Pollinating fauna of a phryganic ecosystem: composition and diversity

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Abstract. A 50-month continuous observation of the pollinator fauna of a 30 ha phrygana plot near Athens revealed an alpha diversity of 666 species which is the highest pollinator diversity recorded so far. Of these, 262 species were Apoidea, of which only three (Apidae) species were eusocial. In comparison with the pollinator fauna of comparable ecosystems in Chile and California, phrygana has a relatively high number of Bombyliidae and especially Syrphidae. Only approximately 20% of the pollinator species occurred in all years of the research period. The very diverse, and shifting pollinator fauna is hypothesized to have brought the evolution of floral characters to a standstill.

A peculiarity of the phryganic ecosystem is a preponderance of pollen as a floral reward and a relative scarcity of nectar. This may be an important factor in the high bee diversity that characterizes the phrygana, and mediterranean ecosystems in general.

Key words. Diversity, mediterranean ecosystems, nectar, phrygana, pollinating fauna.

INTRODUCTION

Despite the first impression of precariousness and poverty, the garrique, or its East Mediterranean counterpart, the phrygana, has a strikingly rich flora (Zohary, 1962; Raven, 1973; Quézel, 1981). This high diversity is maintained in the face of strong environmental pressures, in the first place the prolonged summer drought of the Mediterranean* climate, and in addition the influence of grazing and fires. The vegetation of the Greek phrygana in particular is marked in its physiognomy by seasonally dimorphic shrubs (primarily Thymus capitatus (L.) Hoffmanns. & Link., Satureja thymbra L., Phlomis fruticosa L., and Euphorbia acanthothamnos Heldr. & Sart. ex Boiss.), while therophytes constitute the dominant life form (Margaris, 1980; Quézel, 1981; Polunin & Walters, 1985; Petanidou & Vokou, 1990).

Pollination at an ecosystem level has been dealt with on a number of occasions, and detailed descriptions of the pollinating fauna are available both for systems predominantly characterized by ornithophily (Feinsinger, Swalm & Welt, 1985; Rebele, 1987, and references therein), and by entomophily (Kevan, 1972; Heithaus, 1974, 1979; Moldenke, 1976b, 1979a; Percival, 1974; Pajar, 1974; Moldenke & Lincoln, 1979; Parrish & Bazzaz, 1979; Pleasants, 1980; Arroyo, Primack & Armesto, 1982; Frankie et al., 1983; Primack, 1983; Kratochwil, 1984; Motten, 1986; J. Herrera, 1988; Inouye & Pyke, 1988; McCall & Primack, 1992). Kevan & Baker (1983, 1984) review the field of pollination community ecology as a whole.

The majority of the phryganic plants display a biotic pollination syndrome (Petanidou, 1991a), which implies that pollinators are essential for their reproduction. In spite of this, little attention has been paid so far to the pollinating agents of the phryganic ecosystem. J. Herrera (1988) analysed the anthophilous fauna of a scrub community in SW Spain. Most information on this matter comes from the mediterranean

*In accordance with the proposition by di Castri & Mooney (1973), in this paper ‘Mediterranean’ refers to the Circummediterranean basin, while ‘mediterranean’ refers to all regions of the world with a Mediterranean type climate.

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ecosystems of California and Chile (Moldenke, 1976a, 1979a, b), while the studies by C. Herrera (1987, 1988, 1989) on the pollinator fauna of the seasonally dimorphic shrub Lavandula latifolia Medicus in southern Spain give some fascinating insights, but are not directed to the pollinating fauna as a whole. Armstrong (1979) summarizes what is known on the pollinating fauna of Australia; Whitehead, Giliomee & Rebelo (1987) and Rebelo & Jarman (1987) do the same for fauna of the Cape flora.

The present study focuses on the composition and stability of the pollinating fauna of a Greek phryganic ecosystem. It is part of a broader study of the pollination food web of this ecosystem (Petanidou, 1991a), a small part of which already has been published (Petanidou & Vokou, 1990; Petanidou, 1991b).

