

Role of nesting resources in organising diverse bee communities in a Mediterranean landscape

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Abstract. 1. The habitat components determining the structure of bee communities are well known when considering foraging resources; however, there is little data with respect to the role of nesting resources.

2. As a model system this study uses 21 diverse bee communities in a Mediterranean landscape comprising a variety of habitats regenerating after fire. The findings clearly demonstrate that a variety of nesting substrates and nest building materials have key roles in organising the composition of bee communities.

3. The availability of bare ground and potential nesting cavities were the two primary factors influencing the structure of the entire bee community, the composition of guilds, and also the relative abundance of the dominant species. Other nesting resources shown to be important include availability of steep and sloping ground, abundance of plant species providing pithy stems, and the occurrence of pre-existing burrows.

4. Nesting resource availability and guild structure varied markedly across habitats in different stages of post-fire regeneration; however, in all cases, nest sites and nesting resources were important determinants of bee community structure.

Key words. Bees, community organisation, Mediterranean, nesting guilds, resource availability.

Introduction

Organisation of bee communities is closely related to the floral communities they forage upon, with several key characters having been identified, including floral diversity (e.g. Tepedino & Stanton, 1981; Gathmann *et al.*, 1994), floral abundance (e.g. Banaszak, 1996), and availability of pollen and nectar resources (Petanidou & Vokou, 1990). However, few studies have attempted to quantify the combined effect of these structuring agents (but see Potts *et al.*, 2003a).

In turn, some drivers have been identified that impact directly upon bee communities, while others act indirectly through modification of floral communities or other habitat

characteristics. These drivers include changing land use practices such as agricultural intensification (Banaszak, 1995), habitat fragmentation (Jennersten, 1988) and habitat isolation (Steffan-Dewenter & Tscharntke, 1999), grazing (Potts *et al.*, 2003a), and agrochemical use (O'Toole, 1993). Other important drivers have also been recently identified: fire (Potts *et al.*, 2003b); disease (Watanabe, 1994) and parasite spread (Schmid-Hempel & Durrer, 1991); climate change (Price & Waser, 1998); introduction of non-native plants (Brown & Mitchell, 2001; Chittka & Schürkens, 2001); and competition with managed pollinators (Butz-Huryn, 1997; Steffan-Dewenter & Tscharntke, 2000).

While the forage rewards provided by floral communities are generally accepted as the primary determinants of pollinator community structure, there is an increasing body of evidence suggesting that nest sites and nesting resources may

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also play an important role for bees (e.g. Petanidou & Ellis, 1996). Several studies have investigated particular biotic and abiotic factors influencing nesting success or nest-site selection for single species (e.g. Potts & Willmer, 1997; Wuellner, 1999), yet only two studies to date have provided quantitative evidence showing that nesting resources may have an important role in the structuring of entire communities (Potts *et al.*, 2003a) or key guilds within communities (Cane, 1991). The study of Potts *et al.* (2003a) examined 14 habitat characteristics as predictors of bee community structure; floral characters were the primary determinants, however 5% of the entire bee community structure was explained by the diversity of nesting resources available, and 10% of the structure when only dominant bees were considered. These findings indicate that nesting resources in general play a small but important role in organising bee communities, and direct the present study in partitioning this variation into the function of specific resources and substrates.

Bees exhibit a diverse array of nesting strategies with respect to the part of the habitat they nest in, the type of substrate they use, and the materials required for nest construction. Indeed, bees can be partitioned into several exclusive guilds on the basis of their nesting habits (O'Toole & Raw, 1991), known as miners, masons, carpenters, and social nesters. Miners dominate in many open habitats and excavate holes in the ground that may be lined with glandular secretions. All species of Andrenidae, Melittidae, Oxaeidae, and Fideliidae are miners, as are most Halictidae, Colletidae, and Anthophoridae. Masons generally use pre-existing cavities in which to construct their nests, and these may be pithy or hollow plant stems, small rock cavities, abandoned insect burrows, or even snail shells. Masons are from the family Megachilidae, and they line their nests with materials found within their habitat rather than with glandular secretions. Leaf-cutters are a subgroup of masons, also megachilids from the genus *Megachile* and *Creightonella*; they use pre-existing cavities and line their nest with freshly gathered leaf material. Carpenters excavate their own nests in woody substrate; this habit is found in two genera within the Apidae (*Xylocopa* and *Ceratina*) and one from the Megachilidae (*Lithurgus*). Social nesters use larger pre-existing cavities to build large social nests; members of this guild are all from the Apidae and include honeybees, bumblebees, and stingless bees. Finally, the members of one guild do not construct nests at all, but instead parasitise the nests of other bees and are therefore referred to as cuckoo bees or kleptoparasites. Cuckoo bees have evolved in several families.

