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MICROCLIMATE AND INDIVIDUAL VARIATION IN POLLINATORS: FLOWERING PLANTS ARE MORE THAN THEIR FLOWERS[1]

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Abstract. Variation in pollinator composition at the individual plant level is an important prerequisite for plant specialization on pollinators that does not seem to have been investigated previously. I studied variation in pollinator composition in a southeastern Spanish population of the insect-pollinated shrub *Lavandula latifolia* (Labiatae) and examined its correlates, with particular reference to the distinction between factors intrinsic (flower morphology, nectar standing crop, size of floral display) and extrinsic (sunlight regime, ambient temperature, humidity) to the plants. *L. latifolia* shrubs differed significantly in all intrinsic variables measured, in average irradiance levels (due to site-dependent variation in timing and duration of insolation periods), and in pollinator composition at both the species and order levels. Individual variation in pollinator composition was largely due to differences among insect taxa in their foraging responses to the sunlight mosaic. While some pollinators foraged indiscriminately over that mosaic, others preferred sites characterized by high irradiance. Variation among plants in intrinsic variables was unrelated to differences in pollinator composition, which depended significantly only on the sunlight regime associated with each plant's location in the habitat. Site-specific effects in pollination will generally act to reduce the likelihood of selective pressures by animals on plant traits. Their importance should be greatest in habitats characterized by patchiness in environmental variables that affect pollinator behavior and in plants with pollinator assemblages dominated by ectothermic species.

Key words: flower morphology; individual variation; irradiance; Labiatae; Mediterranean shrubs; microclimate; nectar standing crop; pollinator composition; pollinators and sunlight patterns; Spain; sunlight pattern.

INTRODUCTION

Individual variation in reproductive success is a prerequisite for natural selection, and recent studies on the evolutionary ecology of plant–pollinator systems have increasingly focused on the fitness correlates of individual differences in pollination-related traits (Campbell 1989, Galen 1989, Schemske and Horvitz 1989, Herrera 1993, Mitchell 1993). Central to many of these investigations is the notion that, due to differences in pollination-related attributes (e.g., flower morphology, nectar reward, floral scent), individual plants differ in pollination regime (e.g., behavior, visitation rate and identity of pollinators), which in turn generates fitness differences and thus an opportunity for selection on those features that are ultimately responsible for pollination differences (Waser 1983, Weis and Campbell 1992, Herrera 1995*b*). While many studies have documented that individual variation in floral traits may generate fitness differences via its effects on the pollinating behavior or visitation rate of pollinators (Waser and Price 1981, Klinkhamer et al. 1989, Robertson and Wyatt 1990, Cresswell and Galen 1991, Real and Rathcke 1991), I am not aware of any investigation focusing on individual variation in pollinator composition (but see Schemske and Horvitz 1988, 1989). This represents a serious gap in our knowledge of plant–pollinator relationships. The different taxa pollinating a given plant species ordinarily differ in aspects of pollinating effectiveness, and many authors have emphasized the importance of these differences for plant specialization on pollinators (e.g., Motten et al. 1981, Schemske and Horvitz 1984, Herrera 1987*a*, Wolfe and Barrett 1989, Eckhart 1992, Harder and Barrett 1993). This variation, however, may be evolutionarily irrelevant unless it is associated with differences between individual plants in pollinator composition, *and* the latter are explained by phenotypic, inherent plant attributes. Patterns and correlates of individual variation in pollinator composition are therefore essential to our understanding of the mechanisms involved in the specialization of plants on pollinators.

This paper has two main objectives. The first is to document individual variation in pollinator composition in a southeastern Spanish population of the insect-pollinated shrub *Lavandula latifolia*. The second is to assess the correlates of that variation, with particular reference to the distinction between factors intrinsic (phenotypic) and extrinsic (environmental) to the plants. Differences between individual plants in the

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taxonomic composition of pollinator assemblages may be due to variation in phenotypic features (e.g., floral morphology, nectar abundance, size of floral display), but also to factors unrelated to their phenotypes, such as environmental variables that depend on their particular location in the habitat. Microclimatic variables (e.g., solar irradiance, humidity, ambient temperature) are known to influence pollinator activity and behavior at flowers (Lundberg 1980, Lerer et al. 1982, Willmer 1983, Stone et al. 1988, Stanton and Galen 1989, Herrera 1995*a*), and different pollinators may respond differentially to variation in the physical environment (Gilbert 1985, Herrera 1990*a*). The following questions will be specifically addressed: (1) Do *L. latifolia* plants growing at the same locality differ in pollinator composition? (2) To what extent does this variation depend on intrinsic and extrinsic plant features? (3) Do pollinators differ in their response to those microclimate variables that vary among plants' locations?

