

## LINKING BEES AND FLOWERS: HOW DO FLORAL COMMUNITIES STRUCTURE POLLINATOR COMMUNITIES?

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**Abstract.** Pollinators provide essential ecosystem services, and declines in some pollinator communities around the world have been reported. Understanding the fundamental components defining these communities is essential if conservation and restoration are to be successful. We examined the structure of plant–pollinator communities in a dynamic Mediterranean landscape, comprising a mosaic of post-fire regenerating habitats, and which is a recognized global hotspot for bee diversity. Each community was characterized by a highly skewed species abundance distribution, with a few dominant and many rare bee species, and was consistent with a log series model indicating that a few environmental factors govern the community.

Floral community composition, the quantity and quality of forage resources present, and the geographic locality organized bee communities at various levels: (1) The overall structure of the bee community (116 species), as revealed through ordination, was dependent upon nectar resource diversity (defined as the variety of nectar volume-concentration combinations available), the ratio of pollen to nectar energy, floral diversity, floral abundance, and post-fire age. (2) Bee diversity, measured as species richness, was closely linked to floral diversity (especially of annuals), nectar resource diversity, and post-fire age of the habitat. (3) The abundance of the most common species was primarily related to post-fire age, grazing intensity, and nesting substrate availability. Ordination models based on age-characteristic post-fire floral community structure explained 39–50% of overall variation observed in bee community structure. Cluster analysis showed that all the communities shared a high degree of similarity in their species composition (27–59%); however, the geographical location of sites also contributed a smaller but significant component to bee community structure.

We conclude that floral resources act in specific and previously unexplored ways to modulate the diversity of the local geographic species pool, with specific disturbance factors, superimposed upon these patterns, mainly affecting the dominant species.

**Key words:** *bee diversity; community structure; energy partitioning; fire; grazing; Mediterranean; nectar; nest substrate availability; pollen.*

### INTRODUCTION

Pollinators play a crucial role in ecosystem processes and contribute to the maintenance of both diversity and function. A global pollination crisis has been recognized recently (Allen-Wardell et al. 1998, Kearns et al. 1998, Kevan 1999), and the International Pollinators Initiative (São Paulo Declaration on Pollinators 1999) points to a lack of baseline ecological data for plant–pollinator interactions on which to develop strategies for integrated management of landscapes. The current pollination crisis emphasizes the importance of understanding the fundamental determinants of plant–pollinator community structure; and such knowledge will be necessary to underpin any conservation and restoration efforts.

Key factors responsible for the organization of insect communities have been investigated at many spatial and temporal scales. Several (often not mutually exclusive) hypotheses have been proposed to explain abundance distributions (Wiens 1977, Strong et al. 1984, Russell 1989, Szentkiralyi and Kozar 1991). Principal determinants identified include quantity and quality of forage resources (e.g., Price 1984), the form of species area relationships (e.g., Lawton and Schröder 1977), habitat heterogeneity (e.g., Lawton and Price 1979), host encounter frequency by herbivores (e.g., Southwood 1961), equilibrium theory of island biogeography (e.g., Strong 1979), impact of natural enemies (e.g., Root 1973), and plant structural diversity (e.g., Strong and Levin 1979). To date most work has focused on phytophagous insects, with fewer studies addressing how pollinator communities are structured. Kevan et al. (1997) have demonstrated that the diversity and abundance of pollinators on Canadian blueberry heaths fitted a log-normal model when unaffected

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by a pesticide, and departed from the model when stressed by the pesticide. Food webs constructed using insect visitors of entomophilous flowering plants were found to be compartmentalized in two British grassland communities, with compartments reflecting classic pollination syndromes (Dicks et al. 2002). A survey of a Brazilian reserve by Barbola and Laroza (1993) showed that most species of bee were uncommon, and represented by one or two individuals, with a few species being abundant. A meta-analysis of existing studies (Williams et al. 2001) indicates that bee communities are often rich in rare species and are locally diverse. Other studies have documented the spatial and temporal variability of bee communities (e.g., Moldenke 1979, Ackerman 1983, Hingston 1998).

Competition theory for diversity regulation predicts that the diversity of consumers and resources are positively correlated, as should consumer and resource abundance (MacArthur 1972); these associations have been demonstrated for a tropical insect pollinator community related to its host plants, but without investigation of the rewards involved (Heithaus 1974). Indications that the diversity of nectar, pollen, and flower forms may influence the structure of bee communities have been published (Moldenke 1975, Gathmann et al. 1994, Petanidou and Ellis 1996). Positive relationships have been found between bee abundance and floral abundance (Heithaus 1974, Banaszak 1996), butterfly diversity and floral abundance (Steffan-Dewenter and Tschardt 1997), bee and floral diversity (Banaszak 1996), and pollinator diversity (mainly Hymenoptera and Diptera) and pollen availability (Petanidou and Vokou 1990).

We examined the structure of pollinator communities within a landscape and related this to various aspects of plant community composition and associated reward structure. For our model system, we used northern Israel, which is recognized as a global biodiversity hotspot for entomophilous plants and pollinators, and especially for bees (Dafni and O'Toole 1994, Michener 2000). It has been estimated that, worldwide, 60–70% of flowering plant species are dependent upon insects for pollination (Richards 1986) and bees are the principal pollinating group in most geographic regions (Michener 1979, 2000). We considered the structure of the bee assemblage at four levels: the overall species richness of the bee community, the species abundance relationships within the community, the species richness and abundance within each bee family, and the abundance of the most dominant species. The first two measures aim to describe the overall community organization, while the latter two seek to identify different linkages between particular taxa (family and species) and properties of the floral community. Bee species have characteristic foraging and nesting requirements (Roubik 1989, O'Toole and Raw 1991) and are therefore expected to be associated with specific floral communities; bee families usually comprise species

with broadly similar foraging and nesting habits and so are likely to be linked to particular habitat types.

The two key forage resources for bees are nectar and pollen, and we investigated how the quantity and range of quality of these vary within and across habitat types, and how important they are in determining bee community organization. It has been proposed that in Mediterranean-type ecosystems pollen is the main reward for pollinators (Herrera 1985), with nectar sources being of minor importance (Westrich 1990); however, most studies of reward energetics have concentrated on the role of nectar (but see Petanidou and Vokou 1990 and references therein). Pollen is rarely utilized as an energy source by foraging bees; however, it is the principal constituent of food for developing larvae and therefore will have an important role in defining bee community structure. Other factors influencing plant-pollinator community structure addressed in this study are the availability of nesting sites and substrates and vertebrate grazing, while findings from our studies relating to fire (Potts et al. 2003), habitat heterogeneity, and the impact of non-native invasive pollinators and natural enemies will be published elsewhere.

## MATERIALS AND METHODS

### *Study area*

The study was made in Mount Carmel National Reserve, Israel, during March–May 1999 and 2000. The area has a characteristic Mediterranean climate of hot dry summers (1999 and 2000 monthly means for May to August: maximum temperature  $29.9 \pm 0.8^\circ\text{C}$ , minimum temperature  $22.4 \pm 1.1^\circ\text{C}$ , and precipitation  $0.0$  mm) and cool wet winters (1999 and 2000 monthly means for November to January: maximum temperature  $23.0 \pm 1.1^\circ\text{C}$ , minimum temperature  $14.1 \pm 0.9^\circ\text{C}$ , and precipitation  $116.5 \pm 43.5$  mm). The reserve comprises  $\sim 150$  km<sup>2</sup> of Aleppo pine woodland in a mosaic of differently aged areas of regenerating post-fire vegetation (phrygana). The woodland is composed of *Pinus halepensis* Mill. with several species of multistem dwarf trees and shrubs; *Cistus salvifolius* L., *Salvia fruticosa* Mill., *Pistacia lentiscus* L., and *Quercus calliprinos* Webb. are particularly abundant. Several major fires (1999, 1998 [two burns], 1989, 1983, and 1974) have resulted in large stands of phryganic vegetation that is dominated by *Cistus* spp., *Satureja thymbra* L., *Salvia* spp., with some annual species. Full floristic descriptions of these habitat types are available elsewhere (Zohary 1982).

