



Factors influencing the degree of generalization in flower use by Mediterranean butterflies

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Despite the enormous importance of nectar sources in butterfly ecology, little research has been carried out in determining broad patterns of flower use at the community level. In this paper we report the results of a long-term study (12 years) of the flowers visited by adult butterflies at four sites in northeast Spain encompassing an altitudinal gradient of 1100 m and a rich variety of biotopes. The complete dataset consists of 29 305 recorded flower visits by 100 butterfly and one burnet moth species to 214 different plant species. Our analysis showed firstly that the degree of generalization in flower use is a species trait that remains fairly constant throughout the biotopes and regions occupied by a butterfly species. Related to this pattern, we also found that phylogeny had an important effect on flower use. Of the ecological traits influencing the degree of generalization, the length of the flight period was identified as the most important. Habitat preference was also important, since forest butterflies were more specialized than the butterflies of open habitats. The existence of a link between the degree of generalization in flower use and the degree of larval polyphagy seems more doubtful as we obtained conflicting results that contradict the most plausible biological explanation. Our data provided no support for the hypothesis that rarer species are more specialized than commoner ones, but did seem to confirm a previous finding that body size is not relevant to any explanation of the degree of generalization in adult butterflies.

One of the most characteristic behavioral traits of adult butterflies is that they visit flowers to feed on nectar. The interaction between butterflies and flowers is indeed so strong that the availability of nectar resources invariably appears as one of the main factors explaining – at least in temperate areas – butterfly abundance in semi-natural or natural habitats (Holl 1995, Loertscher et al. 1995, Pywell et al. 2004). Aside from supplying the energy required for flight, nectar intake also plays a predominant role in other life-history traits such as female fecundity (Boggs and Ross 1993, Mevi-Schütz and Erhardt 2005). The distribution of nectar sources also influences patterns of oviposition (Murphy et al. 1984, Grossmueller and Lederhouse 1987, Janz 2005) and emigration and immigration rates in local populations (Kuussaari et al. 1996, Schneider et al. 2003), and therefore has profound implications on the spatial distribution of butterfly populations.

However, despite the enormous relevance of nectar sources to butterfly ecology, surprisingly few studies have ever explored the patterns of flower use at the community level. Although some studies have already noted that certain characteristics make some flower species more attractive than others to butterflies (i.e. 'pollination

syndromes' sensu Faegri and van der Pijl 1979; see also Dicks et al. 2002, Olesen et al. 2007), overall there have been very few attempts to identify the ecological traits that may cause a butterfly species to be a generalist or a specialist in its use of flowers. In general, it has been assumed that butterflies are generalist nectar-feeders and switch between flowers as they become available during their flight periods (Shreeve 1992). Moreover, it is thought that butterflies may act more as 'nectar robbers' than as effective pollinators (Wiklund 1981), a strategy that would preclude the possible co-evolution of narrow plant–pollinator associations and favor instead a pattern of generalization in flower use. On the other hand, some work has revealed the existence of more subtle relationships, including specific sex-preferences in some species (Rusterholz and Erhardt 2000), different innate colour preferences in related genera and species, and constancy in flower use that decreases floral handling time (Weiss 2001). There is also some evidence to suggest that butterfly morphology plays a role in determining flower choice (e.g. short-tongued butterflies do not visit flowers with deep corollas, while butterflies with a high wing load generally prefer clustered or nectar-rich flowers; Corbet 2000).

In a recent paper, Tudor et al. (2004) analyzed the pattern of flower use in an entire British butterfly

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community by using systematic nectaring records obtained during butterfly counts along a transect route. Butterfly species were first classified into generalist or specialist feeders and, in a second step, their degree of feeding generalization was correlated with several life-history traits. Tudor et al. (2004) hypothesized that the greater the number of broods, the longer the flight period, greater adult size, proboscis length, and mobility should all increase the ability of butterflies to access hosts and, therefore, be positively correlated with the degree of generalization in flower use. Similarly, they argued that the occupation of more biotopes (as opposed to habitat specialization) and the use of more larval hosts would also favor this degree of generalization, as in these cases a butterfly will be exposed to more habitats and flower species. They also suggested that butterfly species rareness (measured according to the species' conservation status in the UK) may be negatively correlated with butterflies' generalization in flower use because of the close relationship between rareness and larval feeding specialization (Shreeve et al. 2001). Actually, apart from adult size and proboscis length, all these hypothetical relationships were supported by the data. However, after using multivariate modelling to account for independent effects of life-history traits, Tudor et al. (2004) concluded that the degree of generalization was best explained by the number of larval host plants and three adult-related traits, namely habitat preference, mobility, and the length of flight period. Interestingly, they also found that butterflies preferring woodland biotopes were more specialized in their flower use than those preferring open biotopes.

