Response of plant-pollinator communities to fire: changes in diversity, abundance and floral reward structure

Simon G. Potts, Betsy Vulliamy, Amots Dafni, Gidi Ne'eman, Chris O'Toole, Stuart Roberts and Pat Willmer

Globally, plant-pollinator communities are subject to a diverse array of perturbations and in many temperate and semi-arid systems fire is a dominant structuring force. We present a novel and highly integrated approach, which quantifies, in parallel, the response to fire of pollinator communities, floral communities and floral reward structure. Mt Carmel, Israel is a recognised bee-flower biodiversity hotspot, and using a chronosequence of habitats with differing post-fire ages, we follow the changes in plant-pollinator community organisation from immediately following a burn until full regeneration of vegetation. Initially, fire has a catastrophic effect on these communities, however, recovery is rapid with a peak in diversity of both flowers and bees in the first 2 years post-fire, followed by a steady decline over the next 50 years. The regeneration of floral communities is closely matched by that of their principal pollinators. At the community level we quantify, per unit area of habitat, key parameters of nectar and pollen forage known to be of importance in structuring pollinator communities. Nectar volume, nectar water content, nectar concentration and the diversity of nectar foraging niches are all greatest immediately following fire with a steady decrease as regeneration proceeds. Temporal changes in energy availability for nectar, pollen, total energy (nectar + pollen) and relative importance of pollen to nectar energy show a similar general decline with site age, however, the pattern is less clear owing to the highly patchy distribution of floral resources. Changes in floral reward structure reflect the general shift from annuals (generally low-reward open access flowers) to perennials (mostly high-reward and restricted access flowers) as post-fire regeneration ensues. The impact of fire on floral communities and their associated rewards have clear implications for pollinator community structure and we discuss this and the role of other disturbance factors on these systems.

S. G. Potts, B. Vulliamy and Pat Willmer, School of Biology, Univ. of St Andrews, Scotland, UK, KY16 9TS. Present address for S. G. P.: Centre for Agri-Environmental Research, PO Box 237, Univ. of Reading, Reading, UK, RG6 6AR (s.g.potts@reading.ac.uk). – A. Dafni, Institute of Evolution, Univ. of Haifa, Mt Carmel, IL-31905 Haifa, Israel. – G. Ne'eman, Dept of Biology, Univ. of Haifa, Oranim, IL-36006 Tivon, Israel. – C. O'Toole and S. Roberts, Bee Systematics and Biology Unit, Oxford Univ. Mus. Natl History, Oxford, UK, OX1 3PW.

Mediterranean ecosystems are characterised by exceptional spatial and temporal heterogeneity resulting in a dynamic mosaic of habitats (Rundel et al. 1998). The interaction of geological, topographical, pedological, climatic and anthropogenic factors define the complexity of these regions and are responsible for the generation and maintenance of biological diversity (Blondel and Aranson 1999). This diversity manifests itself both regionally and locally and is reflected in the high levels of endemism reported for plants (Gómez-Campo 1985) and for insects (Baletto and Casale 1991); Myers (1990) considers the Mediterranean basin to be one of the 18 global biodiversity 'hotspots'. Indeed, the flora is particularly rich with an estimated 25 000 flowering plant

species (Quézel 1985) of which the vast majority are mellitophilous (Petanidou and Vokou 1990, Dafni and O'Toole 1994). Bees are the primary pollinators of the region and Michener (1974) notes it as one of the global centres for speciation within this group. Plant-pollinator communities are therefore key contributors to biodiversity and essential to the maintenance of ecosystem function.

The present-day dynamic nature of Mediterranean habitats is driven by the impact of a multitude of disturbance factors, including fire, grazing, fragmentation, changing land-use practices and invasion of non-natives. Fire has a prominent role in organising community structure and has resulted in landscapes comprising complex mosaics of regenerating vegetation and associated fauna. The response of mediterranean flowering plant communities to fire is well documented (Trabaud and Prodon 1993, Arainoutsou 1998, Trabaud 2000, Arianoutsou and Ne'eman 2000); for insect communities considerable literature also exists (e.g. Quinn 1994), but much of this is in non-Mediterranean systems (review by Swengel 2001) or only addresses short-term 'before and after' type comparisons (Ne'eman et al. 2000; Potts et al. 2001a). Studies following a single burnt area as it regenerates are generally impractical as full recovery may take many decades; consequently, the use of space-for-time substitutions offer a practical alternative (Pickett 1989). However, to date, this approach has not been applied to a key functional group, such as pollinators, and never to the floral reward structure supporting them. The response of pollinator communities to fire is of particular importance as effective pollination services within an ecosystem are known to be directly linked to bee community diversity and its response to fire (Potts et al. 2001b).

