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Plant-pollinator biodiversity and pollination services in a complex Mediterranean landscape

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ABSTRACT

Mediterranean landscapes comprise a complex mosaic of different habitats that vary in the diversity of their floral communities, pollinator communities and pollination services. Using the Greek Island of Lesvos as a model system, we assess the biodiversity value of six common habitats and measure ecosystemic 'health' using pollen grain deposition in three core flowering plants as a measure of pollination services. Three fire-driven habitats were assessed: freshly burnt areas, fully regenerated pine forests and intermediate age scrub; in addition we examined oak woodlands, actively managed olive groves and groves that had been abandoned from agriculture. Oak woodlands, pine forests and managed olive groves had the highest diversity of bees. The habitat characteristics responsible for structuring bee communities were: floral diversity, floral abundance, nectar energy availability and the variety of nectar resources present. Pollination services in two of our plant species, which were pollinated by a limited sub-set of the pollinator community, indicated that pollination levels were highest in the burnt and mature pine habitats. The third species, which was open to all flower visitors, indicated that oak woodlands had the highest levels of pollination from generalist species. Pollination was always more effective in managed olive groves than in abandoned groves. However, the two most common species of bee, the honeybee and a bumblebee, were not the primary pollinators within these habitats. We conclude that the three habitats of greatest overall value for plant-pollinator communities and provision of the healthiest pollination services are pine forests, oak woodland and managed olive groves. We indicate how the highest value habitats may be maintained in a complex landscape to safeguard and enhance pollination function within these habitats and potentially in adjoining agricultural areas.

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1. Introduction

Pollinators are well known to provide key ecosystem services to both natural and agro-ecosystems. Pollination is essential for the maintenance of diversity in wild flowers, and is indirectly responsible for the persistence of other guilds that depend upon floral resources, such as herbivores and seed-eaters. Animal pollinators are thought to contribute between

15% and 30% of global food production (McGregor, 1976; Roubik, 1995) and bees are recognised to be the most important pollinating taxon (Delaplane and Mayer, 2000). In the US, economic gains from honeybees (*Apis mellifera*) are estimated to range between \$1.6 and \$5.7 billion (Southwick and Southwick, 1992); in Europe pollination by honeybees is worth approximately €4.25 billion, and pollination by other taxa worth approximately €0.75 billion (Borneck and Merle, 1989). Agricultural crops often depend, at least in part, on unmanaged or 'wild' pollinator populations from adjacent semi-natural habitats for their productivity (Kevan, 1977, 2001; Klein et al., 2003; Kremen et al., 2002, 2004; Ricketts, 2004; Ricketts et al., 2004). However, the economic, biodiversity and aesthetic value of pollinators is known for relatively few systems (e.g., Nabhan and Buchmann, 1997; Delaplane and Mayer, 2000), and there is considerable scope to improve our understanding of the habitat characteristics that moderate the value of plant-pollinator communities.

It is globally recognised that pollinators and the services they provide are under increasing pressure from multiple anthropogenic sources (Kremen and Ricketts, 2000; Kevan, 2001). Major threats identified include: habitat loss and fragmentation (Frankie et al., 1997; Jennersten, 1988; Donaldson et al., 2001; Ricketts, 2004); habitat isolation (Steffan-Dewenter and Tscharntke, 1999; Battacharya et al., 2003); agricultural intensification (Kremen et al., 2002, 2004); agrochemicals (O'Toole, 1993; Kearns et al., 1998); diseases (Watanabe, 1994); parasites (Schmid-Hempel and Durrer, 1991); climate change (Price and Waser, 1998); introduced non-native plants (Brown et al., 2002; Chittka and Schürkens, 2001) and competition with managed pollinators (Gross, 2001; Steffan-Dewenter and Tscharntke, 2000; Thomson, 2004; Paini and Roberts, 2005). Threats to managed pollinators such as honeybees are documented and in some regions of the world significant losses due to disease and competition with Africanised honeybees have been recorded (Ingram, 1996; Kearns et al., 1998; Allen-Wardell et al., 1998). Reliance on a single, or at best a few, species of pollinators for crop production is a high risk strategy given the potential loss of these service providers. Wild pollinators may increasingly provide an 'insurance' for continued crop pollination (Kremen et al., 2002) in addition to their natural function in pollinating wild flowers.

The Mediterranean basin is one of the world's centres of bee speciation (Michener, 1979) and supports some of the most diverse plant-pollinator communities (Michener, 2000). This in part reflects the complex mosaic of habitat types found in the region, which comprises communities that are perpetually subject to a wide range of moderate to intense disturbance factors (Rundel et al., 1998). The biodiversity value of these habitats for pollinators has received some attention (Petanidou and Ellis, 1993, 1996; Potts et al., 2003a), but the services that pollinators provide to flowering plants is still relatively unexplored despite the fact it is known that many wild plants experience significant pollen limitation (Burd, 1994).

This study aims to: (1) assess the biodiversity of a range of typical Mediterranean habitats and identify those supporting the highest diversity of pollinators; (2) quantify the ecosystem services provided by different pollinator assemblages; (3) determine the habitat characteristics associated with the most diverse and effective pollinator communities. This information is essential to underpin directed management seeking to maintain and promote plant-pollinator biodiversity and pollination services in Mediterranean landscapes.