There are, however, several reasons for questioning the validity of these conclusions. First of all, Tudor et al. (2004) did not take into account phylogenetic relationships between species, an omission that may lead to a misinterpretation of the results (Harvey and Pagel 1991, Ives and Zhu 2006). Indeed, the data that is available for mud-puddling behaviour in butterflies points to the existence of a phylogenetic signal in foraging patterns, with marked differences existing in feeding preferences between families (Beck et al. 1999, Boggs and Dau 2004). Moreover, it remains to be seen whether the patterns found in Great Britain can be extrapolated to butterfly communities inhabiting other habitats and regions.

In this study, we use a very extensive dataset encompassing a much wider range of biotopes and butterfly and plant species to examine these issues and test for the generality of the hypotheses raised in Tudor's et al. study. Specifically, our aims were (1) to classify butterfly species as either generalist or specialist nectar feeders using comprehensive records of flower visits from four different Spanish sites; (2) to see how widespread these patterns are among butterfly communities; and (3) to identify the ecological traits that explain the degree of generalization while taking into account the phylogenetic relatedness of species. In a future article, we aim to focus on the role of the plant in plant-pollinator interactions in order to answer questions such as which plant species are most attractive for each butterfly guild and which factors are responsible for ecological variation.

Material and methods

Study sites and data collection

Data were collected between 1996 and 2007 at four different sites in Catalonia (northeastern Spain), where butterflies are regularly monitored by walking fixed routes as part of the Catalan Butterfly Monitoring Scheme (<www.catalanbms.org/>). Monitoring sites have an altitudinal range of 1100 m and represent a rich variety of biotopes, including coastal hay meadows, arable farmland, typical Mediterranean evergreen oak forests, beech forests and montane grasslands (Table 1).

At each site, counts were made on a weekly basis starting on 1 March and ending on 26 September, a total of 30 recording weeks per year. All butterflies within 2.5 m on each side and 5 m in front of the recorder were counted, as per the standard procedure described by Pollard and Yates (1993). We also recorded all the butterflies that were nectaring within the transect route, making sure that they were probing the flowers rather than just resting on them. The complete dataset consists of 29 305 recorded flower visits by 100 butterfly and one burnet moth species to 214 different plant species (Table 1). We excluded the few records (less than 5% of the dataset) of butterflies that could not be identified to species level.

Butterfly and plant nomenclature follow Karsholt and Razowski (1996) and Bolòs et al. (1990), respectively.

Degree of generalization in butterfly-plant interactions

We followed the same approach as Tudor et al. (2004) to measure the degree of generalization in flower use. This approach is based on the assumption that the number of flowers used by butterflies will increase with the number of observations until an asymptotic value is reached that fits the simple power function $Y = c X^z$, where Y is the number of plant species, X is the number of nectaring records for butterfly species, and c and z are fitted constants. The degree of generalization was estimated as the residuals from the adjusted logarithmic curve between the number of observations for each butterfly species and the number of plant species on which they were observed feeding. Following Tudor et al. (2004), we considered a species as 'generalist' if it showed a residual of >2 and as 'specialist' if its residual was <-2 . These cut-off values guarantee the significance of all χ^2 contingency tables in which each observed value is compared to the expected one after fitting the potential distribution.

Factors affecting degree of generalization

According to the hypothetical relationships mentioned earlier, we considered that the following species traits could potentially explain the degree of generalization: (1) phenology, (2) voltinism, (3) wing length, (4) degree of larval polyphagy, (5) habitat specialization, (6) habitat preference, and (7) population abundance.

Phenology was measured as the average number of weeks per season in which a butterfly species was recorded at a site

Table 1. Summary of the main characteristics of the study sites, with the total number of recorded flower visits and numbers of interacting butterfly and plant species. (In brackets, figures after excluding butterflies with less than 20 nectaring records.)

Study site	UTMX	UTMY	Mean altitude (m)	Transect length (m)	Main habitat type	Recording period	Species with nectaring records	No. of records	Plant species with butterfly visits
Closes del Tec	509629	4680432	0.7	1122	abandoned hay meadows	1997-2007	39 (20)	3139 (3015)	51 (17)
El Cortalet	507851	4674362	1.5	4343	riverine forest, hay meadows and arable	1996-2007	43 (21)	6047 (5940)	91 (40)
Can Liro	448922	4615799	332.7	1695	evergreen oak forest and arable	1996-2007	55 (32)	3554 (3409)	89 (26)
El Puig	452320	4627952	1026.9	2029	beech forest and bracken-dominated grassland	1996-2007	87 (52)	16 565 (16 340)	109 (39)
Total							101 (63)	29 305 (28 704)	214 (92)

(excluding zero values for those years when the species was not recorded at the site), while voltinism was a categorical variable distinguishing between species with one (univoltine), two (bivoltine), or three or more (multivoltine) generations per year (data from Tolman and Lewington 1997 and personal observations). Wing length, used as a surrogate of body size, was estimated from data provided by Higgins and Riley (1984) as the mean forewing length in males. For the degree of larval polyphagy, we separated monophagous (i.e. feeding on a single host-plant genus), oligophagous (feeding on several genera within a single plant family), and polyphagous (feeding on several genera belonging to a number of plant families) species (data from Tolman and Lewington (1997) and from personal observations).