Potentially important habitat characteristics previously investigated as being important resources for various nesting guilds are soil texture (Cane, 1991), soil hardness (Brockmann, 1979; Potts & Willmer, 1997), soil moisture (Wuellner, 1999), aspect and slope (Potts & Willmer, 1997), amount of insolation (Weaving, 1989; Jeanne & Morgan, 1992), cavity shape and size (Schmidt & Thoenes, 1992), and diameter of pre-existing holes (Scott, 1994).

Using a hyper-diverse bee assemblage as a model system, this study aims to: (1) quantify the importance of nesting resources in the organisation of overall bee community

structure; (2) determine which guilds are most influenced by nesting resources; and (3) identify the specific habitat characteristics to which the whole community and individual species are responding.

Methods

Sites

The National Reserve on Mt Carmel, Israel, comprises 150 km² of *Pinus halepensis* pine forest. Mount Carmel has a typical Mediterranean climate with cool wet winters and warm dry summers. The reserve now has a mosaic of regenerating post-fire patches, with freshly burnt open habitats, intermediate-aged scrub (phrygana), mature pine forest stands, and all intermediate habitat types. Several major burns have occurred (two in 1998, and one in each of 1989, 1983, and 1974, giving *site ages* of 10, 16, and 25 years); the resultant post-fire regenerating patches are found within large tracts of unburnt pine forest.

Within each burnt area, three 1-ha sites were selected as being representative of that burn age and each was at least 300 m (usually > 600 m) away from another site or boundary with a different vegetation type. This separation distance, though potentially within the foraging range of large solitary and social bees (Wesslerling & Tscharrntke, 1995), is unlikely to compromise the independency of the sites in this study as forage and nesting resources were always found in high concentrations locally within each site. Site details are summarised in Table 1. Full descriptions of the floral communities can be found in Zohary (1982), and more detailed site information can be found in Potts *et al.* (2003a, b).

With this design there is inevitably a degree of pseudo-replication imposed by the structure of the landscape which cannot be experimentally manipulated. However, this potential shortcoming was minimised as far as possible by using independent burns whenever available (e.g. there were two fires in 1998, and two discrete areas of unburnt pine were used as controls) and also separating sites as much as possible. Control sites were selected to be close (> 600 m but < 1 km) to the burnt areas studied and were typical of the large stands of mature pine prior to fire. In view of this a degree of caution is therefore suggested when interpreting findings.

Bee surveys

At each of the 21 sites, bees (Hymenoptera: Apoidea) were monitored throughout the main flight season of February to May in 1999. Five surveys were undertaken at each site spread evenly through the season. Each survey consisted of a 200-m linear transect walk made over 20 min at 08.00, 11.00, and 14.00 hours; these times were chosen to cover the main period of bee activity. A transect started from a random point within the site and was walked in a random direction; all bees encountered within 1.5 m of the observer were recorded. Those species that could be identified

Table 1. Summary of site locations, burn ages, and habitat area used in the 1999 surveys on Mt Carmel, Israel.

Site code	Location	Year burnt	Coordinates (latitude, longitude)	Approximate area (ha)
Den98	Wadi Denia	1998	32° 45.8', 35° 00.1'	100
Hod98	En Hod	1998	32° 41.9', 34° 58.6'	450
Hai89	Hai Bar Reserve	1989	32° 44.9', 35° 01.2'	300
Mit83	Mitla	1983	32° 44.2', 34° 59.6'	400
Etz74	Etzbah	1974	32° 42.4', 34° 58.9'	80
EtzNB	Etzbah	<1950	32° 42.4', 34° 58.8'	240
DenNB	Wadi Denia	<1950	32° 45.7', 35° 00.4'	190

unambiguously while in flight were scored on a recording sheet, while those which could not be were caught using a hand net and retained for identification at Oxford University Museum (U.K.).

As it is extremely difficult and time consuming to locate nesting bees in scrub habitats, this study used surveys of foraging bees as a surrogate. The authors consider the assumption that bees observed foraging in any particular habitat are representative of those nesting to be reasonable.

Family classification was in accordance with Michener (2000), and each species was assigned to the appropriate functional group based on nesting habit: ground nesting miners (designated as ground); mason bees that use rock substrate (masons), hollow stems (stem), pre-existing burrows (old nest), or snail shells (snail); eusocial bees nesting in large cavities (cavity); carpenters (carpenter); and kleptoparasites (cuckoo).