In light of the recent concern for declines in pollinator communities around the world (Allen-Wardell et al. 1998, Kearns et al. 1998) and the lack of fundamental data showing how these communities are structured and respond to disturbance (São Paulo Declaration on Pollinators 1999) we chose to address these issues in a particularly diverse set of bee-flower communities of the eastern Mediterranean. The area is subject to regular and increasingly more frequent, forest fires (Kliot and Keidar 1992). O'Toole and Raw (1991) estimate there to be 3000–4000 species of bees in the Mediterranean with as many as 1500–2000 in Israel alone (Dafni and O'Toole 1994). Mount Carmel National Reserve, Israel, offers the ideal model system to assess, in parallel, the response of plants, forage resources and pollinators to fire. Pollen and nectar are the primary forage for bees and can be quantified in an area-specific manner for both absolute abundance and energy content (Dafni 1992); this has been undertaken for single species of flowering plants but not for complex floral communities. Here we present the first fully integrated study giving quantitative data for the organisation of plant-pollinator communities, with particular emphasis on the associated reward structure, in a replicated series of post-fire habitats encompassing all the major regenerative stages from freshly burnt to fully mature communities.

Materials and methods

Study sites

The Mt Carmel National Reserve, Israel, comprises 150 km^2 of Aleppo pine forest (*Pinus halepensis* Mill.) in various stages of post-fire regeneration. It is composed of natural pines with an understory of *Quercus callipinos* Webb., *Pistacia lentiscus* L., *Cistus salvifolius* L. and several other small trees and shrubs. The area has a typical Mediterranean climate with mild wet winters and hot dry summers. A mosaic of different burn ages has resulted from major fires in 1998, 1989, 1983 and 1974 (Schiller et al. 1997), embedded in a matrix of mature unburnt forests. This chronosequence of burn times facilitated our space-for-time substitution approach. For each burnt patch, three replicate sites of 1 ha were selected, using detailed ground surveys and aerial photographs, as being representative of vegetation for that stage of post-fire regeneration. Site details are summarised in Table 1. Particular care was taken to use sites with similar altitudes, soil types, aspects and slopes; each site was at least 300 m, and most > 600 m, away from the nearest border with a different vegetation type or another site.

A total of 21 sites were used for surveys carried out in 1999 and 2000. Some degree of pseudoreplication is unavoidable owing to the nature of the landscape and inability to experimentally manipulate burn times and areas; however, effects were minimised whenever possible by selecting separate burns (e.g. there were two independent fires in 1998, and two discrete areas of unburnt pine were used as controls) and ensuring sites were spatially separated as far as possible. In view of this we advise a degree of caution when interpreting results. The original set of three sites in the unburnt area of Wadi Denia (DenNB) were completely lost to fire in 1999, so a new set of three sites were established in 2000 (NewNB); surveys at all other sites used the same locations for both years.

The major period of floral bloom and pollinator activity is early March to late May, and five complete surveys were undertaken during this time. Seasonal effects were controlled for by carrying out site surveys in quick succession, so that five clusters of surveys spread across the whole season were obtained. On all days weather data were recorded, and atypical days abandoned to ensure microclimatic variation did not confound survey results.

Table 1. Physical characteristics of survey sites (3 in each patch) in Mount Carmel National Reserve, Israel.

Patch name [1]	Location	Year burnt	GPS	Approximate area (ha)	Altitude a.s.l. (m)	Aspect (°)	Slope (°)	Mean annual precipitation (mm) [2]	Soil type [2]
Den98	Wadi Denia	1998	32°45.8′, 35°00.1′	100	290	247–286	9–17	675	Terra Rossa A1
Hod98	En Hod	1998	32°41.9′, 34°58.6′	450	130	298–320	5–7	625	Terra Rossa A1
Hai89	Hai Bar reserve	1989	32°44.9′, 35°01.2′	300	320	233–296	1–4	725	Rendzina C1
Mit83	Mitla	1983	32°44.2′, 34°59.6′	400	340	216–327	5–12	675	Terra Rossa A2
Etz74	Etzbah	1974	32°42.4′, 34°58.9′	80	180	143–187	4–15	625	Terra Rossa A1
EtzNB	Etzbah	<1950	32°42.4′, 34°58.8′	240	170	178–247	5–9	625	Terra Rossa A1
DenNB (1999 only)	Wadi Denia	<1950	32°45.7′, 35°00.4′	190	320	186–251	12–13	700	Terra Rossa A1
NewNB (2000 only)	Kedumim	<1950	32°43.3′, 35°04.2′	135	290	172–234	6–13	650	Terra Rossa A1

[1] number indicates year of burn; NB indicates 'Not Burnt'.
[2] from Soffer and Kipnis (1980). Terra Rossa A1 = Red; non or slightly calcareous; developed from limestone or dolomite; Terra Rossa A2 = Brown–red; slightly or moderately calcareous; mainly developed from limestone or dolomite; Rendzina C1 = Light brown; moderately calcareous or calcareous; developed from hard chalk or poorly developed nari.