METHODS

The present study was conducted at Daphni, situated approximately 10 km west of the centre of Athens (Fig. 1). The study area was situated in a reserve called ‘Diomedes Botanical Garden of Athens University’, located on the slopes of Mt Aegaleo. The dominant ecosystem type of the reserve is phrygana (Fig. 2); it covers 130 ha. A great part of this area was burned in 1975; during the following years, including the whole observation period, it was effectively guarded against both fire and grazing. The substrate is typical for Greek phryganic ecosystems: calcareous and stony. Pedological data are available for the nearby Mt Hymettus phrygana: there, 48% of the soil dry weight consists of particles 2 mm, while the remaining fraction is characterized as clay loam (Diamantopoulos, 1983). Climatic data for this area are given in Fig. 3.

The study was carried out in a 30 ha section of the reserve, situated at 135–215 m above sea level; the inclination varies between 20 and 30%, the aspect is northern and eastern.

Observations on the flower visitors’ activity began in April 1983, and systematic collecting continued until May 1987. This extended sampling period made possible the establishment of a more complete spectrum of the pollinating fauna, given that pollinator populations may vary significantly in space and time (Moldenke, 1979a; Rathcke, 1988).

As pollinators, all animals were considered that re-
peatedly visit floral units for any reward, meanwhile contacting, with any body part, any of a flower’s reproductive organs; such behaviour may result in pollination of the visited flower (Faegri & van der Pijl, 1979). This definition includes not only well-known pollinating groups like bees and anthophilous flies, but also Heteroptera, Symphyta, etc.

Spiders and ants, despite their presence on flowers, were not considered as regular pollinators.

Spiders were occasionally observed on flowers of some plant species, waiting motionless for insect prey. Their very low interfloral mobility warrants their exclusion as pollinators.

Similarly, ants, although exhibiting considerable activity on open nectar-rewarding flowers (like those of *Euphorbia acanthothamnos* or *Thapsia gargarica* L.) were not regarded as pollinators. Ant contribution to the pollination of flowers has repeatedly been the subject of controversy. The general consensus is that in most cases ants act as nectar thieves rather than as pollinators (Faegri & Van der Pijl, 1979; Kevan & Baker, 1983; C. Herrera, J. Herrera & Espaldar, 1984). Moreover, there is evidence that ant visits to flowers result more in harm than in pollination benefit; Beattie (1982). Beattie *et al.* (1984, 1986) proved that in all cases studied ant-borne pollen results in a reduced seed set.

All 133 plant species visited by pollinators were included in the study. Each was followed throughout its flowering period for at least 2 days out of every 20. Observations were made at approximately every third half hour for each of the co-flowering plant species. The number of pollinator-directed observation hours totalled over 5000.
Diurnal observations started about sunrise and continued till after sunset, when no pollinator was active. Additionally, nocturnal observations were made on the visitors of Capparis spinosa L., the only species in the study area with an exclusively nocturnal anthesis.

Over 18,000 insect specimens (excluding honeybees) were collected to document the details of the pollinator-plant relationships. The insects collected were identified by fifty European taxonomists. Voucher specimens of the insect species are kept by the respective specialists, while a part of the material is conserved in the collection of the senior author. The list of species, with the names of the specialists who carried out the identifications, is available (Petanidou, 1991b).

RESULTS

The pollinating fauna consists entirely of insects. Table 1 summarizes the number of species for the families with more than five species. The total number of pollinator species amounts to 666, 39% of which are bees. High as this number of species is, a saturation graph of the number of species that were recorded from the study site in the course of the 50 months of the field work (Fig. 4) indicates that the alpha diversity of the pollinator fauna must in reality be still somewhat higher.

The material collected contained nine undescribed species (four of Megachiliidae, three of Syrphidae and one each of Bombyliidae and Agromyzidae). Two Tenthredinidae, viz. Tenthredo zona Klug and Macrophaga teutonia (Panzer) are new to the Greek fauna (P. Thomas, pers. comm.). The variation in the number of species that were active each calendar year is shown in Fig. 5. If the fifth, incomplete year of the research period, is disregarded, the difference between the poorest and most species-rich year is of the order of 25%. It would be tempting to relate the low species number of 1986 to the comparatively dry winter season preceding it (247 mm rain in the period from October to May, as opposed to 383 and 353 mm preceding the seasons of 1984 and 1985, respectively). However, the different pollinator groups do not demonstrate a consistent response, neither can we identify a clear correlate to explain the comparatively high values of the year before.