Materials and Methods

Species and study site

Lavandula latifolia Med. (Labiatae) is a low, evergreen, summer-flowering shrub. The composition of the pollinator assemblage, the relation of the plant with pollinators, and other relevant aspects of its reproductive biology have been described elsewhere (Herrera 1987*a*, *b*, 1988, 1989, 1990*a*, *b*, 1991, 1992*a*). *L. latifolia* commonly occurs in the understory of mixed woodlands in the eastern Iberian Peninsula. In the Sierra de Cazorla study region (see below), it has a diverse pollinator assemblage comprising nearly 80 bee, fly, and butterfly species. Pollinator taxa differ in several components of pollinating effectiveness (Herrera 1987*a*, *b*, 1989) and there is also indirect evidence suggesting that they differ in the response to the thermal and radiant environment (Herrera 1990*a*).

I conducted this study in the Sierra de Cazorla (Jaén province, southeastern Spain), at a *L. latifolia* population growing around the intersection of Arroyo Aguaderillos and the track joining Roblehondo and Hoyos de Muñoz, at 1160 m elevation. This is the "Aguaderillos-1" site of earlier studies (Herrera 1988, 1991, where further details may be found). *L. latifolia* plants occupy there the understory of open *Quercus rotundifolia–Pinus nigra* mixed forest. During daytime, understory plants occur in a changing mosaic of insolated and shaded patches whose precise location and spatial characteristics at a given time depend on the size and relative position of overlying tree crowns.

Methods

Data were collected between 20 July and 10 August 1991. This period encompassed about one third of the local flowering season of *L. latifolia* (early July to late September). I chose 15 flowering shrubs haphazardly from the population and marked them at the start of the study. The two most distant plants were 30 m apart, and the nearest ones were 2 m apart. Pollinator censuses were carried out on these plants throughout the study period. Each census lasted for 5 min, during which I closely watched the activity of pollinators at one of the marked shrubs. All flower visitors were visually identified to species, and information from previous studies (Herrera 1987*a*) was used to ascertain their status as pollinators. Pollinators of *L. latifolia* vary over daytime (Herrera 1990*a*), and I paid particular attention to avoid biases due to unequal sampling at different times. Marked plants were censused in turn from dawn to dusk (roughly 0630 to 1900 Greenwich mean time [GMT]; throughout this paper, all times are reported as GMT) according to a random permutation scheme. When a round of censuses was completed on all the plants, a new one was started that used a different random permutation, and this protocol was repeated until the completion of the study. This sampling scheme ensured both a random sampling of pollinator visits to plants and a balanced distribution of censuses among dates, hours, and plants. By the end of the study, 11 plants had been censused on 29 occasions, 3 plants on 30 occasions, and 1 plant on 28 occasions (N = 437 censuses covering 36.4 h in total). All censuses (and concurrent measurements, see below) were conducted in cloudless, calm weather.

In addition to observations on pollinators, I also measured the hygrothermal and radiant environment associated with a given focal plant during each 5-min observation period. Three microclimatic variables were measured in the air at 10 cm from the top of the shrub. Maximum and minimum air temperatures over the census period were recorded using a 0.5 mm diameter Type T thermocouple connected to a recording thermometer. I used the mean of these extreme values to characterize air temperature close to the plant during the census. Air relative humidity was measured using a Vaisala HM 34C Relative Humidity Meter (Vaisala Sensor Systems, Helsinki, Finland). Solar irradiance on the horizontal plane was measured using a LI-COR LI-200SZ Pyranometer Sensor (calibrated spectral range 400-1100 nM) connected to a LI-1000 data logger (LI-COR, Inc., Lincoln, Nebraska, USA). Humidity and irradiance measurements were done immediately after completion of the census period.

Nectar standing crop of the focal plant was also assessed after completing each census. I selected 10 flowers at random, and determined nectar volume using 1-μL micropipettes. The mean value was used to characterize nectar availability during the census. The number of open flowers borne by each marked plant was counted daily (between 1630 and 1730) throughout the study period. The figure obtained for a given plant and date was assigned to all censuses for that plant on that date. This procedure was justified because the number of open flowers on plants experienced only minor variation during daytime.

At the end of the study I collected a sample of flowers (N = 20–25) from each marked shrub to characterize their floral morphology. The protandrous flowers of *L. latifolia* last for several days (Herrera 1990*a*) and experience some morphological change as they pass from male to female stage (C. M. Herrera, *personal observation*). All flowers were collected in the female stage, when morphological change had already occurred. Three linear dimensions were measured for each flower: corolla tube depth (from tube rim to bottom), and maximum width and length of the exposed (external to the calyx), colored portion of the corolla.

