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A land for flowers and bees: studying pollination ecology in Mediterranean communities

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Abstract
Plant–pollinator relationships are of great importance to ecosystem health. Here, we review the importance of Mediterranean habitats for bees, and interactions between plants and pollinators using the pollinator food web approach. We explore the characteristics of reward and attraction in plants, the utility of pollination syndromes and, most importantly, the effect of disturbance and human influence on plant–pollinator communities in the Mediterranean. Finally, we address the major impediment faced in pollination studies in the Mediterranean, i.e., the taxonomic limitation of bees and aculeates in general, and we introduce the 'Melissotheque of the Aegean' a reference bee collection that aims to place some taxonomic capacity in the eastern Mediterranean area.

Key words: *Mediterranean, pollination ecology, plant–pollinator interactions, floral traits, bees, taxonomy, biogeography, conservation biology*

Introduction: Pollination and the Mediterranean region

Plant–pollinator (p–p) relationships embody an essential ecosystem service of often incalculable worth (Kearns et al., 1998). Many angiosperm species are pollinated by animals and as such these mutualisms are under threat from a variety of sources, with declines in pollinator communities witnessed across the world (Kearns et al., 1998; Shepherd et al., 2003). It has, therefore, become imperative that pollination biologists study the ecology of pollinators, the relationship between pollinators and plant communities, and the nature of pollination 'webs' (Kearns et al., 1998; Memmott, 1999; Corbet, 2000).

The Mediterranean-climate regions of the world (southern Europe, California, Chile, South Africa and southern Australia) possess mild, rainy winters and hot, dry summers, and in proportion to their small area, show remarkable species richness, especially in plants and insects (Proctor et al., 1996). These regions are focal points of plant evolution (Proctor et al., 1996), displaying high levels of plant endemism, and are now considered by international conservation groups as five of the twenty-five global biodiversity hotspots (Cowling et al., 1996; Rundel et al., 1998; Mittermeier et al., 1999; Potts et al., 2003a). One of these hotspots, the Mediterranean Basin of southern Europe, contains 7.8% of the world's plant diversity, but represents only 1.6% of the world's area (Blondel & Aronson, 1999). The proportion of the world's terrestrial insects in this area is still unknown (Quézel, 1985; Blondel & Aronson, 1999), but it is considered a centre of bee speciation (Michener, 1979, 2000; O'Toole & Raw, 1991; Proctor et al., 1996; Potts et al., 2001). The Mediterranean Basin supports some of the most diverse p–p communities with approximately 25,000 species of flowering plants, and an estimated 3,000–4,000 species of bees (Blondel & Aronson, 1999; O'Toole & Raw, 1991; Dafni & O'Toole, 1994).

Several theories have been proposed to explain the basis of biodiversity in Mediterranean climates both from a general perspective (see Cowling et al., 1996) and from a more p–p-specific view (see Huston, 1994; Potts et al., 2003a). For insect communities, some determinants of abundance may comprise the quantity and quality of forage, habitat fragmentation, the effect of natural enemies, as well as the composition of plant diversity and nesting sites (Potts et al.,

2003a; and references therein). For plant communities, competition caused by summer drought and low soil nutrients coupled with the regularity of disturbance from fire or grazing, form the basis of a general model to understand relative plant diversity (Huston, 1994). The particularly diverse pollination systems noted in the Mediterranean Basin are set in the backdrop of a heterogeneous landscape, with a long history of moderate to intense disturbance (Rundel et al., 1998; Rundel, 2004) and pressure from the characteristic climatic conditions (Petanidou & Vokou, 1990; Petanidou & Ellis, 1996). Since the mid 1980s, there has been a sharp increase in the number of studies assessing the value of Mediterranean habitats for the biodiversity of pollinators, and for p–p relationships (e.g., Dafni & O'Toole, 1994; Potts et al., 2003a, b, 2004, 2005a; J Herrera, 1988; Petanidou, 1991; Petanidou & Ellis, 1993, 1996; Petanidou et al., 1995a; Petanidou & Potts, 2005). Although most pollination ecology studies from the Mediterranean are on specific pollination cases (Figure 1), there has still been a good general appraisal of p–p interactions at the community level (e.g., J Herrera, 1988; CM Herrera, 1987, 1988, 1992, 1993, 1996; Petanidou, 1991, 1999, 2004; Petanidou & Ellis, 1993, 1996; Petanidou & Vokou, 1990, 1993; Petanidou & Smets, 1995; Petanidou et al., 1995a, b, 2000; Petanidou & Potts, 2005; Potts et al., 2003a, b, 2004, 2005a, b).

In this paper, we review the pollination characteristics of Mediterranean habitats at the community level, stressing the structure of these systems using the pollination food web approach (Memmott, 1999). We highlight the peculiarities of Mediterranean habitats, which make them interesting systems to study, and address the issues of diversity, the p–p food web structure, the reward and attractant basis of the p–p partnership, and the temporal variation of floral and pollination traits. We explore the consequences of local and large-scale disturbances on the mutualistic relationships between pollination partners, and the effect of human management as a device that causes disturbance while also sustaining diversity. We conclude by examining the greatest challenge faced by pollination research conducted in Mediterranean systems, and introduce a programme designed to confront these challenges, the European project ALARM (Settele et al., 2005), which focuses on several research aspects of pollinators and pollination in the Mediterranean region.

Pollination characteristics of the Mediterranean

The importance of Mediterranean habitats for bees

Undoubtedly, a major characteristic of Mediterranean habitats is the diversity of both plants and insects, especially bees (Proctor et al., 1996). The Mediterranean Basin is characterized by a variety of natural and managed habitats that are important for pollination systems. The dominant ecosystem types found in the Mediterranean Basin are *forests,* which are mainly coniferous, *scrub,* typified by evergreen shrubs, and *semi-natural perennial groves* cultivated for centuries using non intensive methods. Scrub is also known as *phrygana* in Greece, *garrigue* in France, *tomillares* in Spain or *coastal sage* in California (Petanidou & Vokou, 1993), and is a characteristically dry ecosystem with woody plants that show
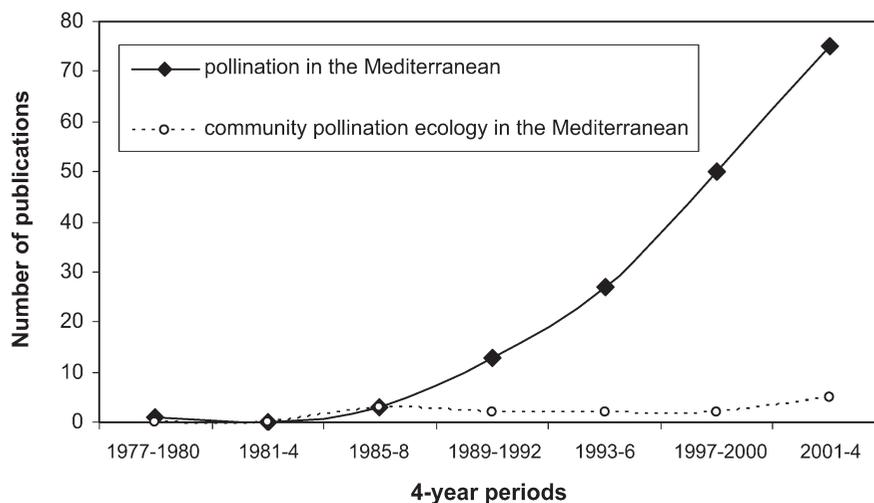