Habitat specialization was assessed by means of the 'species specialization index' (SSI) described by Julliard et al. (2006). Data from the Catalan Butterfly Monitoring Scheme were used to calculate butterfly densities across 17 different habitat types (details in Table 2), as defined by the CORINE Biotopes Manual (Moss et al. 1990). The degree of habitat specialization was then quantified as the variance of average densities within these 17 habitat classes, the coefficient of variation being chosen as a measure of each species' specialization index. These data were also used to identify habitat preference, which separated species preferring open habitats from those preferring woodland habitats. CORINE habitats (Table 2) were first grouped into four broad habitat categories 'scrub' (habitats 31 and 32), 'grasslands' (habitats 34, 35 and 38), 'forests' (habitats 41, 42, 44 and 45), and 'agriculture' (81, 82, 83 and 87), and then the average abundance of each species was calculated for each category. A species was considered to prefer an open biotope when its maximum abundance was obtained in either the 'grasslands' or 'agriculture' categories, or when its greatest abundance was in the 'scrub' category and second greatest abundance in either the 'grasslands' or 'agriculture' categories. A species was considered to prefer woodland biotopes when its maximum abundance was recorded in the category 'forests', or when its maximum abundance was in the 'scrub' category and its second greatest abundance in the category 'forests'. As an exception, *Satyrrium esculi* and *Satyrrium ilicis* were considered to prefer woodland biotopes even though their maximum abundance was recorded in the 'scrub' category and second maximum in the 'grasslands' category. Larvae of both species are restricted to oak trees and adults spend most of the time in the forest canopy where they are easily overlooked during transect counts.

The annual index of abundance at each site – calculated as the sum of weekly counts, following the standard procedure described by Pollard and Yates (1993) – was used as an estimate of population abundance. We used average values for the years 1996–2007, i.e. the period for which nectaring records were available. Population abundance is used here as a surrogate of rareness at local level, to test the hypothesis that rare butterfly species tend to be more specialized in flower use than common species (Tudor et al. 2004).

We did not include in our study two butterfly traits for which we did not have enough data, 'proboscis length' and 'relative proboscis length'. Although these traits may limit

Table 2. Habitat types (with their corresponding CORINE code) used for calculating the ‘Species Specialization Index’. Butterfly abundance was derived from counts on 69 transect routes forming part of the Catalan Butterfly Monitoring Scheme between 1994 and 2007. Data were originally obtained from 314 units representing the 17 habitat types; to avoid pseudoreplication, this number was reduced to 173 independent units after pooling those units representing the same habitat type in the same transect route. To test for possible habitat differences in the degree of generalization in flower use, CORINE habitat types were assigned to one of the four broad habitat categories shown in the final column.

Habitat type	CORINE code	Independent sampling units	Broad habitat type
Unvegetated	62	6	
Heath and scrub	31	3	scrub
Sclerophyllous scrub	32	18	scrub
Mediterranean dry calcareous grasslands and steppes	34	26	grasslands
Montane and subalpine dry calcareous grasslands and steppes	34	6	grasslands
Mediterranean dry siliceous grasslands	35	8	grasslands
Montane and subalpine dry siliceous grasslands	35	3	grasslands
Mesophile grasslands	38	7	grasslands
Broad-leaved deciduous forests	41	4	forests
Coniferous woodland	42	19	forests
Alluvial and very wet forests and brush	44	8	forests
Broad-leaved evergreen woodland	45	21	forests
Water-fringe vegetation	53	4	
Improved grasslands	81	8	agriculture
Cereal grasses	82	14	agriculture
Orchards, groves and tree plantations	83	6	agriculture
Fallow land, waste places	87	12	agriculture

the range of flowers from which nectar can be extracted (Corbet 2000), Tudor et al. (2004) found no relationship between either of them and the degree of generalization in flower use. Moreover, proboscis length has been found to be highly correlated with adult size and wing length (Corbet 2000, Kunte 2007). We also initially considered an index of mobility that distinguished four groups of butterfly species differing in their dispersal ability and population structure (Tudor et al. 2004). However, because of its strong correlation with voltinism (in the general matrix: $r_s = 0.83$, $p < 0.001$), this trait added no further information to the models and was eventually removed from the analyses.