Random sampling of foraging pollinators, along with a detailed characterization of the sunlight regime, were conducted at the study site during 20 July–15 August 1990 as part of other studies (C. M. Herrera, *unpublished data*). To characterize the mosaic of irradiance levels available to pollinators in the forest understory, 60 permanent recording stations were set, regularly spaced at 2-m intervals along a transect that crossed the *L. latifolia* study population. Irradiance was measured periodically from dawn to dusk at all stations during several consecutive days. I also netted individuals of most pollinator species systematically from dawn to dusk while they were visiting *L. latifolia* flowers, and measured solar irradiance at all capture points. Comparisons of irradiance at the capture points of particular insect species with the combined sample of measurements at the permanent sampling points (N = 1620) are used in this study to elucidate patterns of microhabitat selection by pollinators.

Results

Variation in intrinsic and extrinsic variables

Individual plant means for the intrinsic and extrinsic variables considered in this study are summarized in the Appendix. Study shrubs differed significantly in all intrinsic features examined: daily counts of open flowers (χ^2 = 273.6, df = 14, $P \ll 0.0001$; Kruskal-Wallis ANOVA), mean nectar volume per flower in individual censuses (χ^2 = 46.8, df = 14, $P < 0.0001$; Kruskal-Wallis ANOVA), and average (multivariate) floral morphology ($F_{42,959}$ = 17.7, $P \ll 0.0001$; MANOVA). The three descriptors of floral morphology differed significantly among plants (corolla depth: $F_{14,325}$ = 13.2, $P \ll 0.0001$; exposed corolla width: $F_{14,325}$ = 26.2, $P \ll 0.0001$; exposed corolla length: $F_{14,325}$ = 24.9, $P \ll 0.0001$; univariate ANOVAs).

Study plants differed significantly in mean solar irradiance ($F_{14,422}$ = 2.08, P = 0.012), but not in ambient temperature ($F_{14,422}$ = 0.44, P = 0.96) or relative humidity ($F_{14,422}$ = 0.19, P = 0.99). Irradiance on individual plants ranged between 266 ± 221 and 592 ± 376 W/m^2 (mean ± 1 SD, N = 29 measurements per plant). Differences between plants in average irradiance reflect site-dependent variation in timing and duration of direct insolation periods. Irradiance measurements are plotted against time in Fig. 1 (top). The scatter of points in the graph denotes that, at any time of day, *Lavandula latifolia* shrubs fell along a broad gradient of irradiance, ranging from shade (<100 W/m^2) to the time-specific possible maximum (full insolation). Each individual plant had a characteristic temporal pattern of exposure to direct sunlight (Fig. 1, bottom), depending on its location in the forest floor.

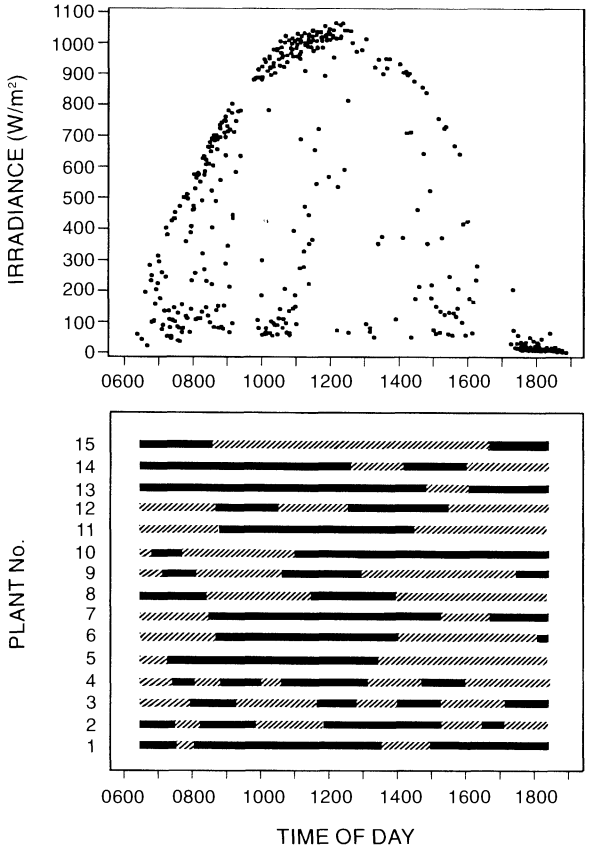

FIG. 1. Daytime variation in solar irradiance on marked *Lavandula latifolia* shrubs. Top graph: Plot of irradiance measurements taken during pollinator censuses (all plants combined, N = 437 census measurements). Bottom graph: Daily pattern of direct insolation (black portion of bars) and shade (hatched portions) periods experienced by marked plants. At a given time, plants were considered to be fully insolated if they received ≥75% of the maximum possible irradiance for the time, otherwise they were considered to be shaded. Time of day is Greenwich mean time.