We selected 21 sites, using the full spectrum of burn ages available, as being representative of all the major post-fire vegetation types on Mt. Carmel (Table 1). Aerial photographs, detailed ground surveys, and reference to the existing literature (Soffer and Kipnis 1980) ensured that all sites were similar with respect to aspect (south or west facing), overall slope ( $<17^\circ$ , though small patches of steep ground were present), altitude

TABLE 1. Summary of survey sites in Mt. Carmel National Reserve, Israel.

Site code	Location	GPS coordinates	Year burnt	Approximate area (ha)
Den98	Wadi Denia	35°00.1' N, 32°45.8' E	1998	100
Hod98	En Hod	34°58.6' N, 32°41.9' E	1998	450
Hai89	Hai Bar reserve	35°01.2' N, 32°44.9' E	1989	300
Mit83	Mitla	34°59.6' N, 32°44.2' E	1983	400
Etz74	Etzbah	34°58.9' N, 32°42.4' E	1974	80
EtzNB	Etzbah	34°58.8' N, 32°42.4' E	<1950	240
DenNB (1999 only)	Wadi Denia	35°00.4' N, 32°45.7' E	<1950	190
NewNB (2000 only)	Kedumim	35°04.2' N, 32°43.3' E	<1950	135

*Notes:* Each area of post-fire vegetation comprised three replicated sites. Site DenNB, used in spring 1999, was completely burnt the following autumn and therefore had to be replaced with an equivalent set of sites in mature woodland (NewNB) for surveys in 2000. Number in site code indicates year of burn; NB indicates "not burned."

(130–340 m asl [above sea level]), mean annual precipitation (625–725 mm), and soil type (Terra Rossa or Rendzina). Other potentially confounding habitat characters, such as logging or unusually intensive grazing, were avoided in site selection. At each site, an area of 1 ha of relatively uniform vegetation typical of that burn age was chosen, always >0.3 km (and usually >0.6 km) away from the nearest border with a different vegetation type or any other site.

Five series of pollinator, flower, nectar, and pollen surveys were carried out during the peak floral blooming and pollinator flight season (late February–May) in 1999 and again in 2000. To minimize the effects of seasonality on our study, all sites were surveyed in quick succession over two weeks, resulting in five series spaced equally across the season (survey 1: late February to early March; survey 2: mid to late March; survey 3: early to mid April; survey 4: late April to early May; survey 5: mid to late May).

Throughout each survey, weather data were recorded using a hand-held temperature humidity meter (HMI, Vaisala, Finland). Any day with particularly unusual conditions (e.g., heavy rain or very high winds) was abandoned and repeated the following day. The March to May mean monthly maximum and minimum temperatures and rainfall during the flowering season for both years ( $23.2 \pm 1.3^\circ\text{C}$ ,  $14.9 \pm 1.3^\circ\text{C}$ , and  $21.8 \pm 10.4$  mm, respectively) were consistent with the long-term averages for 1970–2000 ( $23.2 \pm 1.9^\circ\text{C}$ ,  $13.8 \pm 1.9^\circ\text{C}$ , and  $26.4 \pm 14.5$  mm, respectively) (data from Climatology Branch, Israel Meteorological Service, Bet Dagan, Israel).

#### *Pollinator diversity and abundance surveys*

The pollinating fauna of Mt. Carmel is dominated by bees (Hymenoptera: Apoidea) and most communities comprise >90% bees (Potts et al. 2001; C. O'Toole, *personal communication*); accordingly, our pollinator surveys focused on this group (see Plate 1).

At each site, starting at a randomly selected point each time, a linear transect of 200 m was walked in a random direction over a 20-min period at 0800, 1100, and 1400 h; these times effectively covered the period

of maximum bee activity. The start point (grid reference) and compass direction of transects were randomized using random number tables for each survey. All bee species encountered within 1.5 m of either side of the transect were recorded when unambiguously identifiable on the wing, and those not identifiable caught with an insect net and retained for determination at the Bee Systematics and Biology Unit, Oxford University Museum of Natural History, UK. Family classification was consistent with that of Michener (2000). Overall sampling effort and area were identical across all sites and equally balanced both spatially and temporally.

Full surveys were made in 1999, when abundance was recorded and all caught specimens were kept for determination (2694 individuals). Because the bee fauna of Mt. Carmel National Reserve is under increasing threat from a wide range of disturbance pressures, we decided to reduce the number of individuals captured during the 2000 surveys, while still maintaining equivalent abundance measures. Because total seasonal abundance in 2000 was lower in 16 of the 21 sites and similar in 4 sites, we considered it reasonable to extrapolate the species accumulation curves (plots of the cumulative number of species discovered within a defined area as a function sampling effort) of 1999 with the 2000 recorded abundance measures. We computed species accumulation curves for each site using "BioDiversity Professional" (McAleece 1997), and the fitted curve was used to estimate species richness for each site in 2000; an evaluation of various extrapolation methods is described by Colwell and Coddington (1996). The largest calculated error (95% confidence interval) for any site was  $\pm 0.3$  species on an estimate of 24.2 species. An independent check on the reliability of this method was obtained by capturing subsamples of bees at each site through the season in 2000 (394 individuals) and identifying these; the observed species richness across sites and the estimated species richness were positively correlated ( $r^2 = 0.552$ ,  $P = 0.056$ ,  $n = 21$ ). Thus, we are confident that our calculation of bee species richness in 2000 is an accurate estimate of the actual richness across sites.



PLATE 1. (Left) Honeybee *Apis mellifera* (Apidae) visiting *Satureja thymbra* (Lamiaceae). (Right) Large fast-flying long-tongued male solitary bee, *Habropoda tarsata* (Apidae) hovering in front of *Anchusa undulata* (Boraginaceae). Photographs by Shay Levay.

#### *Floral, nectar, and pollen surveys*

At each site, a 50 m long linear transect, starting from a random point, was marked out in a random direction and a 0.4-m strip along one side of the transect was used to record the species and area coverage of all open flowers that could be visited by bees.

Ten pairs of 1-m<sup>2</sup> quadrats were placed along a second 50-m transect at random distances from the start. Prior to dawn, all the flowers present in each quadrat were covered with 1 mm netting cages to prevent access to visitors. The first set of 10 caged quadrats was used to quantify nectar available without visitation (an index of the “maximum producible nectar”), volumes were determined using microcapillary pipettes (Camlab, Cambridge, UK), and sugar concentration was measured with refractometers modified for small volumes (Bellingham and Stanley, Tunbridge Wells, UK). In parallel, flowers of the same species, and in the same numbers, were assessed in the surrounding habitat for nectar standing crop with open visitation (an index of “available nectar”). All nectar measurements were taken between 0900 and 1100 hours. Individual flower volumes were summed for each survey at each site, and concentrations calculated as the mean per flower per site. Although both methods represent a crude measure of nectar availability (because of our inability to extract all nectar from all flowers, individual variation in temporal nectar production and side effects of caging), they represent time-effective methods of assessment for the purposes of nectar production at the community level. This permitted comparable calculations of nectar energy, volume, mean concentration, and water content per unit area of habitat, for caged and openly visited flowers.