Data analysis

To preclude wrong inferences regarding specialization, butterfly species with less than 20 nectaring records were removed from all analyses (final sample sizes in all datasets in Table 1).

Using the whole dataset, we first tested whether phylogenetic similarity predicted similarity in our dependent variable (i.e. whether related taxa showed a similar degree of generalization in flower use). We pooled data from all four localities and calculated for each butterfly species an average value of its residual from the adjusted logarithmic curves (our measure of degree of generalization). After checking that residuals followed a Gaussian distribution, we tested for differences between butterfly families in mean values (as defined in Wahlberg et al. 2005) with a univariate analysis of variance.

To test for the effect of the different predictors on the degree of generalization while taking into account species relatedness, we performed generalized least square equations (GLS) as implemented in the APE package for R (Paradis et al. 2004). The correlation matrix for species-to-species relatedness was derived from a consensus phylogenetic tree based mainly on papers by Wahlberg and Nylin (2003),

Wahlberg et al. (2005), Braby et al. (2006), Peña et al. (2006), Warren (2006), and unpublished data from R. Vila and N. E. Pierce. All branch lengths were set to be equal and the phylogenetic hypothesis therefore includes only topology. We built individual models for each locality as well as a general model for the whole dataset (calculating for each butterfly species an average value for population abundance and phenology). Voltinism and polyphagy were considered as ordered factors, following increases in the number of generations per year and in the number of host plants on which the larvae develop, respectively. Quadratic terms for these two variables were also included in the models to test for possible non-linear effects.

For comparative purposes, we also report here results obtained with conventional generalized linear models (GLM), without controlling for phylogeny. All the analyses were performed with the R statistical package.

Results

At all four study sites (but also when considering the whole dataset), the number of plants visited by butterflies fitted the power function model well ($p < 0.001$; average $r^2 = 0.70$; Fig. 1A–E), although there was a number of species that performed more or less visits than expected (Table 3). Moreover, we found a consistent pattern in flower use across all butterfly communities, as shown by the high correlation coefficients in pair-wise comparisons of residuals between sites (average $r_p = 0.68$, $n = 14–22$, $p < 0.05$ in all cases). This coincidence was especially strong for the specialists, which were consistently classified as such regardless of the site and the plants they were recorded on.

The degree of generalization differed significantly between butterfly families ($F_{4,58} = 5.669$, $p = 0.0006$; Fig. 2). The Pieridae showed the highest residual values, indicating that the butterflies of this family are the most generalist flower visitors. At the other extreme, the Lycaenidae and Nymphalidae appeared as the most specialized

