Flower traits, habitat, and phylogeny as predictors of pollinator service: a plant community perspective

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Abstract. Pollinator service is essential for successful sexual reproduction and long-term population persistence of animal-pollinated plants, and innumerable studies have shown that insufficient service by pollinators results in impaired sexual reproduction ("pollen limitation"). Studies directly addressing the predictors of variation in pollinator service across species or habitats remain comparatively scarce, which limits our understanding of the primary causes of natural variation in pollen limitation. This paper evaluates the importance of pollination-related features, evolutionary history, and environment as predictors of pollinator service in a large sample of plant species from undisturbed montane habitats in southeastern Spain. Quantitative data on pollinator visitation were obtained for 191 insect-pollinated species belonging to 142 genera in 43 families, and the predictive values of simple floral traits (perianth type, class of pollinator visitation unit, and visitation unit dry mass), phylogeny, and habitat type were assessed. A total of 24,866 pollinator censuses accounting for 5,414,856 flower-minutes of observation were conducted on 510 different dates. Flowering patch and single flower visitation probabilities by all pollinators combined were significantly predicted by the combined effects of perianth type (open vs. restricted), class of visitation unit (single flower vs. flower packet), mass of visitation unit, phylogenetic relationships, and habitat type. Pollinator composition at insect order level varied extensively among plant species, largely reflecting the contrasting visitation responses of Coleoptera, Diptera, Hymenoptera, and Lepidoptera to variation in floral traits. Pollinator composition had a strong phylogenetic component, and the distribution of phylogenetic autocorrelation hotspots of visitation rates across the plant phylogeny differed widely among insect orders. Habitat type was a key predictor of pollinator composition, as major insect orders exhibited decoupled variation across habitat types in visitation rates. Comprehensive pollinator sampling of a regional plant community has shown that pollinator visitation and composition can be parsimoniously predicted by a combination of simple floral features, habitat type, and evolutionary history. Ambitious community-level studies can help to formulate novel hypotheses and questions, shed fresh light on long-standing controversies in pollination research (e.g., "pollination syndromes"), and identify methodological cautions that should be considered in pollination community studies dealing with small, phylogenetically biased plant species samples.

Key words: floral traits; Mediterranean mountain habitats; phylogenetic niche conservatism; phylogenetic signal; plant community; pollinator composition; pollinator functional abundance; pollinator service.

Introduction

Most angiosperm plants are pollinated by animals, and pollinator service is essential to achieve successful sexual reproduction and long-term population persistence (Knight et al. 2005, Harder and Aizen 2010, Ollerton et al. 2011). Considerable research effort has been devoted over the years to elucidate the multiple implications of variation in pollinator service among individuals, species, habitats, or pollination modes. Within this conceptual framework, one traditional line of inquiry has analyzed the *consequences* of variation in pollinator service. This indirect approach to the study of pollinator service includes countless studies showing that insufficient quantity or quality of pollen delivery ("pollen limitation") often entails a reduction in the number or reproductive value of seeds (Gross and Werner 1983, Burd 1994, Harder and Aizen 2010, Bennett et al. 2018); empirical investigations on patterns of variation in pollen limitation among plant taxa, regions, communities or life forms (Johnson and Bond 1997, Larson and Barrett 2000, Vamosi et al. 2006, Alonso et al. 2012, 2013, Bennett et al. 2018); and theoretical treatments formulating evolutionary models (Ashman et al. 2004, Aizen and Harder 2007, Burd 2016, Harder et al. 2016). Thanks to this vast amount of work, the ecological and

evolutionary *consequences* of variable pollinator service at different scales are now reasonably well understood. In contrast, studies directly addressing the *causal factors* explaining variation in pollinator service across species, habitats or regions remain comparatively scarce. This represents an important, albeit insufficiently recognized difficulty for achieving a better understanding of the constellation of factors affecting pollen limitation and reproductive success in animal-pollinated plants. As noted by Ashman et al. (2004: 2419) more than one decade ago, despite the wealth of data on pollen limitation "we [still] remain ill equipped to assess its causes" (see also Vamosi et al. 2013).

Pollinator service, which depends on a combination of pollinator visitation frequency and pollinator composition, is one of the most immediate causal factors contributing to variations in pollen limitation and reproductive success (Gómez et al. 2007, 2010). This is because the intensity of pollen deposition and removal often depends on the frequency of animal visits to flowers (Silander and Primack 1978, Rush et al. 1995, Engel and Irwin 2003; but see also, e.g., Hegland and Totland 2008), and different pollinator types vary in average pollinating efficacy or quality per visit (Herrera 1987, Sahli and Conner 2007, King et al. 2013). Following the lead of early pioneering work (Müller 1883, Knuth 1908, Robertson 1928), information on pollinator visitation frequency and composition has routinely formed part of nearly every published piece of pollination research, and vast amounts of qualitative and quantitative data have steadily accumulated in the literature over many decades. The rather puzzling scarcity of quantitative ecological studies aimed at recognizing predictors of natural variation in pollinator visitation and composition, and thus pollinator service, despite early claims pointing out its ecological significance (McCall and Primack 1992, Primack and Inouye 1993) and the availability of such an enormous literature database can be tentatively interpreted on four distinct grounds. First, with few exceptions (e.g., McCall and Primack 1992, Ollerton et al. 2009, Lázaro et al. 2013) the vast majority of investigations addressing pollinator visitation and/or composition of animal-pollinated plants at the plant community level have examined only small or modest numbers of plant species at a time (see, e.g., Ollerton 2017: Appendix 2 for review). Apart from the likely ecological or taxonomic biases to be expected in small species samples, the narrow range in flower traits, pollinator type, ecological conditions, or taxonomic/phylogenetic affiliation inherent to small samples reduces the statistical power for identifying predictors of pollinator visitation and composition. Second, among the scarce pollination studies dealing with a substantial number of species (>100) very few have applied quantitative methods transcending simple binary scoring of plant–pollinator species associations (Interaction Web Database; *available online*).[2] As

a consequence, attempts at elucidating broad-scale patterns of pollinator visitation and composition in large species samples have often relied on statistically suboptimal, binary plant–pollinator data (Herrera 1996, Waser et al. 1996, Olesen and Jordano 2002). Third, the enormous variety of observational methods and numerical measurements that have been applied so far in pollination studies poses insuperable difficulties for comparing data from different studies (Kearns and Inouye 1993), and also for turning results from different studies into aggregate datasets that could be used for broad quantitative analyses searching for predictors of pollinator visitation and composition. And fourth, irrespective of the methods used to record and numerically represent pollinator visitation and composition, pollination studies have infrequently estimated the uncertainty of whichever estimate of pollinator service was used (but see, e.g., Motten 1986, Inouye and Pyke 1988, McCall and Primack 1992, Gómez et al. 2007, Herrera 2019). This hinders the application of formal statistical tests for addressing explicit hypotheses on predictors of pollinator service, including possible meta-analyses.

This paper presents the results of an investigation designed to assess the importance of pollination-related plant features, evolutionary history, and environmental conditions as predictors of pollinator service in a large sample of plant species from undisturbed montane habitats in southeastern Spain. Quantitative data on pollinator visitation and composition were obtained for a substantial fraction of the regional plant community of insect-pollinated plants, and then related to several floral traits, phylogeny, and type of habitat to evaluate their predictive value. The strength and novelty of this study rest on the combination of an unusually large species sample; considerable pollinator sampling effort; field sampling methods yielding extensively replicated quantitative data on pollinator visitation and composition amenable to powerful statistical analyses; and the application of recent implementations of generalized linear mixed models for the study of pollinator functional abundance (Herrera 2019). The consistent use of mixed linear models where plant species, sampling sites and sampling years were all treated as random effects, will allow drawing of conclusions referred to a broad inference space and answering broad ecological questions whose scope transcends the limits of the specific samples studied (McLean et al. 1991, Bolker 2015, Herrera 2019).