The second set of 10 caged quadrats was used to measure pollen standing crop. In each quadrat, all open anthers, whether freshly dehisced or previously open, were removed and stored in 70% alcohol. These samples were then sonicated for 10 min to release the pollen from open anthers (especially poricidal anthers), fil-

tered through a 0.1-mm mesh to remove most of the plant debris, and the resulting filtrate was then centrifuged at a low speed to obtain a concentrated pollen suspension. The total number of pollen grains and mean pollen grain size were determined by light microscopy, and the mean pollen volume per unit area for each habitat type calculated. Using the regression equation of pollen grain mass on pollen grain volume ( $\text{Ln}[\text{mass}] = 0.95 \times \text{Ln}[\text{volume} \times 10^{-6}] - 12.46$ ) presented in Roulston et al. (2000), an estimate of pollen mass was calculated. This was then used to calculate pollen energy content using a value of 5.69 Kcal/g as the mean of 34 insect-pollinated plants in a similar Mediterranean ecosystem (Petanidou and Vokou 1990). We consider this conversion to be reasonable, as variability across species was small ( $5.69 \pm 0.05$  Kcal/g), and the species used were typical of those in our study (T. Petanidou, *personal communication*). However, some caution is necessary when interpreting results, as energy and nutritional content available from pollen to bee larvae is known to vary with flowering plant species (Roulston and Cane 2000). A more sophisticated method would take specific variability into account and also the quantitative nutritional value of pollen. Our study uses a simple, albeit crude, approach to assess pollen energy availability at the community level as a first step to understanding the role of pollen in organizing bee community structure.

Because nectar and pollen standing crops for each post-fire habitat were available in the same units it was then possible to calculate total energy available to bees (pollen energy + nectar energy) and also the relative importance of each component (P:N ratio).

#### *Analysis of nectar quality*

The quality of nectar resources provided by each site was determined by examining the diversity and abundance of nectar volume and concentration combinations available in each site throughout the season. A 3 × 3 matrix of volume categories (<0.1 μL, 0.1–1.0



TABLE 2. The abundance of all 17 species contributing &gt;0.5% to the total number of bees sampled in Mt. Carmel National Reserve, Israel.

Species	Code	Abundance (%)
<b>Andrenidae</b>		
<i>Andrena grandilabris</i> Perez	<i>And grn</i>	1.6
<i>Andrena rufomaculata</i> Friese	<i>And rfm</i>	0.8
<i>Andrena vetula</i> Lepeletier	<i>And vtl</i>	0.6
<i>Andrena</i> sp. 99/16	<i>And sp 16</i>	0.7
<b>Apidae</b>		
<i>Anthophora dispar</i> Lepeletier	<i>Ant dsp</i>	1.8
<i>Anthophora plumipes</i> Pallas	<i>Ant plm</i>	0.6
<i>Apis mellifera</i> Linnaeus	<i>Apis</i>	32.4
<i>Eucera decipiens</i> Alfken	<i>Euc dcp</i>	0.8
<i>Eucera transversa</i> Vachal	<i>Euc trn</i>	3.5
<i>Eucera</i> sp. 99/06	<i>Euc sp6</i>	0.7
<i>Habropoda tarsata</i> Spinola	<i>Habro</i>	10.4
<b>Halictidae</b>		
<i>Lasioglossum capsicum</i> Morawitz	<i>Las cps</i>	1.7
<i>Lasioglossum malachurum</i> Kirby	<i>Las mlc</i>	0.7
<i>Lasioglossum marginatum</i> Brulle	<i>Las mrg</i>	23.2
<i>Lasioglossum pseudospeocodimorphum</i> Bluthgen	<i>Las psd</i>	0.8
<i>Lasioglossum transitorium</i> Schenck	<i>Las trn</i>	0.8
<b>Megachilidae</b>		
<i>Megachile</i> sp. 99/01	<i>Meg sp1</i>	0.9

$\mu\text{L}$ , and  $>1.0 \mu\text{L}$ ) and concentration categories (<25%, 25–50%, and >50%) was constructed with each independent nectar reading from the surveys assigned to one of the nine possible cells (resource combinations). An independent nectar reading was the mean volume and concentration measure of all the flowers of a given species in each quadrat.

An information statistic (Shannon's index of Evenness [ $E$ ]) was used to measure the evenness of scores across all the categories and was calculated as the ratio of observed diversity to maximum diversity (Magurran 1988). If each cell has the same score, then  $E = 1$ ; if only one category has a score, then  $E = 0$ . A floral community with the greatest variety of nectar sources available (cells with hits) and an even distribution of resources across cells would have the highest values of  $E$  and could therefore be considered to be of the highest quality. Values for all sites of each independent burn age were entered into the matrix to give seven measures of nectar quality for 1999 and 2000.

#### *Measurement of grazing intensity and nesting substrate availability*

Cattle were the primary grazers in Mt. Carmel National Reserve and the only grazers observed in any of the field sites. Concurrent with the floral surveys, cow pat counts along a 100 m long random transect were used to estimate the level of grazing intensity at each site. This method has been used to estimate grazing intensity in other studies (e.g., Abensperg-Traun et al. 1996).

A measure of the availability of nesting sites and nesting materials was made by measuring the abundance of 22 key environmental variables known to be

important for nesting in the various bee guilds present in our study sites (O'Toole and Raw 1991, Potts and Willmer 1997). The nesting categories selected were based upon the combined experience of the authors over three decades of work on Mt. Carmel and effectively cover all nesting habits observed by bees in this locality. The nesting guilds of bees included were miners, masons, leaf-cutters, stem nesters, carpenters, and highly eusocial cavity nesters. The environmental variables recorded were percentage of coverage of bare soil, vegetation, and rock; percentage of flat ground, sloping ground, and cliff; percentage of hard, intermediate, and soft soils; the abundance of dead tree stumps, dead branches, and hollow stems; the number of rodent holes, large, medium, and small rock cavities; the number of insect burrows in wood, insect burrows in soil, and empty snail shells; and the presence/absence of soft leaf material, resin, and flock. For each site an index of nesting substrate diversity was calculated as the mean number of categories with non-zero scores for each survey; and a site mean calculated as the average of all the surveys. The aim was to produce a simple measure reflecting the overall diversity of nesting opportunities available at each site, and not to provide a quantitative analysis of the specific nesting requirements associated with particular guilds of bees; such an extensive treatment of the nesting data is beyond the scope of this analysis.

#### *Statistical analysis*

We used a variety of approaches to explore the relationship between species abundance for the bee communities and the environmental variables measured at the sample sites. As variation was expected to be con-

tinuous, we employed ordination, rather than cluster analysis, using CANOCO version 4.02 (Ter Braak and Smilauer 1999); and detrended correspondence analysis of the species abundance data indicated that the linear (cf. unimodal) ordination method of redundancy analysis (RDA) was most appropriate as gradient lengths were short ( $<2$  SD), indicating that species composition data were homogeneous (Ter Braak and Smilauer 1998). RDA assumes a linear model for the relationship between the response of each taxon and the ordination axis, thus the components (axes) are constrained by linear combinations of environmental variables. Axis 1 uses a constrained multivariate regression model to select the combination of environmental variables that gives the smallest total residual sum of squares with subsequent axes using the remaining variation not previously accounted for. Statistical tests of significance were by Monte Carlo simulations using 199 permutations, and any environmental variables exhibiting collinearity were automatically excluded (i.e., those with a Variance Inflation Factor [VIF]  $> 20$ ; Ter Braak and Smilauer 1998).