Figure 1. Studies on pollination ecology in the Mediterranean Basin. The cumulative number of publications on pollinators and pollination since 1977 are shown, divided into those carried out at the community level and total studies. Original data from The Web of Science (Thomson ISI).

reduced transpiration surfaces (Margaris, 1981) which assist in decreasing the effects of stress caused by summer drought (Aschmann, 1973).

Scrub has been described as the richest bee habitat studied in the Mediterranean (Dafni & O'Toole, 1994; Petanidou & Ellis, 1996; Petanidou & Potts, 2005). Recent comparative studies on Lesvos, Greece, however, have shown that mixed open oak woodlands and managed olive groves are equally high if not higher in species richness (Potts et al., 2005a; Lamborn & Petanidou, unpublished data). Potts and colleagues (2005a), from the pollination services perspective, concluded that pollination levels are highest in burnt and mature pine habitats, while oak woodlands have the highest levels of pollination from generalist pollinator species. Pine forests at different stages of succession, oak woodland and managed olive groves are therefore the three habitats with the greatest overall value for p–p communities, and the provision of the healthiest pollination services in the Mediterranean (Potts et al., 2005a). This highlights the importance of Mediterranean oak woodlands and managed olive groves as pools of biodiversity, habitat types that have been largely ignored in preference to coniferous-related Mediterranean systems (e.g., Margaris, 1976; Petanidou et al., 1995a).

An important feature that enhances bee diversity is the occurrence of nesting sites, which according to many authors is one of the main limiting factors (O'Toole & Raw, 1991; Michener, 2000; Steffan-Dewenter & Tscharntke, 1999, 2002). In a recent study of 21 bee communities in post-fire habitats in the Mediterranean, Potts and colleagues (2005b) found that the composition of communities is strongly related to the diversity of nesting substrates and nest building materials. The amount of bare ground and the availability of potential nest sites were the two main factors that affected the structure of the entire bee community, the composition of guilds and the relative abundance of dominant species. Sloping ground, the coverage of plant species with suitable stems, and the incidence of pre-existing burrows were also found to be important. Among all the habitats examined, freshly burnt scrub had the best combination of these factors, and provided bees with the highest amount of nesting opportunities.

The structure of plant–pollinator food webs in Mediterranean communities

Table I shows an overview of p–p studies carried out on Mediterranean habitats within the Basin. The studies show that bee species make up 30–40% of the total flower-visiting fauna in Mediterranean scrub lands, whereas they are responsible for 37–46% of the total interactions in the community (J Herrera, 1988; Petanidou, 1991). The services bees provide to flowering plants at the community level, though still relatively unexplored, are certainly higher than 70% (Potts pers. comm.). The most species-rich family of bees in the Mediterranean appears to be Megachilidae (see also J Herrera, 1988), followed by Apidae, Halictidae and Andrenidae, whereas Colletidae and Melittidae are the least specious families in the community (Table II).

Flower visitors or guilds other than bees also contribute to the pollination food web of Mediterranean communities. These include: Syrphidae, Bombyliidae and other muscoid flies such as Tachinidae, Sarcophagidae and Anthomyidae; beetles, particularly dominated by Dermestidae, Bruchidae, Buprestidae and Scarabaeidae; butterflies, chiefly Lycaenidae and Pieridae; and wasps, especially Sphecidae and Eumenidae, including also the parasitic Braconidae, Ichneumonidae and Chrysididae (J Herrera, 1988; Petanidou, 1991; Petanidou & Ellis, 1993; *cf.* Table II). The overall p–p community in the Mediterranean is, therefore, rich at both the family and species level.

Considering the overall p–p network from the community perspective (Table I), the bulk of insect visitors have a very restricted pollination niche, being either monotropous (36.2%; Petanidou & Potts, 2005; and 55.6%; J Herrera, 1988) or oligotropous, i.e., visiting 1–3 plant species (65.9%; Petanidou & Potts, 2005; and 83.3%; J Herrera, 1988, respectively). The same relationship is found for the plant niche (oligophily), and all three of these studies revealed a pattern of asymmetric resource use by both plants and pollinators (Petanidou & Potts, 2005). Plants and insects are highly selective within a community when only the resources available during insect activity or the period of plant flowering are considered (Petanidou & Potts, 2005). This selective resource partitioning within the p–p community implies that the Mediterranean pollination food web will have low connectance and be less complicated than is theoretically possible. Mediterranean habitats however, have the highest *residual* connectance after correcting for network size, compared to all other p–p food webs studied to date (Olesen & Jordano, 2002), which could be due to the fact that, within all the systems considered in this paper, the Mediterranean ecosytems were the only year-long active ecosystems encompassing loosely connected data due to the temporal separation of the p–p partners involved.

Asymmetric resource partitioning by both plants and pollinators results in limited community level specialization in Mediterranean systems, which appears to be more marked for insects than plants (Petanidou & Potts, 2005). This asymmetry in the reciprocal use of pollination resources has also been found in other p–p systems (e.g., Bascompte et al.,

Table I. Parameters related to the structure of the plant-pollinator food web in several Mediterranean habitats and communities throughout the Basin. The data have been collected from all community studies on pollination ecology known to have been carried out within the Basin (cf. reference). Interaction is any recorded relationship between a plant and a flower-visiting insect species within a given community. Thus, maximal number of interactions within a community is equal to P × A (i.e. number of plant species visited x number of visiting insect species). Plant phily (referring to a plant) is the number of insect species visiting that plant species within the community. Insect tropy (referring to an insect) is the number of plant species serviced for pollination by the insect species within the community. ⋆ in three replicates (sites).