Overview of freshly burnt, intermediate and mature post-fire vegetation

The vegetation on Mt Carmel comprises three highly intergraded and often poorly defined habitat types through time, which in this study are designated as freshly burnt, intermediate and mature. Fires usually occur in late summer and result in the complete loss of the shrub layer and most of the trees. However, post-fire re-sprouters and post-fire seeders are quick to respond with a massive flush of flowering annuals and a few perennials (e.g. *Asphodelus*) the following spring together with pine seedlings. The habitat is designated as freshly burnt for the following 2–5 years. Perennials (e.g. labiates and *Cistus* spp.) become increasingly abundant and become dominant some 6–10 years post-fire at which time the habitat is best classified as phrygana (intermediate age). Annuals are still present but their abundance declines as *Cistus* spp. become dominant and pine trees increase in size and coverage. For the next 10 years or so, the phrygana shows an increase in pine dominance with perennials still abundant as the vegetation becomes characteristic of high scrubland (still classified as intermediate age). Beyond about 30 years the habitat is designated as mature and perennials and annuals are generally restricted to openings and clearings as the pine canopy becomes enclosed. Finally mature woodland is achieved some 40 years or so post-fire (Arianoutsou and Ne'eman 2000). What results at the landscape level, is a complex mosaic of different post-fire vegetation types locked in continual regeneration. Extensive description of post-fire vegetation can be found elsewhere (Zohary 1982).

Bee diversity and abundance surveys

Previous studies (Potts et al. 2001a) have demonstrated that bees (Hymenoptera: Apoidea) comprise the vast majority (ca 94%) of pollinating insects on Mt Carmel, and we therefore concentrated our survey efforts on this group.

Three randomly selected linear transects of 200 m were walked in 20 min at 08:00, 11:00 and 14:00, which covers the period of maximum bee activity. Individuals that could be unambiguously identified 'on the wing' were recorded, with the remaining individuals being caught and retained for determination at the Bee Systematics and Biology Unit, Oxford Univ. Museum of Natural History.

Surveys were undertaken throughout the flight season of 1999 and yielded 2694 recordings. However, in view of the conservation needs of this sensitive area, we reduced the capture of specimens in 2000, while still recording total abundance (see below). In 2000 the seasonal abundance of bees was lower in 16 of the 21 sites and only marginally higher in the remaining five sites; consequently the extrapolation of the site-specific species accumulation curves of 1999, using the 2000 bee abundances, represented a reasonable approach. Rarefaction curves were computed (Biodiversity Professional version 2, McAleece 1997), and the fitted curve for species accumulation used to estimate species richness for each site in 2000 (description and critique of methods for extrapolation given in Colwell and Coddington 1996). To test the reliability of this method we undertook an independent test of species richness by carrying out smaller scale diversity surveys. Across sites, 394 bees were caught and identified and the

species richness of this observed sample and the estimated species richness had a strong positive correlation ($R^2 = 55.2\%$, $p = 0.056$). We therefore conclude that the estimated bee diversity for 2000 is indeed an accurate measure of the true diversity in our study sites.

Floral, nectar and pollen surveys

Concurrent with the bee surveys, a 50 m linear transect was placed in a random direction and all open flowers, potentially utilisable by bees, were identified and their area coverage estimated in a 0.4 m wide strip along the transect. For a given species, the mean dimensions of a typical flower were recorded and then the number of flowers in the transect estimated to obtain a measure of coverage. A second randomly placed 50 m transect was used for the placement of 10 pairs of 1 m² quadrats, where all flowers in each quadrat were entirely caged at dawn to prevent visitor access. The first set of 10 ('caged') quadrats were used to estimate the 'maximum amount of nectar producible', i.e. nectar standing crop without visitation. Nectar volume was measured for every flower within the quadrat by extraction with microcapillaries (Camlab, UK) and concentration measured with a hand held refractometer modified for small volumes (Bellingham & Stanley, UK). At the same time nectar volume and concentration, for an identical set of uncaged ('open') flower species in equivalent numbers, were determined in the surrounding habitat. This was a measure of actually available nectar, i.e. nectar standing crop with open visitation. While these two methods have limitations (e.g. do not fully take into account individual temporal variation in nectar production and do not allow for complete extraction of nectar from all species), they are appropriate to a community level analysis of nectar availability. The estimates of 'caged' and 'open' nectar standing crops were then used to calculate the energy per unit area of habitat (Dafni 1992). At the community level, 'caged' and 'open' values for nectar energy were highly significantly correlated (1999: $R^2 = 88.1\%$, $n = 21$, $p < 0.001$; 2000: $R^2 = 91.7\%$, $n = 21$, $p < 0.001$) with 'caged' values being approximately 3.3 greater than equivalent 'open' values; accordingly only 'caged' values are presented for other nectar measures (see below).