All species sampled in 1999 were included in the initial RDA with the 14 environmental variables. Because the species abundance distribution of bees was highly skewed (three species comprising 66% of total abundance and nearly half the species represented by singletons), we chose to exclude all species contributing  $<0.5\%$  to total abundance, and the remaining 17 species (Table 2) were entered into a second RDA with the same 14 environmental variables. Nectar parameters entered in to the RDA models were caged values (maximum producible nectar), which were all highly correlated with the equivalent open measurements (available nectar) (see *Results: Nectar and pollen*).

Those environmental factors identified in the RDA as being important for the structuring of bee communities (i.e., significant components of the model), were then selected to test for associations with absolute bee diversity, diversity within families, and abundance of the three dominant species. While many properties of the floral communities are likely to have some degree of autocorrelation (e.g., floral abundance and pollen abundance), those not excluded in the ordination models were explored further to investigate the additive effects of these variables. Where appropriate a Bonferroni correction has been applied to control for Type I errors when repeated tests are used. Regressions between the 14 environmental factors and bee diversity and abundance therefore uses a critical  $P$  value of 0.0036 (0.05/14), which represents a very conservative test.

Several measures of diversity have been proposed (Magurran 1988) with species richness being the most widely used; however, log-series alpha is generally considered the most robust and appropriate statistical measure of diversity (Magurran 1988, Southwood and Henderson 2000). In our study, species richness ( $S$ ) is

presented for two reasons: firstly, it allows our findings to be compared readily with other published works; and secondly,  $S$  and alpha diversity of bees in all sites were very highly correlated ( $r^2 = 0.982$ ,  $P < 0.001$ ,  $n = 21$ ) such that either measure allows the same conclusions.

*Apis mellifera* L. (honey bees) were common at most sites, and though non-native, they have been included throughout our analysis because of their long-term interactions with both native bees and flowers, and we therefore consider them to be in equilibrium with the native bees (see Plate 1). Feral colonies were found in many of the wooded areas of Mt. Carmel (S. G. Potts, B. Vulliamy, A. Dafni, G. Ne'eman, P. Willmer, *personal observations*), and honey bees have been actively managed on a continuous basis in this region for millennia. The dominance and long-term presence of honey bees in many of the communities suggests that the displacement of natives, and resultant change in guild structure, is likely to be a persistent feature of this system. The non-native bumble bee *Bombus terrestris* L. comprised  $<0.1\%$  of all bees surveyed, even though it has been recorded as being much more abundant (Dafni and Shmida 1996), and was therefore also included in the analysis.

The bee species abundance data collected in 1999 were entered into a cluster analysis employing the Bray-Curtis similarity using group-average clustering with single linkage (McAleece 1997); the distance matrix was used to construct a dendrogram of similarity in bee faunas across sites. To investigate the contribution of geographic location on community composition, we correlated similarity in species composition with geographical distance separating each pair of sites. To avoid problems of nonindependence within both matrices of values, we employed the Mantel test based on rank correlations and used a permutation test to calculate significance (Smouse et al. 1986).

## RESULTS

### *General community structure and sampling efficiency*

A total of 170 species of bee were identified from the 1999 and 2000 surveys. Five families were represented across sites: Apidae (61 species), Andrenidae (42 species), Megachilidae (38 species), Halictidae (21 species), and Colletidae (8 species). Many species (47%) were represented by singletons. Using the abundance data for the 116 species collected in 1999 gave a jackknife estimate of total species richness for all the habitats through the entire season as 174 species (BioDiversity Professional; McAleece 1997). Thus, we estimated that we captured representatives of approximately two-thirds of the species present.

Each of the 21 sites had a bee community structure consistent with a log series model ( $P > 0.05$  in all cases for the fit of observed log species abundance distribution to expected distribution under a stochastic

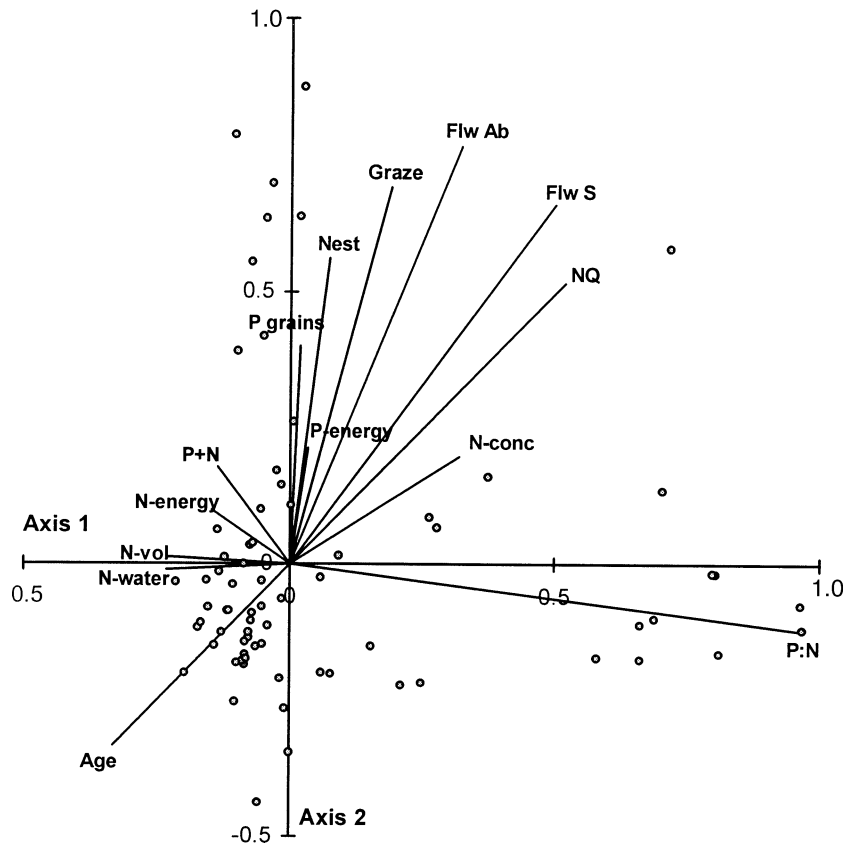


FIG. 1. Ordination diagram from the RDA of the bee abundance matrix comprising all 116 species sampled in 1999. Each point is one or more species, and vector labels refer to environmental factors defined in Table 3. Abbreviations are: Age, site age; Flw S, flower diversity; Flw Ab, flower abundance; Graze, grazing intensity; Nest, nesting substrate diversity; N-energy, nectar energy; N-vol, nectar volume; N-conc, nectar concentration; NQ, nectar quality; P-energy, pollen energy; P grains, number of pollen grains; P:N, ratio of pollen energy to nectar energy; and P + N, total energy.

partitioning model; McAleece 1997). Each community had a small number of abundant species and a large proportion of rare species, indicating that one or a few factors dominate the community (Magurran 1988).