Geographical area	Habitat type	Insect guild	Labour time spent (study months)	Plant species visited (P)	Visiting insect species (A)	Interactions (I)	Plant phily		Insect tropy		Community connectance (I*100)/(A*P)	P/A	A/P	P + A species/labour time	Reference
							Range	Mean ± SE	Range	Mean ± SE					
Greece, Athens	Mature phrygana, 1 site	all insects	50	132	665	3006	1–123	22.77 ± 1.67	1–103	4.52 ± 0.26	3.42	0.2	5.0	15.9	Petanidou, 1991;
		only bees	50	129	262	1390	1–48	10.78 ± 0.80	1–103	5.31 ± 0.52	4.11	0.5	2.0	7.8	Petanidou & Ellis, 1996
Israel, Mt Carmel	High phrygana, several sites merged	bees	6	179	340	921	1–43	5.15 ± 0.53	1–20	2.71 ± 0.16	1.51	0.5	1.9	86.5	Potts et al., 2003a,b; Petanidou & Potts, 2005
Spain, Donana	Garrigue, 1 site	all insects	12	26	180	415	1–86	15.96 ± 3.23	1–17	2.31 ± 0.18	8.87	0.1	6.9	17.2	
Spain, Donana		only bees	12	24	55	155	1–25	6.46 ± 1.01	1–14	2.82 ± 0.36	11.74	0.4	2.3	6.6	J Herrera, 1988
Greece, Lesvos	Freshly burnt pine (low phrygana)⋆	only bees	3	16.3 ± 1.3	18.0 ± 2.4							0.9	1.1	11.4	Potts et al., 2005b
Greece, Lesvos	Intermediate burnt pine (high scrub)⋆	only bees	3	7.0 ± 2.0	15.0 ± 2.3							0.5	2.1	7.3	Potts et al., 2005b
Greece, Lesvos	Mature pine⋆	only bees	3	6.7 ± 2.9	17.0 ± 2.0									7.9	Potts et al., 2005b
Greece, Lesvos	Oak woodland⋆	only bees	3	36.0 ± 2.5	22.7 ± 0.6							1.6	0.6	19.6	Potts et al., 2005b
Greece, Lesvos	Managed olive groves⋆	only bees	3	38.3 ± 4.3	19.0 ± 1.7									19.1	Potts et al., 2005b
Greece, Lesvos	Abandoned olive groves⋆	only bees	3	25.3 ± 2.0	13.0 ± 1.2							1.9	0.5	12.8	Potts et al., 2005b

Table II. Taxonomic structure of the flower-visiting insect groups in three Mediterranean communities analysed by Petanidou & Potts (2005). Numbers in parentheses are percentages over the whole group of insect species found in a site (percentages in regular fonts, separated by a comma from the previous number) or over the total number of species of bees or flies (percentages in italics, without separating comma). Data from Petanidou & Ellis (1993) and Petanidou & Potts (2005).

	Number of species observed		
	Greece	Spain	Israel
All insects	665	180	340
bees	262, (39.4)	55, (30.6)	340
Andrenidae	*49 (18.7)*	*8 (14.5)*	*86 (25.3)*
Anthophoridae	*63 (24.0)*	*14 (25.5)*	*114 (33.5)*
Apidae	*3 (1.1)*	*2 (3.6)*	*1 (0.3)*
Colletidae	*11 (4.2)*	*5 (9.1)*	*22 (6.5)*
Halictidae	*51 (19.5)*	*17 (30.9)*	*44 (12.9)*
Megachilidae	*84 (32.5)*	*7 (12.7)*	*72 (21.2)*
Melittidae	*1 (0.4)*	*2 (3.6)*	*1 (0.3)*
Formicidae	–	7	–
wasps + Symphyta	80, (12.0)	21, (11.7)	–
beetles	72, (10.8)	30, (16.7)	–
flies	188, (28.3)	28, (15.6)	–
Bombyliidae	*45 (23.9)*	*9 (32.1)*	-
Syrphidae	*49 (26.1)*	*16 (57.1)*	-
"muscoid" flies	*88 (46.8)*	*3 (10.7)*	-
butterflies	31, (4.7)	39, (21.7)	–
Heteroptera	31	–	–
Neuroptera	1	–	–

2003; Dupont et al., 2003; Vázquez & Aizen, 2005). At a community level, therefore, the suggestion is that specialized plants and pollinators are associated with generalist partners (Petanidou, 1991; Ollerton, 1996). Conversely, high selectivity (in the sense introduced by Petanidou & Potts, 2005) coupled with temporal resource variability suggests that, within time periods, both plants and insects have a tendency towards specialization.

In conclusion, due to high diversity of both plants and insects, pollination food webs in the Mediterranean are characteristically large, with several loosely connected 'time' or 'partner' guilds. The seasonality of the Mediterranean climate and the presence of guilds of insects over time suggest that the incidence of *sequential mutualists*, those key plant and insect species that connect sub-units at an ecosystem level, are extremely important (Petanidou & Ellis, 1996). In phryganic systems, *Asphodelus aestivus* connects the late winter/spring cohorts, *Hypochoeris achyrophorus* and *Chrysanthemum coronarium* connect the spring cohorts, and *Thymus capitatus* is important for the summer cohorts.

The attractants and rewards in plant–pollinator relationships

Primary attractants for pollinators: Pollen and nectar. The main rewards for pollinators in the Mediterra-

nean are pollen and nectar. Pollen could be the most important reward to pollinators in the Mediterranean as low average rainfall, which in turn affects nectar production (J Herrera, 1985; Petanidou, 1999; Petanidou et al., 1999), could select against plants producing nectar as a sole reward (Petanidou & Vokou, 1990). The importance of pollen for Mediterranean pollination systems is corroborated by both the low number of sole nectar consumers, i.e., butterflies, found in some Mediterranean systems (Petanidou & Ellis, 1993), the high abundance of typically low nectar-producing species (Petanidou & Smets, 1995), and the high numbers of nectar-less deceptive orchids (Dafni & Bernhardt, 1990; Dafni & O'Toole, 1994). Deceptive pollination, found frequently in the Orchidaceae, is when pollinators are offered no nectar or pollen reward for their visits (Dafni, 1984), a common phenomenon in the orchids of the Mediterranean (Dafni & O'Toole, 1994). *Papaver* and *Anemone* are common eastern Mediterranean species that produce no nectar and are important species for pollen alone (Petanidou, 1991; Proctor et al., 1996). Studies of other Mediterranean systems have produced data supporting an important role for pollen and a lesser role for nectar as a pollinator reward (J Herrera, 1985; Petanidou et al., 1999).