Nesting resources surveys

Using existing literature (e.g. Stephen *et al.*, 1969; O'Toole & Raw, 1991; Potts & Willmer, 1997; Michener, 2000) in conjunction with the authors' combined field experience on Mt Carmel, a list of known and potentially important nesting resources was compiled. These resources and the methods used to measure them are listed in Table 2. The resources available for nesting were surveyed twice at each site during 1999, using a 200-m linear transect with 10 1-m² quadrats placed evenly along it. A 1-m² sample unit was considered an appropriate size based on a preliminary assessment of the distribution of resources within habitats.

Statistical approach

A variety of methods was used to explore the relationships between nesting guilds and nesting resources and how these varied between sites of different ages. Differences between the species richness and abundance of bees in each guild with respect to site age were tested using a Generalised Linear Model, and differences between paired means with Tukey's honestly significant test. Changes in nesting resources through time also used the same approach.

Ordination was used to identify associations between bee community structure and nesting resources. Detrended

correspondence analysis of the species data indicated that linear, rather than unimodal, ordination methods were most appropriate, therefore redundancy analysis (RDA) was employed. A first model included all 116 bee species; however, given that more than half of the species in the surveys were represented by singletons, a second model used the 17 species that contributed >0.5% to total abundance. A Monte Carlo global permutation test gave the significance of the canonical axes and the significance of the environmental variable-axis relationships was determined using a Monte Carlo permutation test under a reduced model. Environmental variables were automatically forward selected. The RDA analysis was performed using CANOCO 4.5 (Ter Braak & Smilauer, 1999). The results of the ordinations were used as a guide to test for the strength of associations between specific nesting resources and the abundance of guilds and single species.

Results

Nesting guild structure in habitats of different post-fire age

Total bee species richness shows a curvilinear relationship with site age (Fig. 1a). The number of species is highest in the freshly burnt sites, lowest in the intermediate-aged habitats, and mature habitats show a slightly higher species richness than the intermediate sites. The most speciose guild, the ground nesters, mirrors this pattern with significant differences between mean species numbers ($F_{4,16} = 4.58$, $P = 0.012$): freshly burnt sites have significantly more species than the 16- and 25-year-old sites ($P < 0.05$). The mean number of mason and stem-nesting species varies with site age ($F_{4,16} = 3.71$, $P = 0.025$ and $F_{4,16} = 2.91$, $P = 0.055$ respectively). Masons are more speciose in 10-year-old sites ($P < 0.05$) than in freshly burnt or mature sites. Similarly stem nesters are represented by more species in 10-year-old sites than mature sites ($P < 0.05$). No other guilds show significant changes in species numbers with site age.

The total number of bees is highest in freshly burnt sites and lowest in the 16-year-old sites with intermediate numbers in the mature sites (Fig. 1b). Ground nesting bees dominate the community at all sites, but they decrease steadily in abundance with site age, being least common in the 25-year-old site, and then increase in abundance again in mature sites.

Table 2. Definition, code, and methods for measuring nesting resources in Mt Carmel National Reserve, Israel.

Resource code	Method
Soil	% of exposed ground in a quadrat free of vegetation and litter
Flat	% of ground in a quadrat with slope < 30°
Slope	% of ground in a quadrat with slope 30–60°
Steep	% of ground in a quadrat with slope > 60°
Wood	Amount of dead woody substrate in a quadrat, scored on a categorical scale 0–2
Stems	Number of exposed pithy or hollow plant stems per quadrat
Soft	Number of soil penetrometer (ELE International, Leighton Buzzard, U.K.) readings out of 10 with values < 2.0 kgf cm ⁻²
Medium	Number of soil penetrometer readings out of 10 with values 2.0–4.0 kgf cm ⁻²
Hard	Number of soil penetrometer readings out of 10 with values > 4.0 kgf cm ⁻²
Cavities	Number of large (> 2 cm diameter) cavities in rocks, trees, and rodent holes per quadrat
Old nests	Number of pre-existing insect burrows in the ground or wood per quadrat
Snail shells	Number of empty snail shells per quadrat

kgf, Kilograms of force.

Eusocial cavity nesters are also abundant in all sites, while the other guilds are represented by relatively few individuals. There are, however, no statistically significant differences in the abundance of bees through time for any guild.

Nesting resources in habitats of different post-fire age

The availability of nesting resources varies with site age and mean values are given in Table 3. Not surprisingly, the

