 1990; Westerkamp and Gottsberger 2000; Kevan and Imperatriz-Fonseca 2002; Klein *et al*. 2007; National Research Council 2007). As such, the

need to understand which factors influence species richness and abundance is crucial to promote plant reproduction, bee conservation, and stewardship, and prevent the continued decline of pollinators in a range of habitats (Biesmeijer *et al*. 2006; Williams *et al*. 2010; Winfree 2010). Clearly, habitats will differ dramatically on regional scales with respect to the bee fauna as a whole (Michener 1979); each may have a particular profile of species richness and abundance as some habitats are naturally more productive and/or favour particular bee groups. A general consensus is that managed habitats (*e.g.*, agroecosystems) typically have lower bee species diversity than surrounding natural habitats (Rathcke and Jules 1993; Kremen *et al*. 2002, 2004; Steffan-Dewenter *et al*. 2002; Larsen *et al*. 2005; Cane *et al*. 2006; Klein *et al*. 2007; Sheffield *et al*. 2008a; Williams *et al*. 2010; Watson *et al*. 2011) and that proximity to more natural and/or diverse habitats (*e.g.*, field margins rich in floral resources) typically increases bee diversity (Holzschuh *et al*. 2007; Winfree *et al*. 2007; Jauker *et al*. 2009; Hagen and Kraemer 2010; Roulston and Goodell 2011; Watson *et al*. 2011). However, there is much to be learnt about the response of bees to land-use patterns (Brosi *et al*. 2007, 2008; Carré *et al*. 2009; Calvillo *et al*. 2010).

The pollinator fauna associated with crops grown over wide geographic ranges can show remarkable differences from region to region (*e.g.*, Vincent *et al*. 1994). For instance, the domestic apple, *Malus domestica* Borkhausen (Rosaceae), though originating from Asia, is grown throughout the world and with the exception of the honey bee (*Apis mellifera* Linnaeus; Hymenoptera: Apidae), its pollinators vary greatly from continent to continent, and even within different tree fruit producing areas within single countries. Unfortunately, pollinator data for many crop plants are not complete and many studies of bees in specific agricultural habitats have not provided data that give an accurate representation of the entire fauna within these systems. Most pollinator surveys have been done when the respective crop is flowering (*e.g.*, Brittain 1933; MacKenzie and Winston 1984; Scott-Dupree and Winston 1987; Kevan *et al*. 1997; Gardner and Ascher 2006; Watson *et al*. 2011) as this strategy identifies which species may be visiting the crop(s). However, such restricted sampling will not survey most bee species within

the system, or identify which species use these habitats at other periods during the growing season (Oertli *et al*. 2005). Additionally, these narrow sampling intervals will not reveal the impact that management practices are having, nor the structure or true functional diversity of the bee communities as a whole. Bees display a range of lifestyles, which can be assigned to behavioural or ecological groups or "guilds" (*sensu* Blondel 2003) (Oertli *et al*. 2005; Grixti and Packer 2006; Matteson *et al*. 2008; Wilson *et al*. 2008; Tuell *et al*. 2009). Monitoring the relative abundance and diversity of members of each guild may provide additional information for describing and comparing communities (Tilman and Lehman 2001) as different habitats offer different resources. When used with standard diversity statistics, more information is gained about the factors affecting bee communities, and better conclusions can be drawn with regard to the health of the ecosystem and/or how to improve it.

The main objective of this study was to compare bee communities across a wide range of disturbance levels, from highly managed apple agroecosystems to unmanaged and semi-natural habitats within the Annapolis Valley of Nova Scotia on a "full season" basis. This objective was met by using a sampling regime that was both intensive and extensive in scope. Additionally, the relative proportions of individuals among select bee guilds were compared across habitats to better understand how bee communities respond to ecosystem disruption on long-term scales.

The taxonomic knowledge of bees in Nova Scotia has increased greatly since the publication of the first checklist for the province (Sheffield *et al*. 2003). This arose through both DNA barcoding efforts (Sheffield *et al*. 2009) and taxonomic revisions yielding two new species among the individuals collected (Gibbs 2010; Rehan and Sheffield 2011). Since the last inventory of the province's bee fauna (Sheffield *et al*. 2003), about 25% more species have been found with over 200 species recorded (Sheffield *et al*. 2011).

Materials and methods

Study sites and sampling

Nova Scotia is part of the Acadian Forest Region (Rowe 1972) composed of mixed-forest species and predominated by conifers. The Annapolis Valley (44.9°N–45.3°N, 64.2°W–65.9°W),

with its early springs and warm (mean 17.4°C), dry (435 mm precipitation) summers (Webb and Marshall 1999) is the primary agriculture region of the province. It is ~930 km^2, lying between the North and South Mountains in the south-eastern part of the province (Neily *et al*. 2003). Very little of the original forest remains in the Annapolis Valley due to a long history of intense agriculture; the remaining woodlands consist largely of white and red pine (*Pinus strobus* Linnaeus, *Pinus resinosa* Aiton; Pinaceae), eastern hemlock (*Tsuga canadensis* (Linnaeus) Carrière; Pinaceae), red oak (*Quercus rubra* Linnaeus; Fagaceae), sugar maple (*Acer saccharum* Marshall; Sapindaceae), yellow birch (*Betula alleghaniensis* Britton; Betulaceae), and beech (*Fagus grandifolia* Ehrhart; Fagaceae) (Webb and Marshall 1999; Neily *et al*. 2003).

The sites used in this study, previously described in Sheffield *et al*. (2008a), represent an ecological gradient from highly managed agroecosystems to unmanaged meadow habitats surrounded by woodlands. The four habitat types distinguished were: (1) COMM-A (5 sites), commercially managed apple orchards surrounded by adjacent orchard blocks or other agricultural crops; (2) COMM-B (5 sites), commercially managed orchard blocks isolated from other agricultural areas and/or usually surrounded by adjacent woodland or other nonagricultural land; (3) ABAND (4 sites), abandoned and/or unmanaged orchard sites, which have not been sprayed or otherwise managed for production for at least 10 years; and (4) OLD FIELD (5 sites), unmanaged meadow or open habitats with adjacent woodland. Due to extensive weed control and other standard agricultural practices within the main sampling areas, sites within the COMM-A and COMM-B habitats typically had reduced floral resource diversity and abundance (excluding the crop during its flowering period), though small areas could be found at margins or other areas within these sites. Orchard site selection was facilitated from data collected as part of a "Tree Fruit Census of the Annapolis Valley" (Craig 1998), in particular, the "Orchard Mapping Project" conducted by the Nova Scotia Department of Agriculture and Marketing in 1995.

At each site, nine 12-oz (350 mL) yellow plastic bowl pan traps (Solo® Cup Company, Lake Forest, Illinois, United States of America;

No. PSB2Y 0099) were arranged in a 3 × 3 grid with minimum spacing of 5 m between each pan trap. Within COMM-A and COMM-B, pan traps were placed between trees within the rows to avoid traffic associated with normal orchard management. At each site, a hand-held global positioning system unit was used to measure the centre of the sampling grid, and notes were made on the surrounding habitat. Pan traps were placed in corrugated plastic bases measuring ~30 cm × 30 cm, supported at two ends by 25 cm strips of 1″ × 3″ (2.5 cm × 7.5 cm) lumber and painted with Tremclad® (Beachwood, Ohio, United States of America) grey primer (MFG no. 274103 522) (Fig. 1). A hole was cut into the centre to allow the pan to sit flush with the base surface and filled ~2/3 with a salt water solution with few drops of liquid detergent added to reduce surface tension (Marshall *et al*. 1994). This design was used to avoid suspected visibility problems due to weed and grass build up around the traps, to make trap visibility more equal throughout the season, and to reduce the capture of slugs and other nonvolant invertebrates. Samples were collected weekly from mid-May to mid-October of each year and pans were replaced every sampling period to minimise loss of attractiveness due to fading.

To further characterise the habitat landscape surrounding the sampling sites without an *a priori* classification scheme (*i.e.*, habitat type), the normalised measure of habitat dominance (*hD*) (after O'Neill *et al*. 1988) was calculated for each site using satellite images obtained from Google Earth©. Images of each site were compared with large-scale habitat characteristics observed at the time of study; significant changes in landscape structure had not taken place in the 10-year elapsed period. Satellite images at a common scale were printed and overlaid with a 24 × 24 grid, each grid cell representing 25 m × 25 m, with the central sampling point at the centre of the grid. Habitat dominance was calculated at three levels for each site: (A) the inner 8 × 8 grid, (B) a 16 × 16 grid, and (C) the total 24 × 24 grid. The following landscape classifications were used: (A) tree fruit orchard under intense management, (B) nontree fruit agricultural cropland under intense management, (C) woodland, (D) pasture (no spraying, seasonal mowing), (E) residence, (F) meadow,

Fig. 1. Pan-trap design used in study.

and (G) abandoned orchard. Large bodies of water and paved areas occupying most of the surface of individual grid cells were subtracted from the total grid number. Values of hD range between 0 and 1, with higher values indicating a landscape dominated by only a few cover types; values closer to 0 indicating proportions of land cover that are nearly equal.

Data analysis

For each site, data from all nine pan traps for both years were pooled prior to analysis, as between pan and year differences were not being studied; however, differences in species composition were observed between years, primarily due to the high proportion of singletons. Rank-abundance plots for the pooled years summarised the relationship between species richness and abundance within each of the four habitat categories (Krebs 1998; Magurran 2004). In addition, species abundance data for each habitat were log transformed ($x = \log_2 n_i$) and fitted to a truncated log-normal distribution following Magurran (2004). Goodness of fit of observed to expected values for the truncated

log-normal plot was tested using the Kolmo-gorov–Smirnov test with Lilliefor's correction, as this greatly increases the power of detection of departures from expectation (Sokal and Rohlf 1995), as demonstrated by Kevan *et al*. (1997) for bee communities. Fitting species abundance data to the truncated log-normal plot and measuring the fit have been previously suggested as a means of diagnosing bee communities (Kevan *et al*. 1997); the assumption being that natural "healthy" communities fit this model (Hill and Hamer 1998; Hubbell 2001).