Petanidou & Smets (1995) found that the average amount of nectar produced within a phryganic Mediterranean system is small, with less than 10% of the plant species producing over 0.5 μl of nectar per flower. Some plant species appear to be well adapted to the harsh dry Mediterranean conditions and their nectar secretion seems to be induced by extremities in the local weather (Petanidou & Smets, 1996). *Thymus capitatus,* for example, although flowering at a period typified by extreme heat and drought (June–July), is stimulated by high temperatures to secrete nectar (maximum 32.5°C, Petanidou & Smets, 1996). Yet, in coastal areas, where the sea has a dominant effect on terrestrial habitats, it is not the temperature, but differential humidity that positively affects nectar secretion both in volume and sugar content (Pérez-Bañón, 2000). These examples imply that the factors limiting nectar secretion may have acted in favour of selection of plants with high nectar yields.

Perennials within phrygana have significantly superior nectar yields compared to the therophytes, and the Lamiaceae produce greater volumes than other taxonomic groups (Petanidou & Smets, 1995; Petanidou et al., 2000). Consistent nectar producers are key phryganic species, such as *Asphodelus aestivus*, *Phlomis fruticosa*, *Salvia triloba* and other Lamiaceae. *Capparis ovata* is the best nectar producer in the community and possibly in the Mediterranean, which could be related to its nocturnal anthesis (Eisikowitch et al., 1986; Dafni et al., 1987;

Petanidou et al., 1996) and its notorious ability to gain water (Rhizopoulou, 1990; Rhizopoulou et al., 1997). Perennial species tend to increase their nectar secretion during the mature phryganic stage compared to the early post-fire stage, whereas the opposite holds true for annuals (Petanidou, 1999). Similarly, comparisons of *Satureja thymbra* in burnt and unburnt areas of the Mediterranean showed that standing crops were two times higher in unburnt areas than in burnt ones (Potts et al., 2001).

Secondary attractants of flowers: Colour, shape and other traits. Angiosperm biodiversity is founded to a large extent upon a wide array of traits, such as flower colour, morphology and scent production, which operate to attract pollinators (Proctor et al., 1996; Dafni, 1997). Flower colour is perceived in a different way by insects than by humans (Daumer, 1958 cited in Menzel & Shmida, 1993; Chittka et al., 2001), and it may influence the types of insects visiting flowers and the rates of visitation (see also McCall & Primack, 1992). In the Mediterranean, *Amphicoma* beetles commonly visit red flowers (Dafni et al., 1990) and in Israel the flora displays a distinct colour frequency separation between those flowers potentially visited by flies and beetles, and those visited by Hymenoptera (Mendel & Shmida, 1993).

The main flower colours of the Mediterranean flora are seen in similar proportions to the main flower colours of the world flora (Table III). The majority of the species in the Mediterranean have white or yellow flowers, although in southern Greece, Greek phrygana and Israel, white-flowered species contribute less than yellow-flowered species compared to the world flora. This is counterbalanced by the contribution of blue-flowered (viz. Greece) and violet (viz. Israel) species that may indicate the predominant pollinator types, with bees dominating the Mediterranean climates and flies prevailing at higher altitudes (Diamantopoulos & Margaris, 1981; Kearns, 1992; Totland, 1992). Yellow-flowered plants are commonly considered to attract a variety

of insects, possibly due to the high reflectance of yellow (Kevan, 1983). A review of the northern European literature on p–p relationships indicated that the rank of attraction to yellow-flowered species was wasps, beetles, flies and lastly bees (Willemstein, 1987), but in empirical assessments of Mediterranean phrygana no particular pollinator groups were found to be especially related to yellow flowers (Petanidou, 1991).

Colour alone is not the only factor when examining the attractiveness of flowers to pollinators from different plant species. Intensity, brightness, wavelength content and contrast must also be considered in conjunction with colour vision to build up a full understanding of stimuli to pollinators based on 'colour' (Burkhardt, 1964). The contrast of dark spots on pale backgrounds, for example, is a feature common to several flowering plant species. The most familiar case of 'dark spots' from the Mediterranean is the wild carrot, *Daucus carota*, but dark patches are also present in some deceptive orchids, *Papaver* and *Anemone* species, *Linum pubescens*, and *Tuberaria guttata* (Proctor et al., 1996; Dafni & Giufra, 1999; Lamborn & Ollerton, 2000). It is highly possible that dark spots may represent a short range (90 cm) detection device (Mulligan & Kevan, 1973; Dafni & Kevan, 1997) or be mistaken for already settled insects (Yeo, 1972; Eisikowitch, 1980; Johnson & Dafni, 1998). Dark spots have been found to be attractive to a wide range of pollinators including beetles (Dafni et al., 1990), flies (Eisikowitch, 1980; Westmoreland & Muntan, 1996; Johnson & Dafni, 1998; but see Lamborn & Ollerton, 2000), solitary bees (Bino et al., 1982 cited in Dafni & Giufra, 1999) and honey bees (Free, 1993). The dark central floret of *Daucus carota*, however, does not always increase visitation rates (Lamborn & Ollerton, 2000; Westmoreland & Muntan, 1996) and Darwin (1888) believed it may represent a remnant trait.

The visual perception of insects does not allow them to distinguish shape and form at a distance, although blocks of colour may attract insects to move closer (Kevan, 1983). Smaller flowers are believed to

Table III. The occurrence of flower colours in Greece and Israel. The numbers are percentages of plant species over the floras examined. a) World flora (data from Kevan, 1972); b) Greek flora by Diapoulis, 1947 (data from Diamantopoulos & Margaris, 1981); c) local flora of a phrygana, 133 species (data from Petanidou, 1991); d) flora of Israel, 198 species (data from Menzel & Shmida, 1993).

Flower Colours	Percentage over total flora				
	World[a]	Greek Mountains[b]	Southern Greece[b]	Greek Phrygana[c]	Israel[d]
White	26.5	34	23	21.1	19
Yellow	31.0	33	38	34.6	27
Violet–pink–purple–red	29.0	22	29	29.3	39
Blue	5.5	7	8	10.5	5
Green	7.5	5	3	4.5	10

suffer reduced visitation rates due the insect's inability to detect them (Bell, 1985; Dafni & Kevan, 1997). They compensate for this disadvantage by producing flowers whose outlines show greater dissection and 'flicker' to attract the attention of passing insects (Dafni & Kevan, 1997). Bee flies have shown strong attraction to models of *Linum pubescens* flowers (a Mediterranean herb) with greater dissection in the outline (Johnson & Dafni, 1998). In the flora of Israel, beetles are attracted to those flowers that have the greatest size and the lowest contour density (the relationship between contour length and area, Dafni, 1997). Larger bees visit larger contour-dense flowers than small bees (Dafni & Kevan, 1997).