Variation in pollinator composition

A total of 32 insect species, belonging to the orders Hymenoptera (13 species, accounting for 75.2% of total visits; 1 visit = 1 insect arrival per census), Lepidoptera (14 species, 21.8% of visits), and Diptera (5 species, 3.0% of visits), were recorded during censuses. Species contributing most flower visits were *Apis mellifera* (Apidae, 34.9%), *Bombus terrestris* (Apidae, 12.8%),

TABLE 1. Variation in pollinator composition among marked *Lavandula latifolia* shrubs. Shown are the relative contribution (%) of the 10 major taxa to the total number of pollinator visits recorded for each plant. One visit = 1 insect arrival per census. The rest of the pollinators (N = 22 taxa) accounted collectively for 12.6% of total visits.

Pollinator		Plant no. {Total no. of pollinator visits}														
Species	Order*	1 {5}	2 {19}	3 {29}	4 {6}	5 {15}	6 {66}	7 {19}	8 {14}	9 {32}	10 {37}	11 {46}	12 {17}	13 {26}	14 {34}	15 {71}
		Percentage of pollinator visits														
Anthidiellum breviusculum	H	0	0	10.3	33.3	20.0	16.7	0	0	3.1	16.2	0	11.8	7.7	20.6	8.5
Anthidium florentinum	H	0	0	0	0	6.7	3.0	0	0	0	8.1	4.4	0	0	0	2.8
Apis mellifera	H	20.0	52.6	48.3	50.0	53.3	16.7	36.8	21.4	46.9	43.2	50.0	17.7	34.6	32.4	25.4
Argynnis paphia	L	0	0	0	0	0	1.5	26.3	7.1	0	2.7	2.2	0	3.9	8.8	2.8
Bombus terrestris	H	0	21.0	0	0	6.7	18.2	10.5	28.6	18.8	5.4	8.7	0	15.4	11.8	18.3
Ceratina cyanea + mocsaryi	H	20.0	15.8	3.5	0	0	7.6	0	7.1	9.4	5.4	13.0	47.1	0	5.9	9.9
Fabriciana adippe	L	0	0	3.5	0	0	4.6	0	0	0	5.4	2.2	5.9	3.9	0	5.6
Macroglossum stellatarum	L	0	0	0	16.7	6.7	1.5	0	14.3	6.3	0	4.4	0	7.7	2.9	2.8
Anthophora ochroleuca	H	20.0	0	6.9	0	0	3.0	21.1	14.3	3.1	0	0	0	0	0	1.4
Thymelicus acteon	L	0	10.5	3.5	0	0	15.2	0	0	0	8.1	4.4	11.8	0	0	8.5

* H = Hymenoptera; L = Lepidoptera.

Anthidiellum breviusculum (Megachilidae, 9.9%), *Ceratina cyanea + mocsaryi* (Anthophoridae, 8.9%; these two species are difficult to distinguish in the field and will be treated as a single species in this paper), *Thymelicus acteon* (Hesperiidae, 6.0%) and *Argynnis paphia* (Nymphalidae, 3.4%) (all plants combined, N = 436 pollinator visits).

Plants differed in pollinator composition at the species level (Table 1) and in the relative contribution of hymenopterans (range = 61.5–93.3%), lepidopterans (6.7–31.0%) and dipterans (0–19.2%) to the total number of visits. The statistical significance of individual variation in pollinator composition at the species and order levels were tested using log-linear models that examined the association between plants and taxa (SAS Institute 1990: CATMOD procedure). Most species of pollinators occurred infrequently in censuses and the plant × species table had many empty cells. For this reason, I restricted this test to the 10 species contributing individually >2% of total visits (Table 1). Individual plants differed significantly in pollinator composition at both the species (χ^2 = 270.7, df = 87, $P \ll 0.0001$) and order (χ^2 = 244.1, df = 28, $P \ll 0.0001$) levels.