*Factors affecting the structure of the entire bee community*

*Overall relationships between bee species composition and environmental factors.*—The first ordination used all species sampled in 1999 (Fig. 1) and illustrates the relative importance of the measured environmental variables in the structure of the entire bee community. Both the first canonical axis and all canonical axes were statistically significant under the permutation test ( $F = 1.08$ ,  $P = 0.045$ ;  $F = 1.37$ ,  $P = 0.005$ , respectively). The model resulting from the forward selection of environmental variables identified five significant components (Table 3): nectar quality ( $F = 1.73$ ,  $P = 0.005$ ), P:N ratio ( $F = 2.80$ ,  $P = 0.010$ ), floral diversity ( $F = 1.47$ ,  $P = 0.025$ ), floral abundance ( $F = 2.14$ ,  $P = 0.015$ ), and site age ( $F = 1.40$ ,  $P = 0.035$ ). The cumulative variation explained by four canonical axes

was 39.2%, and the overall contribution of each axis and the correlation of the environmental variables with the axes are summarized in Table 4. Axis 1 was primarily a function of floral diversity and P:N ratio, axis 2 was largely a function of floral abundance, and axis 3 a function of floral diversity and nectar quality.

*Floral diversity and abundance.*—Absolute bee species richness and absolute floral species richness were highly significantly correlated ( $r^2 = 0.519$ ,  $P < 0.001$ ,  $n = 21$ ). Partitioning the floral community into annual (88 species) and perennial (37 species) components demonstrated that bee diversity had a strong positive association with the species richness of annuals ( $r^2 = 0.802$ ,  $P = 0.006$ ,  $n = 21$ ), but was independent of perennial species richness ( $P > 0.1$ ). Bee abundance and floral abundance across sites had a statistically significant positive correlation when years are combined ( $r^2 = 0.123$ ,  $P = 0.023$ ,  $n = 42$ ), although this was nonsignificant when the Bonferroni correction was applied (Table 3). However, the bee abundance in 2000 was better related to the previous year's floral abundance ( $r^2 = 0.414$ ,  $P = 0.002$ ,  $n = 21$ ) than to the current year's ( $P > 0.1$ ,  $n = 21$ ).

TABLE 3. Environmental variables measured concurrently with bee surveys and their contribution to the RDA models, with simple regressions between environmental variables and bee diversity and abundance.

Environmental variable code	Definition	Contribution to RDA model		Simple regression ( $r^2$ )	
		All species	Dominant species only	Bee diversity	Bee abundance
Age	site age; number of years post-fire	0.06*	0.07*	0.34***†	0.31***†
Flw S	flower diversity; species richness of insect-pollinated flowering plants per 100 m <sup>2</sup>	0.06*	0.05‡	0.52***†	0.37***†
Flw Ab	flower abundance; cm <sup>2</sup> coverage of entomophilous flowers per 100 m <sup>2</sup>	0.09*	0.06 NS	0.52***†	0.12*
Graze	grazing intensity; number of dung samples per 100 m <sup>2</sup>	0.05 NS	0.09*	0.02 NS	0.02 NS
Nest	diversity of nest sites and nesting substrates per site	0.05 NS	0.10*	0.04 NS	0.11 NS
N-energy	nectar energy; total KJ of energy in the form of nectar per m <sup>2</sup> of habitat	0.04 NS	0.03 NS	0.01 NS	0.00 NS
N-vol	nectar volume; total ml of nectar per m <sup>2</sup> of habitat	0.03 NS	0.03 NS	0.00 NS	0.00 NS
N-conc	nectar concentration; mean percentage of sugar per site	0.04 NS	0.09‡	0.02 NS	0.01 NS
N-water	nectar water content; total g of water per m <sup>2</sup> of habitat	0.03 NS	0.02 NS	0.01 NS	0.00 NS
NQ	nectar quality; diversity of nectar resources per site	0.07**	0.04 NS	0.55***†	0.55**
P-energy	pollen energy; total KJ energy of entomophilous pollen grains per m <sup>2</sup> of habitat	0.03 NS	0.03 NS	0.03*	0.00 NS
P grains	pollen grains; total number of entomophilous pollen grains per m <sup>2</sup> of habitat	0.04 NS	0.04 NS	0.07 NS	0.05 NS
P:N	pollen to nectar ratio; total pollen energy to total nectar energy ratio	0.13**	0.08‡	0.30*	0.01 NS
P + N	total energy; sum of nectar and pollen energy per m <sup>2</sup> of habitat	...	...	0.06 NS	0.00 NS

Notes: Codes are consistent with figures. Results of Monte Carlo simulation RDA using forward selection of environmental variables are given as proportional contribution to overall model with significance. P + N exhibited collinearity and was therefore excluded from the permutations test. Bee diversity uses 1999 data ( $n = 21$ ), and abundance uses 1999 and 2000 data ( $n = 42$ ); see *Methods* for full explanation.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ; ‡  $P < 0.1$ ; NS,  $P > 0.1$ .

† Indicates the regression is still significant after the Bonferroni correction has been applied (i.e.,  $P < 0.0036$ ).

*Nectar and pollen.*—Nectar energy values for open and caged floral communities were very highly correlated ( $r^2 = 0.917$ ,  $P < 0.001$ ,  $n = 42$ ) with caged values being approximately three times higher. Neither bee diversity nor abundance were associated with nectar volume, nectar concentration, nectar energy, or nectar water content (Table 3). However, nectar quality, defined as diversity of nectar resources, was strongly correlated with floral diversity ( $r^2 = 0.747$ ,  $P < 0.001$ ,  $n = 14$ ) and diverse bee communities were strongly associated with high quality nectar providing sites, ( $r^2 = 0.549$ ,  $P = 0.002$ ,  $n = 14$ ; Fig. 2). This measure of nectar quality was of much greater predictive value than any other measure of nectar.

Bee diversity and abundance were not related to pollen energy availability, total energy availability (P + N), pollen grain number, mean pollen grain size, or P:N ratio (Table 3). Though none of the quantitative measures of pollen traits appear to be important determinants of bee community structure, as expected, they are all closely related to floral abundance: pollen grain number ( $r^2 = 0.552$ ,  $P < 0.001$ ,  $n = 42$ ), pollen energy ( $r^2 = 0.183$ ,  $P = 0.005$ ,  $n = 42$ ), and total energy ( $r^2 = 0.110$ ,  $P = 0.032$ ,  $n = 42$ ).

*Geographic location.*—A cluster analysis using the 1999 species abundance data for the sites grouped in the seven independent burns produced a dendrogram of similarity (Fig. 3). The two most similar sites were

at Etzbah (EtzNB and Etz74), with 58.9% similarity in species abundance composition and were only 0.5 km apart; these were closely followed by the two Denia sites (DenNB and Den98) which had a similarity of 52.6% and were separated by 0.8 km. In contrast, the two freshly burnt sites, Den98 and Hod98, which were 7.5 km apart, shared a similarity of only 42.2%, and the two unburnt sites (DenNB and EtzNB), 6.3 km apart, had a similarity of 37.9%. However, even the most dissimilar sites (Mit83 and EtzNB) still shared at least 27.4% of species. A general pattern of decreasing similarity with distance was apparent when all pairs of sites were considered (Fig. 4), and a statistically significant amount of variation in community similarity was therefore explained by geographical distance (Mantel test:  $r^2 = 0.174$ ,  $P = 0.034$ ) with the greatest changes occurring at the more local scale where sites were separated by <2 km (Fig. 4).

*Factors affecting subcomponents of bee community*

*Dominant bee species and environmental factors.*—For the second ordination analysis, the bee species matrix was reduced from 116 species to 17 by entering those which contributed >0.5% to total abundance, and these 17 species still accounted for 81.9% of the overall bee abundance (Table 2). Just three species were particularly dominant: honey bees, *Apis mellifera* L. (32.4%); *Lasioglossum marginatum* (23.2%); and *Ha-*



TABLE 4. Summary statistics for the four canonical axes of the RDA performed using the matrix containing all bee species and the matrix of environmental variables.