The length of the corolla tube may affect the floral visitors to a plant species. For example, there is a loose correlation between the length of the corolla tube and the length of the bee's tongue in Israeli pollination systems (Menzel & Shmida, 1993). The corolla length of *Satureja thymbra* indicates that nectar would not be accessible for smaller solitary bees with short tongues (Potts et al., 2001), which would restrict the visitor assembly to those bees that can access the nectar. McCall & Primack (1992) found that tubular flowers were visited less often than open flowers in three different communities studied (a woodland-meadow, a Mediterranean scrub, and alpine tundra), with less specialized insects being more common on open flowers.

Are pollination syndromes applicable in the Mediterranean?

The concept of pollination syndromes

Some unrelated plant species display remarkably similar floral traits, which could potentially be the result of convergent evolution (Fǽgri & van der Pijl, 1979). Early observations of unrelated plants and their pollinators led to the establishment of the idea of pollination 'syndromes' (Fǽgri & van der Pijl, 1979; Fenster et al., 2004). Pollination syndromes are sets of floral traits that could conceivably be the result of selection from similar pollinators and are therefore associated with a particular pollinator guild (Fǽgri & van der Pijl, 1979). These 'suites of floral traits' (Fǽgri & van der Pijl, 1979) can be any combination of colour, morphology, scent, nectar composition and phenology (Ollerton & Watts, 2000). The efficacy of pollination syndromes to predict pollinators was demonstrated by Darwin with his a priori deduction that the pollinator of the long-spurred orchid, *Angraecun sesquipedale*, would be a giant hawkmoth (Darwin, 1862, Johnson & Steiner, 2000).

In recent years, the subject of pollination syndromes has suffered repeated critique, and it is firmly established that pollination syndromes should not be used as a replacement for field observations (Ollerton & Watts, 2000; Johnson & Steiner, 2000). One reason for this may be because plant species are limited in their floral design by phylogenetic constraints (Menzel & Shmida, 1993), and so pollination syndromes can not be used as preset methods to describe convergent evolution (Johnson & Steiner, 2000; but see Fenster et al., 2004). In the Israeli flora however, only four families of flowering plants were found to have restricted colour loci, with all other families possessing widespread colour variation (Menzel & Shmida, 1993). Furthermore the function of colour in pollination syndromes has often been given too much weight, as few pollinators have intrinsic preferences for particular colours (Johnson & Steiner, 2000). For example, red tubular flowers with dilute nectar and exerted anthers are often associated with bird pollination in the pollination syndromes concept (Wilson et al., 2004), yet empirical evidence suggests that hummingbird preferences are not inherent but can be learned and modified by conditioning (Proctor et al., 1996). Another criticism of the pollination syndromes concept is the focus of studies on only one type of interaction, compartmentalizing and oversimplifying the p–p relationship at the expense of fully understanding the ecology and evolution of p–p systems (CM Herrera et al., 2002).

The application of pollination syndromes is complicated by the fact that both plants and pollinator species can be specialized or generalized (Johnson & Steiner, 2000). The existence of a syndrome would point towards specialization, yet, for example, the 'fly syndrome' is usually associated with generalist pollination (See Ollerton, 1996 for a full discussion of specialized traits and generalist pollination). Therefore, nature is not as tidy as the pollination syndrome model suggests and subgroups and individual cases are apparent in each syndrome (Waser et al., 1996; Johnson & Steiner, 2000). Due the difficulties of applying pollination syndromes to 'real plants' in many systems including those in the Mediterranean, numerous authors are turning away from the pollination syndromes concept, towards a more integrated assessment of p–p interactions at the community level, using the pollination food web approach (Memmott, 1999) and the study of specialization and generalization.

The concept of p–p specialization proposes that particular phenotypic attributes of flowers promote links with a single pollinator species or guild and is inferred by the concept of pollination syndromes (Waser et al., 1996). In Mediterranean climate regions, it has been speculated that specialized relationships may dominate (Proctor et al., 1996). Many flowers, however, exhibit floral characters that

would be considered specialized, but are often visited by diverse groups of animals (Ollerton, 1996; Johnson & Steiner, 2000). This can be explained by (i) variation in pollinator effectiveness; (ii) equal selection pressures from different groups of pollinators; (iii) when the intensity of selection is temporally differentiated (Ollerton, 1996; Johnson & Steiner, 2000). Methods to quantify specificity, therefore, require more than just species lists of flower visitors as differences between pollinator species, in constancy, visitation rates, behaviour and effectiveness, are likely to exist (Johnson & Steiner, 2000). Ultimately studies to assess specialization in p–p relationships, should involve a determination of effectiveness for each species of flower visitor, preferably involving actual pollen deposition on stigmas after a single visit (Johnson & Steiner, 2000). In challenge to the pollinator effectiveness hypothesis non-coevolved species may be more effective pollinators than co-evolved species. For example, bees deposited more pollen in *Ipomopsis* than hummingbirds (Mayfield et al., 2001, but see also Waser & Price, 1989). Using the pollinator effectiveness criteria however, generalist pollination systems may not be as common as is currently thought.

It has been asserted that generalization in pollination systems are unlikely to produce strong selection pressures for any one set of traits (J Herrera, 1988; Ollerton, 1996; Lamborn & Ollerton, 2000; but see also Waser et al., 1996). Specialized systems, on the other hand, are likely to frequently result in strong selection, and to demonstrate the effects of this selection with the display of adaptations for the partnership (Galen, 1996). Specialized pollination systems could be interpreted as isolating mechanisms (Hodges, 1997), and selection for reproductive isolation could favour the evolution of specialization (Grant & Grant, 1965).

Pollination syndromes in the Mediterranean

In its most simplistic form pollination syndromes are apparent for many different guilds of pollinators in the Mediterranean. For example, the excess of red 'bowl shaped' flowers that repeatedly occurs in a variety of genera in the Mediterranean represents a distinct syndrome that would appear to show adaptations chiefly for pollination by beetles (Dafni et al., 1990; Proctor et al., 1996). In Israel, flowers of this type have been shown to reflect strongly in the red part of the light spectrum (Dafni et al., 1990; Dafni, 1997) which for bees is a dull grey colour (Chittka & Waser, 1997). The red bowl-shaped flower type could be considered generalist in terms of the number of different types of flower visitors it receives, and so only after a thorough assessment of pollinator effectiveness to determine which pollinators are

exerting selection for shape and colour, should the pollination syndromes concept be applied.