2. Methods

2.1. Habitat types and study site selection

The Aegean Sea separates Greece and Turkey and comprises a multitude of islands of varying size (from a few m^2 to 8291 km^2). Lesvos (N38°57′32″–39°23′15″, E25°49′46″–26°36′51″) has an area of 1630 km^2 and is situated in the north east Aegean about 9 km from the Turkish coast at its nearest point. The climate is typically Mediterranean with cool wet winters and hot dry summers (Maheras, 1983). The two major land cover types found on the island are: pine forests occurring in a mosaic of various stages of post-fire regeneration, and small olive groves, most of which are actively managed but some of which are abandoned. In addition there are areas of oak woodland, coastal scrub, urban developments, chestnut forests, salt marshes and a few extensively cultivated lands.

For this study, we identified six distinct habitat types: mature pine forest unburnt for at least 50 years containing open patches (designated mature pine); pine forest in the first 5 years of post-fire regeneration (freshly burnt); pine forest after 10–30 years of post-fire regeneration (intermediate age); mixed oak woodland; olive groves under active management (managed olives); and olive groves that had been abandoned for more than 10 years (abandoned olives).

The mature pine forest is dominated by *Pinus brutia* Ten. with an understory of perennial shrubs including *Cistus salvifolius* L., *Cistus creticus* L., *Lavandula stoechas* L., and *Thymus capitatus* L.. Occasional small open patches also support a range of other perennial and annual flowers. Freshly burnt areas are initially characterised by a flush of flowering annuals in the first 1–5 years, but thereafter perennials become increasingly dominant. Typical flowering plants include *Asphodelus ramosus* L., *Anagallis arvensis* L., *Sinapis arvensis* L. and several species of Fabaceae and Asteraceae. As regeneration continues, perennial species and pine seedlings become more abundant. Intermediate age sites are characterised by high shrubland dominated by *Cistus* spp. and other herbs. The freshly burnt and intermediate age areas covered with vegetation up to 70 cm high, are commonly classified as phryganic vegetation or phrygana. Oak woodlands have an open canopy comprising Valonia oak (*Quercus ithaburensis* subsp. *Macrolepis* (Kotschy) Hedge and Yalt.) with a diverse understory of annuals and perennial shrubs. Olive trees (*Olea europaea* subsp. *oleaster* (Hoffmanns. and Link) Negodi) are cultivated in stands and when managed by ploughing have an understory of many annual flowers. If these stands are abandoned then the vegetation regenerates to include many perennial species found in the phrygana. Descriptions of the habitat types and flowering plant species can be found in (Petanidou and Ellis, 1993, 1996; Detsis et al., 2000; Marathianou et al., 2000).

Using vegetation and topographical maps, in conjunction with aerial photographs, we located areas of each of these six habitat types that were highly representative of those

found across Lesvos. Large blocks of land (>100 ha) of each habitat type were identified and potential sites were selected and ground-truthed to ensure that they were typical of the general area and did not include unusual management practices (e.g., cultivation of other plants, excessive grazing or logging). In each of the six habitat types three 1 ha sites were selected that had a uniform vegetation structure. We ensured that all the sites in each habitat type had similar slopes, aspects and elevations. All sites were at least 0.5 km from any other site or a different habitat type. The location and physical characteristics of each are summarised in Table 1.

2.2. Bee, flower and nectar surveys

Between mid March and late May 2001, three surveys of the flora and pollinating fauna were carried out at the 18 experimental plots (Table 1). The surveys were timed to cover the peak flower blooming period: survey 1, mid March to mid April; survey 2, mid to late April; survey 3, early to mid May. During each round of surveys, sites were sampled in quick succession to reduce seasonal effects, and data were only collected on days with typical weather conditions (i.e., without rain or high winds). Microclimatic data were also recorded and were consistent with long-term averages.

Each bee survey comprised three 200 m long linear transects walked in 20 min at 09:00, 13:00 and 16:00 h. Each transect start point and direction walked were randomly determined using random number tables. All bees unambiguously identifiable 'on the wing' were recorded and all others were caught with a hand net and retained for later identification. Bees were identified and voucher specimens are kept at the Bee Systematics and Biology Unit, Oxford University Museum of Natural History, UK. Some bees observed 'on the wing' could potentially be recorded twice, however, the combined experience of the survey team suggested that this was

an extremely rare event and all reasonable steps were taken to minimise this possibility. There were no marked differences across habitats for the proportion of bees identified on the wing relative to those caught. Time spent handling specimens while walking a transect was subtracted from the overall time to ensure 20 min of actual recording time was used. Bee nomenclature is in accordance with Michener (2000).

Flower surveys were carried out in parallel to the bee surveys and used a 50 × 0.40 m linear belt transect starting at a randomly selected point and moving out in a random compass direction. The species and area coverage of all open flowers that could potentially be visited by bees were recorded. A mean individual flower area for each species was calculated and multiplied by the number of flowers found within the transect. Flower names are consistent with Euro+Med Plant-Base (2004).