Materials and Methods

Study area

Data on pollinator visitation analyzed in this paper were collected during February–December 1997–2018 (with a gap in 2000–2002) in a relatively small area of the Sierras de Cazorla-Segura-Las Villas Natural Park, Jaén Province, southeastern Spain. This region is

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[2] https://www.nceas.ucsb.edu/interactionweb/resources.html

characterized by extensive areas of well-preserved mountain habitats and outstanding biological diversity (Médail and Diadema 2009, Gómez Mercado 2011, Molina-Venegas et al. 2015). Sampling sites ($N = 42$; Appendix S1, distance between sites ≤21 km) were spread over all altitudinal belts of vegetation occurring in the region (elevation range 770–1,920 m above sea level). Study sites were a superset of the $N = 29$ locations studied by Herrera (2019). Major vegetation types from lower to higher elevations included *Quercus rotundifolia*-dominated, Mediterranean evergreen forest and tall scrubland; mixed *Pinus nigra* or *P. pinaster* forest with *Quercus* and *Acer*; and various types of mature *Pinus nigra* forests and woodlands differing in age, height, and tree density.

Plant species sample

Pollinator visitation to flowers was assessed for 191 plant species belonging to 142 genera in 43 families (Table 1). This sample is a superset of the 65 species in 28 families studied by Herrera (2019), and includes species from 73% of families, and ~85% of widely distributed or common species, of entomophilous plants in the Sierra de Cazorla region (Gómez Mercado 2011; C. M. Herrera, *unpublished data*). Mean pollinator sampling date for each species roughly matched its peak flowering date. The seasonal distribution of sampling times in the species sample (Table 1) closely matched the seasonal pattern of flowering times in the region, with most species flowering in June and July. Asteraceae (39 species), Lamiaceae (24 species), Brassicaceae (10), Fabaceae (10), Rosaceae (9), and Cistaceae (8) contributed about one-half of species to the sample. Hemicryptophytes (72 species), chamaephytes (41), geophytes (33), and therophytes (27) were the predominant life forms (Table 1).

Sampling scheme

The goal of this study was to collect quantitative data on pollinator visitation for as many different plant species as possible so that most regional phylogenetic, ecological, and floral diversity was eventually sampled. Considerable attention was paid to avoiding conscious or unconscious biases favoring species from particular habitat types, blooming at convenient times of year, yielding high data/sampling effort ratios, or having particular pollinator types (e.g., easily identifiable or large-sized ones). Obtaining robust quantitative pollinator data for a large, ecologically and phylogenetically unbiased species sample required spanning fieldwork over many years, since pre-established replication rules (see *Pollinator visitation*) limited the number of species that could be sampled per flowering season. About two-thirds of species in the sample ($N = 126$) were sampled for pollinators in only one year and the rest were sampled for two or more years as part of the research on long-term changes in pollinator abundance in relation to climate change reported by Herrera (2019). Pollinator sampling was conducted on a single site in the vast majority of the species considered here ($N = 181$), while 10 species that were part of other investigations were sampled on two or more sites (e.g., *Aquilegia cazorlensis*, *Aquilegia vulgaris*, *Helleborus foetidus*, *Lavandula latifolia*, *Narcissus longispathus*; Table 1). The distribution of pollinator sampling effort among plant species, years and sites is shown in Table 1. Species–year combinations were chosen randomly, subject only to constraints set by time availability, finding suitable populations, and sampling site accessibility, the choice being thus uninformed by, e.g., phenology or flowering intensity (see also Herrera 2019).

Pollinator visitation

Quantitative data on pollinator visitation were obtained by applying the same standardized sampling protocol for all plant species studied (Herrera 2019). The basic sampling unit was the "pollinator census," consisting of a 3-minute watch of a flowering patch whose total number of open flowers was also counted. All pollinators visiting some flower in the focal patch during the 3-minute period were identified (see *Pollinator identification*), and total number of flowers probed by each individual was recorded. Areal extent and number of open flowers in monitored patches were adjusted for each plant species according to flower size and density, so that all pollinator activity in the patches could be confidently monitored from a distance of 1.5–2.0 m. Mean number of flowers in censused patches for each species is shown in Appendix S2: Table S1. Some species had tiny flowers densely packed into compact inflorescences (e.g., Apiaceae, Asteraceae, Dipsacaceae; $N = 53$ species, Table 1), which rendered impractical assessing the number of elemental florets visited by pollinators. In these cases, the number of inflorescences available per patch and visited per census was counted rather than individual flowers, and visitation probabilities (see *Data analysis*) thus actually refer to inflorescences. For simplicity, I will refer to visitation to both single flowers and inflorescences as "flower visitation." In some analyses, however, the two types of visitation units will be considered as levels of the discrete variable "visitation unit," one of the predictors of pollinator visitation considered here ("single flowers" vs. "flower packets"; Appendix S2: Fig. S1; see *Data analysis*).

Census replication rules for each species–site–year combination were as in Herrera (2019). A minimum of 60 censuses spread over three non-consecutive dates should be conducted on ≥20 widely spaced flowering patches with roughly similar flower numbers. On each date, censuses should be distributed from 0.5 to 2.5 h past sunrise (depending on season; censuses started earlier in summer) through one hour past noon, the different patches being watched in random order. Flowers of

TABLE 1. Plant species (N = 191) sampled for pollinator visitation during 1997–2018 in the Sierra de Cazorla mountains, southeastern Spain.

Species (Family)†	Life form‡	Flowering time§	Habitat type¶	Sampling site‖	Years sampled	Sampling effort		
						No. sampling dates	No. pollinator censuses	Flowering units × min
Achillea odorata (Asteraceae)	Hem	175	For-Cl	NCO	2011, 2016	8	147	11,013
Acinos alpinus (Lamiaceae)	Cha	154	For-Cl	VAL	2009	2	94	24,987
Allium roseum (Alliaceae)	Geo	140	Gra	CVA	2011, 2016	4	205	35,592
Allium scorodoprasum (Alliaceae)	Geo	212	Gra	NCO	2014, 2016	7	215	27,336
Allium sphaerocephalon (Alliaceae)	Geo	196	For-Cl	NCO	2016	4	85	4,449
Alyssum simplex (Brassicaceae)	The	108	Gra	NCI	2018	3	85	39,804
Amelanchier ovalis (Rosaceae)	Pha	145	For-Cl	NCO	2017	4	75	41,229
Anarrhinum laxiflorum (Veronicaceae)	Hem	175	Scle	LTO	2004	1	50	13,860
Andryala ragusina (Asteraceae)	The	201	Dis	NCO	2010	3	70	7,230
Anthemis pedunculata (Asteraceae)	Hem	153	Gra	NES	2018	4	95	23,865
Anthericum liliago (Asphodelaceae)	Geo	171	Dms	PLL	2008	2	76	9,840
Anthyllis vulneraria (Fabaceae)	Hem	149	For-In	BJU	2008, 2015	4	140	148,290
Antirrhinum australe (Veronicaceae)	Cha	172	Cli	NCO	2016	4	80	15,369
Aphyllanthes monspeliensis (Aphyllanthaceae)	Hem	157	For-Cl	NCO	2009, 2017	6	200	28,518
Aquilegia cazorlensis (Ranunculaceae)	Geo	163	Cli	BCA, PCC, TGU	2005	10	353	53,262
Aquilegia vulgaris (Ranunculaceae)	Geo	151	Str	BCH, GUA, LCA	2005	8	298	20,484
Arbutus unedo (Ericaceae)	Pha	364	Scle	HMU	2016	2	110	89,100
Arenaria armerina (Caryophyllaceae)	Cha	195	Dol	NCO	2010	4	96	23,193
Arenaria modesta (Caryophyllaceae)	The	162	Dol	LTO	2018	4	110	23,334
Armeria filicaulis (Plumbaginaceae)	Cha	153	Dms	NCO	2010, 2016	7	161	21,795
Armeria villosa (Plumbaginaceae)	Cha	170	Gra	BJU	2007	2	75	5,166
Asphodelus cerasiferus (Asphodelaceae)	Geo	145	For-Cl	PPI	2004, 2015	2	136	17,316
Astragalus incanus (Fabaceae)	Hem	131	Gra	FBE	2013	4	78	37,170
Atropa baetica (Solanaceae)	Hem	182	For-Cl	TGU	2004	2	70	9,033
Bellis perennis (Asteraceae)	Hem	137	Gra	NES	2018	2	110	13,140
Bellis sylvestris (Asteraceae)	Hem	121	Gra	BJU	2016	3	100	18,450
Berberis hispanica (Berberidaceae)	Pha	159	For-Cl	NCT	2011, 2017	4	175	90,336
Biscutella laxa (Brassicaceae)	Cha	124	Dol	NCI	2016	2	120	11,457
Calamintha nepeta (Lamiaceae)	Hem	233	For-In	VAL	2010	3	80	11,859
Campanula dieckii (Campanulaceae)	The	176	Gra	NCO	2007, 2016	5	130	24,222
Campanula mollis (Campanulaceae)	Hem	205	Cli	NCO	2016	4	110	14,064
Carduncellus monspelliensium (Asteraceae)	Hem	180	Dms	RMA	2018	2	115	7,233
Carduus platypus (Asteraceae)	Hem	156	Dis	PPI	2006	2	65	1,656
Carduus tenuiflorus (Asteraceae)	The	168	Dis	LNA	2004	3	81	14,589
Carlina hispanica (Asteraceae)	Hem	228	Dis	VAL	2010, 2015	6	145	10,080
Carlina racemosa (Asteraceae)	The	238	Dis	CAN	2018	4	140	16,980

Table 1. Continued.