An estimate of pollen standing crop was made using the remaining set of 10 caged quadrats. All dehisced anthers, potentially available to bees, were collected and stored in 70% alcohol; in the laboratory they were filtered, sonicated and then centrifuged to give highly concentrated suspensions of relatively pure pollen. Using a light microscope pollen grain number and mean pollen grain size were measured and the total volume of pollen per quadrat computed. To calculate energy per unit habitat we converted volumes to masses using the formula provided by Roulston et al. (2000): $\ln[\text{mass}] = 0.95 \times \ln[\text{volume} \times 10^{-6}] - 12.46$; and then converted mass to energy using the value of 5.7 kcal/g pollen which was the mean of 34 insect-pollinated flowering plants found in an equivalent Mediterranean ecosystem in Greece (Petanidou pers. comm.; Petanidou and Vokou 1990). The pollen and nectar energy per unit habitat used the same units therefore allowing an estimate of total floral reward energy available (P + N) and also an index of the relative importance of each (P:N).

Analysis of nectar niche diversity

An index based on the variety of nectar niches present in each site was generated by partitioning the range of nectar volume and nectar concentration readings into discrete categories. Three volume categories (< 0.1, $0.1–1.0$ and > 1.0 µl) and three concentration categories (< 25, $25–50$ and $> 50\%$) were used to construct a 3×3 matrix with every independent nectar reading at a given site scored in one of the nine cells. Each cell can be viewed as a niche providing a unique resource combination of volume and concentration, and nectar niche diversity was calculated as the total number of cells occupied for that site.

Statistical notes

Clarity of figures is greatly improved by using age means rather than individual sample values. Fig. 1, 3 and 4 present mean values with standard errors based on the replicate sites for each of the independent burnt patches sampled in each year; values for sites from patches of the same age are pooled (i.e. patches burnt in 1998 and also all mature patches), and therefore figures have 9 points (1, 2, 10, 11, 16, 17 25, 26 and > 50 year). However, statistical computations include all 21 sites for each year ($n = 42$). Regression fits stated in the text are for linear functions except for those cases (Fig. 1, 3 and 4) where a logarithmic curve clearly explains a greater proportion of variation in the data. Where neither function shows a significant fit, points through time are simply joined using a dashed line. The similarity of measured parameters across years was undertaken using a t-test for matched pairs (of patch means).

Results

Changes in bee community structure following fire

Bee diversity (species richness) shows a curvilinear decrease with time following a fire (Fig. 1a: $r^2 = 38.1\%$, $n = 42$, $p < 0.001$). Freshly burnt areas support 20–25 species per site while intermediate and mature areas support only 7–12 species. However, when generic

Fig. 1. Changes in bee and flower community structure following fire: a) bee diversity, b) bee abundance, c) floral diversity, and d) floral abundance. Each point is the mean of three replicated sites for that burn age ± SE.
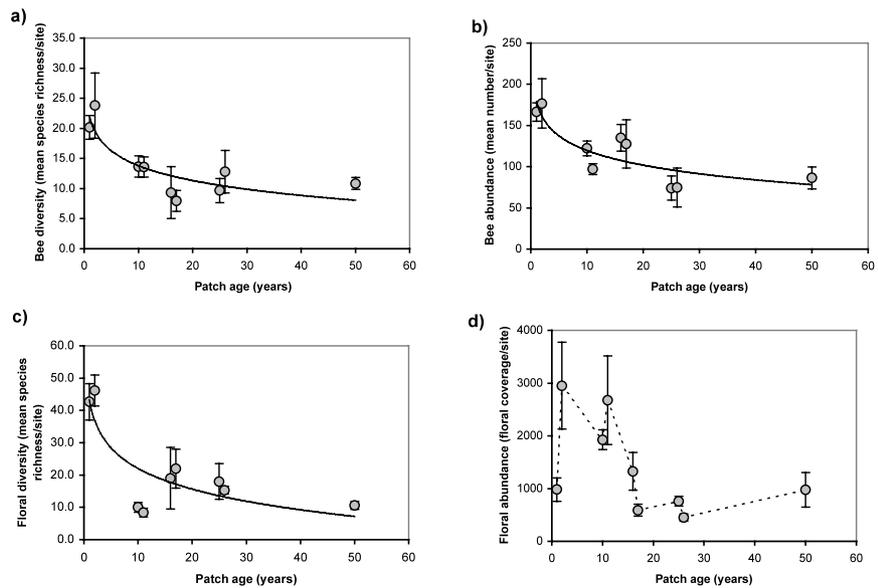
richness is considered there is no change with site age (p = 0.534); generic diversity is fairly constant through the habitats (range 10–17, median 13) whereas species diversity is highly variable (range 22–51, median 26). Using the 1999 data, the partitioning of overall species
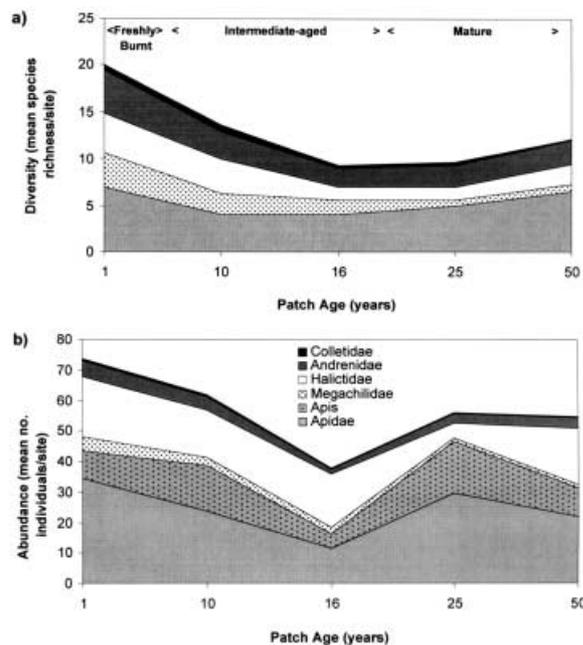