Five nectar parameters were estimated for each site: nectar volume, nectar concentration, nectar energy content, nectar water content and nectar resource diversity. A randomly placed 50 m linear transect was marked and ten 1 m^2 quadrats located along its length. In each quadrat all open flowers were sampled for available nectar using microcapillary pipettes (Camlab, UK) to estimate nectar volume and sugar concentration was measured with refractometers modified for small volumes (Bellingham and Stanley, UK). Flowers were all sampled prior to 08:00 before bee activity increased markedly. Open, rather than 'bagged', flowers were sampled in this experiment as the aim was to obtain a broad estimate of nectar availability at the community level and without needing to accurately quantify nectar production on a species basis. Previous studies have shown that total nectar availability in 'open' and 'bagged' flowers is highly correlated when all species are considered (Potts et al., 2003a) and that this approach is appropriate for habitat comparisons (Potts et al., 2003b). By

Table 1 – Physical characteristics of survey sites on Lesvos, Greece

Site name	Location	Replicate	GPS (lat., long.)	Description	Altitude a.s.l. (m)	Aspect (°)	Slope (°)	Surfacial geology
Freshly burnt	Charamida	1	39.012, 26.595	Phryganic vegetation, burnt in 1999	160	240	20	Peridotites
		2	39.010, 26.593		190	190	15	
		3	39.014, 26.588		128	220	20	
Intermediate burn	Kratigos	1	39.015, 26.596	Phryganic vegetation, burnt in 1977	210	70	15	Peridotites
		2	39.018, 26.597		213	70	30	
		3	39.013, 26.600		195	120	15	
Mature pine	Kratigos	1	39.028, 26.598	Mature pine forest burnt before 1950	475	300	15	Peridotites
		2	39.029, 26.589		450	240	10	
		3	39.031, 26.584		439	10	20	
Oak woodland	Skalohori	1	39.230, 26.028	Mixed oak woodland	192	210	30	Granite, tertiary deposits (tuffs)
		2	39.231, 26.025		188	210	20	
		3	39.232, 26.023		186	210	30	
Managed olive grove	Vatera	1	39.033, 26.168	Olive groves under active management	82	40	20	Peridotites
		2	39.032, 26.163		130	90	10	
		3	39.028, 26.160		103	210	5	
Abandoned olive grove	Vatera	1	39.020, 26.165	Olive groves abandoned for >10 years	109	15	15	Peridotites
		2	39.019, 26.169		118	10	10	
		3	39.015, 26.170		103	20	20	

summing the individual flower nectar volumes for each survey, and calculating the average concentration per site it was possible to estimate a habitat mean for both parameters. Volume and concentration data were then used to calculate nectar energy and water content (Dafni, 1992). Nectar resource diversity was determined by generating an index that quantified the variety of nectar volume–concentration combinations available (Potts et al., 2004). Each mean nectar volume and concentration measurement for each plant species in a given habitat was assigned to an exclusive category using a 3×3 matrix for volume (<0.1, 0.1–1.0 and >1.0 μl) and concentration (<25%, 25–50% and >50%). The number of the categories, of the nine possible, with at least one plant providing that nectar resource were summed to give an index of nectar resource diversity (see Potts et al., 2004 for full details of this method).

2.3. Assessment of pollination services to wild flowers

To measure the effectiveness of whole pollinator communities in delivering pollination services to wild flowers we used pollen grain deposition as a measure of this ecosystem service. We selected three common flower species with contrasting floral morphologies, life histories, pollen and nectar rewards, and growth forms. These were *Asphodelus ramosus* (Liliaceae), *Cistus salvifolius* (Cistaceae) and *Lavandula stoechas* (Lamiaceae) and all three of which were reliant on insects for pollination.

A. ramosus is a tall perennial herb bearing 20–150 large (20–30 mm) white flowers that provide high volumes of dilute nectar in a restricted access corolla, and copious amounts of pollen (Petanidou and Vokou, 1990; Petanidou and Smets, 1995). It was common in all the habitats surveyed and can be considered a 'magnet' species attracting a wide range of medium to large bees and other insect taxa throughout the spring (Ne'eman et al., 2000). Though it is self-compatible, insects are required for effective pollination owing to the position of the anthers and stigma (Schuster et al., 1993). *C. salvifolius* is an evergreen shrub with large white open-access flowers of 30–50 mm; each shrub may bear up to several hundred flowers that provide large amounts of pollen and small volumes of relatively concentrated nectar (Petanidou and Vokou, 1990; Petanidou and Smets, 1995). This species is self-incompatible and entirely dependent upon insect vectors for pollination (Manetas and Petropoulou, 2000), these visitors being a variety of small to large solitary bees, honeybees, beetles and flies. *C. salvifolius* was present in all the sites and was particularly abundant in the post-fire regenerating areas, but much less common in the olive groves. *L. stoechas* is a small aromatic semi-evergreen shrub with dark purple tubular flowers (6–8 mm in length) borne on stubby spikes crowned with conspicuous purple bracts (Blamey and Grey-Wilson, 2000). It provides small volumes of nectar and pollen and is mostly visited by medium- and large-sized bees. This species was found only in the post-fire sites and was never particularly common.

Pollen grain deposition was measured by randomly collecting a minimum of 100 exposed styles of each species at the end of the bee surveys and storing them in individual containers. Within 6 h of harvesting, the stigmas were stained with a mix of phloxine and methyl green, gently crushed between a slide and coverslip, and the number of con-specific pollen grains on the receptive area of the stigma counted under a light microscope (Dafni, 1992).

2.4. Statistical analysis

Counts of bees and flowers, and nectar parameters were pooled for the entire season for each site. Differences between habitat types were analysed using a General Linear Model with site replicate entered as a random factor, and Tukey's simultaneous pairwise comparisons were used to test for differences between pairs of habitats. Count data were transformed using $\log_{10}(x + 1)$. All calculations were performed using Minitab 13.32 and values given in the text are means ± 1 SE.