All species model	Axis 1	Axis 2	Axis 3	Axis 4	Total variance
Eigenvalue	0.134	0.111	0.078	0.068	
Species–environment correlation	0.996	0.976	0.968	0.982	
Cumulative variance of species data (%)	13.4	24.5	32.3	39.2	
Cumulative variance of species–environment relation (%)	18.6	34.1	45.0	54.5	
Sum of all unconstrained eigenvalues					1.000
Sum of all canonical eigenvalues					0.718
Correlation coefficients ( <i>r</i> )					
Age	-0.33	-0.33	-0.15	0.05	
Flw S	0.50***	0.65	0.25***	0.33**	
Flw Ab	0.32	0.75***	-0.01*	0.20***	
Graze	0.19	0.68*	0.13	-0.21***	
Nest	0.07*	0.55	0.35	-0.25***	
N-energy	-0.15**	0.10*	-0.20	0.01***	
N-vol	-0.23*	0.01	-0.39	0.10***	
N-conc	0.32	0.19	-0.21	0.01	
N-water	-0.23	-0.01	-0.38	0.11***	
NQ	0.52	0.50	-0.07***	-0.33***	
P-energy	0.03	0.21	-0.13	0.50	
P grains	0.02	0.39	-0.19	0.52	
P:N	0.96***	-0.12**	-0.04	0.08***	
P + N	-0.14	0.17	-0.25	0.19	

Notes: See Table 3 for definitions of abbreviations. The correlations of the environmental variables with axes are given with their individual significances.  
 \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

*bropoda tarsata* (10.4%). In the ordination diagram, based on the second model (Fig. 5), these three species (underlined) were clearly separated into different sectors of the biplot. Though the first canonical axis was not statistically significant on its own ( $F = 1.40, P > 0.1$ ), when taken together with the other axes, significance was found ( $F = 1.43, P = 0.015$ ). The first two axes displayed in the ordination diagram explained 29.6% of the variation, and the total variation explained

by all the axes was 49.5% (Table 5). Axis 1 had a high loading for grazing, and axis 2 had a high loading for site age (Table 5). Several other environmental characters, namely floral diversity, nectar quality, and nectar concentration, were correlated with axis 2, and these were known to decrease with time after a site was burnt (Potts et al. 2003). Thus, we consider this axis as being

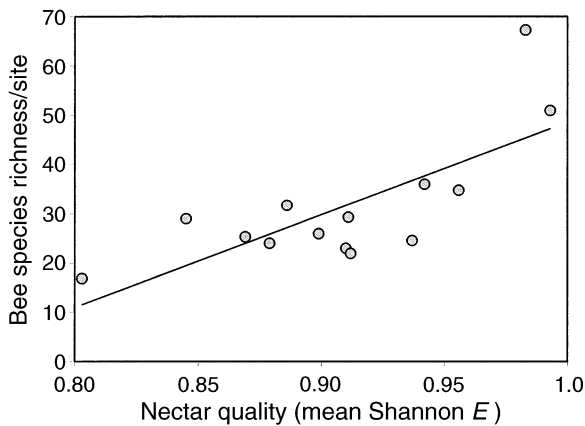


FIG. 2. Bee species richness as a function of nectar quality (mean equitability measure).

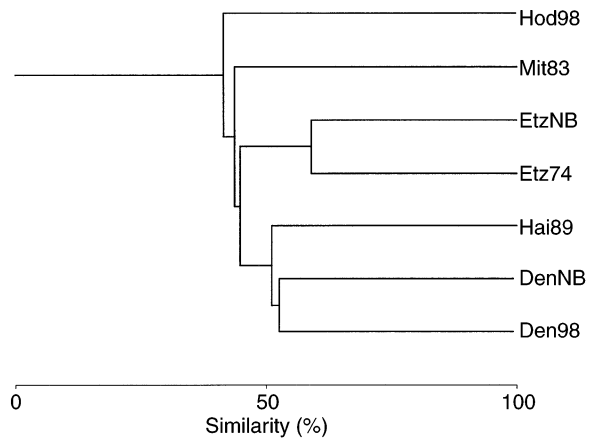


FIG. 3. Dendrogram of cluster analysis of bee species composition across the seven primary sites on Mt. Carmel, Israel (see Table 1). Number following site name indicates the year of burn, and “NB” indicates the site was not burnt.

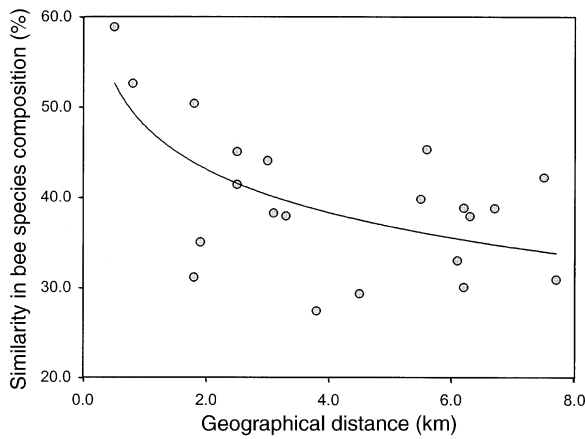


FIG. 4. Plot of similarity in bee species composition against geographical separation for all pairs of sites on Mt. Carmel, Israel.

a function of post-fire age. Forward selection of the environmental variables in the model then showed three statistically significant components: grazing ( $F = 1.88$ ,  $P = 0.015$ ), post-fire age ( $F = 1.84$ ,  $P = 0.030$ ), and nest substrate diversity ( $F = 2.68$ ,  $P = 0.010$ ). Three others approached significance: nectar concentration ( $F = 1.77$ ,  $P = 0.065$ ), P:N ratio ( $F = 1.93$ ,  $P = 0.075$ ), and flower diversity ( $F = 1.53$ ,  $P = 0.100$ ).

*Within family diversity, individual species abundance and environmental factors.*—Partitioning the whole bee community revealed that some species and families were differentially structured by floral resources. Though no relationship was apparent between the entire bee community and quantitative measures of nectar availability, there were some associations for the Apidae subcomponent of the community. For instance, the abundance of the large fast-flying bee, *Habropoda tarsata* (see Plate 1), dominant in all sites during the early part of the season, was positively correlated with both nectar energy ( $r^2 = 0.389$ ,  $P = 0.003$ ,  $n = 21$ ) and total (P + N) energy ( $r^2 = 0.303$ ,  $P = 0.010$ ,  $n = 21$ ), though the latter was not significant after Bonfer-