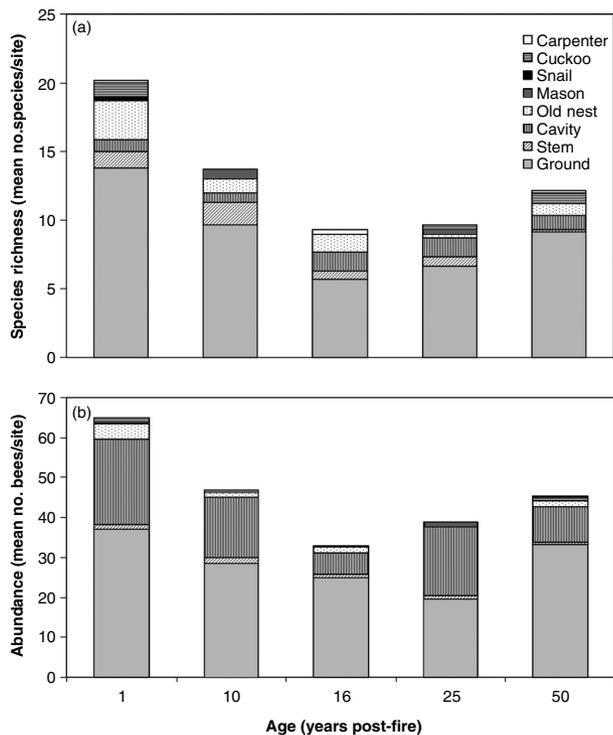


Fig. 1. (a) Species richness, and (b) abundance within bee nesting guilds as a function of site age (time since burnt) for the bee communities of Mt Carmel, Israel. Mature pine sites were burnt before 1950 and labelled as age 50.

availability of soil decreases with post-fire age, with freshly burnt sites having significantly more bare ground available ($F_{4,16} = 7.25$, $P = 0.002$) than all older sites ($P < 0.05$). The freshly burnt sites have 58.6% coverage whereas all other sites have less than 23% coverage. The number of pithy stems available is greater in the 10-year-old site (2.0 per m²) than all other ages (< 1.2 per m²), though the difference is not statistically different.

Relationship between nesting guilds and resources

The redundancy analysis using the entire bee community indicates that bee community structure is significantly correlated with nesting resources (Table 4: sum of all canonical variables = 0.667; $F = 1.34$, $P = 0.004$ for all canonical axes). The first and second axis explain 12.8% and 10.8% of the variance respectively, in the model (Fig. 2a) and four variables are significant: soil (7% of variation explained, $F = 1.55$, $P = 0.024$); cavities (12%, $F = 2.50$, $P = 0.001$); slope (7%, $F = 1.70$, $P = 0.009$); and flat (6%, $F = 1.51$, $P = 0.035$).

Partitioning the bee community into nesting guilds also shows that these are organised by nesting resources (Table 5: sum of all canonical variables = 0.722; $F = 1.73$, $P = 0.025$ for all canonical axes). This model had two significant terms, cavities (9% of variation explained, $F = 3.31$, $P = 0.009$) and old nests (6%, $F = 3.09$, $P = 0.006$), and the first two axes explain 44.3% of the variation (Fig. 2b). The abundance of cavity nesting bees is positively correlated with the number of cavities ($r = 0.482$, $n = 21$, $P = 0.027$) and with steep ground ($r = 0.682$, $n = 21$, $P = 0.001$) available in the habitat. For ground nesters, the guild with the greatest number of species and individuals, species richness is positively correlated with area of bare ground ($r = 0.523$, $n = 21$, $P = 0.015$) and abundance is correlated with availability of hard soils ($r = 0.378$, $n = 21$, $P = 0.091$) though the latter is only marginally significant.

The ordination focusing on only the most numerically dominant species indicates that the structure of this partial community is not as strongly related to nesting variables

Table 3. Mean (\pm SE) availability of nesting resources at sites of different ages.

Characteristic	Site age (years since burnt)				
	1	10	16	25	> 50
Soil	58.6 \pm 9.3	12.2 \pm 6.2	22.5 \pm 8.6	15.9 \pm 5.8	16.5 \pm 5.0
Flat	70.4 \pm 1.6	100.0 \pm 0.0	87.9 \pm 2.7	93.7 \pm 0.9	85.5 \pm 1.6
Slope	20.6 \pm 7.2	0.0 \pm 0.0	12.1 \pm 12.1	1.6 \pm 1.6	14.5 \pm 9.1
Steep	9.0 \pm 3.7	0.0 \pm 0.0	0.0 \pm 0.0	4.7 \pm 2.6	0.0 \pm 0.0
Wood	12.1 \pm 5.1	5.2 \pm 0.7	20.5 \pm 2.0	6.7 \pm 2.6	9.3 \pm 3.0
Stems	0.2 \pm 0.2	2.0 \pm 1.0	0.3 \pm 0.3	1.2 \pm 0.6	1.2 \pm 0.6
Soft	5.4 \pm 0.4	7.3 \pm 0.2	6.2 \pm 0.2	6.3 \pm 1.2	6.9 \pm 0.4
Medium	3.0 \pm 0.3	1.7 \pm 0.2	2.6 \pm 0.2	2.6 \pm 0.9	1.7 \pm 0.3
Hard	1.6 \pm 0.6	1.0 \pm 0.3	1.2 \pm 0.2	1.1 \pm 0.6	1.4 \pm 0.7
Cavities	6.7 \pm 2.9	0.8 \pm 0.6	0.5 \pm 0.3	1.7 \pm 0.9	1.6 \pm 1.1
Old nests	0.2 \pm 0.2	1.0 \pm 0.6	0.0 \pm 0.0	0.3 \pm 0.3	0.0 \pm 0.0
Snail shells	0.8 \pm 0.2	0.2 \pm 0.2	0.7 \pm 0.4	0.6 \pm 0.3	1.0 \pm 0.2