The inverse Simpson's diversity index ($1/D$) was calculated for each site using Species Diversity and Richness IV (SDR) (Pisces Conservation Ltd., Lymington, United Kingdom). Analysis of Variance (ANOVA) with Tukey's test was used to detect differences in the means of the number of species and $1/D$ for each habitat category (Zar 1999). Additionally, to determine the impact of landscape on bee diversity, $1/D$ was regressed against hD at all three spatial scales.

To compare species richness among sites within each of the four habitats, individual-based rarefied estimates ($\pm 95\%$ CI) were calculated

for the pooled data. As the number of bees captured varied among sites within each habitat, data were rarefied down to the following number of randomly sampled individuals to allow a common sampling effort among sites: COMM-A – 40; COMM-B – 50; ABAND – 80; OLD FIELD – 210. Estimates of species richness ($\pm$95% CI) were also calculated for each of the four habitat categories, rarefied to a common sampling of 800 individuals. All rarefaction estimates were obtained using EcoSim (Gotelli and Entsminger 2003), with the default setting of 1000 iterations. In addition, species richness for each habitat type was estimated using two common nonparametric "sample coverage" methods: the Abundance-based Coverage Estimator (ACE) (Chao *et al*. 1993) and the Incidence-based Coverage Estimator (ICE) (Lee and Chao 1994). Both estimates were calculated using EstimateS Version 7.5 (Colwell 2005), with 50 randomisations. An additional "parametric" estimate of species richness (Colwell and Coddington 1994) for each habitat was obtained by adding the number of "hidden species" calculated from the left of the veil line in the truncated log-normal plots to the actual number observed.

Faunal similarity among sites and habitats was compared using the 1-Sørensen incidence-based index (Magurran 2004) calculated using Community Analysis Package III (CAP III) software (Pisces Conservation Ltd., Lymington, United Kingdom); this metric was used to generate average-linkage dendrograms. Cluster analysis was performed in preference to ordination approaches as there were *a priori* expectations that clustering would occur according to habitat assignment (Seaby *et al*. 2004).

Guild structure of the bee communities in each of the four habitat types was compared. Each species was assigned to one of the following eight guilds based on their known natural history (Sheffield *et al*. 2003): (A) solitary ground-nesters (*Agapostemon* Guérin-Méneville, *Andrena* Fabricius, *Calliopsis* Smith, *Colletes* Latreille, *Lasioglossum* Curtis (subgenus *Lasioglossum*), *Macropis* Panzer, *Melissodes* Latreille, *Perdita* Smith, *Pseudopanurgus* Cockerell, *Megachile gemula* Cresson, *Megachile latimanus* Say, *Megachile melanophaea* Smith, *Megachile montivaga* Cresson); (B) social ground-nesters (*Lasioglossum* subgenera *Dialictus* Robertson

and *Evylaeus* Robertson, *Augochlorella* Sandhouse, *Halictus* Latreille); (C) honey bees (*Apis mellifera* Linnaeus); (D) bumble bees (*Bombus* Latreille) other than the social parasitic species; (E) cavity-nesters, including excavators of pithy stems (*Heriades* Spinola, *Hoplitis* Klug, *Hylaeus* Fabricius, *Megachile* Latreille [other than those listed under A], *Osmia* Panzer, *Anthophora terminalis* Cresson, *Ceratina* Latreille); (F) clepto-parasites (*Coelioxys* Latreille, *Epeoloides* Giraud, *Epeolus* Latreille, *Holcopasites* Ashmead, *Nomada* Scopoli, *Sphecodes* Latreille, *Stelis* Panzer, *Triepeolus* Robertson); and (G) social parasites (*Bombus* subgenus *Psithyrus* LePeletier; *B. ashtoni* (Cresson), *B. citrinus* (Smith), *B. fernaldae* (Franklin)). The proportions of bee species and individuals within each guild in the four habitats were compared with multiple comparisons of proportions; data were arcsine transformed using the modified Freemen and Tukey transformation (after Zar 1999). This transformation was chosen as it is preferable to other methods when comparing small and/or large proportions (Zar 1999). In addition, the diversity and relative abundance of the guilds within each habitat were calculated with Shannon's index.

Specimens collected in this study are currently in the Packer collection at York University, Toronto, Ontario, Canada. Representatives will be placed in the Nova Scotia Museum of Natural History in Halifax, Nova Scotia, Canada and in the Royal Saskatchewan Museum, Regina, Saskatchewan, Canada.

Results

A total of 7234 bee specimens, representing 146 species, were sampled in the 2 years combined (see Appendix 1). Great variation was observed in the number of bees collected among sites within the four habitat types (Table 1); sites within the OLD FIELD habitat contributed the highest number of bees (Table 2). Rare bees made up a high proportion of the species collected. Singletons made up 24–67% of species among sites, and resulted in the long tails of the rank-abundance plots (Fig. 2), though differences in the number of singletons were not observed among habitats ($F_{3, 15} = 2.43$, $P = 0.11$) (Table 1). Similarly, the high proportion of singletons affected the fit of the truncated log-normal plots for each habitat (Fig. 3),

Table 1. The number of individuals and species of bee observed at each site; the number (and proportion) of species represented by 10 or fewer specimens and one specimen, respectively; rarified estimates of the number of species expected ($\pm$95% CI) based on 1000 replicated random samplings of 42 (COMM-A), 55 (COMM-B), 83 (ABAND), and 213 (OLD FIELD) individuals from each habitat.

Site	Individuals (*n*)	Species (*S*)	Species with ≤10 individuals	Proportion	Species with one individual	Proportion	Rarified estimate ($\pm$95% CI)
CA1	1184	40	26	0.65	12	0.30	11.6 (8–15)
CA2	134	27	25	0.93	12	0.44	14.8 (11–19)
CA3	95	15	14	0.93	9	0.60	9.3 (6–12)
CA4	42	12	11	0.92	7	0.58	11.7 (11–12)
CA5	68	21	20	0.95	14	0.67	14.6 (11–18)
CB1	195	33	29	0.91	14	0.44	16.1 (12–20)
CB2	77	29	28	0.97	16	0.55	22.8 (19–26)
CB3	55	14	13	0.93	7	0.50	13.3 (12–14)
CB4	247	36	29	0.81	19	0.53	15.8 (12–20)
CB5	314	58	49	0.84	25	0.43	23.2 (19–28)
AB1	83	38	38	1.00	21	0.55	37.2 (36–38)
AB2	231	49	46	0.92	24	0.48	28.8 (24–34)
AB3	419	47	38	0.81	15	0.32	22.9 (18–28)
AB4	378	63	54	0.87	24	0.39	29.7 (24–35)
OF1	235	43	39	0.91	19	0.44	40.9 (38–43)
OF2	312	67	58	0.87	29	0.43	56.2 (51–61)
OF3	556	69	58	0.84	23	0.33	48.2 (43–54)
OF4	2396	74	48	0.65	18	0.24	35.0 (29–41)
OF5	213	44	41	0.93	15	0.34	43.8 (43–44)

Data pooled for the years 2001–2002.
Site coding: CA, COMM-A (sites 1–5); CB, COMM-B (sites 1–5); AB, ABAND (sites 1–4); OF, OLD FIELD (sites 1–5).

Table 2. The total number of bees collected, the number of bee species observed in each of the four habitat types; rarified estimates of the number of species expected ($\pm$95% CI) based on 1000 replicated random samplings of 800 individuals from each habitat; species richness estimated for each habitat based on (A) hidden species revealed in truncated log-normal plots, and the (B) ACE, and (C) ICE estimates. Data pooled for the years 2001–2002; cells sharing letters in column four are not significantly different (Tukey's test, $P = 0.05$).

Habitat	Bees observed	Species observed	Species expected	95% CI	A	B	C
COMM-A	1523	56	44.5	40–49	101	78	91
COMM-B	888	78	75.4	72–78	107	98	113
ABAND	1111	92	85.6	81–89	100	106	118
OLD FIELD	3712	123	79.3	72–87	152	193	219

all significantly deviating from those expected if log-normal (in all cases, $P < 0.01$). More than half (56.2%) of the species captured across all sites were represented by 10 or fewer individuals, ranging between 65–100% across sites (Table 1); no differences were observed among habitats in the number of species represented by at most 10 individuals ($F_{3,15} = 0.47$, $P = 0.71$).