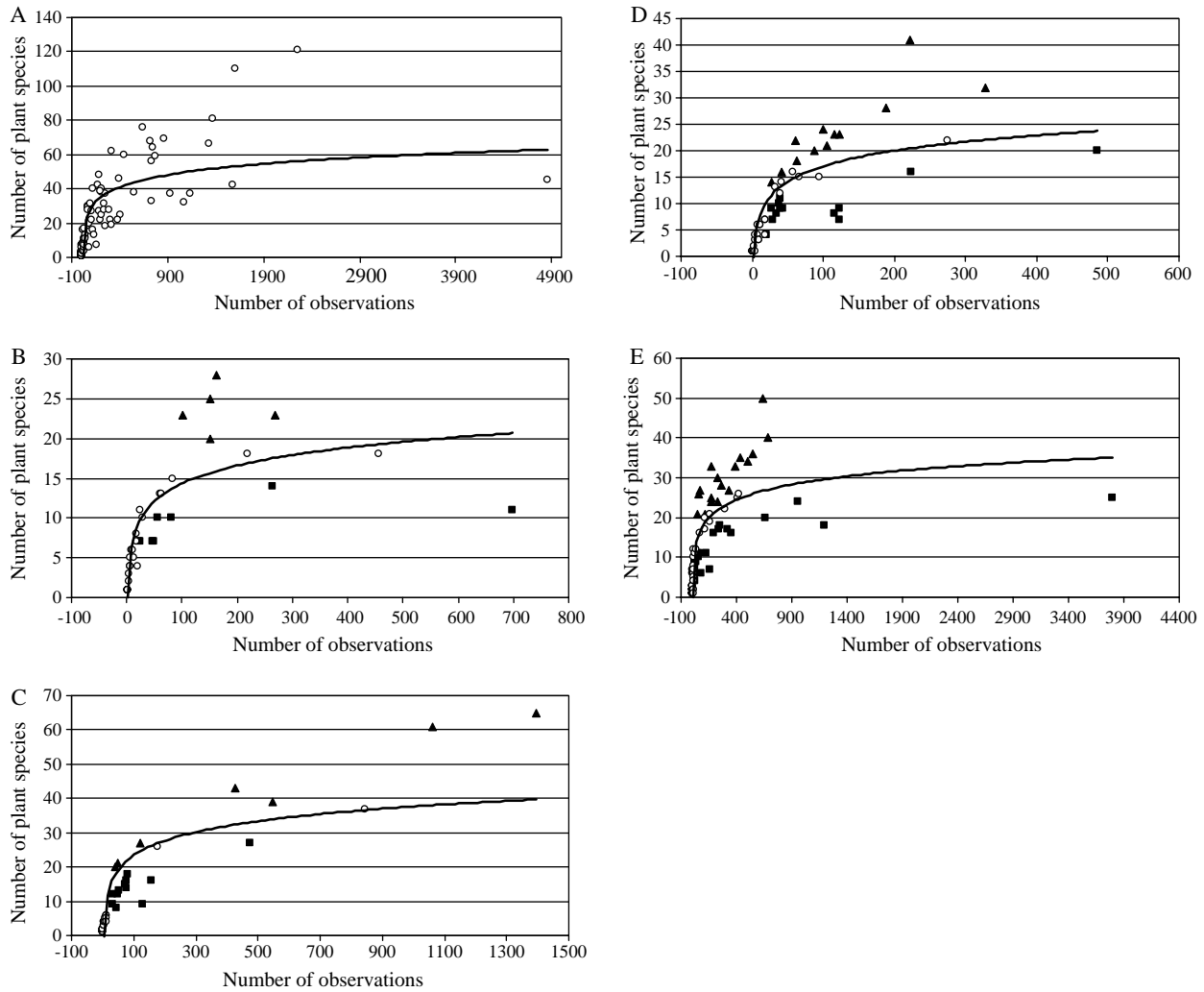


Figure 1. Relationships between the number of observations of butterflies and the number of plant species they visited. At individual sites, black squares correspond to those species considered as specialists (residuals < -2), black triangles to generalists (residuals > 2), and open circles to species adjusting to the model. (A) All sites pooled; (B) Closes del Tec; (C) El Cortalet; (D) Can Liro; (E) El Puig.

families. The a posteriori tests only showed significant differences between Pieridae and Lycaenidae, and Pieridae and Nymphalidae ($p < 0.05$, in both cases). Papilionidae and Hesperiiidae had intermediate levels of generalization (Fig. 2).

Table 4 summarizes the predictor variables with significant effects on the degree of generalization. Phenology and habitat preference appeared as the most important variables in models accounting for phylogenetic relatedness. Both traits were selected in the general model as well as in two out of four site models (or three out of four, if we accept marginally significant results). As expected, butterfly species with long flight periods included a higher number of plants in their diet than species with shorter flight periods. Moreover, in coincidence with Tudor's et al. (2004) results, butterflies from woodland habitats were more specialized than those from open habitats (for the general model: -2.66 ± 1.46 (mean of residuals \pm SE) vs -0.28 ± 0.92 , respectively; Table 3). Larval polyphagy also had significant or marginally significant effects, but not in a consistent way: it showed a quadratic effect when considering the entire

dataset and at one site (El Puig), and a negative linear effect at another site (Can Liro). So, depending on the context, the highest levels of generalization in flower visits were attained by butterflies showing high or intermediate levels of specialization at the larval stage.

We obtained somewhat different results in GLM models when we did not control for species' phylogenetic relatedness. Although phenology also appeared as the main predictor (it had a significant effect on all but one models), habitat preference was only important at the two coastal sites (El Cortalet and Closes del Tec). Moreover, no effect of larval polyphagy was detected at any of the sites.

Finally, wing length and population abundance only reached significant or marginally significant levels at one site (Table 4). The inconsistent results between sites and between GLS and GLM models actually suggest that these two traits are unimportant in determining the degree of generalization in flower use. Likewise, neither voltinism nor habitat specialization seemed to have any effect on our dependent variable, as they never entered the models. This was rather surprising for voltinism, which was

Table 3. Patterns in flower use in butterfly species for which 20 or more flower records were available. Butterflies were classified as generalists if the average of residuals from the fitted models at each site was >2 and as specialists if the average was <-2 . Otherwise, they were taken to have visited the expected number of plant species according to the null model $Y = cX^z$ (where Y is the number of plant species, X is the number of observations of butterflies nectaring, and c and z are fitted constants; see text for details). The main habitat type with which a species is associated (either open or woodland biotopes) is given in the third column. The preferred flower plants used by specialists are shown in the final column.