(Table 6: sum of all canonical variables = 0.580; $F = 0.92$, $P = 0.675$ for all canonical axes). However, there are two significant nesting resources entered into the model (Fig. 2c): soil (12% of variation explained, $F = 2.53$, $P = 0.005$) and cavities (8%, $F = 1.75$, $P = 0.041$). The abundance of four dominant ground-nesting species are positively correlated with the availability of soil: *Lasioglossum transitorium* ($r = 0.732$, $n = 21$, $P < 0.001$); *Lasioglossum caspicum* ($r = 0.427$, $n = 21$, $P = 0.054$); *Andrena rufomaculata* ($r = 0.648$, $n = 21$, $P = 0.002$); and *Eucera transversa* ($r = 0.444$, $n = 21$, $P = 0.044$). The single most common bee in the surveys, the honeybee (32.4% of total bee abundance) is positively correlated with both the number of cavities ($r = 0.486$, $n = 21$, $P = 0.025$) and availability of steep ground ($r = 0.687$, $n = 21$, $P = 0.001$). Cavities and steep ground are also autocorrelated ($r = 0.693$, $n = 21$, $P = 0.001$).

Discussion

For bee communities, habitat quality depends upon two sets of environmental characteristics: those related to foraging requirements and those related to nesting requirements. The idea of *partial habitats* (Westrich, 1996) highlights the need for both these complementary resources to be available locally to bee species, even if spatially segregated within the habitat. The role of foraging resources (pollen and nectar sources) has been clearly demonstrated

for bee communities (e.g. Petanidou & Vokou, 1990), but the relative importance of nesting resources has received relatively little attention (but see Cane, 1991). Given that an earlier study indicates that 5–10% of bee community organisation is influenced by the availability of nesting resources (Potts *et al.*, 2003a), this study clearly demonstrates that several specific resources are key factors influencing community structure.

For the entire bee community and the dominant species within the community, approximately 40% of the variation in species-abundance pattern is explained by the availability of nesting resources (Tables 4 and 6); and when the community is analysed in terms of guild structure 61% of the variation is accounted for (Table 5). Two nesting resources consistently contribute to the models: the availability of bare ground and the occurrence of suitable nesting cavities. The area of exposed earth for ground-nesting bees to nest in has been suggested as a possible limiting factor for Mediterranean bee communities (Petanidou & Ellis, 1996); however, this is the first study to quantify the effect for an entire community. The abundance of ground nesting bees varies markedly across sites and is highest in freshly burnt areas. One of the most obvious impacts of burning is the clearance of vegetation and consequent exposure of bare ground, which is highest immediately post-fire and then decreases as the plant community regenerates. The absolute abundance of four dominant ground-nesting species is positively correlated with the area of soil available within a site. The analysis indicates that it may not be only the quantity but

Table 4. Redundancy analysis for the entire bee community of 116 species.

	Axis 1	Axis 2	Axis 3	Axis 4	Total variance
Eigenvalues	0.128	0.108	0.073	0.069	
Species–environment correlation	0.988	0.963	0.979	0.944	
Cumulative percentage variance of species data	12.8	23.6	30.9	37.8	
Cumulative percentage variance of species–environment data	19.2	35.4	46.3	56.7	
Sum of all eigenvalues					1.00
Sum of all canonical eigenvalues					0.667