Species richness varied considerably among habitats (Table 1); the mean number of species observed was highest in OLD FIELD and ABAND, and lowest in COMM-A; no differences were observed between COMM-A and COMM-B, or between COMM-B and ABAND (Tukey's test, $P = 0.05$; Table 2; Fig. 4). Rarified estimates for each habitat (*i.e.*, sites combined) indicated that COMM-A had fewer species than the other three habitats, which did not differ significantly (Table 2, "Species Exp"; Fig. 5). In contrast, addition of "hidden species" from the

Fig. 2. Species rank (X-axis) versus log abundance (Y-axis) for bees collected within each habitat type; data pooled for 2001–2002.
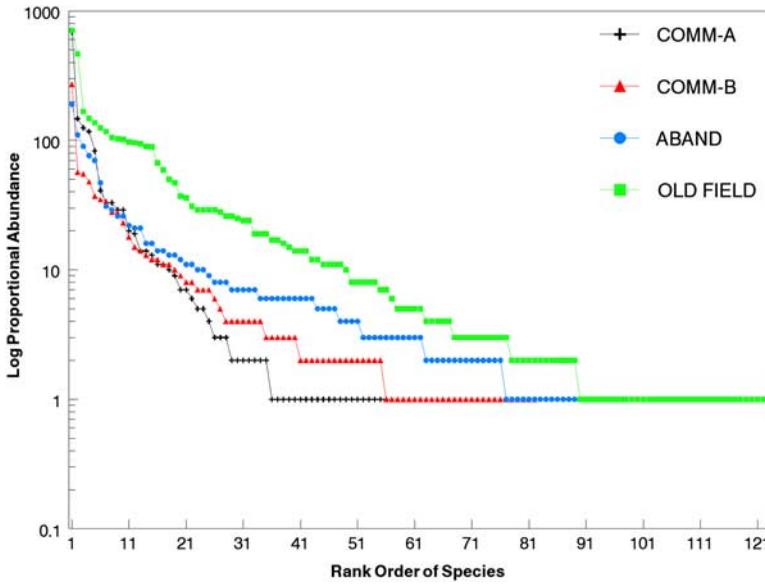
Fig. 3. Truncated log-normal plots of observed (solid bars) and expected (triangles) number of bee species (Y-axis) in each abundance octave (X-axis; $\log_2$ scale), and estimated number of "unseen" species (diagonal striped bars) in the (A) COMM-A, (B) COMM-B, (C) ABAND, and (D) OLD FIELD habitats for 2001–2002. Kolmogorov–Smirnov test for normality with Lilliefors adjustment do not support a log-normal distribution for any habitat type.
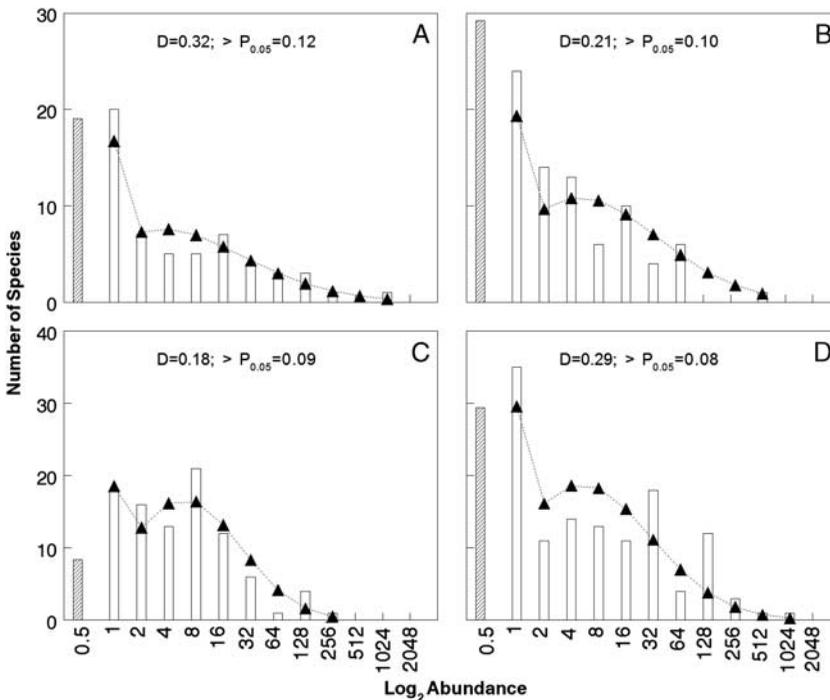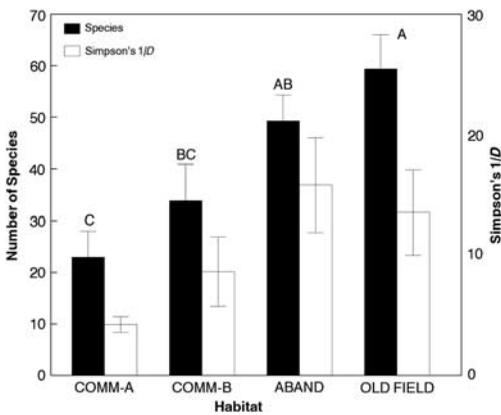
left of the veil line to the actual number of species observed (Figs. 3A–3D; Table 2; compare "Species Obs" to column A) and both ACE (Table 2, "B") and ICE (Table 2, "C") estimators suggested that COMM-A, COMM-B, and ABAND had equally low species richness; all three habitats having species richness estimates much lower that OLD FIELD (Table 2). Contrasting with species richness estimates, no significant differences in diversity ($1/D$) were observed among habitats ($F_{3, 15} = 3.03$,

Fig. 4. Mean ($\pm$SE) of the number of species and Simpson's $1/D$ index for the four habitat types. Bars sharing letters are not significantly different (Tukey's test, $P = 0.05$); no differences were observed in $1/D$.

$P = 0.062$), but COMM-A had the lowest mean index value (Fig. 4).

Most of the COMM-A sites clustered together and separately from the remaining sites. Sites within COMM-B, ABAND, and OLD FIELD showed no distinct pattern of clustering by habitat type (Fig. 6A). Similarly, COMM-A was the least similar to the other habitats, whereas COMM-B most closely resembled ABAND (Fig. 6B).

The managed orchards (COMM-A, COMM-B) had significantly higher proportions of solitary ground-nesting species and individuals (Figs. 7–8, Guild A), while ABAND and OLD FIELD had the lowest. In contrast, no differences were found among habitats with respect to the proportion of social ground-nesters (Figs. 7–8, Guild B), honey bees (Guild C), nor the nonparasitic bumble bees (Guild D) (Figs. 7–8). Cavity-nesting bees (Guild E) were most common in ABAND and OLD FIELD, accounting for over 20% of the species and almost 15% of the bees captured (Figs. 7–8); in contrast, this guild made up only ~1% of the bees in COMM-A (Fig. 8) even though 7% of the species in this habitat belonged to this guild (Fig. 7). Cleptoparasites (Guild F) were proportionally most abundant in ABAND, but almost nonexistent in COMM-A (Figs. 7–8). The proportional abundances of the social parasite *Bombus (Psithyrus)* (Guild G; not shown) showed no differences among habitats. Supporting these overall trends

Fig. 5. Rarefaction plot for each habitat type for the years 2001–2002. Dashed vertical line indicates the sample size (900) of randomly selected individuals for habitat comparison.
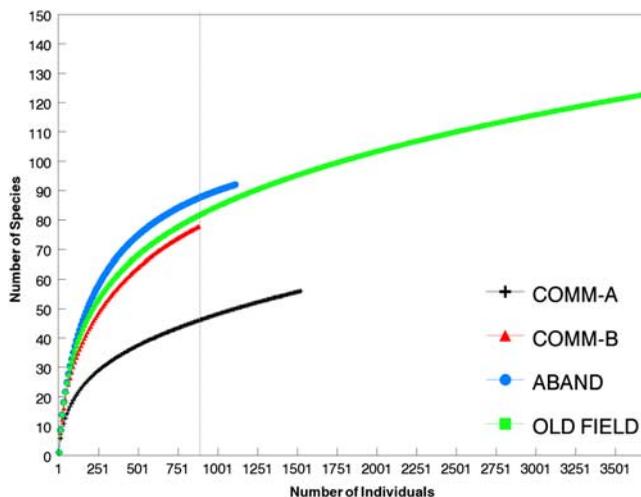
Fig. 6. Average linkage dendrograms of dissimilarity (1-Sorenson index) (top X-axis) for: (A) all sites, and (B) the four habitat types. CA, COMM-A (sites 1–5); CB, COMM-B (sites 1–5); AB, ABAND (sites 1–4); OF, OLD FIELD (sites 1–5).
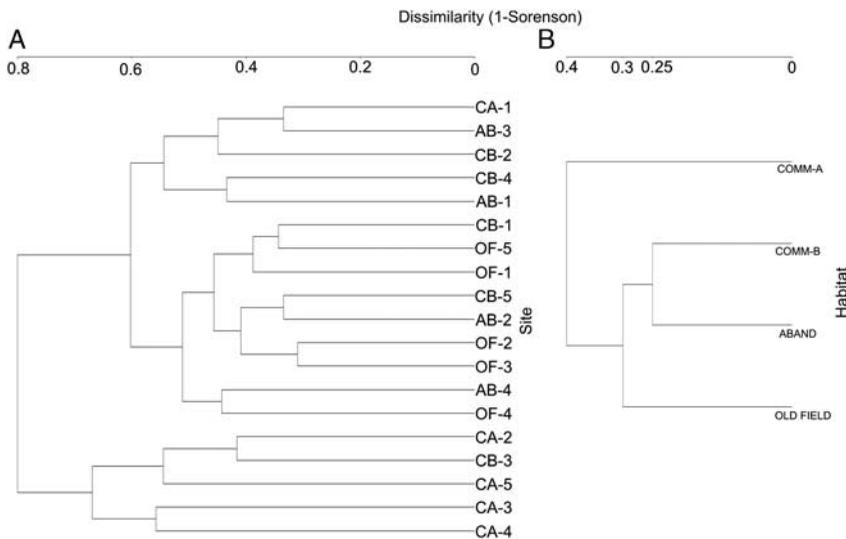
for guild structure, the Shannon H′ index, based on the proportion of species in each of the eight guilds did not differ greatly among habitats, but showed great variability when the relative abundance of individuals in each guild was considered (Table 3). In general, OLD FIELD and ABAND displayed the highest guild diversity, while COMM-A was the lowest (Table 3).

Landscape structure had a strong influence on bee diversity (Fig. 9). At the smallest scale bee diversity decreased as hD increased (Fig. 9A) with many of the sites with low species diversity being dominated by managed orchard cover (Fig. 10, top graph). As a larger proportion of the surrounding landscape was included, a weak relationship was observed between bee diversity and hD (Fig. 9B) and at the largest scale, bee diversity increased as hD increased (Fig. 9C), though primarily in landscapes dominated with nonagricultural habitat (Fig. 10, lower graph).