Species (Family)†	Life form‡	Flowering time§	Habitat type¶	Sampling site‖	Years sampled	Sampling effort		
						No. sampling dates	No. pollinator censuses	Flowering units × min
Catananche caerulea (Asteraceae)	Hem	172	For-In	NCI	2006, 2017	6	150	5,214
Centaurea calcitrapa (Asteraceae)	Hem	189	Dis	RHO	2005, 2015	4	126	9,249
Centaurea graminifolia (Asteraceae)	Hem	177	Gra	NCO	2018	3	105	4,590
Cerastium gibraltaricum (Caryophyllaceae)	Cha	163	Gra	NCO	2016	3	85	19,215
Chaenorhinum macropodum (Veronicaceae)	Hem	155	Dol	AGU	2007	4	85	12,378
Chiliadenus glutinosus (Asteraceae)	Hem	216	Dol	NCO	2014	4	83	5,805
Chondrilla juncea (Asteraceae)	Hem	229	Dis	NCO	2014, 2017	7	175	8,871
Cirsium acaule (Asteraceae)	Hem	225	Gra	NCO	2016	3	105	1,239
Cirsium monspessulanum (Asteraceae)	Hem	222	Str	CBE	2014	4	75	4,629
Cirsium pyrenaicum (Asteraceae)	Hem	224	Str	VAL	2010, 2015	6	140	8,982
Cirsium vulgare (Asteraceae)	Hem	227	Dis	VAL	2016	2	110	3,021
Cistus albidus (Cistaceae)	Pha	113	Scle	LFR	2017	3	100	3,423
Cistus monspeliensis (Cistaceae)	Pha	152	Scle	HMU	2007, 2016	4	154	7,569
Cistus salviifolius (Cistaceae)	Pha	114	Scle	LFR	2017	3	81	2,586
Cleonia lusitanica (Lamiaceae)	The	169	Scle	VAD	2003	2	60	9,705
Clinopodium vulgare (Lamiaceae)	Hem	191	For-In	NCO	2010	3	70	9,831
Convolvulus arvensis (Convolvulaceae)	Geo	193	Dis	NCO	2015	3	80	4,845
Coris monspeliensis (Primulaceae)	Cha	166	Dms	RMA	2011	3	80	25,542
Crataegus monogyna (Rosaceae)	Pha	175	For-Cl	LME	2013	3	90	46,800
Crepis albida (Asteraceae)	Hem	158	Dol	FBE	2010	3	67	1,806
Crocus nevadensis (Iridaceae)	Geo	39	Gra	CVA	2017	2	90	2,703
Daphne gnidium (Thymelaeaceae)	Pha	227	Scle	AME	2014	3	100	36,738
Daphne laureola (Thymelaeaceae)	Pha	93	For-In	GUA	2017	3	105	149,985
Digitalis obscura (Veronicaceae)	Cha	161	Scle	PPO	2004, 2014	4	140	18,201
Draba hispanica (Brassicaceae)	Cha	115	Cli	NCO	2018	2	102	13,137
Echinospartum boissieri (Fabaceae)	Cha	174	Dms	NCO	2011	4	95	27,747
Echium flavum (Boraginaceae)	Hem	146	Dis	BJU	2008, 2015	4	160	39,180
Erinacea anthyllis (Fabaceae)	Cha	145	Dms	CLA	2004, 2015	2	136	99,420
Erodium cazorlanum (Geraniaceae)	Hem	158	Dol	FBE	2010	3	75	3,156
Erodium cicutarium (Geraniaceae)	The	113	Dis	FBE	2015	3	71	8,889
Erophila verna (Brassicaceae)	The	94	Gra	CVA	2018	3	90	71,025
Eryngium campestre (Apiaceae)	Hem	223	Dis	NCO	2014, 2017	9	250	35,964
Eryngium dilatatum (Apiaceae)	Hem	198	For-Cl	NCO, RMA	2009, 2015	7	200	38,841
Erysimum cazorlense (Brassicaceae)	Hem	148	Dol	LCA	2013	4	125	11,577
Filipendula vulgaris (Rosaceae)	Hem	171	Gra	NCO	2010	3	72	6,027
Fumana baetica (Cistaceae)	Cha	169	Dol	NCO	2011, 2017	8	160	15,054

TABLE 1. Continued.

Species (Family)†	Life form‡	Flowering time§	Habitat type¶	Sampling site‖	Years sampled	No. sampling dates	No. pollinator censuses	Flowering units × min
Fumana paradoxa (Cistaceae)	Cha	182	Dol	PTE	2018	2	106	19,005
Fumana procumbens (Cistaceae)	Cha	175	Dol	RMA	2008	3	101	5,238
Galatella linosyris (Asteraceae)	Hem	262	For-Cl	NCO	2018	4	120	32,466
Galium verum (Rubiaceae)	Hem	194	Gra	NCO	2016	4	85	168,930
Geranium molle (Geraniaceae)	The	150	Dis	NES	2018	3	102	28,737
Geum sylvaticum (Rosaceae)	Hem	123	For-In	CVA	2018	3	122	7,413
Gladiolus illyricus (Iridaceae)	Geo	175	Gra	NCO	2004, 2014, 2015	7	190	15,216
Gymnadenia conopsea (Orchidaceae)	Geo	160	Str	NCI	2014	3	110	25,323
Helianthemum apenninum (Cistaceae)	Cha	150	Dms	VAL	2007, 2016	5	165	10,593
Helianthemum oelandicum (Cistaceae)	Cha	145	Dms	NCO	2010, 2017	6	167	20,445
Helleborus foetidus (Ranunculaceae)	Cha	63	For-In	LNA, RHO	1998, 1999, 2012, 2013	21	1,786	54,921
Hepatica nobilis (Ranunculaceae)	Hem	109	For-In	FRE	2018	2	90	14,535
Himantoglossum hircinum (Orchidaceae)	Geo	147	For-Cl	NCO	2017	4	66	11,847
Hormathophylla baetica (Brassicaceae)	Cha	112	Dol	FBE	2013	2	41	23,355
Hormathophylla spinosa (Brassicaceae)	Cha	176	Dms	LME	2013	3	90	60,960
Hyacinthoides reverchonii (Hyacinthaceae)	Geo	124	Cli	NCO	2018	4	105	10,392
Hypericum caprifolium (Clusiaceae)	Hem	198	Str	VAL	2015	3	76	14,649
Hypericum perforatum (Clusiaceae)	Hem	193	For-Cl	NCO	2010, 2016	9	140	27,825
Inula montana (Asteraceae)	Hem	170	Dms	NCO	2015, 2017	6	155	6,669
Iris foetidissima (Iridaceae)	Geo	170	Str	CVA	2013	3	90	4,230
Iris planifolia (Iridaceae)	Geo	68	Gra	CZA	2017	2	100	3,339
Jasonia tuberosa (Asteraceae)	Hem	218	Gra	NCO	2014	3	70	4,389
Jonopsidium prolongoi (Brassicaceae)	The	121	Gra	BJU	2016	3	97	41,631
Jurinea humilis (Asteraceae)	Hem	166	Dms	RMA	2011	3	92	2,373
Klasea nudicaulis (Asteraceae)	Hem	171	Gra	NCO	2016	3	75	5,622
Klasea pinnatifida (Asteraceae)	Hem	169	For-Cl	NCO	2015, 2017	5	165	9,480
Knautia subscaposa (Dipsacaceae)	Hem	167	Gra	BJU	2007, 2015	4	177	12,687
Lamium amplexicaule (Lamiaceae)	The	112	Dis	FBE	2010	2	76	22,698
Lavandula latifolia (Lamiaceae)	Cha	220	Scle	AAG, AUB, CCA, CBE, LNA, RTE	1997, 2014, 2015, 2016	19	818	424,803
Leontodon longirrostris (Asteraceae)	The	174	Gra	FBE	2010	3	65	3,663
Leucanthemopsis pallida (Asteraceae)	Hem	132	Dol	FBE	2013	4	70	7,773
Linaria aeruginea (Veronicaceae)	Hem	155	Dol	AGU	2007	4	71	2,397
Linaria verticillata (Veronicaceae)	Hem	163	Cli	NCO	2016	3	75	19,107
Linaria viscosa (Veronicaceae)	The	155	Dol	LTO	2016	3	105	97,596
Linum bienne (Linaceae)	The	177	Gra	NCO	2007, 2016	7	172	36,426