Correlates of variation in pollinator composition

Three separate between-plant similarity matrices were computed that reflected the degree of resemblance in pollinator composition and intrinsic and extrinsic features. Similarity in proportional pollinator composition at the species level was computed using Renkonen's percentage similarity index (Krebs 1989). Similarity in intrinsic features (number of open flowers, mean nectar standing crop per flower, and the three descriptors of floral morphology) was obtained using Cattell's transformation of the matrix of Euclidean distances computed on standardized individual means (Sneath and Sokal 1973). Among extrinsic variables, only irradiance was considered, as no significant differences between plants were found in ambient temperature and relative humidity. Plants were characterized by the sequence and duration of sunlit and shaded periods during daytime (Fig. 1, bottom), and pairwise similarity values were obtained using a simple matching coefficient for binary, presence–absence data (Krebs 1989).

Similarity between plants in the taxonomic composition of their pollinator assemblages (STC) is plotted against similarity in intrinsic (SI) and extrinsic (SE) features in Fig. 2. The statistical significance of these relationships was tested using ordinary Mantel's permutation tests with 10,000 repetitions (Manly 1991). The regression coefficient for the relationship STC-SI (0.052) did not differ significantly from zero (P = 0.35), while that for STC-SE (0.428) did differ (P = 0.0034). In a further analysis, I applied Manly's (1991) extension of Mantel's test to three matrices. In this case, which is conceptually analogous to a multiple regression, I used STC as the dependent variable, and SI and SE as the independent ones. The estimated R^2 for the multiple regression model (0.189) was statistically significant (P = 0.0079). The partial regression coefficient of STC on SI (0.076) was not significant (P = 0.292), while the coefficient on SE (0.432) was significant (P = 0.0028) (randomization tests with 10,000 repetitions, conducted using routines in Manly [1991] and Press et al. [1992]). Similarity among plants in pollinator composition was therefore unrelated to similarity in intrinsic features, and depended significantly only on similarity in daily sunlight pattern. An identical conclusion was obtained when proportional similarity between

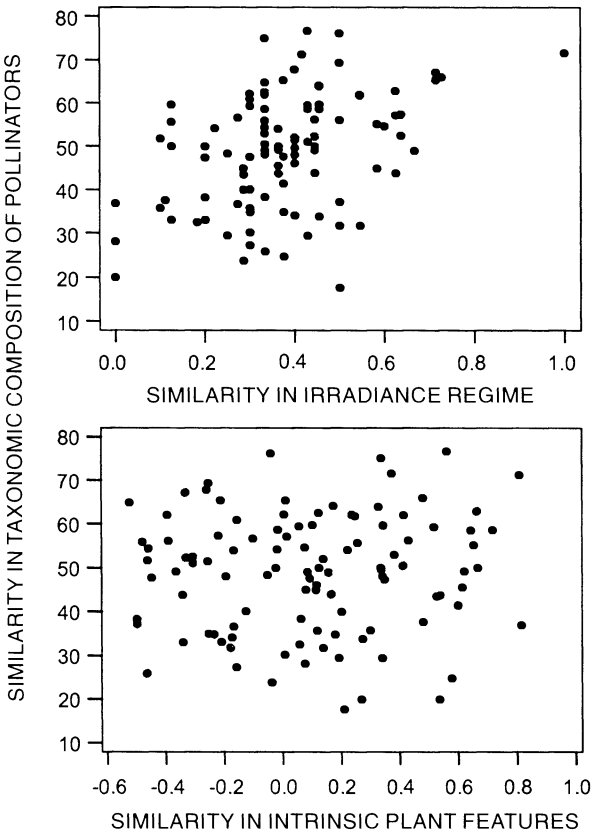

FIG. 2. Relationship among marked plants between pairwise similarity in pollinator composition and similarity in irradiance regime (top graph) and similarity in intrinsic plant features (bottom graph; similarity index based on information on number of open flowers, nectar standing crop, and three descriptors of floral morphology). See *Results: Correlates of variation in pollinator composition* for description of similarity indices used.

plants in pollinator composition was assessed using numbers of flowers visited instead of numbers of visits (results not shown).

Pollinator responses to microclimate

To determine if the results obtained in the preceding section are due to differential response of pollinators to microclimatic variation, I examined the effects of irradiance, temperature, and humidity on the probability of occurrence in censuses of major pollinator taxa, using logistic regression (SAS Institute 1990: LOGISTIC procedure) and individual censuses as sampling units. Separate regressions were run for each pollinator, using occurrence in censuses (presence or absence) as the dependent variable, and the three associated microclimatic variables as independent ones. Pollinators differed in the extent and nature of their response to microclimatic variables (Table 2). Occurrence in censuses was significantly affected by microclimatic variable in some species (two bees and three butterflies), but not in others (four bees and one day-flying moth). Among the former, solar irradiance had a significant effect in all cases, temperature in two cases, and no significant effect of relative humidity was found for any species (Table 2).