Fig. 2. Changes in bee family composition following fire for sites sampled in 1999: a) species richness of bees, and b) abundance of individuals within each family. Honeybees (*Apis mellifera*) are plotted separately as they were the single most abundant species; total abundance in Apidae therefore includes *A. mellifera*.

richness by family reveals different responses through time (Fig. 2). Apidae and Andrenidae species richness are highest immediately following a burn, then decline with intermediate-aged sites before increasing slightly as maturity is approached (Fig. 2a). Similarly, within the Megachilidae and Halictidae, richness is greatest in freshly burnt sites but both show a significant and continuous decline with time ($r^2 = 26.1\%$, n = 21, p = 0.018 and $r^2 = 16.8\%$, n = 21, p = 0.065 respectively).

The abundance of bees varies markedly with site age for both the whole community (Fig. 1b) and for its component guilds (Fig. 2b). Total bee numbers decline steadily in the first 25 years post-fire, but thereafter are fairly constant ($r^2 = 41.7\%$, n = 42, p < 0.001). The numbers of Apidae, Andrenidae and honeybees (*Apis mellifera*) are lowest in intermediate burn times with Halictidae and Colletidae showing no clear pattern and Megachilidae a decrease in abundance with time ($r^2 = 16.6\%$, n = 21, p = 0.067). Descending order of abundance across most sites is: Apidae (excluding *A. mellifera*) > Halictidae > Andrenidae > Megachilidae > Colletidae, with *A. mellifera* being highly variable depending upon the local proximity of hives. Overall bee community structure is very similar across sample years for both bee diversity (t = − 0.37, n = 21, p = 0.716) and bee abundance (t = 1.34, n = 21, p = 0.194).

Changes in flower community structure following fire

The change in species richness (Fig. 1c) and abundance (Fig. 1d) of flowering plants through time closely mirrors that of the bee community. Species richness is highest (40–50 spp.) immediately following a burn and

then sharply declines in the following decade (ca 10 spp.) before increasing slightly in the following years (10–20 spp.). The overall decrease shows a significant curvilinear fit ($r^2 = 21.0\%$, n = 42, p = 0.010) though the 10 and 11 year old sites fall well below the curve. Annuals are the dominant component of the flora in the first year after fire (50.5 ± 10.5 spp.) and thereafter occur in much lower numbers (13.0 ± 3.2 spp; range 5–23) in all burn times. Perennial species, however, remain relatively less common from immediately after fire until site maturity (11.9 ± 1.7 spp; range 5–18).

Floral abundance is relatively low the first year after fire before attaining a maximum the following year (Fig. 1d); abundance then declines steadily ($r^2 = 41.7\%$, n = 42, p < 0.001) for the following three decades and becomes asymptotic as maturity is reached.

Floral diversity and floral abundance are very similar for all sites across sampling years (t = − 0.06, n = 21, p = 0.950 and t = − 0.52, n = 21, p = 0.609 respectively).

Changes in nectar, pollen and energy rewards following fire

Absolute nectar volume and absolute water content of nectar per unit area of habitat show no clear pattern with site age (Fig. 3a, c; p = 0.234 and p = 0.214 respectively). Nectar concentration shows a significant steady decline with time ($r^2 = 60.2\%$, n = 42, p = 0.001) from 50–55% in freshly burnt sites to 35–40% in mature sites (Fig. 3b). Similarly, nectar niche diversity decreases significantly over time (Fig. 3d: $r^2 = 72.8\%$, n = 14, p = 0.020) from 7 to 4–5 out of 9 niches available. Pollen grain number per unit area decreases with site age ($r^2 = 13.7\%$, n = 42, p = 0.016) while mean pollen grain size remains constant through time (p > 0.1; mean = 56.6 ± 5.3 μm (42)).