	Residuals	Habitat	Specialist preferences
Generalists			
<i>Pieris napi</i>	16.93	open	
<i>Pieris rapae</i>	16.33	open	
<i>Anthocharis cardamines</i>	10.95	woodland	
<i>Leptidea sinapis</i>	10.55	woodland	
<i>Boloria dia</i>	10.05	open	
<i>Issoria lathonia</i>	9.08	open	
<i>Aricia agestis</i>	8.08	open	
<i>Pyrgus malvoides</i>	7.72	open	
<i>Thymelicus sylvestris</i>	5.69	open	
<i>Polyommatus icarus</i>	4.67	open	
<i>Coenonympha pamphilus</i>	4.27	open	
<i>Pieris brassicae</i>	4.07	open	
<i>Melitaea cinxia</i>	3.45	open	
<i>Lycaena phlaeas</i>	3.12	open	
<i>Maniola jurtina</i>	2.89	open	
<i>Lasiommata megera</i>	2.50	open	
Null model			
<i>Aglais urticae</i>	1.91	open	
<i>Carcharodus alceae</i>	1.37	open	
<i>Aporia crataegi</i>	1.28	open	
<i>Pontia daplidice</i>	0.64	open	
<i>Gonepteryx rhamni</i>	0.55	woodland	
<i>Melitaea trivialis</i>	0.43	open	
<i>Ochlodes venata</i>	0.39	woodland	
<i>Colias crocea</i>	0.25	open	
<i>Iphiclidia podalirius</i>	-0.34	open	
<i>Cynthia cardui</i>	-0.52	open	
<i>Gonepteryx cleopatra</i>	-0.57	open	
<i>Inachis io</i>	-0.87	woodland	
<i>Vanessa atalanta</i>	-1.07	open	
<i>Melitaea athalia</i>	-1.08	open	
<i>Aricia cramera</i>	-1.15	open	
<i>Papilio machaon</i>	-1.26	open	
<i>Polyommatus semiargus</i>	-1.51	open	
<i>Pararge aegeria</i>	-1.71	woodland	
Specialists			
<i>Melitaea deione</i>	-2.02	open	<i>Scabiosa columbaria</i>
<i>Argynnis aglaja</i>	-2.14	open	<i>Centaurea pectinatus</i> , <i>Mantisalca salmantica</i>
<i>Callophrys rubi</i>	-2.22	woodland	<i>Vicia cracca</i>
<i>Thymelicus acteon</i>	-2.87	open	<i>Cirsium arvense</i> , <i>Rubus ulmifolius</i> , <i>Scabiosa atropurpurea</i> , <i>S. columbaria</i>
<i>Libythea celtis</i>	-2.93	woodland	<i>Salix atrocinerea</i>
<i>Argynnis adippe</i>	-3.41	open	<i>Sambucus ebulus</i>
<i>Plebejus argus</i>	-3.66	open	<i>Limonium vulgare</i> , <i>Lotus corniculatus</i>
<i>Erebia meolans</i>	-3.67	open	<i>Jasione montana</i> , <i>Thymus serpyllum</i>
<i>Lycaena alciphron</i>	-3.97	open	<i>Anthemis triumfetti</i> , <i>Thymus serpyllum</i>
<i>Coenonympha arcania</i>	-4.35	open	<i>Thymus serpyllum</i>
<i>Cacyreus marshalli</i>	-4.70	open	<i>Oxalis</i> sp.
<i>Pyronia cecilia</i>	-4.92	open	<i>Medicago sativa</i> , <i>Mentha suaveolens</i> , <i>Scabiosa atropurpurea</i>
<i>Polygonia c-album</i>	-5.02	woodland	<i>Rubus ulmifolius</i> , <i>Rubus</i> sp.
<i>Satyrus esculi</i>	-5.25	woodland	<i>Rubus ulmifolius</i> , <i>Rubus</i> sp.
<i>Celastrina argiolus</i>	-5.51	woodland	<i>Lythrum salicaria</i> , <i>Rubus</i> sp.
<i>Anthocharis euphenoides</i>	-5.60	woodland	<i>Biscutella laevigata</i>
<i>Melitaea phoebus</i>	-5.69	open	<i>Carduus nigrescens</i>
<i>Leptotes pirithous</i>	-5.71	open	<i>Limonium vulgare</i> , <i>Lythrum salicaria</i> , <i>Medicago sativa</i>
<i>Pyronia tithonus</i>	-6.32	open	<i>Mentha suaveolens</i> , <i>Oenanthe lachenalii</i> , <i>Origanum vulgare</i>
<i>Brintesia circe</i>	-6.36	open	<i>Buddleia davidii</i>
<i>Lampides boeticus</i>	-6.43	open	<i>Limonium vulgare</i> , <i>Medicago sativa</i>
<i>Brenthis daphne</i>	-7.02	woodland	<i>Rubus</i> sp.
<i>Argynnis paphia</i>	-7.12	woodland	<i>Buddleia davidii</i> , <i>Rubus</i> sp.
<i>Aphantopus hyperantus</i>	-7.41	woodland	<i>Rubus</i> sp.
<i>Zygaena trifolii</i>	-7.75	open	<i>Lotus corniculatus</i>
<i>Hipparchia semele</i>	-7.77	open	<i>Rubus</i> sp.
<i>Pyronia bathseba</i>	-7.97	woodland	<i>Rubus</i> sp.
<i>Hipparchia alcyone</i>	-8.21	open	<i>Arctium minus</i>
<i>Melanargia lachesis</i>	-10.05	open	<i>Cirsium arvense</i> , <i>Scabiosa atropurpurea</i> , <i>S. columbaria</i> , <i>Trifolium pratense</i>
<i>Satyrus ilicis</i>	-10.83	woodland	<i>Rubus</i> sp.
<i>Satyrus acaciae</i>	-13.24	open	<i>Achillea millefolium</i>