The inconstant presence of many of the species implies that they play but a limited role in the pollination ecology of the ecosystem. One might suppose that these less constant species would belong to taxa that are of more or less marginal pollination efficiency, like Heteroptera, Symphyla, wasps etc. This,
however, is not borne out. The distribution of species over the year classes is hardly modified when one concentrates on the most strongly anthophilous families: Bombyliidae, Syrphidae and the bee families. From this it must be concluded that there is only a rather small core of constantly present pollinator species, with a much larger shifting fringe of accompanying species. These fringing species are equally likely to belong to the strictly anthophilous families, and there is no reason to assume that they have a reduced pollination efficiency, other than by their unpredictable occurrence.

Out of the 262 bee species, only three are eusocial; among them only the honeybee (Apis mellifera Linnaeus) displays a considerable pollinating activity.

FIG. 4. Total number of pollinator species known from the Daphni phrygana at the end of the 1st through 49th month of the observation period. Vertical bars denote year limits.

FIG. 5. Number of species of the various pollinator groups that were recorded in the years 1983–87. Each bar gives the number of species as a percentage of the total number of species recorded from that group over all years (values on top of the graph). (Note that observations were made from April 1983 to May 1987).
The bumblebees *Megabombus argillaceus* (Scopoli) and *Bombus terrestris* (Linnaeus), in contrast, were only occasional visitors.

Four of the nine species of SympHYTA (*Arge scita* Mocsary, *Cuneala dahlii* (Klug), *Tenthredo zona*, and *T. zonula* Klug) occur regularly in large numbers on the flowers of some phryganic plant species. Although SympHYTA are generally considered poor pollinators, this observation might indicate a more pronounced role of this group.

In the phryganic ecosystem, Lepidoptera species contribute only to a very limited extent to the pollinating fauna. For instance, Kratochwil (1988) found fifty-six butterfly species in a small plot in SW Germany, against twenty-nine in the Greek site. Sphingidae are represented by one species only, viz. *Macroglossum stellatarum* (Linnaeus), which moreover exhibits extremely limited activity.

Lepidoptera (with the exception of the primitive Micropterigidae, that are absent from the ecosystem under consideration) form the only comprehensive exclusively nectarivorous group of insect pollinators. Among them, the highly energy demanding, endothermic, hawk moths depend (like the obligatory nectarivorous birds) on an abundant supply of nectar.

Although not rich in species, the Coleoptera families Alleculidae, Dasytidae, Dermestidae, Mordellidae, and Scarabaeidae exhibit considerable pollinating activity. In contrast to Coleoptera, Heteroptera (except the mirid genus *Psallus*) are only irregular flower visitors.

### DISCUSSION

### Diversity

The Mediterranean basin is not the only region with a Mediterranean climate, i.e. a climate with a hot dry summer and a wet mild winter. Other regions with such a climate are parts of southern Africa, SW Australia, California and Chile (Aschmann, 1973). Concomitantly, the biota of these regions show parallelisms that are generally recognized (albeit not without criticism, cf. Milewski, 1983, and Barbour & Minnich, 1990). In particular, Mediterranean ecosystems of California and Chile have often been compared (e.g. di Castri, 1973; Thrower & Bradbury, 1973; Mooney, Parsons & Kummerow, 1974; Parsons & Moldenke, 1975; Cody et al., 1977, Cody & Mooney, 1978), and the composition and evolution of their pollinator fauna has been studied by Moldenke in a number of publications (mainly 1976a, 1979a, b).

Unfortunately, Moldenke’s data are difficult to interpret at times. In particular, in Cody et al. (1977) and in his 1979b paper he states that he leaves out of consideration an unspecified group, consisting of an ‘enormous number of minute individuals of several flower visiting species’ that he supposes to be ineffi-

### Table 2. Number of pollinator species (S), by major groups, in the Greek phryganic ecosystem, in relation to a Chilean matorral and a Californian chaparral (unburned and burned 2 years previously). (American data after Moldenke, 1979b).

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<th>Greek phrygana</th>
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<td>Apoidea</td>
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<td>‘muscid flies’</td>
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<td>‘wasp’</td>
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<tr>
<td>Coleoptera</td>
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<td>Syrphidae</td>
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<td>Bombyliidae</td>
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<td>Lepidoptera</td>
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<td>Birds</td>
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Total pollinator species = 666, 281, 309, 254.