Energy available in the form of nectar and also total energy (nectar + pollen) are highly variable through time without any apparent pattern (Fig. 4a, c: p = 0.903 and p = 0.514 respectively); the large SE's are indicative of the patchiness of floral rewards in these habitats. There may be a weak negative trend in total energy available through time if the unusually high value for the 25 year old site is excluded (this mean is greatly inflated due to the inclusion of a single large flowering plant in a single quadrat on a single day which resulted in a nectar score several orders of magnitude greater than any other value). Total energy is 1.5–4.0 kJ/ha/d in the first decade after fire and then drops to < 1.5 kJ/ha/d thereafter. Energy available in the form of pollen only (Fig. 4b) exhibits a significant decrease with site age ($r^2 = 17.0\%$, n = 42, p = 0.007), declining from ca 1.0 kJ/ha/d initially to 0.5 kJ/ha/d at maturity. In addition to this general trend, there may be a peak at intermediate times after fire (years 10 and 11) which coincides with the dominance of the polleniferous *Cistus* spp. The ratio of pollen:nectar energy (P:N) may gradually decay with age though this is only marginally significant (Fig. 4d: $r^2 = 9.5\%$, n = 42, p = 0.065); freshly burnt sites have a P:N of approximately 8 which decreases to 2 at maturity, but with some sites as clear outliers. However, in nearly all cases (Fig. 4d) the ratio is greater than unity, indicating that the energy available in the form of pollen is greater than that available from nectar (mean P:N = 2.3 ± 0.4 (42)).

Comparing values for nectar and pollen parameters between 1999 and 2000 showed no difference between years: nectar energy (t = − 0.10, n = 21, p = 0.920), nectar volume (t = − 0.65, n = 21, p = 0.522), nectar concentration (t = 1.59, n = 21, p = 0.129), nectar water
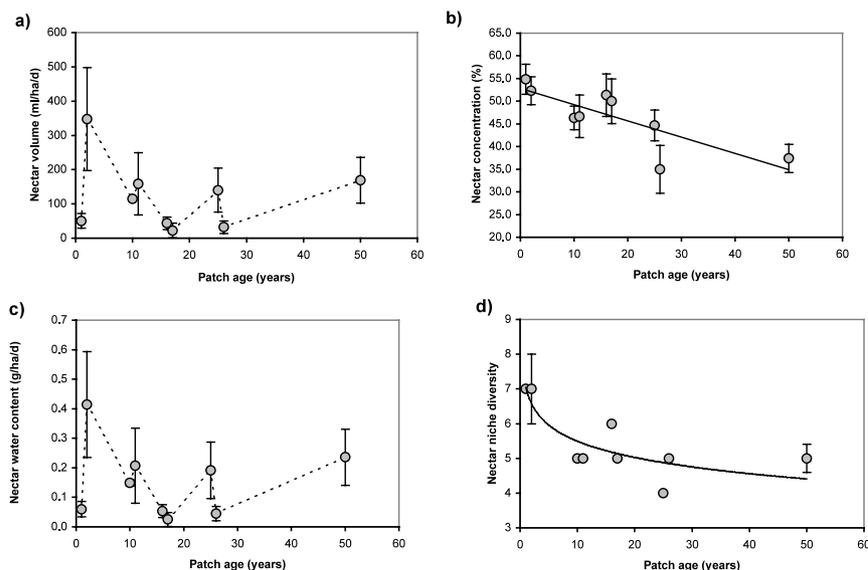

Fig. 3. Variation in nectar parameters with site age: a) nectar volume per unit habitat area, b) mean nectar concentration, c) nectar water content per unit habitat area and d) nectar niche diversity (see text for details). Each point is the mean of three replicated sites for that burn age ± SE.