The relationships between bee community structure, flower community structure and pollination services were explored using a variety of techniques. Separate ordinations for the entire bee community and only the common species (>0.5% of total abundance) were made using CANOCO 4.02 (Ter Braak and Smilauer, 1999) with flower and nectar parameters entered as the environmental variables. Redundancy analysis (RDA) was employed because a detrended correspondence analysis of the species-abundance data indicated that a linear model was appropriate. Statistical tests of significance were made using Monte Carlo global permutation tests under a reduced model for the canonical axes (1000 permutations) and environmental variable–axis relationships; environmental variables were automatically forward selected. Significant environmental factors identified in the ordination models were then correlated with bee diversity and the abundance of the common species. To investigate the link between pollinator community structure and pollination services, an additional ordination was undertaken with pollen grain deposition of the three test plants as response variables and the abundance of the common bee species as the environmental variables.

To test whether the variability in species composition is spatially structured after accounting for the six different habitat types a partial Mantel test (Mantel, 1967) was carried out. This was calculated using Pearson's correlation and a permutation test (Legendre and Legendre, 1998; Smouse et al., 1986) with 5000 permutations to test for significance. The dissimilarity matrix for sites based on species composition was calculated using the Bray-Curtis measure of dissimilarity (Legendre and Legendre, 1998). The dissimilarity matrix for sites based on distances was calculated using Euclidean distances, as was the dissimilarity matrix for sites based on habitat. Results using all bee species gave a Mantel statistic of $r = -0.09028$ ($P = 0.92$) and for common species a Mantel statistic of $r = -0.09756$ ($P = 0.94$). In both cases this indicates that there is no evidence that sites which have similar species composition are spatially close together, or in other words that there is no evidence that dissimilarity in species composition between sites is a function of the geographical distance between sites. Analysis was carried out using functions from the package *vegan* (Oksanen et al., 2005) in the statistical computing programme R (R Development Core Team, 2005).

3. Results

3.1. Biodiversity of bees and flowers across habitats

A total of 5584 bees were recorded with 130 species represented. Habitats differed markedly in both the abundance and diversity of bees present (Table 2). Of the post-fire regenerating sites, the mature pine forests had the highest overall diversity (36 species), followed by the freshly burnt habitats (31), with intermediate burn age areas being least diverse (28). Oak woodlands were more species rich than any of the post-fire habitats (45). Of all habitats surveyed, the actively managed olive groves had the most bee species (50), and the abandoned groves the fewest (20). The significant difference in mean diversity across sites ($F_{10,5} = 3.71$, $P = 0.037$) was accounted for by the difference between the oak woodland and abandoned olive sites ($P = 0.0248$).

Bee abundance also varied across sites (Table 2) with a general trend of decreasing bee numbers as post-fire sites matured: freshly burnt had 1408 bees; intermediate age yielded 1061 and mature sites 484. Oak woodlands (1572) supported the greatest number of individuals, and managed olives (693) had many more bees than abandoned olives (366). There was a significant difference in mean numbers across sites ($F_{10,5} = 3.61$, $P = 0.040$) with oak woodland having more bees than abandoned olive groves though this was only marginally significant ($P = 0.0685$).

Oak woodlands and both types of olive groves had many more flowering plant species (all >25 per replicate) than any of the post-fire sites (Table 2). These differences were highly significant ($F_{10,5} = 26.34$, $P < 0.0001$), with all post-fire habitats being less diverse than oak woodlands (all $P < 0.004$) and managed olive groves (all $P < 0.02$). Managed groves were more diverse than abandoned groves ($P = 0.0563$). There was no significant difference in diversity between oak woodlands and managed olive groves, or between abandoned olive groves and any post-fire habitat.

Oak woodlands also had the highest abundance of flowers, followed by managed olive groves and freshly burnt areas, all of which had many more flowers than intermediate age burnt sites, mature sites and abandoned olive groves (Table 2). However, high variation across replicates of a given habitat type meant that there were no significant differences in mean floral cover between habitats ($F_{10,5} = 2.50$, $P = 0.102$).

Mean nectar volume ($F_{10,5} = 10.05$, $P = 0.001$), nectar energy content ($F_{10,5} = 10.26$, $P = 0.001$) and nectar water content ($F_{10,5} = 9.52$, $P = 0.001$) all varied significantly between habitat types. Freshly burnt sites always had the highest values ($P < 0.005$ in all cases). There were no significant differences in mean nectar concentration across habitats ($F_{10,5} = 2.63$, $P = 0.163$).

3.2. Pollination services across habitats

For *Asphodelus*, the number of con-specific pollen grains deposited varied significantly between habitats (Table 2: $F_{10,5} = 21.20$, $P < 0.001$). Burnt and mature pine sites both had significantly higher values than all other sites ($P < 0.02$ in all cases), though there was no difference in grain counts between the burnt and mature sites.

Numbers of grains deposited on *Cistus* varied significantly between sites (Table 2: $F_{10,5} = 17.40$, $P < 0.001$) but there were no differences between post-fire sites. Managed olives had significantly higher grain counts than abandoned olives ($P = 0.0077$) and oak woodlands had more grains deposited ($P < 0.04$ in all cases) than all other habitats except managed olive groves.

Pollen grain numbers found on *Lavandula* were significantly different across post-fire sites (Table 2: $F_{2,4} = 14.29$, $P < 0.001$) with higher counts in the burnt habitat than in either the intermediate age ($P < 0.0001$) or mature pine ($P = 0.0029$) habitats. There were no differences between intermediate and mature sites.