*Remainin insects* = Nematocera + Neuroptera + Homoptera.
cient pollen vectors, citing as examples two genera of Apoidea, one of Bibionidae and one of Bombyliidae. The effect of this exclusion on his summary data cannot be properly assessed, but his alpha diversity values are clearly to be regarded as lower estimates. Moreover, some of his groupings are undefined; this applies in particular to his ‘muscoid flies’ that presumably (but not certainly) equal Diptera minus Nematocera, Bombyliidae, and Syrphidae. (That is the sense in which we use the term in the present paper.) A comparison of the pollinator faunas of the Mediterranean ecosystems of California, Chile, and Greece, taking Moldenke’s (1979b) data at face value, is presented in Table 2. This comparison shows an astonishingly high alpha-diversity in the phrygana, viz., a total pollinator fauna of 666 species, considerably higher than the 254 and 309 in the burned and unburned Californian chaparral and the 261 species in the Chilean matorral. Moldenke (1975, 1976b) mentions as an example of an ‘extremely high diversity’ a chaparral covered site at Stanford University (California) with 484 species of flower visitors.

Within the Mediterranean itself, our results can only be compared with those of J. Herrera (1988) who studied the pollinating fauna of the woody vegetation (thirty species) of a 4 ha site in SW Spain (Doñana National Park). The pollinator array here consisted of 187 species, a species richness that the author considered ‘very high’. Accounting for the differences in methodology and number of plant species included in the study, his result is remarkably congruous with ours.

The difference in diversity between the European and the American Mediterranean ecosystems may be attributed, at least in part, to the fact that Moldenke restricted his sampling to the main blooming period, and to the shorter duration of Moldenke’s observation period (2 versus 4 years). Given the very high numbers of specimens captured by Moldenke, viz., in round numbers, 18,000, 70,000 and 48,000 for the unburned and burned Californian chaparral and the Chilean matorral, respectively, it is very probably that Moldenke sampled all available species. In the first 24 months the Daphni survey had produced 493 species (Fig. 3), far more than the typical chaparral/matorral of Table 2 (although strikingly similar to that of the Stanford site). It must therefore be concluded that the strong contrast in alpha-diversity between the Greek phrygana on the one hand, and that of the Californian and Chilean chaparral/matorral on the other, is essentially real.

The successional stage, 8 years after a fire may be another case in point. Force (1981) reported a very high abundance of anthophilous insects in a chaparral during the first postburn years, probably attracted by the profuse bloom of annual plants.

Data on pollinator diversity of other ecosystem types are not easy to provide from the literature, essentially because the study area and habitat diversity usually remain unspecified. The data we summarize below may nevertheless serve to bring our results into perspective.

In a monumental, but almost forgotten study on the pollination ecology of the north-eastern part of Belgium, MacLeod (1893–1894) listed a fauna of 491 insect species. Kratochwil (1988) found 102 bee species and fifty-six butterflies during a 2-year study of a 0.4 ha site in SW Germany; he gives no data on other pollinator groups. A long-term study of a site of approximately 3 ha, mainly covered by Calluna- and Corynephorus-heath, on the island of Öland (S Sweden) brought as many as seventy-nine bee species to the fore (Janzon & Svensson, 1984).

In a study on the flower visitors of a Californian altitudinal transect, Moldenke (1975) found species numbers ranging from seventeen (for a sea bird colony), then fifty (a sea-level weed community), sixty-three (almost sea-level oak-madrone forest), seventy-seven (alpine tundra), etc., then rising to 426 for a grassland at 1500–1800 m, and finally the Stanford University chaparral mentioned above, at 150 m, with 484 species. Moldenke & Lincoln (1979) found between seventy-seven and 145 pollinator species in various montane ecosystems in Colorado. A one-season study of a pavement plain at approximately 2500 m in southern California yielded a pollinator fauna of 156 species (O’Brien, 1980).

The classical long-term study by Müller (1881) on the pollination fauna of the Alps brought 841 insect species to the light. Arroyo, Primack & Armesto. (1982) studied the pollinator fauna of a much more restricted area at three altitudinal zones of the Andes of central Chile (subandean: 2200–2600, cushion zone: 2700–3100, and subnival zone: 3200–3600 m) throughout one flowering season. They recorded 109, seventy-six and thirty-nine species in these zones, respectively. These numbers refer to the main pollinator fauna, that consisted of Hymenoptera, Rhopalocera, and Diptera; for the pollinator groups of secondary importance (hummingbirds, beetles, and moths) no numbers are given. Primack (1978, 1983) collected 228 pollinator species at four sites on the South Island.
of New Zealand at altitudes ranging from 600 to 1800 m, thereby refuting Heine’s (1937) opinion of the relative poverty of the pollinator fauna of that region.