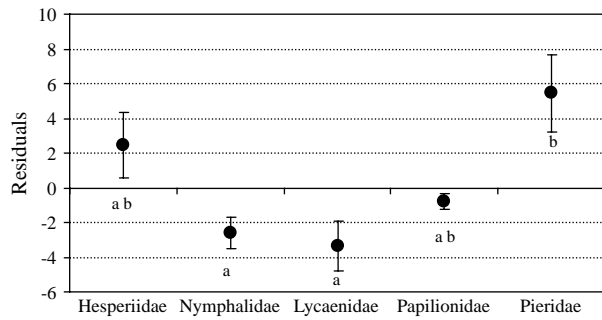


Figure 2. Taxonomic differences in generalization in flower use between butterfly families. Bars indicate SE of the mean. The different letters below the bars refer to statistically significant differences ($p < 0.05$; Tukey HSD post hoc tests) between groups.

always positively correlated with the length of flight period ($p < 0.05$, in all cases).

Discussion

In this study we used what is probably the most extensive existing dataset on flower use by butterfly communities (nearly 30 000 records of flower visits collected over a period of 12 years from four Mediterranean sites). A first interesting finding was the high consistency in the pattern of generalization in particular butterfly species, regardless of the assemblage to which they belonged. The same conclusion was reached when we compared our data with that of Tudor et al. (2004), which also used a high number of records of flower visits along a butterfly transect. A total of 19 out of 23 butterfly species appearing in the British dataset were also common at our sites and for 14 of these species their classification as either generalists or specialists was the same in both studies ($p = 0.02$) (Table 3). Taken together, these results suggest that the degree of generalization in flower use is a species trait that remains fairly constant across the biotopes and regions occupied by these butterfly species.

In a similar way, we also found that the effects of phylogeny were important, as shown by the significant effect of family in the ANOVA analysis. A broad pattern revealed by our data is that Pieridae typically behave as generalists, while a large proportion of the Nymphalidae and the Lycaenidae act as more specialized feeders (Fig. 2). Although not surprising (i.e. closely related taxa tend to share traits as a consequence of common ancestry), these results highlight the need to take phylogenetic relatedness into account in any analysis aimed at identifying the ecological factors underlying the degree of generalization in flower use by butterflies. In fact, as reported here, somewhat different conclusions were reached when phylogeny was not considered in the modelling process.

Of the various predictors considered in our study, the length of the flight period was the most important at three of the four sites, as well as when pooling data from all the sites. This finding agrees well with the idea expressed by Shreeve (1992) to the effect that butterflies are mainly opportunistic nectar feeders that use resources as they become available during the season. This was also readily apparent from the high number of plant species visited at the study sites by single butterfly species with long flight periods. We recorded as many as 65 plant species for the most generalist species (*Pieris napi*) at El Cortalet, with an average of 40.8 plant species per site or 58% of all plant species with butterfly records.

This generalist pattern of flower use can be detrimental for plant reproductive biology, because insects visiting many different species of flowers can promote heterospecific pollen transfer and stigma clogging with pollen from other species (Chittka et al. 1999, reviewed by Morales and Traveset 2008). The role of butterflies in mutualistic pollinator interactions could be even more limited if they mainly act as ‘nectar robbers’ that take nectar without collecting pollen (Courtney et al. 1981, Wiklund 1981, Lazri and Barrows 1984). However, the opposite view – that butterflies may be important pollinators for plants – has also been put forward (Jennersten 1984, Murphy 1984), and there are a number of well-documented

Table 4. Summary of predictor variables explaining the degree of generalization in flower use by butterflies. GLS models took into account the phylogenetic relatedness of butterfly species. GLM models did not control for phylogeny and are shown here for comparison. Significant values appear in bold type.