Data on microhabitat use by pollinators obtained in 1990 suggest that patterns of occurrence in censuses revealed by logistic regressions actually reflect microhabitat selection by pollinators. Frequency distributions of irradiance values at pollinator capture points (= habitat use) are shown in Fig. 3 along with the frequency distribution at permanent sampling stations (= availability) for the five species whose probability of occurrence in censuses was significantly affected by irradiance (Table 2). Four of these exhibited distinct patterns of microhabitat selection in relation to irradiance, as revealed by significantly greater average irradiance at capture points than at permanent sampling stations (*Anthidiellum breviusculum*: $\chi^2 = 100.9$, $P \ll 0.001$; *Ceratina cyanea* + *mocsaryi*: $\chi^2 = 85.3$, $P \ll 0.001$; *Fabriciana adippe*: $\chi^2 = 9.8$, $P = 0.002$; *Thymelicus acteon*: $\chi^2 = 27.3$, $P \ll 0.001$; Kruskal-Wallis ANOVAs).

DISCUSSION

As in other plants (Horvitz and Schemske 1990, Waser and Price 1990, Pettersson 1991, Eckhart 1992), the composition and abundance of *Lavandula latifolia* pollinators vary annually, seasonally, and among populations (Herrera 1988). This study shows that variation occurs also at a restricted spatial scale within populations, as shrubs within a radius of a few dozen metres differed significantly in pollinator composition at both the insect species and order levels. As the study encompassed only a fraction of the local flowering season of *L. latifolia*, the nature and extent of individual variation in pollinator composition reported here may differ from that for the whole flowering period. Possible differences, however, are not expected to be substantial because study dates roughly corresponded to those when diversity and abundance of *L. latifolia* pollinators were around their seasonal maxima (Herrera 1988).

L. latifolia shrubs differed in floral morphology, nectar standing crop, and number of open flowers (intrinsic variables). The variation in size of floral display was mainly due to plant differences in number of inflorescences, the major determinant of flower production in this species (Herrera 1991), and only secondarily to slight differences among shrubs in flowering phenology. Among the extrinsic, site-dependent variables considered, significant among-plant variation was found for average irradiance, which reflected differences among plant locations in sunlight patterns. Plants did not differ, however, in average ambient temperature and relative humidity. This suggests that mixing of the air near the ground was sufficient to prevent the appearance of consistent, small-scale temperature or humidity mosaics (Geiger 1965). All the intrinsic variables considered in this study have been shown to in-

TABLE 2. Summary of logistic regression analyses testing for the effect of irradiance, air temperature, and relative humidity on the probability of occurrence of major pollinator species in censuses.

Species†	Irradiance		Relative humidity		Temperature		Significance of the model‡	
	χ^2	P	χ^2	P	χ^2	P	χ^2	P§
Responsive species								
Anthidiellum breviusculum	12.45	.0004	0.00	NS	7.53	.006	62.85	***
Argynnis paphia	6.82	.009	0.29	NS	3.81	NS	21.97	***
Ceratina cyanea + *mocsaryi*	6.47	.011	0.01	NS	5.11	.024	33.43	***
Fabriciana adippe	3.84	.05	0.00	NS	1.48	NS	12.99	*
Thymelicus acteon	8.06	.004	0.53	NS	0.67	NS	25.51	***
Non-responsive species								
Anthidium florentinum	1.96	NS	0.42	NS	0.14	NS	2.46	NS
Anthophora ochroleuca	0.06	NS	0.42	NS	1.26	NS	4.96	NS
Apis mellifera	1.15	NS	0-59	NS	0.91	NS	9.35	NS
Bombus terrestris	0.88	NS	0.98	NS	0.00	NS	4.23	NS
Macroglossum stellatarum	3.23	NS	0.29	NS	0.01	NS	5.82	NS

† Individual species have been classed into "Responsive" and "Non-responsive" categories, according to the overall significance of their respective regression models.

‡ "Significance of the model" refers to the combined influence of the explanatory variables alone (i.e., not considering the significance of the intercept).

§ To account for simultaneity of tests, significance levels were adjusted for increased Type I error using Bonferroni method.