TABLE 1. Continued.

Species (Family)†	Life form‡	Flowering time§	Habitat type¶	Sampling site‖	Years sampled	Sampling effort		
						No. sampling dates	No. pollinator censuses	Flowering units × min
Linum narbonense (Linaceae)	Cha	158	For-Cl	GUA, NCO	2016	5	85	18,060
Linum tenue (Linaceae)	The	171	Gra	LNA	2014, 2017	6	190	10,941
Lithodora fruticosa (Boraginaceae)	Cha	154	Dms	NCO	2009, 2016	7	185	72,195
Lonicera arborea (Caprifoliaceae)	Pha	173	For-Cl	CPA	2007	2	65	8,154
Lysimachia ephemerum (Primulaceae)	Geo	183	Str	CVA	2009, 2017	5	200	39,603
Lythrum salicaria (Lythraceae)	Geo	238	Str	CAN	2018	3	110	17,274
Mantisalca salmantica (Asteraceae)	Hem	199	For-Cl	NCO	2010, 2016	6	160	8,535
Marrubium supinum (Lamiaceae)	Cha	164	Gra	NES	2004, 2014	7	160	72,465
Mentha aquatica (Lamiaceae)	Hem	228	Str	CAN	2018	3	110	9,942
Merendera montana (Colchicaceae)	Geo	248	Gra	NCO	2014	4	120	6,876
Narcissus bujei (Amaryllidaceae)	Geo	65	Scle	CZA	2008, 2017	4	205	11,889
Narcissus cuatrecasasii (Amaryllidaceae)	Geo	113	For-In	FBE	2010, 2011	5	214	34,080
Narcissus hedraeanthus (Amaryllidaceae)	Geo	86	Gra	FBE, NCI	2013, 2017	5	205	20,703
Narcissus longispathus (Amaryllidaceae)	Geo	90	Str	GUA, LCA	2006, 2015	8	295	32,859
Narcissus triandrus (Amaryllidaceae)	Geo	113	For-In	CBA	2018	3	125	13,338
Nepeta tuberosa (Lamiaceae)	Hem	172	Str	NCI	2006	2	60	25,815
Ononis pusilla (Fabaceae)	Cha	158	Dol	FBE	2010	3	79	18,483
Ononis spinosa (Fabaceae)	Cha	204	Gra	CLA	2016	3	100	12,780
Orchis coriophora (Orchidaceae)	Geo	175	Gra	NCO	2004, 2015	2	120	29,514
Origanum virens (Lamiaceae)	Hem	198	For-Cl	VAL	2015	3	77	25,209
Ornithogalum umbellatum (Hyacinthaceae)	Geo	142	For-Cl	BJU	2010, 2016	6	160	24,837
Orobanche haenseleri (Orobanchaceae)	Geo	180	For-In	LNA	2013	3	96	11,154
Papaver dubium (Papaveraceae)	The	177	Dis	NCO	2018	3	85	3,363
Parnassia palustris (Saxifragaceae)	Hem	263	Str	FRE	2018	2	70	5,583
Petrorhagia nanteuilii (Caryophyllaceae)	The	178	For-Cl	NCO	2011	4	70	9,744
Phlomis herba-venti (Lamiaceae)	Hem	183	Gra	PMA	2005, 2014	4	150	74,397
Phlomis lychnitis (Lamiaceae)	Cha	178	Scle	CLE	2004, 2014	2	151	18,546
Pilosella pseudopilosella (Asteraceae)	Hem	176	Gra	NCO	2016	4	66	3,840
Pistorinia hispanica (Crassulaceae)	The	170	Dol	LTO	2004, 2014	5	161	133,569
Plumbago europaea (Plumbaginaceae)	Cha	226	Dis	NCO	2014, 2017	8	205	64,245
Polygonatum odoratum (Ruscaceae)	Geo	142	For-In	GUA	2013	4	138	16,353
Potentilla caulescens (Rosaceae)	Hem	225	Cli	PPI	2018	3	125	25,518
Primula acaulis (Primulaceae)	Hem	111	For-In	FBE, LCA	2010, 2011	5	153	26,256
Prolongoa hispanica (Asteraceae)	The	165	Dol	LTO	2018	3	88	4,032
Ptilostemon hispanicus (Asteraceae)	Cha	224	Dis	VAL	2010	3	65	1,977
Ranunculus bulbosus (Ranunculaceae)	Geo	155	Gra	NES	2018	3	100	14,289

TABLE 1. Continued.

Species (Family)†	Life form‡	Flowering time§	Habitat type¶	Sampling site‖	Years sampled	Sampling effort		
						No. sampling dates	No. pollinator censuses	Flowering units × min
Ranunculus ficaria (Ranunculaceae)	Geo	127	For-In	NCO	2018	3	108	6,282
Ranunculus malessanus (Ranunculaceae)	Geo	120	Gra	NCI	2015	3	95	11,760
Rhagadiolus edulis (Asteraceae)	The	165	For-In	LNA	2018	3	95	14,361
Roemeria argemone (Papaveraceae)	The	145	Gra	BJU	2016	4	90	4,338
Rosa canina (Rosaceae)	Pha	160	For-Cl	PMA	2014	3	75	6,948
Rosa micrantha (Rosaceae)	Pha	181	For-Cl	NCO	2010, 2017	7	145	10,422
Rosa sicula (Rosaceae)	Pha	175	For-Cl	NCO	2014	3	80	4,749
Rosmarinus officinalis (Lamiaceae)	Pha	140	Scle	GUA	2004, 2017	4	166	88,515
Rubus ulmifolius (Rosaceae)	Pha	191	For-Cl	RHO	2012	2	95	5,061
Salvia lavandulifolia (Lamiaceae)	Cha	185	Scle	AGU	2009	2	72	6,912
Salvia verbenaca (Lamiaceae)	Hem	133	Dis	BJU	2015	3	90	5,727
Santolina rosmarinifolia (Asteraceae)	Cha	192	Dms	NCO	2010, 2015	8	130	29,889
Saponaria ocymoides (Caryophyllaceae)	Hem	153	For-In	VAL	2004, 2017	2	141	70,680
Satureja intricata (Lamiaceae)	Cha	193	Dms	NCO	2010, 2015	6	147	68,655
Saxifraga haenseleri (Saxifragaceae)	Hem	132	Dol	FBE	2013	4	77	34,758
Scabiosa andryaefolia (Dipsacaceae)	Hem	182	For-Cl	BCA	2005	2	62	2,175
Scilla paui (Hyacinthaceae)	Geo	121	Gra	NCI	2015	3	90	16,113
Scorzonera albicans (Asteraceae)	Hem	160	Dol	NCO	2016	5	70	4,323
Sedum album (Crassulaceae)	Cha	185	Dms	NCO	2010, 2017	5	165	7,305
Sedum mucizonia (Crassulaceae)	The	172	Dol	LTO	2013	3	100	71,640
Senecio doria (Asteraceae)	Hem	222	Str	CBE	2014	4	74	6,042
Seseli montanum (Apiaceae)	Geo	266	For-Cl	NCO	2018	4	120	20,079
Sideritis incana (Lamiaceae)	Cha	178	Dol	RMA	2008, 2014	6	130	54,819
Silene colorata (Caryophyllaceae)	The	155	Dis	LTO	2016	4	92	16,218
Silene psammitis (Caryophyllaceae)	The	149	Dol	GUA	2004, 2016	4	132	21,645
Sisymbrella aspera (Brassicaceae)	Hel	171	Str	NCO	2010, 2016	8	180	39,942
Sisymbrium crassifolium (Brassicaceae)	Hem	146	For-Cl	LCA	2013	3	70	14,814
Solidago virgaurea (Asteraceae)	Hem	235	For-In	CBE	2018	3	100	14,112
Sonchus aquatilis (Asteraceae)	Hem	232	Str	CBE	2018	3	91	4,866
Stachys officinalis (Lamiaceae)	Hem	190	Gra	NCO	2010, 2015	8	138	49,356
Taraxacum laevigatum (Asteraceae)	Hem	145	Gra	NES	2018	3	120	6,459
Teucrium aureum (Lamiaceae)	Cha	180	Dms	NCO	2006, 2014	4	142	106,956
Teucrium rotundifolium (Lamiaceae)	Cha	176	Cli	NCO	2007, 2016	6	181	49,818
Teucrium webbianum (Lamiaceae)	Cha	192	Dms	RMA	2009	4	81	8,535
Thymus mastichina (Lamiaceae)	Cha	169	Scle	LNA	2004, 2014	5	160	80,343
Thymus orospedanus (Lamiaceae)	Cha	153	Dms	VAL	2004, 2016	4	163	172,485