Site	Predictor variable	GLS				GLM			
		value	SE	t-value	p-value	value	SE	t-value	p-value
All sites	phenology	0.663	0.151	4.367	<0.001	0.693	0.183	3.794	<0.001
	larval polyphagy ²	-4.912	1.377	3.567	<0.001	-1.880	1.207	-1.558	0.125
	habitat	2.581	1.273	2.027	0.048	1.884	1.543	1.221	0.227
Closes del Tec	phenology	0.754	0.216	3.485	0.005	0.774	0.262	2.954	0.013
	habitat	6.779	3.335	2.032	0.067	6.851	3.746	1.829	0.095
El Cortalet	habitat	16.416	5.915	2.775	0.020	18.378	6.445	2.851	0.017
	wing length	-0.822	0.409	-2.011	0.072	-0.397	0.405	-0.982	0.349
	phenology	1.023	0.685	1.496	0.166	1.187	0.628	1.890	0.088
Can Liro	larval polyphagy	-4.706	1.620	-2.905	0.008	-1.482	1.972	-0.752	0.460
	habitat	5.311	1.862	2.853	0.009	2.246	2.381	0.943	0.356
	phenology	0.490	0.268	1.829	0.081	0.831	0.285	2.912	0.008
El Puig	phenology	0.923	0.183	5.047	<0.000	0.840	0.197	4.264	<0.000
	larval polyphagy ²	-3.264	1.627	-2.006	0.051	-1.970	1.370	-1.438	0.158
	IA	-0.002	0.006	-0.398	0.692	-0.012	0.005	-2.151	0.037

examples that indicate the existence of a close relationship between plant and pollinator (Levin and Berube 1972, Cruden and Hermann-Parker 1979, Johnson and Bond 1992). In this sense, our data also revealed considerable feeding specialization in some cases (Table 3). Moreover, a generalist pattern of foraging at species level does not exclude flower constancy at individual level, which can promote a more efficient pollination service. Indeed, several behavioral studies have identified flower constancy in otherwise highly generalist butterflies (e.g. *Pieris rapae*, *P. napi* and *Thymelicus sylvestris*; Lewis 1989, Goulson and Cory 1993, Goulson et al. 1997). Certainly, detailed quantitative studies are urgently needed to clarify the role of butterflies as pollinators.

Habitat preference appeared as the second most important factor in determining the degree of feeding specialization. Forest butterflies were more specialized than butterflies preferring open habitats, as has been previously reported by Tudor et al. (2004). This observed pattern is probably related to the fact that flower diversity tends to be lower in woodland than in open habitats, at least in temperate regions. However, this idea remains to be tested with field data, and other hypotheses cannot be discarded at present. In any case, as suggested by Tudor et al. (2004), the greater specialization of forest butterflies is relevant for conservation and habitat management as it shows the need to maintain certain flower species that may act as key resources for these insects (e.g. brambles *Rubus* spp.; see Table 3). This question becomes even more pertinent in those areas where the rarest and most endangered butterfly species appear in association with forests, as occurs in the British study.

The effect of the degree of larval polyphagy on the degree of generalization was shown to be context-dependent and was only detected when accounting for phylogeny. Such a finding does not support Tudor's et al. (2004) hypothesis as, contrary to their prediction, the highest degree of generalization in flower use was observed in species with monophagous or oligophagous larvae, rather than in species with polyphagous larvae. In fact, the lack of a convincing biological explanation for the patterns found, together with the conflicting results depending on the modelling approach, seem to indicate that the association between larval polyphagy and the pattern of flower use by adult butterflies is weak and equivocal.

An important result claimed by Tudor et al. (2004) was that rarer species are more specialized in nectar feeding than commoner ones. However, our findings do not support this at all. We believe that this discrepancy stems from the fact that the rarer species in the British site were typical of woodland habitats, where, as we have already shown, there is a tendency for butterflies to be more specialists in flower use.

Finally, despite the high correlation between adult size and proboscis length, and the greater range of flowers (either those with deep or shallow corollas) that can be used by butterfly species with a long proboscis, we found no relevant effect for body size on the degree of flower generalization by adult butterflies. This finding, also obtained by Tudor et al. (2004), may be attributable to a phenomenon of partitioning of floral resources among butterfly communities, similar to that described for bum-

blebees (Pyke 1982). Short-tongued butterflies might well be more efficient when feeding on shallow flowers than long-tongued butterflies, leading to their exclusion from part of their potential range of floral resources. Recent work showing functional constraints on proboscis length (Kunte 2007), together with experimental evidence of competitive exclusion for nectar resources in butterfly communities (Kunte 2008), makes the above hypothesis certainly worth exploring in the future.

In conclusion, the analysis of an extensive dataset encompassing a large number of plants and butterflies in a wide range of biotopes has enabled us to detect a number of patterns of flower use at the community level. We found both phylogenetic and ecological correlates with the degree of generalization in flower use, which provide a useful framework for further investigations in the field of plant-animal interactions.

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