Percival (1974), dealing with the pollination ecology of about 10 ha of coastal scrub in Jamaica, found an anthophilous fauna composed of no more than fifty species, including three bird and five ant species. Heithaus (1974) reported a range in diversity from sixty-nine to 586 in Costa Rican tropical ecosystems. The fact that the pollinator diversity in the phryganic site exceeds that of even the Central American rain forest is surprising indeed.

Stability

The number of pollinator species that play a central role in the ecosystem naturally cannot be simply equated with the total diversity score. In the absence of sufficiently detailed data on abundance and efficiency of pollinator species, their year to year constancy is the best estimator. The number of pollinator species that have been recorded in at least three calendar years amounts to 223, and this value may be used as describing the total number of ‘important’ pollinators. However, we have no explanation for the inconstancy of what we called above the ‘fringing’ species, and by the same token we cannot exclude the possibility that the core species in another 5 year period, or under somewhat different climatological circumstances, would become just as inconstant.

If a pollinator assemblage is to exert an effective selective pressure upon the plant species in an ecosystem it is intuitively clear that the pollinators of an individual plant species should behave more or less similarly towards their host. C. Herrera (1989) demonstrated that, even where there is a constant and limited set of pollinators (like the one moth, one butterfly and four bees regularly pollinating Lavandula latifolia) different pollinator species may impose different, even opposing, selection pressures on floral traits, thereby effectively cancelling each other. Our results now show that, at least in the phrygana, the pollinator fauna moreover is neither constant in composition nor limited in species number. Only a minority of the few plant species of the phrygana are more or less oligophiline; of the entomophilous species, 121 (91%) are served by five or more pollinator species (Petanidou, 1991a).

We hypothesize that under such a regime of selective noise, floral evolution has come to a standstill (or it must be that the omnipresent honeybee is still able to influence floral evolution to some degree). The concept of stasis that is the core of the Punctuated Equilibria theory comes to the mind. If stasis then is a result of a diverse and shifting pollinator fauna, the prerequisite for a punctuation must be the reduction of the pollinator fauna to its barest minimum. Conceivably, the glacial minima formed the theatre for such a scenario. In these periods not only was the pollinator diversity strongly reduced, but population sizes of both plants and pollinators were often close to minimum, permitting all aspects of quantum evolution.

In a fruitful attempt to link island ecology models to pollination biology, Feinsinger, Wolfe & Swarm (1982) confirmed that the reduction of the number of pollinators on a relatively small island (in their case hummingbirds on Tobago) has important effects on the reproductive biology of the plants; pollinator services to plants were more erratic and of a lesser constancy and quality, and the plants tended to invest more in pollinator attraction. It would be worthwhile to elaborate this line of research in the insect-dominated Greek lowland; island situations, either through habitat fragmentation or as actual, phrygana-covered islands, abound in all sizes and degree of isolation.

Composition

no birds, no bats

A glance at Table 2 confirms the well-known general absence of bird pollinators in western Palearctic ecosystems. Both Egypt and Israel have one species of nectarivorous bird, and the presence of several indigeneous plants with a clearly ornithophilous syndrome on the Canary Islands demonstrates their subrecent presence (Vogel et al., 1984), but otherwise Europe lacks this element in its biota (Ford, 1985). This places the mediterranean ecosystem of Europe in a unique position, because not only its counterparts in North and South America have an important part of bird pollinators, but also the one in southern Africa, where ± 4% of the flora is bird-pollinated (Rebelo, 1987) and south-western Australia, where this fraction is as high as 15% (Keigherry, 1982). The fauna of mediterranean Australia and southern Africa stands even more apart in the role non-flying mammals play there as pollinators (Milewski, 1983; Rebelo & Breytenbach, 1987; Rebelo & Jarman, 1987). The strong depen-
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Dobat & Peikert-Holle (1985) draw a map of chiropterophily, showing that this pollination mode extends from tropical Africa over Egypt and the Levant into southern Turkey and Cyprus, where Roussettus aegyptiacus (E. Geoffroy) occurs naturally. Greece is thus barely missed by this largely tropical pollination mode, but the treeless phrygana would not be a suitable habitat anyhow.