TABLE 1. Continued.

Species (Family)†	Life form‡	Flowering time§	Habitat type¶	Sampling site‖	Years sampled	Sampling effort		
						No. sampling dates	No. pollinator censuses	Flowering units × min
Thymus serpylloides (Lamiaceae)	Cha	168	Dms	NCT	2011	3	75	36,750
Trifolium campestre (Fabaceae)	The	179	Gra	NCO	2011	3	82	40,479
Ulex parviflorus (Fabaceae)	Pha	88	Scle	CVA	2018	3	125	72,840
Urginea maritima (Hyacinthaceae)	Geo	236	Scle	VAD	2014, 2017	10	220	14,838
Valeriana tuberosa (Valerianaceae)	Hem	136	Gra	BJU	2010, 2015	6	165	8,412
Verbascum giganteum (Scrophulariaceae)	Hem	218	Dis	CME	2018	3	115	19,905
Verbascum sinuatum (Scrophulariaceae)	Hem	217	Dis	LTO	2018	3	115	21,207
Viburnum tinus (Adoxaceae)	Pha	111	Scle	HMU	2017	3	90	39,126
Vicia onobrychioides (Fabaceae)	Hem	162	For-Cl	NCO	2016	4	65	18,966
Vicia pseudocracca (Fabaceae)	The	154	For-Cl	GUA	2006	2	73	34,260
Viola cazorlensis (Violaceae)	Cha	151	Cli	BCA, AGU, PTE	2005, 2007, 2015	6	123	26,625
Viola odorata (Violaceae)	Hem	112	For-In	FBE	2010, 2011	5	198	22,950

† With only minor exceptions, nomenclature follows the standard flora for the region (Blanca et al. 2011).
‡ Raunkiaer life forms: Cha, chamaephyte; Geo, geophyte; Hel, helophyte; Hem, hemicryptophyte; Pha, phanerophyte; The, therophyte.
§ Mean date of pollinator censuses, expressed as days from 1 January.
¶ Habitat types: Cli, Cliffs; Dis, Disturbances; Dol, sandy or rocky dolomitic outcrops; Dms, dwarf mountain scrub dominated by cushion plants; For-Cl, forest clearings and edges; For-In, forest interior; Gra, grasslands and meadows; Scle, Tall Mediterranean sclerophyllous forest and scrub; Str, Banks of permanent streams or flooded areas surrounding springs.
‖ Codes for the *N* = 42 sampling sites as in Appendix S1: Table S1, where location details are also shown. See Appendix S1: Fig S1 for a map.

about one-third of species studied are not available to pollinators in the afternoon, as their corollas wither, close, or fall shortly after noon, and earlier studies in the area have also shown that insect pollinator activity declines considerably in the afternoon (Herrera 1990, 1995*a*; C. M. Herrera, *personal observations*). For four species (*Daphne gnidium*, *D. laureola*, *Origanum virens*, *Silene colorata*) there was some circumstantial evidence suggesting the existence of additional crepuscular or nocturnal pollinators (e.g., crab spiders with captured moths). Several factors precluded fulfilling all the preceding rules for some species in some sites or years, including long spells of poor weather, logistic problems and destruction of flowering patches by herbivorous mammals. Number of distinct sampling dates, number of censuses, and flower-minutes of observational effort for every species are summarized in Table 1. This study is based on pollinator visitation data obtained in a total of 24,866 pollinator censuses carried out on 510 different dates and accounting for a total watching effort of 5,414,856 flower-minutes. With the only exceptions noted in *Acknowledgments* (*Helleborus foetidus*, *Aquilegia vulgaris*), I conducted all censuses throughout this study personally, thus results are unaffected by inter-observer heterogeneity.

Pollinator identification

Pollinators recorded during censuses were identified using the methods described by Herrera (2019). Insect taxonomists that contributed identifications for this study are listed in *Acknowledgments*. Out of a total of 30,463 individual pollinators recorded in censuses, 79.1% were identified to species, 4.1% were assigned to cryptic species pairs of congeneric species, and 15.6% were identified to genus. Orders will be the only taxonomic level considered in this paper. Close-up photographs of pollinators visiting flowers were taken routinely during censuses using a DSLR digital camera and 105 mm macro lens. These photographs were used for insect identification, keeping photographic vouchers of pollinators, and ascertaining the pollinating status of different insect taxa. Only taxa whose individuals contacted anthers or stigmas, or had visible pollen grains on body surfaces, are considered as pollinators in this study.

Data analysis

Pollinator visitation.—Two probabilistic measurements will be used here as complementary descriptors of pollinator service, namely "patch visitation probability" and "flower visitation probability," which depict the probability of a flowering patch or a single flower being visited by some pollinator during a 3-minute census. These two measurements estimate pollinator service from the viewpoint of the local flowering plant population and single flowers, respectively. Each pollinator census provided point estimates of patch visitation (probability of at least one flower in a patch being probed during a 3-minute period) and flower visitation (probability of an individual flower being probed during a 3-minute period) probabilities, and replication of censuses allowed calculation of parameter estimates in models and associated uncertainty measurements. See Herrera (2019) for additional details and discussion on the motivation and advantages of framing pollinator functional abundance in these probabilistic terms.

The broad-scale pattern of interspecific variation in proportional pollinator composition in the sample of species studied was explored by performing nonmetric multidimensional scaling (NMDS) on the matrix of pairwise interspecific dissimilarity (Bray-Curtis distance) in proportional importance of the four major insect orders. NMDS provided an objective assessment of major trends in pollinator composition occurring in the sample. Computations were performed with the function metaMDS in the package vegan (Oksanen et al. 2019) for the R computing environment (R Core Team 2018; all statistical analyses in this paper were carried out using R). To assess the relative importance of interspecific variation in the species sample in relation to variation between sites and years, total sample variance in patch and flower visitation probabilities was dissected into components due to variance among plant species, sampling sites, and sampling years. Generalized linear mixed models were fitted to pollinator census data, where plant species, sampling site and sampling year were included as random effects, an intercept as the only fixed effect, and patch and flower visitation probabilities were the response variables, modeled as binomial processes. For each response variable, independent analyses were conducted for all pollinator taxa combined and for each major insect order separately.