Discussion

Agroecosystems typically have lower bee diversity than surrounding natural habitats (Rathcke and Jules 1993; Kremen *et al*. 2002, 2004; Steffan-Dewenter *et al*. 2002; Larsen *et al*. 2005; Cane *et al*. 2006; Klein *et al*. 2007;

Sheffield *et al*. 2008a; Williams *et al*. 2010), and the establishment or maintenance of set-asides, hedgerows, natural borders, and corridors throughout agricultural landscapes has long been known to increase pollinator species richness and abundance within these settings (Corbet 1995; Shepherd *et al*. 2003; Greenleaf and Kremen 2006; Pywell *et al*. 2006). Bees respond favourably to increased proximity to and increased proportions of natural habitat rich in floral food resources (Scott-Dupree and Winston 1987; Banaszak 2000; Richards 2001; Roulston and Goodell 2011; Watson *et al*. 2011), and the number of species observed (Tables 1–2; Fig. 4), rarified estimates of species richness (Fig. 5) and diversity (1/D) (Figs. 4, 9–10) generally support this. Bee species richness in the habitats dominated by agricultural land (COMM-A) was lower than in agricultural landscapes with adjacent woodlands and/or natural habitats (COMM-B).

Landscapes dominated by crops, whose flowers may serve as rich sources of pollen and nectar for bees during the flowering period (Banaszak 2000; Westphal *et al*. 2003; Tscharntke *et al*. 2005; Hagen and Kraemer 2010; Watson *et al*. 2011), are generally not good bee habitat. Bee diversity at the smallest scale was lowest in sites with the highest hD (Fig. 9A) when the site was dominated by agriculture habitat (Fig. 10, top graph). At a larger

Fig. 7. The proportion of the bee species representing each guild within each habitat type (nontransformed data). Bars sharing letters within each guild are not significantly different (multiple comparisons of proportions, $q_{0.05,\,4} = 3.633$; after Zar 1999). Guild A = solitary ground nesters; Guild B = social ground nesters; Guild C = *Apis mellifera*; Guild D = bumble bees; Guild E = cavity-nesters; Guild F = cleptoparasitic bees.
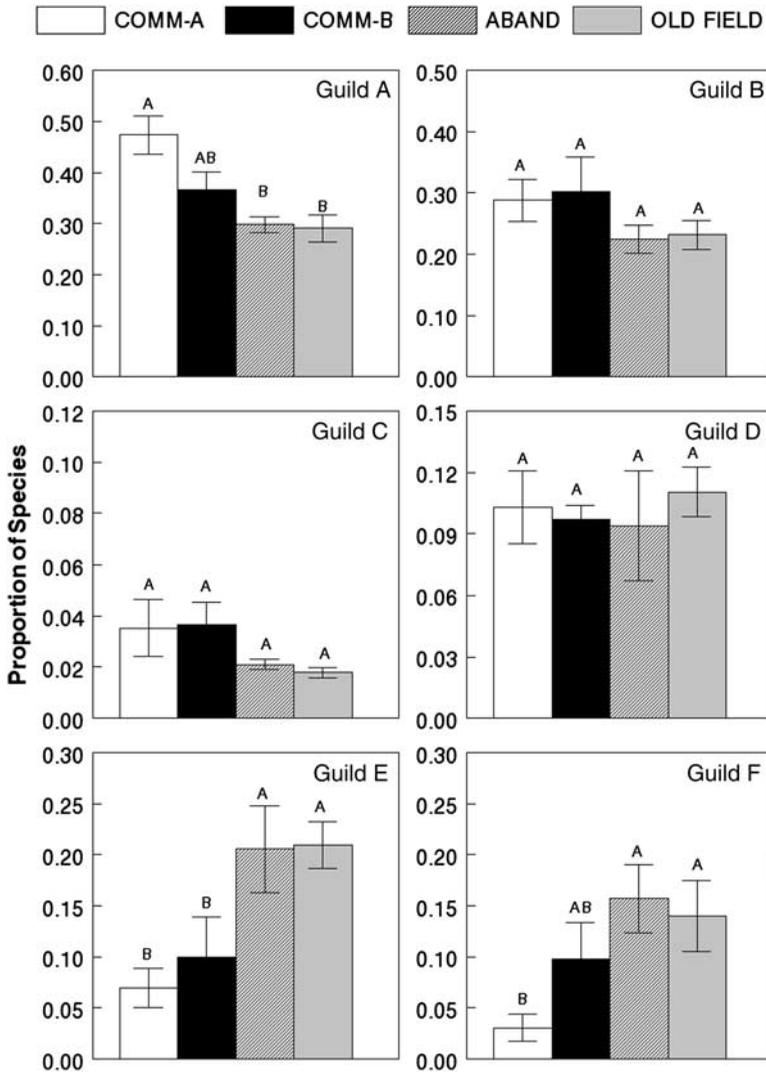
scale, bee diversity increased with *hD* (Fig. 9C), though this trend was linked to sites dominated by more natural habitat (Fig. 10, bottom graph). These results are also consistent with the known benefits of unmanaged semi-natural areas adjacent to agricultural land; for the most part, variation in the quantity and quality of resources available to bees is dependent on the characteristics of the surrounding landscape (Kremen *et al*. 2002; Blanche *et al*. 2006; Pywell *et al*. 2006; Sheffield *et al*. 2008a, 2008b; Hagen and Kraemer 2010; Watson *et al*. 2011).

Cluster analysis of bee fauna similarity among sites also supported this; most sites within COMM-A clustered together, with no clear pattern separating the other three habitats (Fig. 6A). This suggests that a wider range of bee species, normally restricted to more naturalised habitats, are able to use agroecosystems with higher proportions of unmanaged habitat. In an analysis of agricultural landscapes, Banaszak (2000) indicated that having at least 25% of the landscape maintained as wild or refuge habitat would support bee populations adequately.

Fig. 8. The proportion of the total number of bees representing each guild within each habitat type (nontransformed data). Bars sharing letters within each guild are not significantly different (multiple comparisons of proportions, $q_{0.05,4} = 3.633$; after Zar 1999). Guild A = solitary ground nesters; Guild B = social ground nesters; Guild C = *Apis mellifera*; Guild D = bumble bees; Guild E = cavity-nesters; Guild F = cleptoparasitic bees.
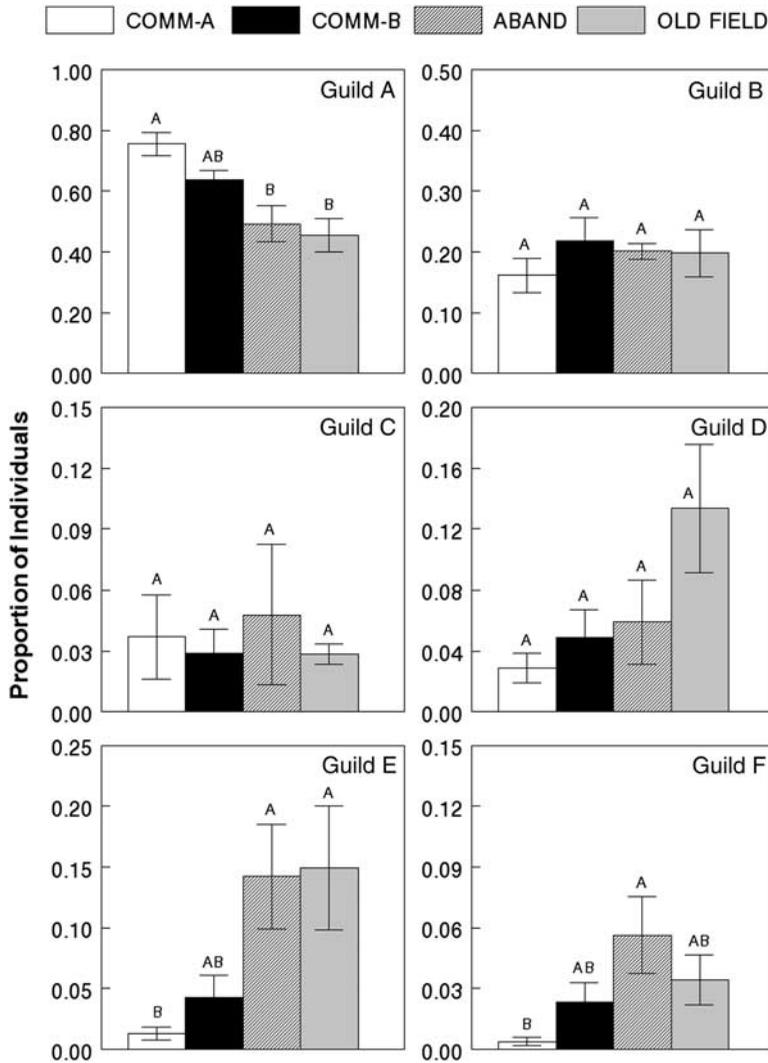

With this in mind, agroecosystems can be managed for pollinators by providing habitat with additional food and nesting resources (Tscharntke *et al.* 2005; Pywell *et al.* 2006; Sheffield *et al.* 2008b; Winfree 2010).

However, the other species richness estimators used in this study, though supporting that COMM-A had the fewest species, also suggested that intermediate sites (COMM-B, ABAND) have significantly fewer species than OLD FIELD. When "hidden" species were included

Table 3. Shannon H′ index for the guild structure of each habitat type, and the pooled habitats based on the proportional species richness, and the proportional abundance of bees in each guild.