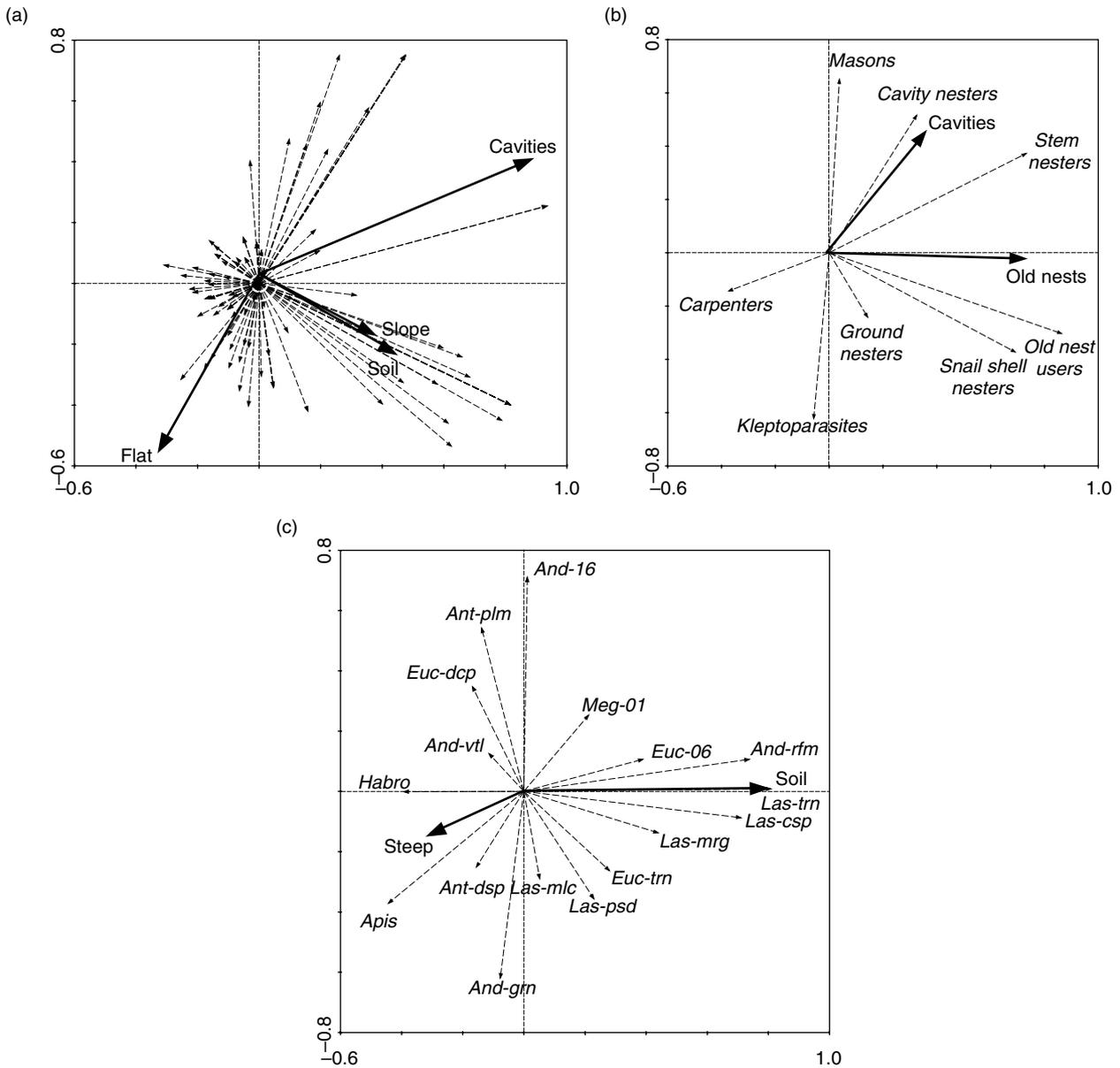


Fig. 2. Redundancy analysis biplots showing correlation between species and nesting resource variables for: (a) the entire bee community (116 species); (b) bee nesting guilds; and (c) the dominant 17 species within the community. Solid line vectors represent significant environmental variables as defined in Table 2, and dashed line vectors represent species/guilds. Abbreviations for species are: *And-grn*, *Andrena grandilabris*; *And-rfm*, *Andrena rufomaculata*; *And-vtl*, *Andrena vetula*; *And-16*, *Andrena* sp. 99/16 (Andrenidae); *Ant-dsp*, *Anthophora dispar*; *Ant-plm*, *Anthophora plumipes*; *Apis*, *Apis mellifera*; *Euc-dcp*, *Eucera decipiens*; *Euc-trn*, *Eucera transversa*; *Euc-06*, *Eucera* sp. 99/06; *Habro*, *Habropoda tarsata* (Apidae); *Las-csp*, *Lasioglossum caspicum*; *Las-mlc*, *Lasioglossum malachurum*; *Las-mrg*, *Lasioglossum marginatum*; *Las-psd*, *Lasioglossum pseudospecodimorphum*; *Las-trn*, *Lasioglossum transitorium* (Halictidae); *Meg-01*, *Megachile* sp. 99/01 (Megachilidae).

also the quality of soil that is important. The proportion of hard soil may be related to the abundance of ground-nesting bees in the study, a finding reported for other hypogeous bee species (Potts & Willmer, 1997, 1998). The slope of the ground may also be a further quality component of the ground, and it is a significant factor in organising the whole bee community; various ground nesting Hymenop-

tera have demonstrated preferences for particular slopes and aspects (e.g. Weaving, 1989; Potts & Willmer, 1997).