Floral and ecological predictors.—Three species-specific floral features were examined as potential predictors of pollinator visitation: class of floral perianth, type of pollinator visitation unit (single flower vs. flower packet; Appendix S2: Fig. S1), and mean dry mass of visitation unit ($\log_{10}$-transformed for the analyses). All plant species were characterized for each of these three variables (Appendix S2: Table S1). Two discrete perianth classes were recognized, corresponding respectively to open, more or less bowl-shaped, non-restrictive perianths ("open perianth" hereafter, $N = 123$ species), and closed, tubular, sympetalous or otherwise restrictive perianths ("restrictive perianth" hereafter, $N = 68$ species). Mean dry mass of the visitation unit was obtained for each species by weighing samples of flowers or flower packets collected at census localities. Samples were dried in an oven until constant mass prior to weighing. Dry mass of the visitation unit was used here as a convenient surrogate for overall size, which could influence pollinator visitation through effects on pollen or nectar production. The broad heterogeneity in morphology and structure of visitation units occurring in the sample precluded

dissection of flowering unit mass into components with different functionalities in relation to pollinators that were comparable across species. This should be inconsequential in the context of overall analyses because of the expected positive relationship between overall flower size and pollinator reward or attraction (e.g., Plowright 1981, Herrera 1985, Stanton and Preston 1988).

To assess possible environmental influences on pollinator service, each plant species was assigned to one of the following nine habitat types (total species per habitat in parentheses): vertical rock cliffs (nine species); local disturbances caused by humans, large mammals, or natural abiotic processes (21); sandy or rocky dolomitic outcrops (23); dwarf mountain scrub dominated by cushion plants (21); forest edges and large clearings (30); forest interior (18); patches of grasslands and meadows on deep soils in relatively flat terrain (35); tall, dense Mediterranean sclerophyllous forest and scrub (17); banks of permanent streams or flooded/damp areas around springs (17). Individual species' assignments to habitat types are shown in Table 1. In the case of species that occurred in more than one of these habitat types (~15% of total), the assignment considered only the habitat where pollinator censuses were conducted, for it was impractical to sample these species in all habitats where they occurred. This should be inconsequential to results, since plant species and sampling sites were treated as random effects in the analyses (see next paragraph) and conclusions on variation among habitats referred to a broad inference space beyond the limits of the specific samples studied.

Two sets of generalized linear mixed models were fitted to the data to test the effects on patch and flower visitation probability of species-specific floral traits (perianth type, visitation unit type, visitation unit mass) and habitat type, respectively, which were in each case included as fixed effects. In each set of analyses, independent models were fitted using as response variables the visitation probability by all pollinators combined and by each major insect order considered separately. Binomial error distribution and logit link function were used in all models, and plant species, sampling site, and sampling year were included as random effects. For a large subset of species considered here, Herrera (2019) found that in the vast majority of species the number of flowers per patch was directly related to patch visitation probability, and inversely related to flower visitation probability. Furthermore, in the study area patch and flower visitation probabilities increased from winter through spring to summer (C. M. Herrera, *unpublished data*). To account statistically for these effects, the number of flowers in each censused patch (scaled and centered) and the date of the census (expressed as days from 1 January, scaled and centered) were included in all models as fixed-effect covariates.

All generalized linear mixed models in this paper were fitted with the glmer function in the lme4 package (Bates et al. 2015). They were checked for overdispersion using function dispersion_glmer from the blmeco library (Korner-Nievergelt et al. 2015). Weak overdispersion of some models was fixed by adding observation-level random effects to the data (Bolker 2015). Statistical significance of fixed effects was determined by analysis of deviance-based, Type II Wald chi-square tests using the ANOVA function from the car package (Fox and Weisberg 2011). Confidence intervals of fixed effect parameter estimates were obtained using the profile likelihood method implemented in the confint.merMod function of the lme4 package. The function ggpredict from the ggeffects package (Lüdecke 2018) was used to compute marginal effects of single predictors on measurements of pollinator visitation holding constant the rest of fixed effects in the model.

Phylogenetic effects.—The relationship between pollinator visitation and plant phylogeny was examined by constructing a phylogenetic tree for the set of species studied and testing for the presence of a phylogenetic signal in the species means for patch and flower visitation probability, for all pollinators combined and separately for each major insect order. The phylogenetic tree was obtained using the phylomatic function in the brranching package and the default storedtree = "R20120829" (Chamberlain 2018). Tree branch lengths were set to unity and polytomies resolved randomly using utility functions compute.brlen and multi2di in the ape package, respectively (Paradis and Schliep 2018). Phylogenetic signal in pollinator visitation, defined as "a tendency for related species to resemble each other more than they resemble species drawn at random from the tree" (Blomberg and Garland 2002) was assessed with Pagel's λ. This statistic, which assumes a Brownian motion model of quantitative trait evolution, seems strongly robust to incompletely resolved phylogenies or suboptimal branch-length information, and can be used to assess the strength, or "effect size," of phylogenetic structuring (Münkemüller et al. 2012, Molina-Venegas and Rodríguez 2017). To identify relevant "local hotspots" of phylogenetic autocorrelation contributing disproportionately to overall phylogenetic signal in pollinator visitation, local Moran's I (I_i) was computed for each tip of the phylogenetic tree. This local indicator of phylogenetic association (LIPA; Keck et al. 2016) allows for the decomposition of global phylogenetic signal into the contributions due to individual observations, and the LIPA for each tip in the phylogeny gives an indication of the extent of significant phylogenetic clustering of similar values around that tip (Anselin 1995). Computations were performed using the package phylosignal (Keck et al. 2016), and statistical significance of Pagel's λ and I_i was tested by randomization.

A regression approach (Grafen 1989) based on phylogenetic generalized least squares (PGLS; Paradis 2012, Symonds and Blomberg 2014) was adopted to evaluate the importance of habitat type as predictor of patch and flower visitation probabilities after statistically

accounting for the phylogenetic correlations underlying pollinator visitation data. Generalized linear mixed models were fitted to species mean values using restricted maximum likelihood estimation, with either mean patch or mean flower visitation probabilities as response variables. For each response variable, separate analyses were performed for all pollinators combined and for each major insect order separately. Phylogenetic correlations were incorporated into the models by setting the variance–covariance structure between species to match that expected under a Brownian motion process of evolution on the phylogenetic tree (Paradis 2012, Symonds and Blomberg 2014). Computations were performed with function gls in the nlme package (Pinheiro et al. 2018). The covariance structure between species was obtained from the phylogenetic tree using the corBrownian function of the ape package (Paradis 2012, Paradis and Schliep 2018).

RESULTS

The pollinators

Regional assemblage.—Hymenoptera (47.5% of individuals), Diptera (19.9%), Coleoptera (16.8%), and Lepidoptera (15.2%) accounted for nearly all pollinators recorded (N = 30,463 individuals) in the N = 191 plant species studied. Three additional insect orders, Hemiptera, Neuroptera, and Orthoptera, contributed altogether 0.5% of all individuals and will not be considered hereafter. Coleoptera, Diptera, Hymenoptera, and Lepidoptera were recorded in 62.3%, 88.5%, 97.9%, and 62.3% of plant species studied, respectively.

Pollinators identified at least to genus (N = 30,121) belonged to 314 insect genera. Diptera (106 genera) exhibited the highest generic diversity, followed in decreasing order by Hymenoptera (86), Lepidoptera (62), and Coleoptera (53). Bees (families Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae) accounted for nearly all the Hymenoptera recorded (95.5% of individuals). Truncated genus abundance curves for the 20 most abundant genera in each order are shown in Appendix S3: Fig. S1. Dominance was similarly high in all orders, with a few genera accounting for most individuals in every case: *Anthrenus*, *Lobonyx*, and *Dasytes* were the three most abundant genera of Coleoptera (36.9% of total); *Sphaerophoria*, *Bombylius*, and *Eristalis* of Diptera (32.9%); *Argynnis*, *Thymelicus*, and *Melanargia* of Lepidoptera (41.0%); and *Bombus*, *Andrena*, and *Lasioglossum* of Hymenoptera (33.5%).