	Habitat category			
H′ based on	COMM-A	COMM-B	ABAND	OLD FIELD
Species	0.64	0.71	0.72	0.73
Abundance	0.33	0.52	0.59	0.59

Fig. 9. The diversity of bees (Simpson's $1/D$) versus landscape dominance (hD) for each site at three landscape levels surrounding the sampled area: (A) 200 m × 200 m, (B) 400 m × 400 m, and (C) 600 m × 600 m.
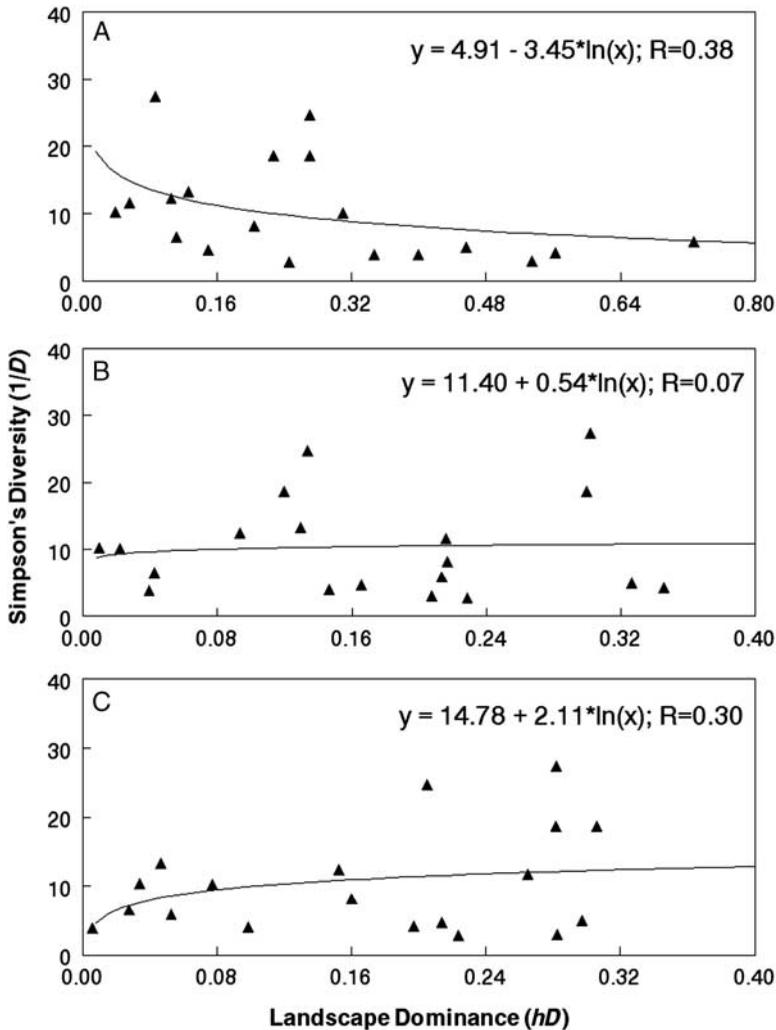

in truncated log-normal plots, or when the data were analysed with ICE or ACE, the two types of commercial orchard habitats (COMM-A, COMM-B) did not differ from each other, and neither differed from unmanaged orchards (ABAND) (Table 2; columns "A–C"). These results have important implications as they suggest that agroecosystems with intermediate levels of natural habitat do not have increased bee species richness, results that contradict the observed species richness and results from rarefaction. As such, species richness metrics alone are not always enough to accurately describe the influence of increasing levels of natural habitats

on bee communities, which certainly are important, nor can these metrics alone be used to diagnose bee community health.

Fitting species richness and abundance data to a truncated log-normal distribution has been suggested as a diagnostic for the assessment of ecosystem health (Hill and Hamer 1998; Hubbell 2001), including for bee communities (Kevan *et al*. 1997). Natural communities, which have species abundance distributions that fit a truncated log-normal distribution, are regarded as being mostly independent and large enough to survive with little immigration (reviewed by Hughes 1986), thus are considered "healthy".

Fig. 10. The proportion of each type of habitat cover (left Y-axis) and diversity of bees (Simpson's $1/D$) (right Y-axis) for each site at three landscape levels surrounding the sampled area: 200 m × 200 m (top), 400 m × 400 m (middle), and 600 m × 600 m (bottom). Legend: "**A**", tree fruit orchard under intense management; "**B**", nontree fruit agricultural cropland under intense management; "**C**", woodland; "**D**", pasture (no spraying, seasonal mowing); "**E**", residence; "**F**", meadow; and "**G**", abandoned orchard.
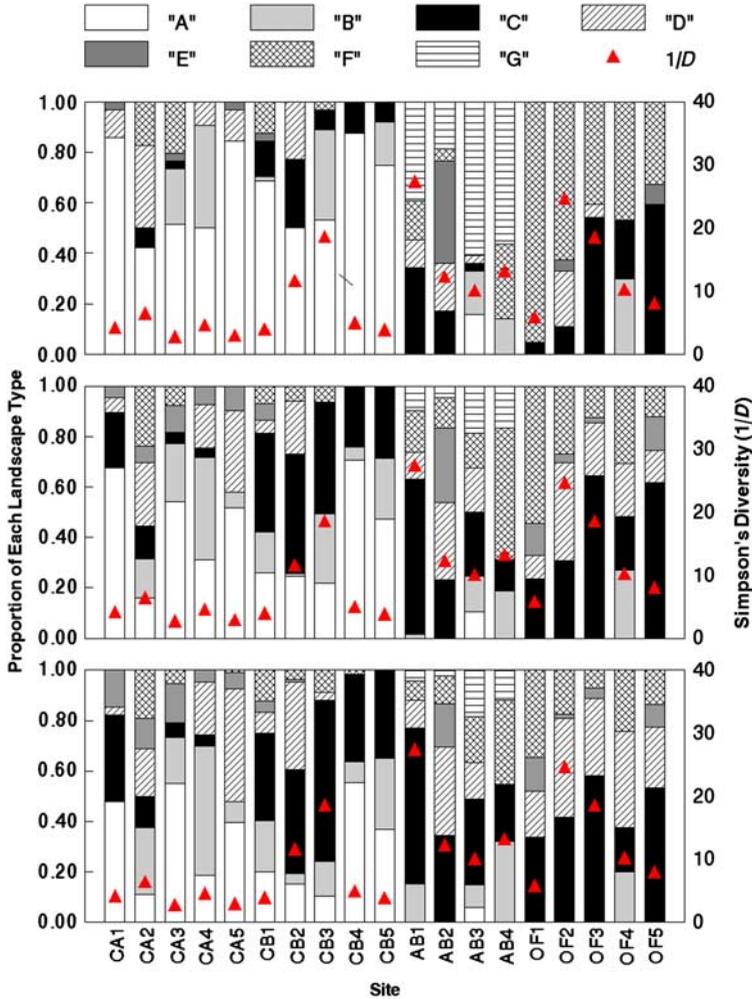
In contrast, disrupted, stressed, or nonnatural communities deviate from the log-normal (Preston 1948, 1980; Kevan *et al*. 1997; Hill and Hamer 1998). In this study, rare species made up a high proportion of the fauna, and their presence influenced the shapes of rank-abundance plots (Fig. 2) and contributed to the lack of fit in truncated log-normal plots for all habitats (Fig. 3). The log-normal communities in the study of Kevan *et al*. (1997) consisted of species visiting lowbush blueberry flowers in commercial field settings, not the entire bee community

within the habitat (*i.e.*, nonblueberry visitors) throughout the season, and departures from log-normal were attributed to differing management regimes and pesticide stress. However, lack of fit to the truncated log-normal may also be due to insufficient sampling (Preston 1948), but this interpretation (and the use of the log-normal distribution in general), has come into question (Williamson and Gaston 2005). In the present study, "hidden" or uncaptured species were numerous in all habitats (Fig. 3) though greatest in COMM-A and OLD FIELD, and the use of

one sampling method only (*i.e.*, yellow pan traps) may have influenced total species capture. Not all bees respond equally to yellow pan traps, and a range of coloured pans (Toler *et al.* 2005) supplemented with other sampling methods (Roulston *et al.* 2007; Westphal *et al.* 2008; Grundel *et al.* 2011; Nielsen *et al.* 2011) give fuller representation of bee faunas. Hill and Hamer (1998) discuss some of the problems associated with appropriate choice of sampling methods for various taxa. However, as a standard colour and number of pan traps were used in the present study, the biases are consistent across sites, and estimates of richness for the Nova Scotia bee fauna, just over 200 species (Sheffield *et al.* 2011), agree favourably with limits estimated for the OLD FIELD habitats, and the pooled habitats examined in this study.

In other studies of bee communities (*e.g.*, Griswold *et al.* 1997; Potts *et al.* 2003), the log-series distribution was considered the most accurate descriptive abundance model. Preston (1948) regarded the log-series distribution the result of sampling from a log-normal community, the sample being less independent with a large number of rare species due to higher rates of immigration (reviewed by Hughes 1986). Interestingly, Magurran and Henderson (2003) suggested that both log-normal and log-series distributions might be reflective of ecological communities; the "core" species (*i.e.*, those which are persistent, abundant, and biologically associated with the habitat) whose abundance are described by the log-normal distribution, and "occasional" species (*i.e.*, those which occur infrequently, are typically low in abundance, and have differing habitat requirements from the core species) that follow a log-series distribution. Magurran and Henderson (2003) suggest that the lack of fit associated with the presence of rare species in real data sets (*e.g.*, Fig. 3) may be a combinatory result of these distributions. As such, this has potential implications for describing and diagnosing bee communities using the log-normal distribution, and this method on its own (which is also reliant on species richness and abundance data) may also be insufficient.