Roubik (1992) suggests that the availability of suitable cavities may limit the number of eusocial bee colonies in warm temperate areas, although this remains untested. In this system, the availability of potential nesting cavities is an important structuring agent for the overall bee community,

Table 5. Redundancy analysis for bee nesting guilds.

	Axis 1	Axis 2	Axis 3	Axis 4	Total variance
Eigenvalues	0.253	0.190	0.116	0.052	
Species–environment correlation	0.959	0.918	0.891	0.880	
Cumulative percentage variance of species data	25.3	44.3	59.9	61.1	
Cumulative percentage variance of species–environment data	35.1	61.4	77.5	84.7	
Sum of all eigenvalues					1.00
Sum of all canonical eigenvalues					0.722

Table 6. Redundancy analysis for dominant bee species within the community (i.e. those with abundance >0.5% of total).

	Axis 1	Axis 2	Axis 3	Axis 4	Total variance
Eigenvalues	0.156	0.112	0.072	0.062	
Species–environment correlation	0.922	0.958	0.93	0.968	
Cumulative percentage variance of species data	15.6	26.8	33.9	40.1	
Cumulative percentage variance of species–environment data	26.9	46.3	58.4	69.2	
Sum of all eigenvalues					1.00
Sum of all canonical eigenvalues					0.580

for the cavity nesting guild and for the abundance of honeybees. Feral colonies of honeybees were encountered during the surveys on Mt Carmel, and hives are banned from within the National Reserve; however, a significant proportion of honeybees recorded are likely to be from hives adjacent to the park boundary. Therefore it is not possible to determine the proportion of honeybees relying upon natural cavities for their nesting requirements.

The abundance of stem nesting bees and the availability of suitable stems were both highest 10 years post-fire, when the vegetation was dominated by dwarf shrubs such as *Salvia fruticosa*, which have pithy stems. Stems did not feature in any of the models, however, which probably reflects the relatively low species richness and abundance of this guild. Nevertheless, in the ordination using guilds the vectors for stems and stem-nesters were in very similar directions (not shown on Fig. 2b) though not significantly associated. The same visual concurrence was found for carpenter bees and the availability of woody substrates, and the lack of significance can again be attributed to their relative rarity.

Clearly, nesting resources in addition to foraging resources need to be considered when examining the organisation of bee communities. Much attention has focused upon improving the floral resources available for bees and many conservation and agri-environmental schemes use land management practices to conserve and enhance floral communities. However, relatively little effort has been focused upon the complementary and critical need for nesting resource provision. Successful habitat management requires both these partial habitats to be available to support diverse bee communities and the pollination services they provide.

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References

- Banaszak, J. (1995) *Changes in Fauna of Wild Bees in Europe*. Pedagogical University, Bydgoszcz, Poland.
- Banaszak, J. (1996) Ecological bases of conservation of wild bees. *The Conservation of Bees* (ed. by A. Matheson, S. L. Buchmann, C. O'Toole, P. Westrich and I. H. Williams), pp. 55–62. Academic Press, London.
- Brockmann, H.J. (1979) Nest site selection in the golden digger wasp, *Sphex ichneuomoneus* L. (Sphecidae). *Ecological Entomology*, **4**, 211–224.
- Brown, B.J. & Mitchell, R.J. (2001) Competition for pollination: effects of pollen of an invasive plant on seed set of a native congener. *Oecologia*, **129**, 43–49.
- Butz-Huryn, V.M. (1997) Ecological impacts of introduced honey bees. *Quarterly Review of Biology*, **72**, 275–296.
- Cane, J.H. (1991) Soils of ground-nesting bees (Hymenoptera: Apoidea): texture, moisture, cell depth, and climate. *Journal of Kansas Entomological Society*, **64**, 406–413.
- Chittka, L. & Schürkens, S. (2001) Successful invasion of a floral market. *Nature*, **411**, 653.
- Gathmann, A., Greiler, H.J. & Tschardtke, T. (1994) Trap-nesting bees and wasps colonizing set-aside fields: succession and body size, management by cutting and sowing. *Oecologia*, **98**, 8–14.