Fig. 4. Variation in energetic parameters with site age: a) nectar energy per unit habitat area, b) pollen energy per unit habitat area, c) total energy (pollen + nectar) per unit habitat area, and d) ratio of pollen energy to nectar energy (P:N) per unit area. Each point is the mean of three replicated sites for that burn age $\pm$ SE.
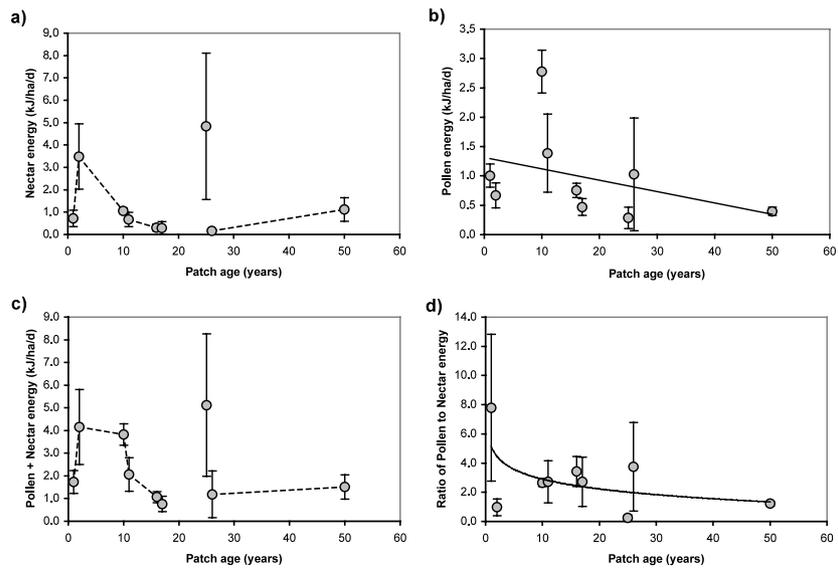
content (t = -0.70, n = 21, p = 0.492), nectar niche diversity (t = 0.0, n = 21, p = 1.000), pollen energy (t = 1.50, n = 21, p = 0.149), pollen grain number (t = -0.89, n = 21, p = 0.386), pollen grain size (t = 2.07, n = 21, p = 0.052), total energy (t = 27, n = 21, p = 0.788) and P:N (t = 88, n = 21, p = 0.391).

Discussion

Bee-flower community structure in response to fire

The plant-pollinator communities of Mount Carmel National Reserve show characteristic regeneration patterns following fire. Bee and flower communities are most diverse during the first two years after a burn and follow the same asymptotic decrease during the next five decades until they reach a minimum in mature sites (Fig. 1a,c). The temporal change in bee diversity closely mirrors that of the flora, as would be expected from resource tracking by the bee community.

Immediately following a substantial burn there is a catastrophic loss of both flowers and bees, but of an extremely short duration. The majority of flower species are fire-adapted as post-fire resprouters or seedling recruiters (Keely 1986), and bees are well known for their high mobility and can rapidly re-colonise freshly available habitats (Michener 1979). Stem-nesting guilds and those with shallow soil burrows are likely to suffer the highest mortality rates. Those with deeper burrows will escape the immediate effects of the fire, as the heating effect of intense fires is generally confined to 10–20 cm of soil depth (Christensen 1994), with the

result that many soil micro-invertebrates survive the direct effects of fire (Sgardellis et al. 1995, Brosa 2000). This coupled with the long flight range of some bees (e.g. 360–600 m for bumblebees, Dramstad 1996; 200–800 m for solitary bees, Wesserling and Tscharntke 1995) allow utilisation of fresh floral resources by bee populations from the surrounding unburnt vegetation. This type of rapid recolonisation has also been documented for flower-feeding insects in chaparral burns (Force 1981) and a variety of other habitats (Swengel 2001).

As floral regeneration proceeds, with the progressive loss of floral richness, most bee families become less speciose (Fig. 2a). The Apidae are an exception, as this family diversifies beyond intermediate-aged sites; this is linked to the general replacement of annuals by long-corolla-tubed perennials in mature vegetation on which long-tongued Apidae tend to specialise.

Changes in the overall abundance of bees and flowers correspond to the same general pattern exhibited by diversity changes, with early post-fire maxima (Fig. 1b,d). After an initial peak in floral coverage in year two, which coincides with the first flowering season of the dominant nectariferous perennial *Salvia fruticosa*, overall floral abundance declines as vegetation maturity is reached. Total bee numbers also follow this trend, though within most families there is no clear response through time. The exception is Megachilidae, whose numbers steadily decrease; this may be associated with nesting resources rather than floral characteristics, as they prefer to nest in habitats with more open areas and pithy plant stems (O'Toole and Raw 1991), which become increasingly scarce with site age (pers. obs.).

Nectar volume, concentration and niche diversity responses to fire

Community level changes in the structure of nectar rewards following fire are complex, and subject to a diverse suite of environmental factors modulating nectar production, including floral community composition, resource availability, vegetation architecture and microclimate. While nectar-providing plants are characterised by a specific decline in diversity and abundance through time, only nectar concentration and niche diversity follow this trajectory (Fig. 3). Nectar volume (Fig. 3a), and nectar water content (Fig. 3c), are highly variable through time. Despite the overall loss of floral cover with approaching maturity (Fig. 1d), the increasing dominance of nectar-rich perennials over annuals results in a continued substantial supply of nectar. Variability in volume and water content is high for many post-fire ages and indicates the heterogeneous nature of this resource. Indeed, equivalent-aged sites may have similar floristic richness and cover yet the community is composed of different groups of species with contrasting nectar provisioning profiles.