Individual plant species' assemblages.—Nearly all species studied had taxonomically diverse pollinator assemblages at the insect order level (Appendix S3: Table S1). Only 14 species (7.3% of total) had pollinators belonging to single insect orders (e.g., Diptera: *Saponaria ocymoides*; Hymenoptera: *Digitalis obscura*, *Iris foetidissima*, *Ononis spinosa*; Lepidoptera: *Gymnadenia conopsea*), while as many

as 152 species (79.6% of total) had pollinators from three or four different insect orders (Appendix S3: Table S1). With few exceptions, the proportional contributions of Coleoptera and Lepidoptera were consistently low in most plant species, while the relative importance of Diptera and, particularly, Hymenoptera varied extensively (Appendix S3: Fig. S2). Ordination analysis of the matrix of interspecific dissimilarity in proportional importance of the four major insect orders revealed an essentially continuous, bivariate distribution of species over the reduced two-dimensional space obtained (Fig. 1). The cloud of points was roughly centered on the bivariate origin (0, 0), which corresponded to comparable contributions of the four insect orders, and there was no evidence of clusters or gaps indicative of the presence in the sample of distinct groups of species with contrasting, differentiated pollinator types (Fig. 1). Some species falling around or beyond the periphery of the rather compact 191-species cluster did have pollinator assemblages strongly dominated by single insect orders. These included, for instance, *Gymnadenia conopsea*, *Carduus platypus* (Lepidoptera), *Saponaria ocymoides*, *Arenaria modesta* (Diptera), *Cistus monspeliensis*, *Daphne laureola* (Coleoptera), *Digitalis obscura*, and *Helleborus foetidus* (Hymenoptera; Fig. 1; see Appendix S3: Table S1 for details).

Sample variance components of pollinator visitation

For all pollinator taxa combined, variation among plant species in pollinator visitation probabilities was by far the chief source of sample variance in the whole data set, and results were comparable for patch and flower visitation probabilities (Table 2). Closely similar results were obtained when variance components due to species, sites, and years were computed only for subsets of species that were sampled on more than one year (N = 65 species, Appendix S4: Table S1) or more than one site (N = 10 species, Appendix S4: Table S2). For the whole species sample, similar patterns held when separate analyses were conducted for each major insect order, although there existed some differences among orders in the variance structure of patch and flower visitation probabilities. Sample variance due to interspecific variation was highest for visitation by Coleoptera and Lepidoptera, and lowest for Diptera and Hymenoptera (Fig. 2), thus denoting greater interspecific heterogeneity in patch and flower visitation probabilities by the former two pollinator groups.

The important interspecific variation in pollinator visitation occurring in the sample was also apparent in the broad range of species means for patch and flower visitation probabilities (Fig. 3), which spanned nearly three orders of magnitude. Mean patch visitation probability per 3-minute period ranged between 0.0049 (*Viola cazorlensis*) and 0.9857 (*Jasonia tuberosa*), or a 200-fold variation. Mean flower visitation probability ranged between 0.0033 (*Linaria verticillata*) and 0.644 (*Scabiosa andryaefolia*), or a 195-fold variation. Reciprocals of these
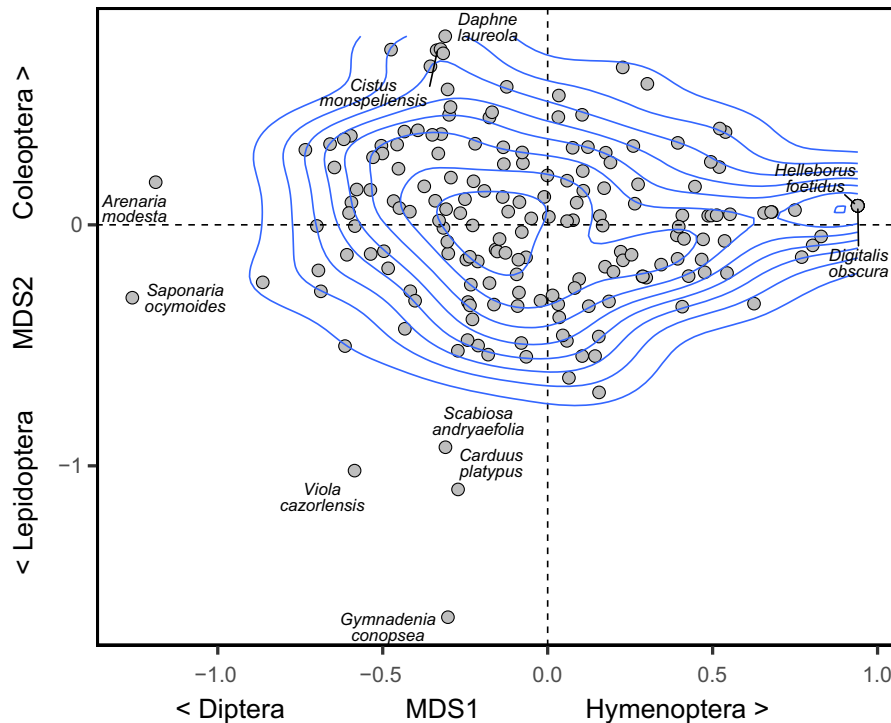
Fig. 1.   Distribution of the $N = 191$ plant species studied over the plane defined by the two axes (MDS1, MDS2) obtained by applying nonmetric multidimensional scaling to the matrix of pairwise interspecific dissimilarities in proportional pollinator composition (percent individuals contributed by each major insect order; data shown in Appendix S3: Table S1). Annotations along the two ordination axes are intended to provide rough indications of the main trends of variation underlying the two axes. Blue contour lines show the results of a two-dimensional kernel density estimation, depicted to emphasize the essentially continuous, bivariate distribution of species over the MDS1–MDS2 plane. A selection of "outlier" plant species characterized by exclusive or nearly exclusive dominance of Coleoptera (top), Diptera (left), Lepidoptera (bottom) or Hymenoptera (right) in their pollinator assemblages are individually identified in the graph.

figures indicate that the estimated time between consecutive insect visits to individual flowers, or "waiting time" between consecutive visits, ranged between 4.7 minutes (*S. andryaefolia*) and 15.2 h (*L. verticillata*). The shapes of frequency distributions of species means differed markedly for patch and flower visitation probabilities. While species means for patch visitation probability were roughly symmetrically distributed around the median, the distribution of species means for flower visitation probability was strongly skewed to the right, with most species falling around the lowermost extreme of the flower visitation probability range (Fig. 3).

Pollinators and floral features

All pollinators combined.—Generalized linear mixed models fitted to pollinator census data that included pollinator census date (days from 1 January) and number of flowers per patch as fixed-effect covariates, revealed that patch and flower visitation probabilities by all pollinators combined were significantly related to perianth type (open vs. restrictive), visitation unit type (single flower vs. flower packet), and mass of visitation unit ($\log_{10}$-transformed; Appendix S5: Table S1). In general, patch

and flower visitation probabilities tended to be higher for flowers with open perianths or arranged in flower packets, and visitation probabilities increased with increasing mass of visitation unit (Fig. 4). Nevertheless, simple interpretations of the effects of floral traits on pollinator visitation were precluded by the statistically significance of two- and three-way interactions between predictors (Appendix S5: Table S1).

Interactions of floral traits on predicted marginal effects on patch and flower visitation probabilities, all pollinators combined, are illustrated in Fig. 4. Single flowers with open perianths had predictably higher visitation probabilities than single flowers with restrictive perianths over most of the range of visitation unit mass. This relationship did not hold when visitation units consisted of flower packets, for which visitation probabilities were higher for flowers with restrictive perianths for much of the range of visitation unit mass. In flowers with open perianths, but not in those with restrictive perianths, patch and flower visitation probabilities increased steadily with increasing mass of visitation unit. In flowers with restrictive perianths, predicted patch and flower visitation probabilities declined with increasing mass of visitation unit when visitation units were single flowers,

TABLE 2. Variance components of patch and flower visitation probability (all pollinators combined) accounted for by plant species, sampling site, and sampling year in the data set studied.

Random effect	Variance (95% confidence interval)	
	Patch visitation probability	Flower visitation probability
Plant species (N = 191)	1.429 (1.143–1.805)	1.610 (1.304–2.015)
Sampling site (N = 42)	0.147 (0.059–0.363)	0.491 (0.270–0.939)
Sampling year (N = 19)	0.068 (0.026–0.178)	0.235 (0.122–0.519)

Notes: Variance components were obtained by fitting generalized linear mixed models to the pollinator census data (N = 24,866 pollinator censuses), with species, site, and year as random effects and the intercept as the only fixed effect. Response variables were modeled as binomial processes. Patch visitation probability is the probability of at least one flower in a patch being probed during a 3-minute period. Flower visitation probability is the probability of visitation of an individual flower during a 3-minute period.

but the trend was reversed when visitation units consisted of flower packets.