*$P < 0.05$; ***$P < 0.001$; NS = not significant.

fluence plant or flower discrimination by insect pollinators in one or another species (e.g., Galen and Newport 1987, Schmid-Hempel and Speiser 1988, Klinkhamer et al. 1989, Cresswell and Galen 1991, Real and Rathcke 1991, Eckhart 1992). Furthermore, pollinator taxa often differ in their response to variation in some of these variables (Kay 1982, Eckhart 1992). I thus expected that intrinsic variables could partly account for plant differences in pollinator composition in *L. latifolia*. Under the conditions of this study, however, individual variation in intrinsic variables had no measurable effect on differences among shrubs in pollinator composition, which depended more on differences in the sunlight regime. It could be argued that individual variability of *L. latifolia* in the intrinsic variables considered, although statistically significant, may have been unusually small in absolute terms and thus unable to induce pollinator selectivity and variation in pollinator composition. This may be true for mean nectar standing crop, which was consistently small and differed little between plants (see Appendix), but does not apply to the other four variables. The mean number of open flowers per plant exhibited five-fold variation (32–158 flowers), and the coefficients of variation for plant means of the descriptors of floral morphology (3.8%, 11.8%, and 9.4% for tube depth, corolla width, and corolla height, respectively) fell within the range observed for other insect-pollinated species (Kearns and Inouye 1993: Table 9-1, Herrera 1995*b*).

A number of studies have documented that physical environmental factors may constrain the activity of pollinators, influence their behavior at flowers (Corbet 1990, Herrera 1995*a*, and references therein), and become critical determinants of plant reproductive success via their effects on pollinators (Eisikowitch and Galil 1971, Martínez del Río and Búrquez 1986, Murcia 1990). To the best of my knowledge, however, no study has previously examined the influence of the physical environment on the pollination regime of individual plants. Beattie (1971) found for a forest-floor violet that "the precise location of the plant relative to gaps in the canopy directly affected the frequency of insect visits", and suggested that "the immediate locality of a plant may be of prime importance in its pollination", but provided no quantitative results. In that case, as in *L. latifolia*, the spatio-temporal pattern of sunlight on the forest floor was the major determinant of individual differences in pollination regime.

Variation among *L. latifolia* shrubs in pollinator composition was mainly the result of differences among insect taxa in their foraging responses to the spatio-temporal mosaic of sun and shade patches. While some pollinators foraged indiscriminantly over that mosaic, others selected sites or times characterized by high irradiance (see also Herrera 1990*a*). Microhabitat-selective pollinators were butterfly and small-sized bee species, while indiscriminate (with regard to irradiance) foragers were medium- to large-sized bees and one day-flying hawk moth. The contrasting microhabitat selection patterns of these two groups of species must be related to differences in thermal biology and thermoregulatory methods. Indiscriminate foragers are endotherms, which regulate body temperature mainly by physiological means (Herrera 1992*b*, Heinrich 1993; C. M. Herrera, *unpublished data*), while species of selective foragers are ectotherms, which thermoregulate behaviorally and rely on solar radiation to keep suitable flight temperature (Kingsolver 1985, Pivnick and McNeil 1986; C. M. Herrera, *unpublished data*).

Insects pollinating *L. latifolia* differ broadly in flow-

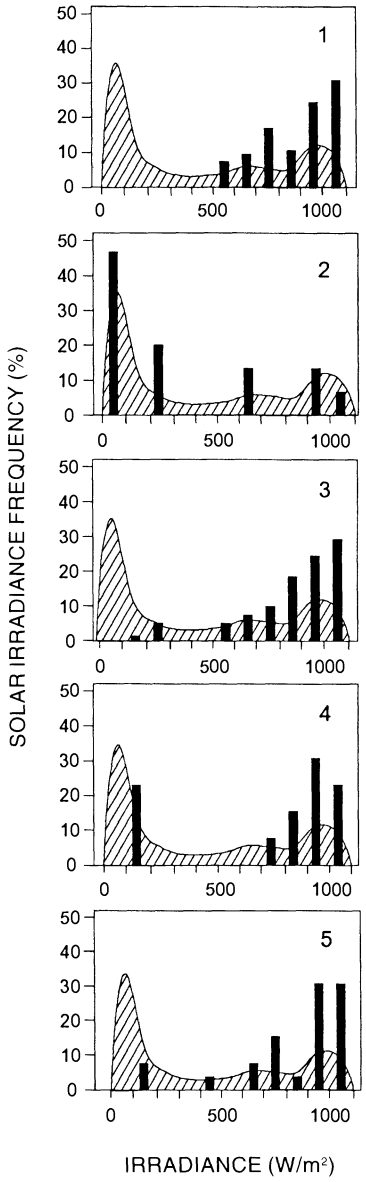

FIG. 3. Frequency distribution of solar irradiance at capture points of selected pollinator species (filled bars). In each graph, the frequency distribution of irradiance values in the habitat, measured from dawn to dusk along a permanent transect, also is shown for comparison (shaded area). Species included are those whose probability of occurrence in censuses was significantly affected by irradiance (Table 2). (1) *Anthidiellum breviusculum*; (2) *Argynnis paphia*; (3) *Ceratina cyanea* + *mocsaryi*; (4) *Fabriciana adippe*; (5) *Thymelicus acteon*.