In the core flowering plant *Satureja thymbra* (Lamiaceae) nectar volumes were significantly higher in an unburnt area than in an eight year post-fire site (Potts et al. 2001b). This temporal 'snapshot' demonstrates that changes in floral reward availability in response to fire may be marked in a single species; however, at the community level the overall pattern of rewards may be very different. The current study is based on area-specific nectar production, whereas the study on *S. thymbra* focussed on a 'per plant' basis. Both provide useful information in describing the rewards available to foragers, with the former more relevant for explaining community structure and the latter for visitation patterns.

The clear decline in the mean concentration of nectar available through time (Fig. 3b) is a function of both floral morphology and gross vegetation architecture. Freshly burnt sites typically support extensive blooms of open access annuals that produce relatively small amounts of nectar and, in addition, these sites are devoid of tree cover leading to increased exposure to the sun and wind, factors known to concentrate nectar (Corbet et al. 1979). In contrast, mature sites have more long-corolla-tubed flowers, especially perennials, with higher nectar volumes, and are also shaded by the canopy. In immature sites, this combination of factors results in concentrated nectar-providing communities that would be expected to support foragers adapted to this resource. Indeed, the Andrenidae and Halictidae comprise short-tongued bees that are more efficient at collecting small volumes of relatively concentrated nectar than similar sized long-tongue equivalents (Harder 1983) and these families are most speciose in recently burned sites (Fig. 2a). This close association between andrenids and annuals has also been indicated in another fire-driven system in Greece (Petanidou and Ellis 1996).

Nectar volume and concentration can both be combined to define a set of potential foraging niches, and given the variation in these two parameters across sites it follows that nectar niche diversity should also be linked to site age (Fig. 3d). The decline in the number of niches available reflects the transition from an annual-dominated flora to a perennial-dominated flora and a steady loss with age of the low-volume, high-concentration niches provided by annuals. All sites had high-volume and low- to medium-concentration niches supplied by the ubiquitous biannual *Asphodelus aestivus* (Liliaceae), but the supplementation of this by a variety of annuals creates more niches in young sites. The fundamental importance of nectar niche diversity in organising pollinator community structure has been demonstrated for the post-fire habitats of Mount Carmel (Potts, unpubl.).

Energy availability in response to fire

Energy availability has a pivotal role in structuring consumer communities and we present two novel aspects of this relating to pollinators: first we have quantified the absolute energy content of the primary resources used by bees on a per unit area basis, and second we have tracked the changes in these measures through an entire cycle of post-fire recovery.

Total energy in the system is greatest in the first decade and the associated bee fauna is at its most diverse and abundant during this period (Fig. 4c). The temporal profile of nectar energy (Fig. 4a) and its dependent variable total energy (nectar plus pollen energy (P + N); Fig. 4c) match closely that of the volume profile in Fig. 3a; with the exception of the outlying point for the 25 year old site which was the result of a single highly unusual sample (note large SE). Ignoring this data point, the general conclusion is that nectar energy peaks in year 2, and thereafter remains fairly constant through time. The 2 year peak coinciding with the massive flush of *Salvia*. Beyond 2 years, the intermediate-aged communities are dominated by *Cistus* spp. which are primarily pollen producers with little or no nectar, and nectar energy is particularly low during this post-fire stage.

Pollen energy availability declines over time in tandem with floral abundance (Fig. 4b); recently burnt sites are dominated by a relatively continuous cover of r-selected annuals, and consequently are pollen rich. Pollen is the main food source for developing bee larvae, while nectar is primarily used by adult bees to sustain foraging activity; the balance between these two resources will ultimately define bee community structure. However, total energy content of pollen does not

necessarily correspond to the energy available to the consumer (Roulston and Cane 2000), therefore we advise cautionary interpretation of pollen-related data.

In terms of the relative importance of these energy sources, pollen may be considered dominant as the ratio between the pollen and nectar energy (P:N) is >1 in most sites (Fig. 4d). However, pollen importance declines with site age as it is a property of the changing floral communities following fire and therefore subject to the shift from annuals to perennials. It is often suggested that pollen is the primary reward in Mediterranean plant-pollinator systems (Herrera 1985, Petanidou and Vokou 1990), and we provide the first quantitative validation of this. P:N is one of the most important factors in organising bee community structure (unpubl.) and its age-related magnitude has key implications for understanding bee-flower relations at the community level.

Clearly understanding how reward structure links floral and pollinator communities and how all three interact and respond to disturbance is central to any conservation measures aiming to restore and protect these communities (São Paulo Declaration on Pollinators, 1999). Given the extensive background literature available on plant-pollinator associations of single species and small groups of species, there is a need to extend our current knowledge to embrace these complex interrelations at the scales at which landscape management practices operate. Only in this way can we identify the key factors maintaining the integrity of these communities and predict how various disturbance regimes will effect the organisation of floral, reward and pollinator abundance and diversity.

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