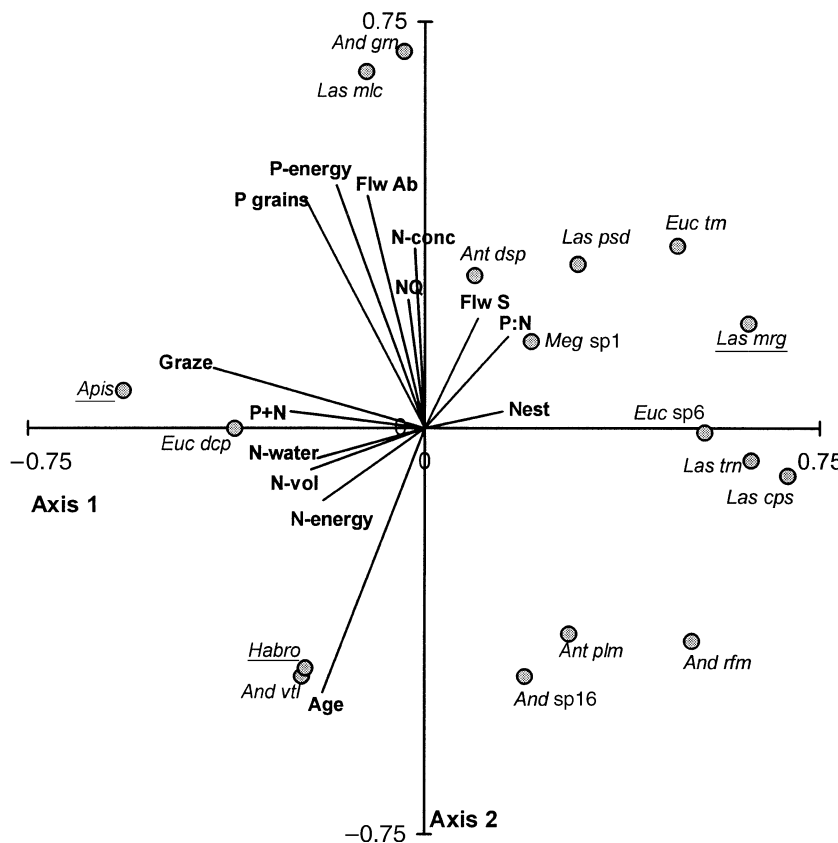


FIG. 5. Ordination diagram from the RDA of the bee abundance matrix comprising only the 17 most dominant species (abundance > 0.5%). Vector labels refer to environmental factors defined in Table 3. Abbreviations are: Age, site age; Flw S, flower diversity; Flw Ab, flower abundance; Graze, grazing intensity; Nest, nesting substrate diversity; N-energy, nectar energy; N-vol, nectar volume; N-conc, nectar concentration; N-water, nectar water content; NQ, nectar quality; P-energy, pollen energy; P grains, pollen grains; P:N, ratio of pollen energy to nectar energy; and P + N, total energy. Species codes are given in Table 2. The three species with the greatest abundances are underlined: *Apis*, *Apis mellifera*; *Las mrg*, *Lasioglossum marginatum*; *Habro*, *Habropoda tarsata*.

TABLE 5. Summary statistics for the four canonical axes of the RDA performed using the matrix containing the dominant 17 bee species and the matrix of environmental variables.

Dominant species model	Axis 1	Axis 2	Axis 3	Axis 4	Total variance
Eigenvalue	0.167	0.129	0.107	0.089	
Species–environment correlation	0.907	0.967	0.945	0.983	
Cumulative variance of species data (%)	16.7	29.6	40.2	49.5	
Cumulative variance of species–environment relation (%)	22.9	40.7	55.4	67.7	
Sum of all unconstrained eigenvalues					1.000
Sum of all canonical eigenvalues					0.726
Correlation coefficients ( <i>r</i> )					
Age	−0.19	−0.49***	0.21	−0.12	
Flw S	0.10	0.20***	−0.01	0.24*	
Flw Ab	−0.11	0.43	−0.01	0.55	
Graze	−0.40*	0.11***	0.15*	0.03	
Nest	0.15	0.03***	0.00	−0.26**	
N-energy	−0.19	−0.13***	−0.16	−0.17*	
N-vol	−0.22	−0.08***	−0.23	−0.31*	
N-conc	−0.02	0.33***	−0.69***	0.05	
N-water	−0.20	−0.06***	−0.23	−0.31*	
NQ	−0.03	0.24***	−0.28	0.30	
P-energy	−0.17	0.45	−0.07	0.03	
P grains	−0.23	0.42	−0.02	−0.08	
P:N	0.16	0.17*	−0.11**	0.85***	
P + N	−0.25	0.03	−0.20	−0.15	

Notes: See Table 3 for definitions of abbreviations. The correlations of the environmental variables with axes are given with their individual significances.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

roni correction. The abundance of *Apis mellifera* was positively, but nonsignificantly, correlated with grazing intensity ( $r^2 = 0.690$ ,  $P = 0.021$ ,  $n = 21$ ) and nectar-rich plants are often associated with intensely grazed areas of Mt. Carmel (A. Dafni and G. Ne'eman, *personal observations*); this link is apparent from the ordination biplot (Fig. 5). These two species were the most abundant within the Apidae and were closely related to resource availability, even though the family as a whole showed no close linkage to environmental variables ( $P > 0.1$ ).

In contrast, the Megachilidae appear to be organized by both nectar and pollen resources. Species richness within this family was related to floral diversity ( $r^2 = 0.682$ ,  $P < 0.001$ ,  $n = 21$ ), and P:N ratio ( $r^2 = 0.386$ ,  $P = 0.003$ ,  $n = 21$ ) was a good predictor of the number of individuals recorded within this family.

The diversity within the second most speciose family, Andrenidae, was positively associated with floral diversity ( $r^2 = 0.276$ ,  $P = 0.015$ ,  $n = 21$ ) and possibly the diversity of annuals ( $r^2 = 0.505$ ,  $P = 0.074$ ,  $n = 21$ ). Of the remaining two families, the Halictidae were most diverse in communities with high P:N ratios ( $r^2 = 0.377$ ,  $P = 0.004$ ,  $n = 21$ ), and the highly dominant *Lasioglossum marginatum* was linked to pollen-rich sites (those with a high P:N ratio) and areas providing good nesting opportunities (Fig. 5). However, the Col-

letidae showed no particular association, though this family was only represented by a total of 10 individuals from eight species in the whole survey.

## DISCUSSION

Mt. Carmel National Reserve, Israel, supports a diverse bee fauna, which shows great variation over space and time. The entire bee community comprises many rare species, even at the local level, and this phenomenon of widespread rarity is consistent with many large-scale bee surveys (Barbola and Laroca 1993, Williams et al. 2001, but see Pearson 1933, Kevan et al. 1997). This may reflect a high proportion of "transient" species typically associated with highly disturbed habitats (Rundel et al. 1998) or that many species of bee typically occur at low densities throughout their range. An alternative explanation may be that this pattern is characteristic of leptokurtic dispersal (Bosart and Prowell 1998). Relative to distances expected if dispersals are normally distributed, a leptokurtic distribution is skewed to a lower mean with a long tail encompassing rare long-range dispersal events; and this pattern is found in some insect species (e.g., Aikman and Hewitt 1972). The net result is that bee communities may include many rare species from relatively distant populations not supported locally. The high proportion of rare bees may therefore result in "loose"

linkages between floral and bee community structure, such that a nontrivial proportion of the variation cannot be explained by floral community characteristics, nest site availability, or geographical location alone.

The first ordination, using all bee species, explained 39% of variation in bee community structure (Fig. 1). Nectar quality and the relative abundance of pollen (P:N ratio) are the two principle components (Table 3) of floral communities that appear to be important in organizing gross community structure of the flower-visiting fauna. Absolute diversity of bees is strongly related to the diversity of flower species, especially annuals, and it is the variety of nectar-foraging resources that appears to be the defining factor. Though floral diversity and nectar resource diversity are correlated, the ordination analysis shows that these two habitat characteristics are additive in their influence on bee community structure. This is a novel finding that should direct attention away from crude estimates of mean nectar concentration or mean volume of nectar available. It is consistent with the idea that a high diversity of resources promotes a high diversity of consumers in insect communities (e.g., Price 1984), with the number of foraging niches being positively related to the number of nectar and pollen profiles and flower types available. In effect, different bee guilds show different associations.