3.3. Bee and flower community structure

The organisation of the whole bee community of 130 species was significantly linked with floral community (Fig. 1, Table 3: Redundancy Analysis, sum of all canonical variables = 0.454; $F = 1.19$, $P = 0.014$ for all canonical axes). There were three significant variables in the model: flower species richness (9% of

Table 2 – Summary of mean bee, flower, nectar and pollen grain deposition values for each habitat type						
Parameter	Freshly burnt	Intermediate burn	Mature pine	Oak woodland	Managed olive grove	Abandoned olive groves
Bee species richness (species/site)	18.0 ± 2.4	15.0 ± 2.3	17.0 ± 2.0	22.7 ± 0.6	19.0 ± 1.7	13.0 ± 1.2
Bee abundance (individuals/site)	469 ± 70	354 ± 81	161 ± 32	524 ± 149	231 ± 57	122 ± 18
Flower species richness (species/site)	16.3 ± 1.3	7.0 ± 2.0	6.7 ± 2.9	36.0 ± 2.5	38.3 ± 4.3	25.3 ± 2.0
Flower abundance (cm^2/site)	3793 ± 1760	486 ± 153	162 ± 63	8307 ± 4230	5235 ± 1614	770 ± 272
Nectar volume (ml/ha/day)	41.1 ± 12.2	2.5 ± 2.1	4.5 ± 2.1	3.0 ± 1.5	0.8 ± 0.4	4.6 ± 3.3
Nectar concentration (% sucrose)	35.5 ± 1.3	20.3 ± 10.2	27.6 ± 8.2	46.5 ± 6.4	47.0 ± 4.7	35.3 ± 0.5
Nectar energy (kJ/ha/day)	1.44 ± 0.40	0.07 ± 0.06	0.15 ± 0.10	0.14 ± 0.07	0.04 ± 0.02	0.16 ± 0.12
Nectar water (g/ha/day)	0.33 ± 0.10	0.02 ± 0.02	0.04 ± 0.02	0.02 ± 0.01	0.01 ± 0.01	0.04 ± 0.03
Nectar resource diversity (categories)	4.0	2.0	3.0	3.0	2.0	1.0
Asphodelus pollen grains (no./stigma)	40.3 ± 2.1	30.3 ± 1.6	37.0 ± 2.6	29.8 ± 3.1	33.0 ± 3.2	30.4 ± 2.0
Cistus pollen grains (no./stigma)	26.3 ± 3.1	16.6 ± 1.7	26.8 ± 4.1	45.7 ± 2.9	37.6 ± 2.4	26.6 ± 1.9
Lavandula pollen grains (no./stigma)	46.3 ± 3.7	34.7 ± 2.0	38.4 ± 3.7	–	–	–

Means are based on the pooled seasonal total for each of three replicated sites, except for nectar resource diversity which are the pooled value for all three replicates within a habitat. *Lavandula* was only recorded in three habitats.
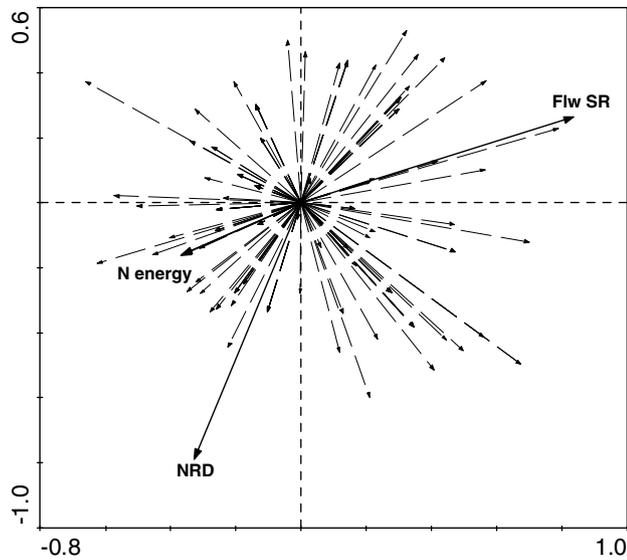
Fig. 1 – Redundancy analysis biplot showing correlation between the whole bee community and the floral community. Solid line vectors represent significant environmental variables: 'Flw SR', flower species richness; 'N energy', nectar energy content; 'NRD', nectar resource diversity. Dashed line vectors represent bee species.
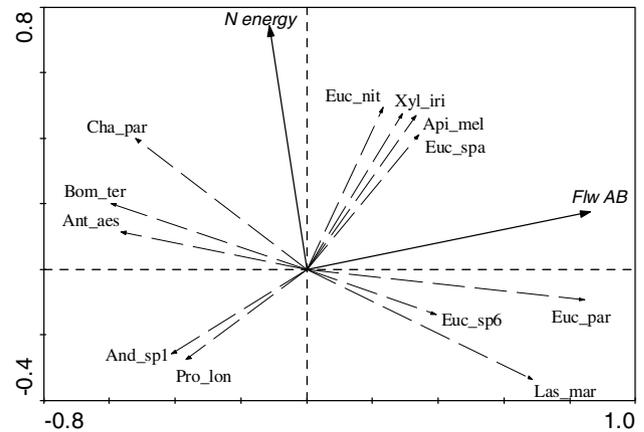

Fig. 2 – Redundancy analysis biplot showing correlation between the abundance of the 12 most common bee species and the floral community. Solid line vectors represent significant environmental variables: 'Flw AB', flower abundance and 'N energy', nectar energy content. Abbreviation for bee species are: Api_mel, *Apis mellifera*; Bom_ter, *Bombus terrestris*; Las_mar, *Lasioglossum marginatum*; Ant_aes, *Anthophora aestivalis*; Xyl_iri, *Xylocopa iris*; And_sp1, *Andrena* sp. 2001/2001; Euc_par, *Eucera parvula*; Euc_nit, *Eucera nitidiventris*; Pro_lon, *Protosmia longiceps*; Euc_spa, *Eucera* sp nov. aff. *spatulata*; Cha_par, *Chalicodoma parietina*; and Euc_sp6, *Eucera* sp. 2001/2006.