- Jeanne, R.L. & Morgan, R.C. (1992) The influence of temperature on nest site choice and reproductive strategy in temperate zone *Polistes* wasp. *Ecological Entomology*, **17**, 135–141.
- Jennersten, O. (1988) Pollination of *Dianthus deltoides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. *Conservation Biology*, **2**, 359–366.
- Michener, C.D. (2000) *The Bees of the World*. Johns Hopkins University Press, Baltimore.
- O'Toole, C. (1993) Diversity of native bees and agroecosystems. *Hymenoptera and Biodiversity* (ed. by J. LaSalle and I. Gauld), pp. 69–106. Commonwealth Agricultural Bureau International, London.
- O'Toole, C. & Raw, A. (1991) *Bees of the World*. Sterling Publishing, New York.
- Petanidou, T. & Ellis, W.N. (1996) Interdependence of native bee faunas and floras in changing Mediterranean communities. *The Conservation of Bees* (ed. by A. Matheson, S. L. Buchmann, C. O'Toole, P. Westrich and I. H. Williams), pp. 201–226. Academic Press, London.
- Petanidou, T. & Vokou, D. (1990) Pollination and pollen energetics in Mediterranean ecosystems. *American Journal of Botany*, **77**, 986–992.
- Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G., O'Toole, C., Roberts, S. & Willmer, P.G. (2003b) Response of plant–pollinator communities following fire: changes in diversity, abundance, and reward structure. *Oikos*, **101**, 103–112.
- Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G. & Willmer, P.G. (2003a) Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology*, **84**, 2628–2642.
- Potts, S.G. & Willmer, P.G. (1997) Abiotic and biotic factors influencing nest-site selection by *Halictus rubicundus*, a ground nesting halictine bee. *Ecological Entomology*, **22**, 319–328.
- Potts, S.G. & Willmer, P.G. (1998) Compact housing in built-up areas: spatial positioning of nests in aggregations of a ground-nesting bee. *Ecological Entomology*, **23**, 427–432.
- Price, M.V. & Waser, N.M. (1998) Effects of experimental warming on plant reproductive phenology in a subalpine meadow. *Ecology*, **79**, 1261–1271.
- Roubik, D.W. (1992) Loose niches in tropical communities: why are there so few bees and so many trees? *Effects of Resource Distribution on Animal–Plant Interactions* (ed. by M. D. Hunter, T. Ohgushi and P. W. Price), pp. 327–354. Academic Press, San Diego.
- Schmid-Hempel, P. & Durrer, S. (1991) Parasites, floral resources, and reproduction in natural populations of bumblebees. *Oikos*, **62**, 342–350.
- Schmidt, J.O. & Thoenes, S.C. (1992) Criteria for nest site selection in honey-bees (Hymenoptera: Apidae) – preference between pheromone attractants and cavity shapes. *Environmental Entomology*, **21**, 1130–1133.
- Scott, V.L. (1994) Phenology and trap selection of three species of *Hylaeus* (Hymenoptera, Colletidae) in upper Michigan. *Great Lakes Entomologist*, **27**, 39–47.
- Steffan-Dewenter, I. & Tschardtke, T. (1999) Effects of habitat isolation on pollinator communities and seed set. *Oecologia*, **121**, 432–440.
- Steffan-Dewenter, I. & Tschardtke, T. (2000) Resource overlap and possible competition between honey bees and wild bees in central Europe. *Oecologia*, **122**, 288–296.
- Stephen, W.P., Bohart, G.E. & Torchio, P.F. (1969) *Biology and External Morphology of Bees*. Oregon State University, Corvallis.
- Tepedino, V.J. & Stanton, N.L. (1981) Diversity and competition in bee–plant communities on short-grass prairie. *Oikos*, **36**, 35–44.
- Ter Braak, C.J.F. & Smilauer, P. (1999) *Canoco for Windows, Version 4.02*. Microcomputer Power, Ithaca, New York.
- Watanabe, M.E. (1994) Pollination worries rise as honey bees decline. *Science*, **265**, 1170.
- Weaving, A.J.S. (1989) Habitat selection and nest construction behaviour in some Afrotropical species of *Ammophila* (Hymenoptera: Sphecidae). *Journal of Natural History*, **23**, 847–871.
- Wesseling, J. & Tschardtke, T. (1995) Das Heimfidevermögen von Stechimmen und die Verinselung von Lebensräumen. *Mitteilungen der Deutschen Gemeinschaft für Allgemeine und Angewandte Entomologie*, **10**, 323–325.
- Westrich, P. (1996) Habitat requirements of central European bees and the problems of partial habitats. *The Conservation of Bees* (ed. by A. Matheson, S. L. Buchmann, C. O'Toole, P. Westrich and I. H. Williams), pp. 1–16. Academic Press, London.
- Wuellner, C.T. (1999) Nest site preference and success in a gregarious, ground-nesting bee *Dieuomia triangulifera*. *Ecological Entomology*, **24**, 471–479.
- Zohary, M. (1982) *Vegetation of Israel and Adjacent Areas*. Reihe A. (Naturwissenschaften) no. 7. Wiesbaden, Göttingen, Germany.

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