In systems with a large proportion of generalist species, pollination syndromes are more difficult to apply. In phrygana and other Mediterranean ecosystems, the occurrence of high plant and pollinator diversity is accommodated by a generalized use of pollination resources by the majority of either partners, in which a large percentage of specialist pollinators are served (Petanidou & Potts, 2005). In a generalized p–p food web, where divergence in the pollinator community is narrow in comparison to systems with other groups of pollinators (e.g., mammals or birds), the chance of distinguishing clear pollination syndromes diminishes significantly. For example, in a plant community of 133 species visited by 655 potential pollinator species in Greece, no clear pollination syndrome was detected even though trends were apparent (Petanidou, 1991). In fact, many insects consistently visited non-typical flowers (e.g., beetles visited Fabaceae and Lamiaceae flowers), and time and flower availability were the major drivers of the partnerships (Petanidou, 1991).

What shapes pollination characteristics in the Mediterranean?

Temporal variation in plant–pollinator characteristics

The peculiar Mediterranean climate of mild, wet winters followed by hot, dry summers establishes the provision for plants to flower throughout the year with the main growth period in winter and a peak of flowering in the spring, March–May (Diamantopoulos & Margaris, 1981; Dafni & O'Toole, 1994; Petanidou et al., 1995a; Petanidou & Ellis, 1996). Pollinator populations can to some degree be sustained all the way through the year although their abundance is often reduced in the autumn and winter months of October–February (Petanidou, 1991, 2004; Dafni & O'Toole, 1994; Petanidou & Ellis, 1996). This decrease is more dramatic for bees than for flies (Petanidou, 1991; Petanidou & Ellis, 1996). The strong differentiation of plant flowering allows for the segregation of plants into major seasonal guilds (spring, autumn, winter; Petanidou et al., 1995a). Pollinating insects also appear in season guilds with a clear spring fauna (subdivided into at least three major turnovers), a summer, a winter, and an autumnal fauna (Petanidou et al., 1995a; Petanidou & Ellis, 1996).

The glut of spring flowers has been described as a 'buyers market' for pollinators, with flowering plants outnumbering pollinators (Dafni & O'Toole, 1994). This probably leads to an increase in investment in rewards and advertisement on behalf of the plants as they compete for pollinators early in the year

(Cohen & Shmida, 1993; Petanidou, 2004). During this period of high diversity, both plants and insect partners appear highly selective; yet, outside this period, they are much less so (Petanidou, 2004). This selectivity could be the result of time constraints, although it is unclear how this may be an inherent characteristic of the system, or possibly just because the ability to be selective and still achieve reproductive assurance for both parties is available during this period. In the summer, the opposite trend is found and a 'sellers market' is set up with an over-abundance of pollinators in relation to flowers (Dafni & O'Toole, 1994; Petanidou et al., 1995a; Petanidou, 2004). Nectar is often limited in summer and few plant species support a wide range of pollinators (J Herrera, 1985; Petanidou & Vokou, 1990, 1993; Petanidou & Smets, 1995). In autumn, large flowers follow 'discovery advertisement' with low nectar quantities (Dafni, 1996). Thus, there is a significant temporal compartmentalization of resources in the Mediterranean (Dafni & O'Toole, 1994; Dafni, 1996).

The climate, in particular the summer drought, turns time into a critical parameter for Mediterranean communities and shapes many pollinator-related plant characteristics. For example, flowering phenology in the Mediterranean is not constrained by phylogeny as it is in continental communities (Kochmer & Handel, 1986). In Mediterranean plant communities, multiflorous (bearing many small flowers) and pauciflorous (with < 10 relatively large flowers, compared to the plant body) species are strongly differentiated throughout the year, with pauciflorous species mainly restricted to the autumn–winter flowering period and multiflorous species to the spring-summer (Cohen & Shmida, 1993; Petanidou et al., 1995a). This divergence in flowering time, coupled with the differential pollination investment strategies of these two groups, has been regarded as a reflection of the variation in competitive environments at these times of year, with multiflorous species considered better competitors than pauciflorous ones. However, because pauciflorous species mainly flower in autumn and early spring in temperate regions as well, we do not believe that their flowering phenology in the Mediterranean should be interpreted as the result of a shift in flowering time to avoid competition with multiflorous species as hypothesized by Dafni and Dukas (1986), and Dafni and Werker (1982) for some geophytes. Rather, it seems that a pre-adaptation has enabled these genera to flourish and diversify after the time when the local summer-rain climate changed into the present winter-rain climate, approx. 3.2 million years BP (Suc, 1984; Petanidou et al., 1995a).

The strong seasonality of Mediterranean communities may have severe drawbacks for p–p relationships. The composition of the flower-visiting fauna may fluctuate enormously between seasons and years (CM Herrera, 1988; Quaranta et al., 2004). For example, CM Herrera (1988) recorded only 35.7% of the pollinator taxa through all his six-year study period. Similarly, over a four-year study of pollinators in Greek phrygana only 20% of the total pollinating fauna, consisting of 665 species, were recorded in all years (Petanidou, 1991), with a 25% difference between the most species-rich and the most species-poor years (Petanidou & Ellis, 1993, 1996). This phenomenon was insect-specific and not related to plant phenology (Petanidou, 1991). The erratic presence of so many insect species implies that their role in the pollination ecology of the ecosystem is limited, yet, interestingly, the more highly fluctuating species belonged to the major pollinating taxa (e.g., bee-flies, hover flies and bees) as well as marginal taxa (e.g., Heteroptera, Symphyta and wasps). Greek phrygana has a small core of consistently present pollinator species, with a much larger fringe of accompanying species equally likely to belong to strictly anthophilous families. There is no reason to assume that these fringe species will have any reduction in pollination effectiveness other than by their unpredictable occurrence.

Another potentially climate-specific phenomenon is the low occurrence of parasitic bees in Mediterranean communities. Bee parasitism in the Mediterranean is about 15%, while at higher altitudes the rate is nearer to 30% (Petanidou et al., 1995b). This low incidence of bee parasitism may be attributable to the unpredictability of the climate, and to the consequences of this on the phenology and size of the host populations (Petanidou et al., 1995b).