As indicated by Büchs *et al.* (2003), assessment of "biodiversity" (= "species richness") alone as a method of evaluating habitats and/or stewardship practices is lacking in many regards

as it does not consider the complex interactions within communities. This shortcoming applies equally to the use of the truncated log-normal plot for diagnosing bee communities. Bees constitute an incredibly diverse assemblage of life histories, social structure, nesting biology, lifestyles, *etc.* (Michener 2007; Packer 2010; Williams *et al.* 2010), which can be categorised as guilds. Members of each guild have differing requirements, and thus may be categorised as "core" and "occasional" species (as per Magurran and Henderson 2003), so it is somewhat unreasonable to generalise the bee community as a whole, especially if habitat comparisons and/or health evaluation are the subjects of investigation. In this study, habitat type had large impacts on the proportional abundance of different bee guilds (Figs. 7–8), with strong negative responses to intense agriculture observed in the abundance of cavity-nesting bees and cleptoparasites; members of these guilds became more numerous in sites containing higher proportions of natural habitat (Figs. 7–8). In contrast, solitary ground-nesting bees were proportionally most abundant in agricultural landscapes (Figs. 7–8), though this may be more an artifact of the lack of other guilds.

As has been demonstrated (Tilman and Lehman 2001; Tabor and Aguirre 2004; Oertli *et al.* 2005; Scrosati *et al.* 2011), incorporating guilds into ecological studies may offer additional insights into the overall ecological balance maintained within habitats and/or the influence of disturbance. Most terrestrial communities require that functional diversity be maintained; loss of important guilds may ultimately lead to community collapse (Peterson *et al.* 1998). Species data alone do not provide information on functional diversity, though most species within a community can be categorised within functional guilds. Community resilience to disturbance is facilitated not by having diverse species assemblages only, but how species diversity is distributed among functional guilds (Walker 1992; Walker *et al.* 1999; Elmqvist *et al.* 2003). As disturbances intensify, changes in guild composition may signify detrimental impacts much earlier and more effectively than species alone. Therefore, knowing the relative proportions of different bee guilds within natural habitats, and monitoring how the guilds respond to habitat disturbances or land management practices may offer a more accurate guideline as to the quality

of bee communities in managed/semi-managed landscapes compared with species richness data when considered alone.

Acknowledgements

References

Banaszak, J. 2000. Effect of habitat heterogeneity on the diversity and density of pollinating insects. *In* Interchanges of insects between agricultural and surrounding landscapes. *Edited by* B. Ekbom, M.E. Irwin and Y. Robert. Kluwer Academic Publishers, Dordrecht, Netherlands. pp. 123–140.

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., *et al.* 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science, **313**: 351–354.

Blanche, K.R., Ludwig, J.A., and Cunningham, S.A. 2006. Proximity to rainforests enhances pollination and fruit set in orchards. Journal of Applied Ecology, **43**: 1182–1187.

Blondel, J. 2003. Guilds or functional groups: does it matter? Oikos, **100**: 223–231.

Brittain, W.H. 1933. Apple pollination studies in the Annapolis Valley, Nova Scotia. Canadian Department of Agriculture Bulletin, New Series, **162**: 1–198.

Brosi, B.J., Daily, G.C., and Ehrlich, P.R. 2007. Bee community shifts with landscape context in a tropical countryside. Ecological Applications, **17**: 418–430.

Brosi, B.J., Daily, G.C., Shih, T.M., Oviedo, F., and Durán, G. 2008. The effects of forest fragmentation on bee communities in tropical countryside. Journal of Applied Ecology, **45**: 773–783.

Büchs, W., Harenberg, A., Zimmermann, J., and Weiß, B. 2003. Biodiversity, the ultimate agri-environmental indicator? Potential and limits for the application of faunistic elements as gradual indicators in agroecosystems. Agriculture, Ecosystems & Environment, **98**: 99–123.

Calvillo, L.M., Ramírez, V.M., Parra-Tabla, V., and Navarro, J. 2010. Bee diversity in a fragmented landscape of the Mexican neotropic. Journal of Insect Conservation, **14**: 323–334.

Cane, J.H., Minckley, R., Roulston, T., Kervin, L.J., and Williams, N.M. 2006. Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. Ecological Applications, **16**: 632–644.

Carré, G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Cripps, J., *et al.* 2009. Landscape context and habitat type as drivers of bee diversity in European annual crops. Agriculture, Ecosystems & Environment, **133**: 40–47.

Chao, A., Ma, M.-C., and Yang, M.C.K. 1993. Stopping rules and estimation for recapture debugging with unequal failure rates. Biometrika, **80**: 193–201.

Colwell, R.K. 2005. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5 [online]. Available from http://viceroy.eeb.uconn.edu/EstimateS [accessed 12 October 2012].

Colwell, R.K. and Coddington, J.A. 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society of London, Series B, **345**: 101–118.

Corbet, S.A. 1995. Insects, plants and succession: advantages of long-term set aside. Agriculture, Ecosystems and Environment, **53**: 201–217.

Craig, W. 1998. Tree fruit census of the Annapolis Valley. Production Technology Branch, Nova Scotia Department of Agriculture and Marketing, Kentville, Nova Scotia, Canada.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., *et al.* 2003. Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment, **1**: 488–494.

Gardner, K.E. and Ascher, J.S. 2006. Notes on the native bee pollinators in New York apple orchards. Journal of the New York Entomological Society, **114**: 86–91.

Gibbs, J. 2010. Revision of the metallic species of *Lasioglossum (Dialictus)* in Canada (Hymenoptera, Halictidae, Halictini). Zootaxa, **2591**: 1–382.

Gotelli, N.J. and Entsminger, G.L. 2003. EcoSim: Null models software for ecology version 7.72 [computer program]. Jericho, Vermont, United States of America.

Greenleaf, S.S. and Kremen, C. 2006. Wild bee species increase tomato production and respond differently to surrounding land use in northern California. Biological Conservation, **133**: 81–87.

Griswold, T., Parker, F.D., and Tepedino, V.J. 1997. The bees of the San Rafael Desert: implications for the bee fauna of the Grand Staircase-Escalante National Monument. *In* Proceedings of the Grand Staircase-Escalante National Monument Science Symposium, Cedar City, Utah. *Edited by* L.M. Hill. United States Department of the Interior Bureau of Land Management, Salt Lake City, Utah, United States of America. pp. 175–186.

Grixti, J.C. and Packer, L. 2006. Changes in the bee fauna (Hymenoptera: Apoidea) of an old field site in southern Ontario, revisited after 34 years. The Canadian Entomologist, **138**: 147–164.

Grundel, R., Frohnapple, K.J., Jean, R.P., and Pavlovic, N.B. 2011. Effectiveness of bowl trapping and netting for inventory of a bee community. Environmental Entomology, **40**: 374–380.

Hagen, M. and Kraemer, M. 2010. Agricultural surroundings support flower-visitor networks in an Afrotropical rain forest. Biological Conservation, **143**: 1654–1663.

Hill, J.K. and Hamer, K.C. 1998. Using species abundance models as indicators of disturbance in tropical forests. Journal of Applied Ecology, **35**: 458–460.

Holzschuh, A., Steffan-Dewenter, I., Kleijn, D., and Tscharntke, T. 2007. Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context. Journal of Applied Ecology, **44**: 41–49.

Hubbell, S.P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, United States of America.

Hughes, R.G. 1986. Theories and models of species abundance. American Naturalist, **128**: 879–899.

Jauker, F., Diekötter, T., Schwarzbach, F., and Wolters, V. 2009. Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. Landscape Ecology, **24**: 547–555.

Kevan, P.G., Clark, E.A., and Thomas, V.G. 1990. Pollination: a crucial ecological and mutualistic link in agroforestry and sustainable agriculture. Proceeding of the Entomological Society of Ontario, **121**: 43–48.

Kevan, P.G., Greco, C.F., and Belaoussoff, S. 1997. Log-normality of biodiversity and abundance in diagnosis and measuring of ecosystem health: pesticide stress on pollinators on blueberry heaths. Journal of Applied Ecology, **34**: 1122–1136.

Kevan, P.G. and Imperatriz-Fonseca, V.L. 2002. Pollination bees: the conservation link between agriculture and nature. Ministry of Environment, Secretariat for Biodiversity and Forests, Brasília-DF, Brazil.

Klein, A.M., Vassiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., *et al.* 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society, Series B, **274**: 303–313.

Krebs, C.J. 1998. Ecological methodology, 2nd ed. Harper and Row, New York, New York, United States of America.

Kremen, C., Williams, N.M., Bugg, R.L., Fay, J.P., and Thorp, R.W. 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. Ecology Letters, **7**: 1109–1119.

Kremen, C., Williams, N.M., and Thorp, R.W. 2002. Crop pollination from native bees at risk from agricultural intensification. Proceedings of the National Academy of Sciences, **99**: 16812–16816.

Larsen, T.H., Williams, N.M., and Kremen, C. 2005. Extinction order and altered community structure rapidly disrupts ecosystem functioning. Ecology Letters, **8**: 538–547.

Lee, S.-M. and Chao, A. 1994. Estimating population size via sample coverage for closed capture-recapture models. Biometrics, **50**: 88–97.

MacKenzie, K.E. and Winston, M.L. 1984. Diversity and abundance of native bee pollinators on berry crops and natural vegetation in the lower Fraser Valley, British Columbia. The Canadian Entomologist, **116**: 965–974.

Magurran, A.E. 2004. Measuring biological diversity. Blackwell Publishing, Malden, Massachusetts, United States of America.

Magurran, A.E. and Henderson, P.A. 2003. Explaining the excess of rare species in natural species abundance distributions. Nature, **422**: 714–716.

Marshall, S.A., Anderson, R.S., Roughley, R.E., Behan-Pelletier, V., and Danks, H.V. 1994. Terrestrial arthropod biodiversity: planning a study and recommended sampling techniques. Supplement to the Bulletin of the Entomological Society of Canada, **26**: 1–33.