er visitation rate, proportion of visits resulting in pollen delivery to the stigma, amount of pollen deposited and removed per floral visit, and flight distance between consecutive flower visits (Herrera 1987*a*, *b*, and *unpublished data*). Some of the sun-loving species (e.g., *Anthidiellum breviusculum*, *Ceratina* spp., *Thymelicus acteon*) pollinate flowers infrequently, deposit and remove small pollen loads, and have intermediate average flight distances between consecutively visited flowers (Herrera 1987*a*). In contrast, irradiance-indifferent bees (e.g., *Apis mellifera*, *Bombus terrestris*, *Anthophora ochroleuca*) pollinate flowers very often, deposit and remove large pollen loads, and fly short distances between flowers. Individual variation in pollinator composition found in this study should thus not be dismissed as inconsequential for plant reproduction, as it will presumably translate into differential reproductive success. This view is supported by evidence that experimentally induced pollination regimes differing in pollinator composition produce seeds that differ in the probability of giving rise to established seedlings (C. M. Herrera, *unpublished data*).

Patchiness in the light environment may induce individual variation in growth, photosynthesis, herbivory, and reproduction of forest understory plants (Thompson and Willson 1978, Maiorana 1981, Moore and Willson 1982, Louda et al. 1987, Chazdon 1988, Piper 1989, Niesenbaum 1994, and this study). Sunlight patchiness, however, is only one possible cause of site-specific effects. Patch size and location of neighboring flowering or fruiting plants, for example, may also decisively influence the reproductive success of forest plants (Manasse and Howe 1983, Denslow 1987, Sowig 1989, Sargent 1990, Laverty 1992). In plant–animal interactions, site-specific effects will generally reduce the likelihood of animals exerting selective pressures on plant traits, as the outcome of the interactions will partly depend on features over which the plants can exert no or little influence (Herrera 1986). Due to this potential role in constraining the adaptation of plants to animals, site-specific effects deserve more consideration than they have received so far in evolutionary ecological studies of plant–animal interactions. In plant–pollinator systems, site-specific effects should most likely occur in habitats characterized by patchiness in biotic or abiotic variables that affect pollinator behavior (e.g., microclimate, simultaneously flowering plants). When microclimatic variables are involved, site-specific effects should be most important in situations where ectothermic pollinators prevail and unfavorable weather often limits their activity. Tests of these predictions should help to evaluate to what extent flowering plants are, from the viewpoint of pollinators, more than the flowering-related phenotypic attributes routinely considered in pollination ecology studies.

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APPENDIX

Individual means for intrinsic and extrinsic plant variables considered in this study of *Lavandula latifolia* shrubs in Spain.

Plant no.	No. of open flowers	Nectar volume (μL/flower)	Exposed corolla width (mm)	Exposed corolla length (mm)	Corolla tube depth (mm)	Irradiance (W/m^2)	Temperature (°C)	Relative humidity (%)
1	42.8	0.039	4.52	4.31	6.70	266.1	26.5	24.1
2	65.1	0.025	4.98	4.29	7.11	564.7	28.0	23.0
3	60.0	0.020	4.94	3.92	6.86	574.3	28.1	22.2
4	40.5	0.025	4.37	3.63	6.92	461.2	27.4	24.3
5	83.7	0.026	4.50	4.07	6.75	540.6	28.0	22.2
6	130.9	0.018	5.19	4.75	7.09	451.6	26.9	23.0
7	39.1	0.020	4.05	3.87	6.97	407.1	26.8	22.5
8	32.4	0.045	5.05	4.22	6.97	348.3	26.1	24.4
9	120.5	0.022	4.35	3.82	6.96	591.6	28.3	23.6
10	58.2	0.012	4.61	4.26	6.38	561.8	27.9	24.0
11	158.4	0.021	5.84	4.97	6.97	507.7	26.8	23.4
12	31.8	0.045	4.26	3.94	7.06	469.0	27.2	24.2
13	58.9	0.012	5.35	4.28	7.03	339.1	26.8	22.7
14	102.1	0.018	6.03	4.89	7.58	381.3	27.0	22.4
15	142.9	0.021	5.02	4.50	7.24	575.2	27.6	22.1