The effect of disturbance

Plant–pollinator relationships in many areas of the world are under rising pressure from anthropogenic sources, such as habitat fragmentation and isolation (Steffan-Dewenter & Tscharntke, 1999, 2002), pesticide use (O'Toole, 1993; Kevan, 2001), changes in land use (Kearns et al., 1998), fire (Petanidou & Ellis, 1996; Potts et al., 2001, 2003b), biological invasions (Brown & Mitchell, 2001; Chittka & Schurkens, 2001), competition with managed pollinators (Steffan-Dewenter& Tscharntke, 2000), and climate change (Price & Waser, 1998; Warren et al., 2001). Disturbance is a frequent and persistent feature in the Mediterranean and could be considered the main driver of Mediterranean ecosystem dynamics (Cowling et al., 1996; Rundel et al., 1998; Rundel, 2004). The main disturbances occurring in the basin are caused by anthropogenic sources, fire being the factor that may be of both natural and anthropogenic origin.

The effect of local disturbances (fragmentation, fire and grazing)

The long history of human habitation, disturbance, geographical barriers and extreme climate conditions have served to form a heterogeneous Mediterranean landscape that can only be described as fragmented (Blondel & Aronson, 1999; Pérez-Bañón et al., 2003). Human-induced disturbances, such as development or agriculture, have eroded many natural systems, fragmenting the landscape and modifying the structure and distribution of plant communities. The structure and spatial distribution of plant communities may in turn have an effect on the number of pollinator visits and on the composition of deposited pollen (Kunin, 1997; Steffan-Dewenter & Tscharntke, 2002). For example, small populations or small patches of plants within a larger population may receive less flower visitors and more hetero-specific pollen (Steffan-Dewenter & Tscharntke, 2002). Empirical evidence from artificially established populations has shown that visitation rate can increase in small populations, but pollinators prefer large populations (Mustajärvi et al., 2001). Fragmentation and isolation effects on plant and pollinator communities can, under particular conditions, result in a decrease in abundance and species richness of pollinators, particularly bees, through the destruction of nest-sites and food plants (Kearns et al., 1998; Steffan-Dewenter & Tscharntke, 1999). In natural and semi-natural fragmented populations, pollen limitation may be a frequent phenomenon (Steffan-Dewenter & Tscharntke, 2002). Populations isolated in oceanic islands can also exhibit pollen limitation, as demonstrated by some populations of *Medicago citrina*, which, without bees, are only visited by flies (Pérez-Bañón et al., 2003). Although plant species may suffer lower reproductive success in isolation, the fact that they may be subject to different selective pressures under different pollinators could be an important factor for increased biodiversity, and highlights the significance of barriers and fragmentation in the Mediterranean, to which man has contributed for millennia (Blondel & Aronson, 1999).

In the Mediterranean, intensive grazing and fire have radically altered the natural vegetation, creating a mosaic of ecosystems in different stages of degradation and succession (Naveh, 1982; Blondel & Aronson, 1999). This mosaic is composed of rich, semi-open woodland, shrubland and grassland, and depleted, scrub, maquis and rock desert (Naveh, 1982). Both fire and grazing are considered as agents of widespread disturbance, since both reduce the amount of biomass over large areas. Several studies suggest that fire and grazing have distinct, but interactive effects on diversity (Noy-meir, 1995).

Fire is regarded as less selective, and while it creates space for adventitious species, these can rapidly be eliminated by the regeneration of species that were present before the fire (Trabaud, 1994). The disturbance caused by fire has a massive effect on the structure of the community in general and on bee communities in particular (Potts et al., 2001, 2003b). The successional stages following fire are initially bad for bee communities, but recovery is rapid due to an increase in annuals and nesting opportunities (e.g., bare soil), and shows a peak of diversity after two years, thereafter following a steady decline for the next fifty years (Table IV; Petanidou & Ellis, 1996; Ne'eman et al., 2000; Potts et al., 2003a). Entomophilous plants closely mirror their pollinator communities (Potts et al., 2003a). The structure of bee communities in post-fire habitats is dependent among other things on post-fire age, floral diversity and floral abundance (Tables I, IV; Petanidou & Ellis, 1996; Potts et al., 2000, 2003b, 2005a).

Bee diversity is most strongly associated with the diversity of annuals (Potts et al., 2003b) and grazing, when moderate and well managed, can support annuals and restrict the growth of perennials (Petanidou & Ellis, 1996; Potts et al., 2005a). In fact, many ecosystems in the Mediterranean are halted from climax communities by the preponderance of grazing, a condition believed by some to be the form of 'climax succession' in the Mediterranean (Grove & Rackham, 2002). Having been used as a major management tool in the past, moderate levels of grazing have contributed to ecosystem function (Petanidou & Ellis, 1996), and helped to maintain equilibrium between the woody and herbaceous fragments (Naveh, 1982). On the other hand, grazing can lead to soil erosion and desertification when it is excessive and uncontrolled (Mairota et al., 1998). Furthermore, grazing may help to increase the spread of non-native invasive plant species in Mediterranean-climate grasslands, which may disrupt native p–p interactions (Kimball & Schiffman, 2003). In present day Mediterranean countries, about 90% of the food requirements for sheep and goats are met by free grazing (Pulina et al., 1995 cited in Vulliamy, 2003), and grazing is in the most part uncontrolled, a condition that is seriously affecting the environment (Giourga et al., 1998; Petanidou et al., 2004). In some areas, such as Crete and the Aegean islands, hundreds of years of intensive grazing have resulted in severe land degradation and many authors believe overgrazing to be one of the most serious threats to the Mediterranean landscape as a whole (Petanidou & Ellis, 1996; Grove & Rackham, 2002).

Grazing may have positive effects on bees of the phrygana. When grazing is absent, a homogeneous

Table IV. Summary of attributes correlated with succession after fire. The two columns denote young and mature phrygana.

Attribute	freshly burnt	mature scrub (>10 years)	Reference
General characteristics			
system	open	closed	
competition level	low	high	
fire risk	low	high	
Plant component			
dominant plant form in flower	annuals	perennials	Petanidou et al., 1995
self-pollinating plants	many	few	Petanidou & Ellis, 1996
Lamiaceae in flower	almost none	well represented	Petanidou & Vokou, 1993; Petanidou & Ellis, 1996
Floral rewards			
nectar	low volumes; high concentrations; many nectar niches	high volumes; medium concentrations; fewer nectar niches	Petanidou, 1999, Potts et al., 2001, 2004
main floral reward	pollen	nectar + pollen	Petanidou & Vokou, 1990; Petanidou & Ellis, 1996
Insect component			
bee tongue length	only short-tongued	short + long-tongued	Petanidou & Ellis, 1996
bee size	only small-sized	small + large-sized	Shmida, Petanidou & Ellis, 1996
nest habits	all types; highest percentage of soil-nesters	soil-nesters in decline; pithy or hollow stem-nesters; wood-nesters	Potts et al., 2005a
Andrenidae	dominant	subdominant	Petanidou & Ellis, 1996
Megachilidae	relatively few	dominant	Petanidou & Ellis, 1996
cleptoparasites	none	few	Petanidou & Ellis, 1996; Potts (per. com.)