bees

As a general rule, the number of bee species is high in arid and semiarid temperate regions (Linsley, 1958; Michener, 1974, 1979; Moldenke, 1976a, 1979b; Heithaus, 1979; Roubik, 1989, 1992; Shmida & Dukas, in press). To find 262 species of Apoidea in a restricted area of phrygana is nevertheless exceptional. Moldenke put forward two factors that may explain the general pattern: first, the large area of vegetationless soil, that provides ample opportunity for ground-nesting species; and second, the frequent occurrence of fire, which results in the presence of many dead branches thereby giving twig-nesting species many nesting opportunities. In the case of the phrygana a coarse soil texture and the presence of stones certainly provide opportunities for species using free spaces in the soil, or cementing a nest in the open.

There may exist a more general explanation, however. The present winter-rain Mediterranean climate replaced a previous summer-rain climate in this region 3.2 mya (Syc, 1984). In the phryganic ecosystem pollen, rather than nectar, constitutes the main floral reward (J. Herrera, 1985; Petanidou & Vokou, 1990). This is probably a general adaptation in many of the plant species to drought stress, because nectar has to be kept at a sufficiently low level of viscosity to be acceptable to pollinators. Bees are (with Masaridae) strongly dependent on pollen as food for their larvae, and the shift in the flora from nectar to pollen as the main reward for pollinators may well have been an important factor in the high diversity of bees in the phrygana. It is possible that the same explanation holds for other arid and semiarid ecosystems as well, but pertinent data on the proportions of pollen and nectar are not yet available. An indication is that Anderson, Buys & Johannsmeier (1983, cited by Whitehead, Giliomee & Rebelo, 1987) note that the Cape flora lacks dominant entomophilous plants with a good nectar yield. However this may be, the bee fauna of Chile, South Africa, and Australia is by far not so extremely rich in species as that of the Mediterranean and California (Armstrong, 1979; Michener, 1979; Whitehead, Giliomee & Rebelo, 1987).

Moldenke (1976a) surveyed the taxonomic composition of the bees of the Mediterranean faunas of Chile and five subdivisions of Mediterranean California. Not surprisingly, in a comparison of the fauna of the restricted Daphni study site with the faunas of these extensive regions (Fig. 6), the first one does not score highest. It is the more interesting that even then the diversity of the Daphni bee fauna exceeds that of the whole of Mediterranean Chile. In comparison with the Californian bee faunas, the Greek one is notable by its slightly higher proportion of Megachilidae and a somewhat low proportion of Anthophoridae and Andrenidae. Seen in another light, it is noteworthy that the relative frequencies of the different bee families vary to such a limited degree in three regions so geographically disparate as Chile, California, and Greece. The only truly deviant feature is the high proportion of Colletidae in Chile. The conclusion is inescapable that the similarity in climate and vegetation exerts an overpowering convergent influence.

Colletidae have a high preponderance in the southern hemisphere, even constituting about 50% of the relatively depauperate bee fauna of Austria (Michener, 1979). In the pollinating fauna of the New Zealand mountains (Primack, 1983) the bee fauna consisted of two Halictidae and fourteen Colletidae (next to four introduced Apidae).

Nectar limitation may be a factor in the restriction of the remarkably unimportant bumblebee species, but a climatological factor may play a role as well. In more temperate climates than the Mediterranean one, the role of the endothermic bumblebees becomes larger, in both number of species and individuals (Michener, 1974, 1979; Willmer, 1983). Conversely, towards the tropical zone the importance of social bees rises as well, as argued by Roubik (1989) probably because under tropical conditions true eusociality is strongly favoured (as exemplified by Apis species, the subgenus Bombus (Fervidobombus), Euglossini and Meliponini).

As noted by Simpson & Neff (1983), pollen may have a high nutritious value, yet it is relatively slowly digested. Adult bees therefore still need a supply of
nectar to cope with their immediate energy needs. At the ecosystem level, therefore, a certain quantity of nectar, even if limited, remains an indispensable commodity. Without doubt, the species both most in need of this resource, and most effective in harvesting it, is the honeybee. This suggests a vigorous competitive interaction with the remainder of the pollinator fauna, which is exacerbated by its broad host plant spectrum: honeybees were observed visiting 105 out of the 133 entomophilous plant species in the phrygana (Petanidou, 1991a). Holm (1988) found extremely few pollinating insects in southwestern Australia, and hypothesized that they have been outcompeted by imported honeybees (see also Moldenke, 1976b; Percival, 1974; Douglas, 1977; Kevan & Baker, 1983; Vaughton, 1992).