Table 3 – Redundancy analysis for the whole bee community of 130 species					
	Axis 1	Axis 2	Axis 3	Axis 4	Total variance
Eigenvalues	0.096	0.083	0.069	0.064	
Species–environment correlation	0.974	0.969	0.951	0.960	
Cumulative % variance of species data	9.6	17.9	24.8	31.2	
Cumulative % variance of species–environment data	21.2	39.4	54.5	68.7	
Sum of all eigenvalues					1.000
Sum of all canonical eigenvalues					0.454

variation explained, $F = 1.52$, $P = 0.001$); nectar resource diversity (7%, $F = 1.36$, $P = 0.01$); and nectar energy content (7%, $F = 1.27$, $P = 0.083$). The first and second axes explain 9.6% and 8.3% of the variance respectively in the model. Overall bee and flower species richness were highly significantly correlated ($r = 0.481$, $n = 18$, $P = 0.044$) and overall bee abundance was marginally statistically correlated with nectar resource diversity ($r = 0.427$, $n = 18$, $P = 0.078$).

Selecting only the bee species contributing >0.5% to the total abundance of the community left 12 species that comprised 85.5% of total numbers. The species were: *Apis mellifera* L. (Apidae), 65.4% of numbers; *Bombus terrestris* L. (Apidae), 7.4%; *Lasioglossum marginatum* Brulle (Halictidae), 2.8%; *Anthophora aestivalis* Panzer (Apidae), 2.3%; *Xylocopa iris* Christ (Apidae), 1.6%; *Andrena* sp. 2001/2001[1] (Andrenidae),

1.4%; *Eucera parvula* Friese (Apidae), 1.2%; *Eucera nitidiventris* Mocsary (Apidae) 0.9%; *Protosmia longiceps* Morawitz (Megachilidae), 0.7%; *Eucera* sp. nov. aff. *spatulata* (Apidae), 0.7%; *Megachile* (*Chalicodoma*) *parietina* Geoffroy (Megachilidae), 0.6%; and *Eucera* sp. 2001/2006 (Apidae) 0.5%. The abundance of these common species was strongly related to the structure of the floral community (Fig. 2, Table 4: redundancy analysis, sum of all canonical variables = 0.558; $F = 1.81$, $P = 0.013$ for all canonical axes). Two significant floral parameters were entered into the model: floral abundance (20% of variation explained, $F = 3.90$, $P = 0.002$) and nectar energy content (9%, $F = 1.87$, $P = 0.074$). The abundance of four bee species was positively correlated with floral abundance: *Apis mellifera* ($r = 0.508$, $n = 18$, $P = 0.031$); *Eucera parvula* ($r = 0.896$, $n = 18$, $P < 0.001$); *Eucera*. sp nov. aff. *spatulata* ($r = 0.424$, $n = 18$, $P = 0.079$); and *Lasioglossum marginatum* ($r = 0.595$, $n = 18$, $P = 0.009$). The abundance of *Xylocopa iris* ($r = 0.437$, $n = 18$, $P = 0.070$) and Megachile (*Chalicodoma*) *parietinum* ($r = 0.418$, $n = 18$, $P = 0.084$) were a positive function of the amount of nectar energy available.

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[1] Several species in this study are undescribed and so without published descriptions. We have therefore separated material into Recognisable Taxonomic Units and designated them as sp. 2001/2001, etc.

Table 4 – Redundancy analysis for the 12 most common species					
	Axis 1	Axis 2	Axis 3	Axis 4	Total variance
Eigenvalues	0.246	0.113	0.087	0.069	
Species–environment correlation	0.969	0.647	0.913	0.862	
Cumulative % variance of species data	24.6	35.9	44.6	51.5	
Cumulative % variance of species–environment data	44.1	64.3	79.8	92.1	
Sum of all eigenvalues					1.000
Sum of all canonical eigenvalues					0.558

3.4. Pollination services and bee community structure

The variations in the number of pollen grains deposited on *Aphodelus*, *Cistus* and *Lavandula* stigmas were explained by the abundance of the common bee species (Fig. 3, Table 5: redundancy analysis, sum of all canonical variables = 0.558; $F = 4.74$, $P = 0.004$ for all canonical axes). Three bee species were significant contributors to the model: *Andrena* sp. 2001/2001 (29% of variation explained, $F = 6.60$, $P = 0.007$); *Anthophora aestivalis* (18%, $F = 4.89$, $P = 0.017$); and *Xylocopa iris* (11%, $F = 4.79$, $P = 0.035$). However, the two most common spe-

cies across all habitats, the social bees *Apis mellifera* and *Bombus terrestris*, were not significant in the model. Three species were correlated with the number of *Cistus* pollen grains deposited: *Xylocopa Iris* ($r = 0.534$, $n = 18$, $P = 0.027$); *Eucera parvula* ($r = 0.558$, $n = 18$, $P = 0.020$); and *Eucera*. sp nov. aff. *spatulata* ($r = 0.449$, $n = 18$, $P = 0.070$). The abundance of none of the common species was significantly correlated with grain deposition in *Asphodelus* or *Lavandula*. *Cistus* was the only flowering plant where pollen grain counts were a positive function of total bee diversity ($r = 0.476$, $n = 18$, $P = 0.053$) and total bee abundance ($r = 0.445$, $n = 18$, $P = 0.074$).