Matteson, K.C., Ascher, J.S., and Langellotto, G.A. 2008. Bee richness and abundance in New York City urban gardens. Annals of the Entomological Society of America, **101**: 140–150.

Michener, C.D. 1979. Biogeography of the bees. Annals of the Missouri Botanical Garden, **66**: 277–347.

Michener, C.D. 2007. The Bees of the world, 2nd ed. Johns Hopkins University Press, Baltimore, Maryland, United States of America.

National Research Council. 2007. Status of pollinators in North America. National Academies Press, Washington, DC, United States of America.

Neily, P.D., Quigley, E., Benjamin, L., Stewart, B., and Duke, T. 2003. Ecological land classification for Nova Scotia. Vol. 1 – Mapping Nova Scotia's terrestrial ecosystems. Report DNR, 2003–2. Nova Scotia Department of Natural Resources, Truro, Nova Scotia, Canada.

Nielsen, A., Steffan-Dewenter, I., Westphal, C., Messinger, O., Potts, S.G., Roberts, S.P.M., *et al.* 2011. Assessing bee species richness in two Mediterranean communities: importance of habitat type and sampling techniques. Ecological Research, **26**: 969–983.

Oertli, S., Muller, A., and Dorn, S. 2005. Ecological and seasonal patterns in the diversity of a species-rich bee assemblage (Hymenoptera: Apoidea: Apiformes). European Journal of Entomology, **102**: 53–63.

O'Neill, R.V., Krummel, J.R., Gardner, R.H., Sugihara, G., Jackson, B., DeAngelis, D.L., *et al.* 1988. Indices of landscape pattern. Landscape Ecology, **1**: 153–162.

Packer, L. 2010. Keeping the bees: why all bees are at risk and what we can do to save them. HarperCollins Publishers Ltd, Toronto, Canada.

Peterson, G., Allen, C.R., and Holling, C.S. 1998. Ecological resilience, biodiversity, and scale. Ecosystems, **1**: 6–18.

Potts, S.G., Vulliamy, N., Dafni, A., Ne'eman, G., and Wilmer, P. 2003. Linking bees and flowers: how do floral communities structure pollinator communities? Ecology, **84**: 2628–2642.

Preston, F.W. 1948. The commonness, and rarity, of species. Ecology, **29**: 254–283.

Preston, F.W. 1980. Noncanonical distributions of commonness and rarity. Ecology, **61**: 88–97.

Pywell, R.F., Warman, E.A., Hulmes, L., Hulmes, S., Nuttall, P., Sparks, T.H., *et al.* 2006. Effectiveness of new agri-environment schemes in providing foraging resources for bumblebees in intensively farmed landscapes. Biological Conservation, **129**: 192–206.

Rathcke, B.J. and Jules, E.S. 1993. Habitat fragmentation and plant–pollinator interactions. Current Science, **65**: 273–277.

Rehan, S.M. and Sheffield, C.S. 2011. Morphological and molecular delineation of a new species in the *Ceratina dupla* species-group (Hymenoptera: Apidae) of eastern North America. Zootaxa, **2873**: 35–50.

Richards, A.J. 2001. Does low biodiversity resulting from modern agricultural practice affect crop pollination and yield? Annals of Botany, **88**: 165–172.

Roulston, T.H. and Goodell, K. 2011. The role of resources and risks in regulating wild bee populations. Annual Review of Entomology, **56**: 293–312.

Roulston, T.H., Smith, S.A., and Brewster, A.L. 2007. A comparison of pan trap and intensive net sampling techniques for documenting a bee (Hymenoptera: Apiformes) fauna. Journal of the Kansas Entomological Society, **80**: 179–181.

Rowe, J.S. 1972. Forest regions of Canada. Department of the Environment, Canadian Forestry Service, Ottawa, Ontario, Publication 1300: 1–172.

Scott-Dupree, C.D. and Winston, M.L. 1987. Wild bee pollinator diversity and abundance in orchard and uncultivated habitats in the Okanagan Valley, British Columbia. The Canadian Entomologist, **119**: 735–745.

Scrosati, R.A., van Genne, B., Heaven, C.S., and Watt, C.A. 2011. Species richness and diversity in different functional groups across environmental stress gradients: a model for marine rocky shores. Ecography, **34**: 151–161.

Seaby, R.M.H., Henderson, P.A., and Prendergast, J.R. 2004. Community analysis package Version 3.2 [computer program]. Pisces Conservation Ltd, Lymington, United Kingdom.

Sheffield, C.S., Dumesh, S., and Cheryomina, M. 2011. *Hylaeus punctatus* (Hymenoptera: Colletidae), a bee species new to Canada, with notes on other non-native species. Journal of the Entomological Society of Ontario, **142**: 29–43.

Sheffield, C.S., Hebert, P.D.N., Kevan, P.G., and Packer, L. 2009. DNA barcoding a regional bee (Hymenoptera: Apoidea) fauna and its potential for ecological studies. Molecular Ecology Resources, **9** (s1), 196–207.

Sheffield, C.S., Kevan, P.G., Smith, R.F., Rigby, S.M., and Rogers, R.E.L. 2003. Bee species of Nova Scotia, Canada, with new records and notes on bionomics and floral relations (Hymenoptera: Apoidea). Journal of the Kansas Entomological Society, **76**: 357–384.

Sheffield, C.S., Kevan, P.G., Westby, S.M., and Smith, R.F. 2008a. Diversity of cavity-nesting bees (Hymenoptera: Apoidea) within apple orchards and wild habitats in the Annapolis Valley, Nova Scotia, Canada. The Canadian Entomologist, **140**: 235–249.

Sheffield, C.S., Westby, S.M., Smith, R.F., and Kevan, P.G. 2008b. Potential of bigleaf lupine for building and sustaining *Osmia lignaria* populations for pollination of apple. The Canadian Entomologist, **140**: 589–599.

Shepherd, M., Buchmann, S.L., Vaughan, M., and Black, S.H. 2003. Pollinator conservation handbook. The Xerces Society, Portland, Oregon, United States of America.

Sokal, R.R. and Rohlf, F.J. 1995. Biometry. W.H. Freeman and Co., New York, New York, United States of America.

Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., and Tscharntke, T. 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology, **83**: 1421–1432.

Tabor, G.M. and Aguirre, A.A. 2004. Ecosystem health and sentinel species: adding an ecological element to the proverbial "canary in the mineshaft". EcoHealth, **1**: 226–228.

Tilman, D. and Lehman, C. 2001. Biodiversity, composition, and ecosystem processes: theory and concepts. *In* The functional consequences of biodiversity: empirical progress and theoretical extensions. *Edited by* A.P. Kinzig, S.W. Pacala and D. Tilman. Princeton University Press, Princeton, New Jersey, United States of America. pp. 9–41.

Toler, T.R., Evans, E.W., and Tepedino, V.J. 2005. Pan-trapping for bees (Hymenoptera: Apiformes) in Utah's west desert: the importance of color diversity. Pan-Pacific Entomologist, **81**: 103–113.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., and Thies, C. 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecology Letters, **8**: 857–874.

Tuell, J.K., Ascher, J.S., and Isaacs, R. 2009. Wild bees (Hymenoptera: Apoidea: Anthophila) of the Michigan highbush blueberry agroecosystem. Annals of the Entomological Society of America, **102**: 275–287.

Vincent, C., de Oliveira, D., Bélanger, A., and Chiasson, H. 1994. Aménagement des insects pollinisateurs et régie des insects ravageurs du fraisier. *In* Colloque sur l'apiculture et al pollinisation. Edited by Conseil des Productions Végétales du Québec, Inc. Montréal, Québec, Canada. pp. 81–92.

Walker, B.H. 1992. Biological diversity and ecological redundancy. Conservation Biology, **6**: 18–23.

Walker, B.H., Kinzig, A.P., and Langridge, J. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. Ecosystems, **2**: 95–113.

Watson, J.C., Wolf, A.T., and Ascher, J.S. 2011. Forested landscapes promote richness and abundance of native bees (Hymeoptera: Apoidea: Anthophila) in Wisconsin apple orchards. Environmental Entomology, **40**: 621–632.

Webb, K.T. and Marshall, L.B. 1999. Ecoregions and ecodistricts of Nova Scotia. Crops and Livestock Research Centre, Research Branch, Agriculture and Agri-Food Canada, Truro, Nova Scotia; Indicators and Assessment Office, Environmental Quality Branch, Environment Canada, Hull, Québec, Canada.

Westerkamp, C. and Gottsberger, G. 2000. Diversity pays in crop pollination. Crop Science, **40**: 1209–1222.

Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., *et al.* 2008. Measuring bee diversity in different European habitats and biogeographical regions. Ecological Monographs, **78**: 654–671.

Westphal, C., Steffan-Dewenter, I., and Tscharntke, T. 2003. Mass flowering crops enhance pollinator densities at a landscape scale. Ecology Letters, **6**: 961–965.

Williams, N.M., Crone, E.E., Roulston, T.H., Minckley, R.L., Packer, L., and Potts, S.G. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. Biological Conservation, **143**: 2280–2291.

Williamson, M. and Gaston, K.J. 2005. The lognormal distribution is not an appropriate null hypothesis for the species-abundance distribution. Journal of Animal Ecology, **74**: 409–422.

Wilson, J.S., Griswold, T., and Messinger, O.J. 2008. Sampling bee communities (Hymenoptera: Apiformes) in a desert landscape: are pan traps sufficient? Journal of the Kansas Entomological Society, **81**: 288–300.

Winfree, R. 2010. The conservation and restoration of wild bees. Annals of the New York Academy of Sciences, **1195**: 169–197.