**butterflies and moths**

The combined effect of low nectar supply and honey-

bee competition is possibly the limiting factor for the butterfly species, in particular the highly energy-demanding Sphingidae. A poverty in butterflies similar to that in the Daphni site is noted by Shmida & Dukas (in press) for Israel, and by Whitehead, Giliomee & Rebele (1987) and McCall & Primack (1992) for the Cape pollinating fauna; the latter authors explain this by the high prevailing wind speeds and the limited number of suitable larval foodplants. Maybe, however, these low butterfly richness values are but an expression of the general trend that Lepidoptera seem to take only a limited share in the pollination of temperate ecosystems. MacLeod (1893-1894) mentions only thirty-five Lepidoptera species (7%) from N Belgium. In contrast, butterflies are usually important pollinators in the tropics. Percival (1974), for instance, counted sixteen butterfly species among the forty-two 'true' insect pollinators in a Jamaican coastal ecosystem, and Haber & Frankie
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Müller (1880) expressed the opinion that the importance of Lepidoptera pollinators rises also in mountainous areas, basing himself on the observation of 220 flower visiting Lepidoptera recorded by him in the Alps, against seventy-nine species in the lowland (26 and 9%, respectively, of the total number of species recorded in both situations). Primack (1983) captured fifty-three Lepidoptera species (only four of which are Rhopalocera) in the New Zealand mountains, out of a total fauna of 228 species. Also more or less in agreement with this is the result of Arroyo, Primack & Armesto (1982) who found that the number of Rhopalocera in the Andes declines but little from the subandean to the subnival zone (viz. twelve to nine). The data of Moldenke (1976b) also support Müller’s generalization, in that they show nineteen Lepidoptera species (excl. Sphingidae; 25% of the local richness) in an alpine tundra in California, which should be compared with an average percentage of 12% over three sites at subalpine altitudes, 6% at mid-elevation (four sites) and 6% at sea level (four sites). Moldenke (1979b) makes the interesting comment that in alpine ecosystems many moths, unable to be active at the prevailing low night-time temperatures, fly during the day. Because nocturnal pollinators generally tend to be underestimated in censuses, this shift in diel activity pattern might well be the explanation of the apparently high alpine Lepidoptera diversity. (In the Spanish site studied by J. Herrera (1988) three plant species were expected to be moth-pollinated, and therefore special nocturnal censuses were executed. As a result, the Lepidoptera in his survey include, next to fourteen butterflies and a hawkmoth, no less than twenty-three moth species).

flies

Most numerous and active among Diptera families are the anthropophilous flies, viz. Bombyliidae and Syrphidae. The first family is represented by approximately the same percentage in the Mediterranean ecosystems of Greece, California, and Chile (Table 2). Contrariwise, Syrphidae are quite species-rich in Greece and rather much so in Chile, while being poorly represented in California. Syrphidae as a group have little resistance against spells of hot and dry weather (V. S. van der Goot, pers. comm.). Next to muscid flies, they are the most common pollinators in the cool and wet New Zealand mountains (Primack, 1983). A possible explanation of their low abundance in California therefore may be that, in the words of Aschmann (1973) ‘Along the parameter of winter concentration of rainfall and extreme summer drought California may be said to have the most Mediterranean climate of the world’. Moldenke (1979b) reports that the Chilean site receives 52 cm of annual precipitation, against 32 cm in California (and 37 cm in Athens). The fact that in Greece many Syrphidae have an activity period in, or extending into winter or spring fits well in this explanation (Petanidou, 1991a).

Muscid flies take a large part in the pollination in arctic habitats; in the study of Kevan (1972) they consisted of twenty-two out of a total of thirty-three species. In temperate N Belgium their share is reduced to 27% (MacLeod, 1893–1894). At subalpine levels in California (Moldenke, 1976b) this value ranges from 16 to 28%, whereas it has low values in an alpine tundra (6%) and at sea level (0–6%). In this light, the proportion of muscid flies in the Greek phrygana (13%) is rather high.

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