4. Discussion

4.1. Plant-pollinator biodiversity across habitats

Overall bee diversity, measured as species richness, changes with the age of a site following fire. Mature pine woodland, regenerating for more than 50 years after a burn, had more species than freshly burnt habitats, which in turn had more species than areas of intermediate post-fire age. The mean number of species was similar in all three habitats, so that at any one time they support comparable levels of bee diversity however, the greater overall species numbers in mature pine woodlands indicates that species turnover is considerably greater here. This is consistent with the observation that mature post-fire habitats tend to be more heterogeneous in nature, having had sufficient time to diversify following a major burn that initially produced relatively uniform stands of vegetation (Arianoutsou and Ne'eman, 2000). Mature pine sites have many rarer bee species, since the highest diversity is also coupled with the lowest abundance, reflecting the steady decline in bee numbers as succession proceeds (Potts et al., 2003a). This suggests that allowing adequate time for regeneration towards climatic vegetation is important for maintaining high bee diversity within a landscape.

The mixed oak woodland had a more diverse bee community than all of the fire-driven habitats. However, the areas
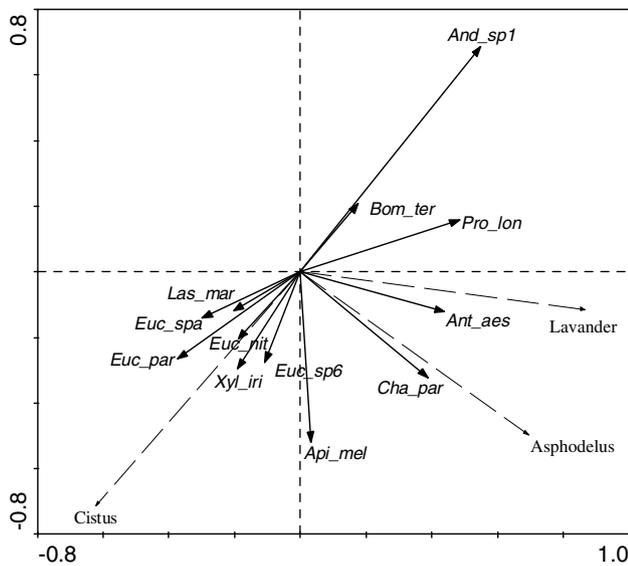

Fig. 3 – Redundancy analysis biplot showing correlation between the pollination services (pollen grain deposition) of test plants and common bee species. Solid line vectors represent the bee species (see Fig. 2 for abbreviations). Dashed vectors are the plant species: *Asphodelus ramosus*, *Cistus salvifolius* and *Lavandula stoechas*.

Table 5 – Redundancy analysis for pollen grain deposition on the three test plants					
	Axis 1	Axis 2	Axis 3	Axis 4	Total variance
Eigenvalues	0.540	0.256	0.124	0.045	
Species–environment correlation	0.967	0.946	0.948	0	
Cumulative % variance of species data	54.0	79.6	91.9	96.4	
Cumulative % variance of species–environment data	58.7	86.6	100.0	0	
Sum of all eigenvalues					1.000
Sum of all canonical eigenvalues					0.919

with the highest bee species richness were the olive groves under active management, and the most species-poor areas were the olive groves that had been abandoned from agriculture. The maintenance of working groves therefore appears to be important in supporting more diverse bee communities which are lost once production ceases. Managed olive groves are regularly ploughed which increases the abundance and diversity of ruderals species and also prevents the dominance of any particular species. Another key structural element of managed groves appears to be the boundary areas where perennials thrive and have a function analogous to field margins in arable habitats.

The observed differences in bee diversity are closely linked to the floral communities upon which the bees forage. Whether considering the entire bee assemblage of 130 species (Fig. 1) or the abundance of the 12 most common species (Fig. 2), the abundance and diversity of flowers are significant structuring elements. The highest bee species richness in the oak woodlands and managed olive groves is mirrored in the high floral diversity recorded in these habitats. The observed patterns in bee and flower diversity in post-fire habitats are consistent with other fire-driven systems in the Mediterranean (Petanidou and Ellis, 1996; Potts et al., 2003a).

Two characteristics of the floral community found to be important for bees are the amount of nectar energy available and the variety of nectar types present. Bee diversity in this Mediterranean landscape appears to be very much driven by the diversity of flowers and the diversity of nectar resources as has been shown for similar sites in Israel (Potts et al., 2003b). The abundance of common species is strongly associated with the overall abundance of flowers, and of energy available in the form of nectar. Other studies have also identified flower diversity and abundance as important elements structuring bee communities (e.g., Banaszak, 1996; Steffan-Dewenter and Tscharntke, 1997). Indeed the numbers of the most common species, *Apis mellifera*, and of three other common species, were positively correlated with the number of flowers in a given habitat; and two large, high energy-demanding bee species were clearly linked to energy available in the form of nectar.

4.2.   *Pollination services across habitats*

Pollination services, measured as con-specific pollen grain delivery in flowers with open visitation, varied markedly between habitats. Results from two of the test plants, *Asphodelus ramosus* and *Lavandula stoechas*, both having corollas with restricted access and so requiring more specialist visitors (primarily bees), indicated that pollination services were highest in the freshly burnt habitats, which is consistent with these areas having high overall bee abundance. The mature pine woodlands also had comparable levels of open pollination in *Asphodelus* but had many fewer bees than the burnt areas. Therefore, either the component of the bee fauna providing pollination services to *Asphodelus* in this mature community must be better represented than in the burnt areas, or the ratio of pollinators to floral resources must be higher in the mature sites. Indeed pine woodlands were relatively depauperate in flowers that were usually only found in open glades that were highly attractive to bees. This situation can

be considered a "sellers market" (Cohen and Shmida, 1993) where consumers are forced to concentrate on limited resources. We can conclude that pollination services to restricted access flowers is highest in burnt areas, followed by mature woodlands with intermediate aged sites, with olive groves and oak woodlands providing the lowest levels.