Winfree, R., Griswold, T., and Kremen, C. 2007. Effect of human disturbance on bee communities in a forested ecosystem. Conservation Biology, **21**: 213–223.

Zar, J.H. 1999. Biostatistical analysis, 4th ed. Prentice Hall, Upper Saddle River, New Jersey, United States of America.

Appendix 1. The number of individuals of each bee species collected in each habitat type, and the total number of individuals.

Species	COMM-A	COMM-B	ABAND	OLD FIELD	Total
Andrena algida Smith	1	0	9	0	10
Andrena alleghaniensis Viereck	0	0	2	6	8
Andrena asteris Robertson	0	0	0	8	8
Andrena barbilabris (Kirby)	3	1	1	5	10
Andrena canadensis Dalla Torre	0	0	0	5	5
Andrena carlini Cockerell	14	55	12	8	89
Andrena ceanothi Viereck	2	2	2	1	7
Andrena crataegi Robertson	11	4	2	0	17
Andrena dunning Cockerell	0	2	0	0	2
Andrena forbesii Robertson	0	1	0	0	1
Andrena heraclei Robertson	0	0	0	1	1
Andrena hippotes Robertson	29	3	5	3	40
Andrena hirticincta Provancher	1	0	0	0	1
Andrena mandibularis Robertson	0	12	0	1	13
Andrena mariae Robertson	7	0	0	2	9
Andrena melanochroa Cockerell	0	3	1	1	5
Andrena milwaukeensis Graenicher	2	0	3	2	7
Andrena miranda Smith	0	0	0	3	3
Andrena miserabilis Cresson	1	0	7	5	13
Andrena nivalis Smith	0	1	1	1	3
Andrena nubecula Smith	1	1	0	0	2
Andrena regularis Malloch	1	0	0	1	2
Andrena rufosignata Cockerell	0	3	0	1	4
Andrena rugosa Robertson	0	0	0	1	1
Andrena sigmundi Cockerell	0	0	0	1	1
Andrena thaspii Graenicher	0	0	1	1	2
Andrena tridens Robertson	0	0	0	1	1
Andrena vicina Smith	3	1	3	0	7
Andrena wheeleri Graenicher	4	6	24	37	71
Andrena wilkella (Kirby)	147	12	90	31	280
Andrena w-scripta Viereck	1	9	2	3	15
Calliopsis andreniformis Smith	20	9	14	67	110
Perdita octomaculata (Say)	0	0	3	167	170
Pseudopanurgus nebrascensis (Crawford)	0	1	0	1	2
Anthophora terminalis Cresson	0	0	6	0	6
Apis mellifera Linnaeus	33	28	47	90	198
Bombus ashtoni (Cresson)	0	1	1	1	3
Bombus borealis Kirby	2	3	3	11	19
Bombus citrinus (Smith)	0	2	0	4	6
Bombus fernaldae (Franklin)	0	0	0	1	1
Bombus fervidus (Fabricius)	7	14	8	125	154
Bombus impatiens Cresson	3	2	6	25	36
Bombus perplexus Cresson	0	1	1	1	3
Bombus rufocinctus Cresson	0	0	2	8	10
Bombus sandersoni Franklin	0	0	0	1	1
Bombus ternarius Say	1	23	7	97	128
Bombus terricola Kirby	2	4	5	17	28
Bombus vagans Smith	1	10	10	28	49
Ceratina calcarata Robertson	4	15	31	103	153
Ceratina dupla Say	1	1	8	15	25

Appendix 1. *Continued*

Species	COMM-A	COMM-B	ABAND	OLD FIELD	Total
Ceratina mikmaqi Rehan and Sheffield	0	3	2	5	10
Epeoloides pilosulus (Cresson)	0	0	0	2	2
Epeolus autumnalis Robertson	0	0	0	1	1
Holcopasites calliopsidis (Linsley)	0	0	1	0	1
Melissodes druriella (Kirby)	1	1	1	26	29
Nomada articulata Smith	0	0	3	1	4
Nomada bishoppi Cockerell	1	0	0	2	3
Nomada capitalis Mitchell	1	4	6	0	11
Nomada cressonii Robertson	0	2	11	11	24
Nomada cuneata (Robertson)	0	1	2	1	4
Nomada imbricata Smith	0	0	5	0	5
Nomada inepta Mitchell	0	0	1	0	1
Nomada lepida Cresson	0	0	0	1	1
Nomada maculata Cresson	0	1	5	0	6
Nomada pygmaea Cresson	0	0	1	0	1
Nomada sayi Robertson	0	2	1	0	3
Nomada subrutila Lovell and Cockerell	0	0	2	1	3
Triepeolus pectoralis (Robertson)	1	0	0	0	1
Colletes inaequalis Say	1	0	0	0	1
Colletes simulans Cresson	0	1	0	0	1
Hylaeus affinis (Smith)	0	0	0	1	1
Hylaeus annulatus (Linnaeus)	0	0	1	12	13
Hylaeus basalis (Smith)	0	1	4	8	13
Hylaeus mesillae (Cockerell)	0	0	6	14	20
Hylaeus modestus Say	2	11	16	46	75
Agapostamon virescens (Fabricius)	125	7	110	466	708
Augochlorella aurata (Smith)	0	0	1	12	13
Halictus confusus Smith	9	8	13	103	133
Halictus ligatus Say	10	11	76	117	214
Halictus rubicundus (Christ)	5	3	8	29	45
Lasioglossum albipenne (Robertson)	0	5	21	2	28
Lasioglossum athabascence (Sandhouse)	0	1	2	5	8
Lasioglossum cinctipes (Provancher)	1	0	0	0	1
Lasioglossum coriaceum (Smith)	11	57	6	29	103
Lasioglossum cressonii (Robertson)	5	28	5	31	69
Lasioglossum divergens (Lovell)	13	37	4	9	63
Lasioglossum ephialtum Gibbs	2	4	3	43	52
Lasioglossum imitatum (Smith)	33	18	24	66	141
Lasioglossum laevissimum (Smith)	117	13	6	148	284
Lasioglossum leucocomum (Lovell)	29	0	10	99	138
Lasioglossum leucozonium (Schrank)	684	271	190	708	1853
Lasioglossum nigroviride (Graenicher)	0	4	2	4	10
Lasioglossum novascotiae (Mitchell)	0	1	0	0	1
Lasioglossum oblongum (Lovell)	0	1	1	4	6
Lasioglossum pectorale (Smith)	1	0	0	1	2
Lasioglossum perpunctatum (Ellis)	14	7	2	106	129
Lasioglossum pilosum (Smith)	83	1	25	138	247
Lasioglossum planatum (Lovell)	1	2	7	19	29
Lasioglossum sagex (Sandhouse)	1	0	2	20	23
Lasioglossum sheffieldi Gibbs	0	0	0	26	26
Lasioglossum subversans (Mitchell)	0	2	0	0	2

Appendix 1. *Continued*

Species	COMM-A	COMM-B	ABAND	OLD FIELD	Total
Lasioglossum tenax (Sandhouse)	0	0	0	1	1
Lasioglossum versans (Lovell)	19	35	16	20	90
Lasioglossum viridatum (Lovell)	0	1	2	29	32
Lasioglossum zonulum (Smith)	41	48	26	89	204
Sphecodes atlantis Mitchell	0	0	2	3	5
Sphecodes autumnalis Mitchell	0	0	0	24	24
Sphecodes clematidis Robertson	0	0	0	4	4
Sphecodes confertus Say	0	0	0	2	2
Sphecodes coronus Mitchell	0	2	0	6	8
Sphecodes cressonii (Robertson)	0	2	4	24	30
Sphecodes dichrous Smith	0	0	0	3	3
Sphecodes johnsonii Lovell	0	0	0	1	1
Sphecodes levis Lovell and Cockerell	0	0	0	2	2
Sphecodes minor Robertson	0	0	0	1	1
Sphecodes persimilis Lovell and Cockerell	0	0	0	1	1
Sphecodes prosphorus Lovell and Cockerell	0	0	0	2	2
Sphecodes prostygius Mitchell	0	1	0	1	2
Sphecodes ranunculi Robertson	0	0	4	1	5
Sphecodes stygius Robertson	0	1	0	4	5
Sphecodes townesi Mitchell	0	1	0	0	1
Coelioxys porterae Cockerell	0	0	0	2	2
Coelioxys rufitarsis Smith	0	0	0	2	2
Coelioxys sodalis Cresson	0	3	8	8	19
Heriades carinatus Cresson	0	0	0	1	1
Hoplitis pilosifrons (Cresson)	0	0	2	11	13
Hoplitis spoliata (Provancher)	0	1	2	50	53
Megachile centuncularis (Linnaeus)	0	0	0	1	1
Megachile frigida Smith	0	0	16	2	18
Megachile gemula Cresson	0	1	3	11	15
Megachile inermis Provancher	0	7	6	17	30
Megachile latimanus Say	0	0	1	1	2
Megachile melanophaea Smith	6	34	70	94	204
Megachile montivaga Cresson	0	0	1	0	1
Megachile pugnata Say	0	0	0	1	1
Megachile relativa Cresson	0	1	7	10	18
Osmia atriventris Cresson	1	4	6	7	18
Osmia bucephala Cresson	0	0	1	16	17
Osmia caerulescens (Linnaeus)	0	2	3	3	8
Osmia inermis (Zetterstedt)	0	0	0	1	1
Osmia proxima Cresson	0	0	3	14	17
Osmia simillima Smith	0	2	14	3	19
Osmia tersula Cockerell	2	2	7	19	30
Stelis foederalis Smith	1	2	4	8	15
Stelis vernalis Mitchell	0	0	0	1	1
Macropis nuda (Provancher)	0	0	0	3	3

Data pooled for two years (2001–2002). Species list arranged alphabetically by family, genus, species.