Reducing the community to its 17 dominant species in the second ordination (Fig. 5) revealed that grazing intensity and post-fire age were primary organizing factors, with an indication that a non-floral resource, namely nesting substrate diversity, may also be important (Table 3). Fire and grazing have prominent roles in the structuring of many aspects of Mediterranean-type ecosystems (Rundel et al. 1998), including vegetation, and core bee species are therefore expected to respond to these perturbations.

Both models account for ~40–50% of the variation in the composition of the bee community (Tables 4 and 5), which, based purely on floral community characteristics, is large, considering the highly fluctuating and unpredictable nature of many bee communities (reviewed by Williams et al. 2001). Our findings have identified several components of floral communities that may have important functions in explaining the compartmentalization found in some flower-visiting communities (Dicks et al. 2002). Of the remaining variation not explained by floral community structure, a smaller, but significant amount, was accounted for by the effect of geographical separation on species composition between sites (Fig. 4). This is a particularly striking finding given that some bees are capable of flying distances comparable to those which separated our study sites (e.g., 360–600 m for bumble bees [Dramstad 1996], 200–800 m for solitary bees [Wes-serling and Tscharnke 1995]). However, given that most species on Mt. Carmel were small to medium-sized solitary bees and resources were generally locally

abundant, we might expect most of the bees to forage relatively short distances (10s rather than 100s of meters). Honey bees on Mt. Carmel were from both feral colonies and hives, and capable of flying distances greater than our site separations, and so may have been found in higher numbers in some sites, even if nests/hives were scarce. Our experimental design attempted to minimize, as far as possible, the effects of bee movement on the composition of bees sampled in our surveys by selecting sites widely separated from each other and situated within large tracts of uniform vegetation. The aim was to sample areas where bees would nest and forage within patches of similar vegetation rather than areas where bees would move between patches of different habitat. However, this is a wide-ranging difficulty for any study that surveys bees in a landscape where there is habitat heterogeneity on a scale comparable to that of bee flight distances; indeed there are few landscapes that are uniform enough for this not to be a problem (e.g., areas of intensive agriculture).

The linkage between bee and flower diversity at the overall community level is accounted for by the strong associations found within the Andrenidae and Megachilidae, which appear to be absent from the Apidae. In a phryganic community similar to the one we studied, but in Greece, Petanidou and Ellis (1996) demonstrated an association between flower visitation by Andrenidae and the diversity of annuals. Our data support this linkage, with the diversity of andrenids closely matched to the diversity of all flowers and more specifically to annuals. Indeed, Andrenidae are short-tongued bees and therefore are often restricted to shallow, open-access flowers, traits that are characteristic of many annual species. In a contrasting system (set-aside field in Germany), Gathmann et al. (1994) established that habitats with greater floral diversity presented trap-nesting bees (mainly megachilids) with better and richer food resources. Our findings suggest that it is the availability of pollen relative to nectar that is the crucial property of floral communities that determine the composition of Megachilidae and Halictidae on Mt. Carmel.

Overall bee abundance is a positive function of the abundance of flowers in a particular habitat, such that habitats with abundant flowers have greater possibilities for partitioning of available resources. In a study of short-grass prairie communities, there was no clear relationship between floral and bee abundance (Tepe-dino and Stanton 1981), and the authors suggest that in any given year, floral abundance determines the number of nest cells that can be provisioned, rather than the number of adult bees present. There is some evidence in our data that the previous season's floral abundance may be a better predictor of the current season's bee abundance, which is of course likely, as the current generation of offspring developed on the resources provisioned to the nest in the previous season and so de-



pended upon local availability of pollen and nectar at that time.

Though we have identified a crude relationship between plant and pollinator abundance at the community level, we have not found a clear linkage using any quantitative nectar character. Because pollen is considered the primary reward of phryganic systems (Herrera 1985), it is not surprising that nectar energy availability is unimportant for organizing the community as a whole (though it may be important for individual species), and our findings give quantitative support to this. Relative pollen availability (P:N ratio) is important in structuring the size and richness of the entire bee fauna, and particularly the Megachilidae and Halictidae, whereas absolute energy from pollen is at best poorly predictive. It has been shown that pollinator diversity generally increases with the pollen energy content of entomophilous flowering species in a Mediterranean ecosystem (Petanidou and Vokou 1990). However, it may be that pollen energy is not the key property of pollen that is important to bees; indeed, it may be protein content or composition, as this is the primary protein source for developing larvae. Grains vary interspecifically in their protein content and ratio of lipid:carbohydrate energy (Baker and Baker 1983), and these two components will differ in their nutritional value to developing bee brood (Roulston and Cane 2000). Pollen quality has yet to be fully examined as a possible determinant of bee community structure; an approach calculating biochemical composition of pollen across a series of habitats and relating this to the bee fauna is needed.

Two dominant species within the bee community, *Apis mellifera* and *Habropoda tarsata* (both Apidae), however, may depend on the high energy availability in the form of nectar. *H. tarsata* is a very large, fast-flying, and consequently, high energy-demanding species and is most abundant in mature woodland and unburnt areas where the flora is dominated by nectariferous perennial flowering plants. Similarly, honey bees may be able to exploit high-energy resource patches within a habitat much more effectively than their solitary counterparts by virtue of their recruitment-based foraging system (Roubik 1989). Thus, habitats with the greatest energy are able to support the most and/or largest honey bee colonies. The abundance of solitary bees in comparison appears not to be limited solely by energy but by other habitat component(s).

The high degree of similarity in bee faunas across all sites (Fig. 3) indicates that the community is composed of generalist species able to utilize a wide range of floral resources with many less common species utilizing the particular suite of post-fire regenerating flora found at a given site. In the highly dynamic landscape of Mt. Carmel, niche overlap appears to be high with a large proportion of generalist bee species utilizing a range of contrasting habitats in close proximity to each other. This is concordant with the findings of Moldenke

(1975), who suggests that in Californian plant-pollinator communities there may be greater selective pressure for pollinator specialization in more predictable and stable environments. Consequently, in our highly disturbed system, widely separated areas of equivalent burn age may be expected to share fewer common species than spatially proximate sites of different ages (Fig. 4). No pair of sites was >59% similar, and the remaining differences are consistent with other studies that have reported high levels of species turnover in geographically proximate areas (e.g., Herrera 1988, Minckley et al. 1999). Similar and low similarity values were found for closely situated bee communities in blueberry fields (Kevan et al. 1997), and the authors suggest this is to be expected as the reconstitution of sites following disturbance, in this case pesticide application, is likely to follow a distinct pattern of recolonization. In the same way, we argue that the burn-age-specific floral community structure acts to modulate the composition of the local geographic species pool of bees as the communities re-establish. Fire and grazing are important disturbance factors influencing floral community structure; both of these factors deserve further study (Potts et al. 2003). In addition, the role of nest site (and substrate) availability in structuring Mediterranean bees communities is often suggested (e.g., Petanidou and Ellis 1996), but our data provide the first quantitative evidence to support this.

Floral community composition, reward structure, and geographical locality were all found to be fundamental in organizing the bee community structure in the mosaic of habitats making up Mt. Carmel National reserve in Israel. Our approach indicates that an understanding of the underlying ecological interactions between plants and pollinators at a variety of spatial scales is essential if we are to conserve and restore many of the threatened communities found worldwide (São Paulo Declaration on Pollinators 1999). The broad methods applied here, in conjunction with other more specific studies, will help underpin any landscape management strategies aiming to maintain adequate pollination services for both natural and agricultural systems.

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