In contrast, the open/unrestricted access species, *Cistus salvifolius*, had the highest pollen grain delivery in the oak woodlands where bees were both most abundant and most diverse. Petanidou (1991) reports *Cistus* being visited by a broad range of taxa relative to other co-flowering species. Pollination services were also high in the managed olive groves and *Cistus* was significantly better pollinated here than in groves that had been abandoned. Though statistically there was no difference in pollination of the three post-fire habitats, the intermediate-aged site received the lowest level of services. *Cistus* was therefore a useful indicator of overall bee diversity and abundance. Inventories of pollinators are time consuming, particularly in diverse areas such as the Mediterranean, and using pollen grain deposition on *Cistus* and other common and easily accessible flowers could potentially be an effective surrogate for estimating pollinator species richness.

Our analysis indicates that the most common flower visitors were not the primary pollination service providers (Fig. 3). Specifically, honeybees (65% of all bees) and bumblebees (7%) do not appear to be significant pollinators of the three flower species. In our model, *Andrena* sp. 2001/2001 accounted for 29% of variation in pollen deposition but made up only 1.6% of bee abundance. Two other species were important pollinators, *Anthophora aestivalis* and *Xylocopa iris*, and provided 18% and 11% of the services respectively yet contributed only 2% each to bee numbers. Therefore, solitary bees contribute a disproportionately very large amount to overall pollination services based on the three test species in a range of Mediterranean habitats. Studies in other systems have also concluded that the commonly held conception that honeybees are the primary pollinators may not always be correct (Kevan et al., 1990; Westerkamp, 1991).

4.3.   *Protecting and enhancing the biodiversity value of pollinators and pollination services*

Based on bee and flower diversity and the levels of pollination services provided we conclude that the three highest value habitats are mature pine woodland, oak woodland and managed olive groves. In the patchwork landscape of the Mediterranean basin it is therefore important to protect these habitat types in order to ensure effective pollination of wild plants, especially given that >60% of all flowering plant species studied are pollination limited (Burd, 1994). Provision of pollination services to adjacent areas with agricultural crops requiring insect-mediated pollination may also be enhanced by maintaining 'healthy' semi-natural habitats in the landscape (Kremen et al., 2002; Klein et al., 2003). Traditionally farmers have relied on honeybees for most crop and orchard pollination, but our results indicate that they are of more limited value than is often appreciated. Furthermore, recent losses of honeybees due to *Varroa* and tracheal mites (Allen-

Wardell et al., 1998) mean that reliance on this single species may no longer be possible and the services provided by 'native' unmanaged bees may be of increasing importance (Kearns et al., 1998; Kremen et al., 2002).

In the post-fire regenerating system, burnt areas supported diverse and effective pollinator communities, but the persistence of these habitats is relatively short lived before they mature into intermediate-aged habitats which have the lowest species diversity and lowest level of pollination services. Mature pine forests take more than 50 years to regenerate (Arianoutsou and Ne'eman, 2000) and have a relatively high biodiversity value. Most of the high plant-pollinator species richness is linked with open patches found throughout the mature pine stands which enhance the overall diversity of what is generally considered to be a relatively depauperate habitat (Verroios and Georgiadis, 2002). Fires are increasing in frequency in many areas around the Mediterranean basin (and in other mediterranean systems) and many intermediate-aged areas are re-burnt before becoming mature woodlands (Schiller et al., 1997). Repeated burning and overgrazing tend to keep pine woodland locked in early successional stages of regeneration (Rundel et al., 1998). It should therefore be a high priority to protect mature pine forests from inappropriate fire and grazing regimes in order to safeguard pollinators (Kreuss and Tscharntke, 2002), as well as other species (Swengel, 2001), and so maintain their ecosystem functions.

The continued management of olive groves should also be encouraged to enhance local plant-pollinator biodiversity. Abandoned olive groves quickly revert to a state not dissimilar to intermediate-aged burnt habitats with few bee and flower species and the lowest levels of pollination provision. Non-intensive olive farming is generally declining around the Mediterranean (Loumou and Giourga, 2003) and there are opportunities to use agri-environmental schemes to ensure that these groves can still provide diverse flower communities for pollinators and for important herbivorous species. Environmentally-friendly management of temperate orchards in Europe has resulted in more diverse plant-pollinator communities (Steffan-Dewenter and Leschke, 2003), and a similar situation may be achievable in olive groves, though olives themselves do not require biotic pollination.

Protection of other natural habitats, such as the oak woodlands in Greece, should also be sought as they support high levels of bee and flower diversity and often have species components complementing those found in the post-fire and olive grove systems. Indeed, the oak sites had the highest overall levels of generalist (open-access) pollination found in this landscape. The use of *Cistus* as a rapid assessment method for pollinator diversity may also be helpful for identifying other habitats types of high conservation importance.

At the landscape level it would evidently be most effective to maintain a diverse mosaic of all these high-biodiversity-value habitats (Rundel et al., 1998). Given the perpetual exposure of these areas to disturbance and dynamic nature of the system, long-term maintenance of biodiversity and ecosystem function would benefit by reducing the risk of losing any single component.

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