shrub layer is formed and bare ground is lost, reducing nesting places for bees (Petanidou & Ellis, 1996). The positive effect of grazing on pollinator diversity is a pattern found across the world. For example, the number of Andrenids increased in Oklahoma when forbs replaced grasses following grazing, and bare soil for nesting was exposed (Smith, 1940 cited in Vulliamy, 2003). Similarly, grazing was found to be beneficial to bumblebees on Salisbury plain in the UK (Carvell, 2002). In New Mexico, however, protection from grazing increased plant diversity (Floyd et al., 2003), which some authors have suggested is strongly linked to pollinator diversity (Petanidou & Ellis, 1993, 1996). In Greece (island of Lesvos) and Israel, Vulliamy (2003) found that grazing decreased the mean height of vegetation, but only in the intermediate post-fire age sites, as grazing animals prevented the growth of shrubs in various patches rather than decreasing the height of the vegetation overall. The number of bee visitors tended to be higher at the site edges than in the centres of the patches, which was hypothesized to contribute to the bees' optimal foraging, as less effort was needed per reward gained. These results are interesting, because they show that patchiness may benefit those bees which visit the shrubs making up the main areas, as well as those who benefit from the increase in herb flowers within the patches. This is corroborated by recent results on Lesvos (Greece), where the highest bee diversity, especially for large

bees, was found in sites with the highest grazing pressure (Kapsali et al., 2005).

The effect of land management

Agricultural land use: Modern versus traditional. Modern agricultural practices have several characteristics that make poor habitats for wild bees and other pollinators (Kearns et al., 1998; Kevan & Phillips, 2001). One of the most influential practices is the tendency to grow monocultures of crops, which reduces floral diversity and subsequently has an impact on the diversity of insects (Kearns et al., 1998). Pesticide use, especially when it is misused, is also reducing pollinator abundance and diversity (Batra, 1981; Kearns et al., 1998; Shepard et al., 2003). Furthermore, marginal land is continually being farmed, leading to the reduction of nesting sites and the loss of wild vegetation which supports pollinator communities (Kearns et al., 1998; Steffan-Dewenter & Tscharntke, 1999).

Where traditional agricultural practices in the Mediterranean have been abandoned, mainly in the 1960s and 70s, pesticide use has become a potential threat to pollinator communities and their associated plant partners (Kearns et al., 1998; Shepherd et al., 2003). While all pollinators are probably affected by these agrochemicals, most of the work on pollinator loss has been based on managed honeybee colonies (O'Toole, 1993; Kearns et al.,

1998; Kevan, 2001). The loss of wild bees and other pollinators from pesticide use has largely been ignored to date in the Mediterranean, a fact that could partly be attributed to the serious shortfall in surveys and taxonomic characterization of pollinating insects in this area.

Pollinator communities in the Mediterranean where intensive farming is commonplace may well suffer from these modern agricultural practices. On the other hand, traditional methods of land management still carried out in many regions of the Mediterranean, particularly olive and fruit production, may have beneficial effects on pollinator communities (Petanidou & Potts, 2005; Lamborn & Petanidou, unpublished data). Olive grove management is of great value to pollinator communities as they often contain ploughed sections, which support a diversity of annual plants and unploughed and terraced parts, which create niches for the perennial plants. Often the two management regimes are found within a small area, and sustain a large diversity of bee species (Potts et al., 2005a; Lamborn & Petanidou, unpublished data).

Bee-keeping. Competition between honey bees and wild pollinators is believed to affect the abundance, distribution and relative success of wild pollinators (Kato et al., 1999; but see Steffan-Dewenter & Tscharntke, 2000; and Paini, 2004 for a review). Few studies have evaluated the effect of honey bees on wild pollinators or plants in the Mediterranean (see Paini, 2004), and these have focused on particular plant species and not on community level interactions (e.g., Dupont et al., 2004). Even though there is a lack of studies specifically from the Mediterranean, there is a general trend in many areas, which suggests that an increase in bee-keeping is detrimental to both wild pollinators and plants, and to the interactions between the two (Petanidou & Ellis, 1996; Kato et al., 1999; but see also Donovan, 1980; and Steffan-Dewenter & Tscharntke, 2000). These detrimental effects can take the form of reduced nectar available to wild pollinators which may serve to limit their population sizes (Kato et al., 1999). In addition, honey bees tend to spend more time on individual flowers, and to move less frequently between inflorescences than wild bees do, which may promote geitonogamy and self pollination in the visited plant species, a trend that may ultimately reduce genetic diversity in plant populations and restrict their ability to adapt to environmental stresses (Dupont et al., 2004).

Conclusions and challenges

As in the rest of the world, there is a good level of knowledge of specific p–p interactions in the Mediterranean, but a lack of necessary studies at a community level (Memmott, 1999; Petanidou & Potts, 2005). These studies are imperative if we are to explore the evolution of mutualisms (Jordano, 1987), quantify the effects of agricultural policies on biodiversity (e.g., Klinger et al., 1992) or attempt to restore damaged ecosystems (Memmott, 1999). Additionally, the objective of understanding the structure of the pollinator communities will be biased if only a few species of plants or pollinators are studied or studies are temporally limited (Waser et al., 1996; Petanidou & Ellis, 1996; Memmott, 1999; Ollerton & Cranmer, 2002; Vázquez & Aizen, 2003, 2006; Medan et al., 2005).

In response to the 'pollination crisis' (Kearns et al., 1998), it is imperative that studies of p–p relationships in the Mediterranean be supported by additional investment in taxonomic expertise (Dafni & O'Toole, 1994), without which it will be extremely difficult to investigate p–p food webs and to undertake the conservation management of pollinator communities. In fact, taxonomic limitation is a foremost concern of pollination ecologists in the Mediterranean, particularly the eastern Mediterranean areas, where the lack of reference collections and relevant taxonomic keys is a major obstacle to community-level pollination studies. In order to address this problem, a reference collection of Aegean insects, held at the University of the Aegean, has been established through the auspices of the European project ALARM (**A**ssessing **LA**rge-scale environmental **R**isks for biodiversity with tested **M**ethods) (Settele et al., 2005). The main objectives of this collection, called 'The Melissotheque of the Aegean', are to counteract this regional imbalance, and place some taxonomic capacity in the eastern Mediterranean area. The ALARM project is also conducting several community-level pollination studies in the eastern Mediterranean, which will ultimately serve to increase our understanding of these important and diverse systems.

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