Major insect orders.—Patch and flower visitation probabilities by each major insect order were significantly related to perianth type, visitation unit type, and mass of visitation unit, and in every case, there were also statistically significant interactions among floral traits (Appendix S5: Table S1). Major insect groups differed

widely in detailed aspects of the relationships between visitation probabilities and combinations of floral features, as shown by the interaction graphs shown in Fig. 4. Among plants with single flowers and open perianths, visitation by Coleoptera and Hymenoptera, but not by Diptera and Lepidoptera, increased steeply with increasing visitation unit mass. In species with single flowers and restrictive perianths, in contrast, there was a steep decline in visitation by Diptera and Lepidoptera, but not by Coleoptera and Hymenoptera, with increasing visitation unit mass. In plants with flower packets as visitation units, patch and flower visitation probabilities by Hymenoptera and, particularly, Lepidoptera, increased with increasing visitation unit mass, while visitation by other groups remained stable (Diptera) or declined slightly (Coleoptera), and patterns were closely similar for species with open and restrictive perianths. Taken together, these results denote sharply contrasting, complex responses of the four major insect groups to interspecific variation in individual floral features and, particularly, the different trait combinations represented in the large set of plant species studied.

Pollinators and phylogenetic relationships

The phylogenetic tree depicting evolutionary relationships among the plant species studied is shown in Appendix S6: Fig. S1. The hypothesis that mean values of patch and flower pollinator visitation probabilities for individual plant species were independent from their
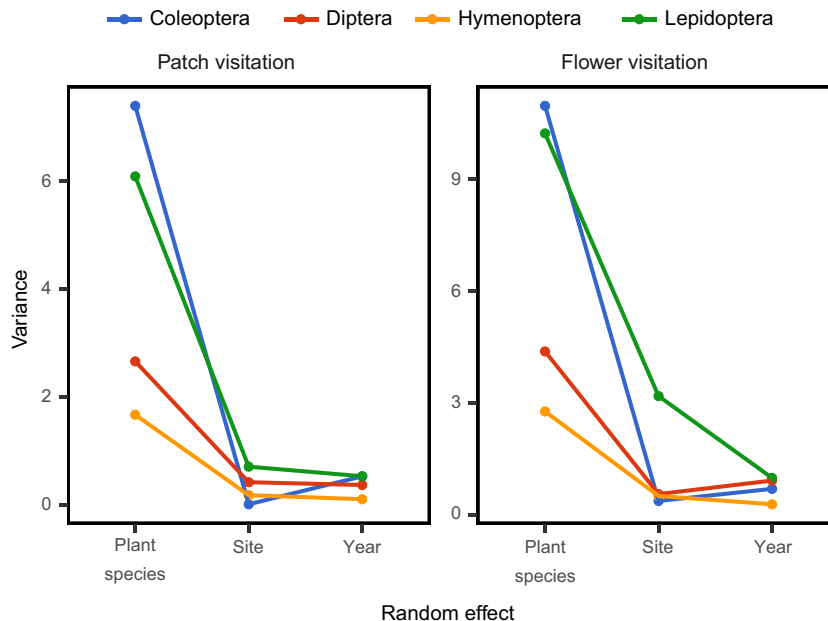

FIG. 2. Variance components of patch and flower visitation probability accounted for by plant species, sampling site, and sampling year in the data set studied, estimated separately for each major insect order. Patch visitation probability is the probability that some flower in a focal flowering patch is probed in 3 minutes and flower visitation probability is the probability that one individual flower is probed in 3 minutes. See Table 2 for the results for all pollinators combined.
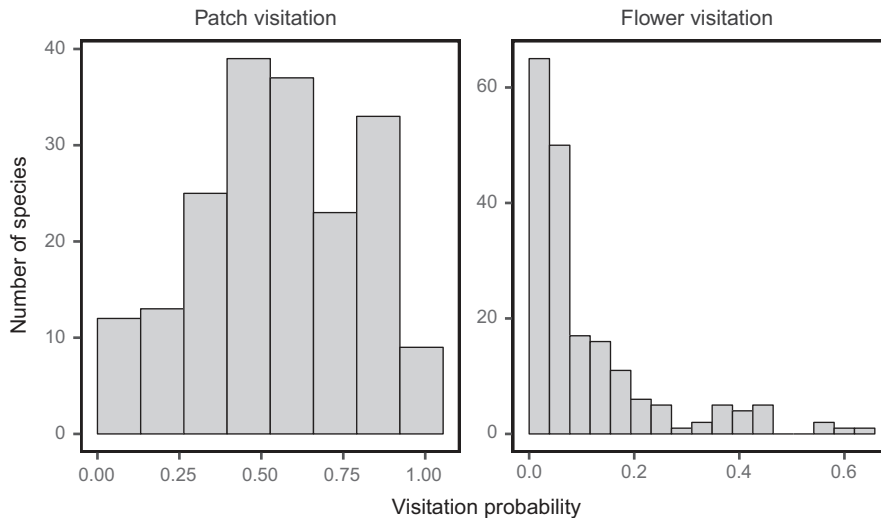
Fig. 3.   Frequency distributions of plant species means for patch (probability that some flower in a focal flowering patch is probed in 3 minutes) and flower (probability that one individual flower is probed in 3 minutes) pollinator visitation probabilities, all pollinators combined (N = 191 species).

location in the phylogenetic tree was rejected. Tests for the presence of a phylogenetic signal for patch and flower visitation probability yielded statistically significant results, irrespective of whether tests referred to all pollinators combined or to individual insect orders considered separately (Table 3). The magnitude of phylogenetic structuring of patch and flower visitation probability, as assessed with Pagel's λ, varied among insect orders, being strongest for Coleoptera and weakest for Diptera and Lepidoptera (Table 3).

For all pollinators combined, global phylogenetic signal in the whole species sample mostly reflected a trend of increasing patch and flower visitation probabilities running from basal clades through more derived ones (Fig. 5). Nevertheless, the phylogenetic signal was not homogeneously distributed across the phylogenetic tree. There were statistically significant phylogenetic correlation hotspots characterized by low pollinator visitation probabilities within the Monocots, Ranunculales, and some Lamiales, while the Asterales as a whole exemplified a large, distinct hotspot of local phylogenetic correlations characterized by high patch and flower visitation probabilities (Fig. 5).

Separate consideration of patch and flower visitation probabilities by major insect groups revealed well-defined, order-specific patterns in the distribution of statistically significant autocorrelation hotspots in the phylogeny. For Coleoptera, distinct hotspots of high-visitation probabilities were associated with Malvales, Rosales, and some clades in Asterales, and one large hotspot of low visitation was associated with Lamiaceae (Fig. 5). The Diptera exhibited statistically significant hotspots of high visitation associated with Caryophyllales and some clades in Asterales, and significant hotspots of low visitation in some clades of Monocots and Lamiales. For the

Hymenoptera, significant hotspots of high visitation were restricted to Asterales, while hotspots characterized by low visitation occurred in several scattered clades within Monocots, Ranunculales, and Caryophyllales. Hotspots of high visitation by Lepidoptera were restricted to Asterales, while a large hotspot characterized by low visitation comprised all clades from Monocots to Rosales. The combination of the preceding trends led to several distinct patterns in pollinator composition associated with higher-level plant taxa and phylogenetic position. For example, species of Caryophyllales were simultaneously characterized by high-Diptera and low-Hymenoptera visitation; species of Malvales by high visitation by Coleoptera and low visitation by Hymenoptera and Lepidoptera; species of Lamiales by low visitation of Coleoptera and Diptera; and most species of Asterales by a combination of high Hymenoptera and Lepidoptera visitation (Fig. 5).

Pollinators and habitat type

All pollinators combined.— Visitation by all pollinators combined varied widely among habitats. Generalized linear mixed models that included pollinator census date (days from 1 January) and number of flowers per patch as fixed-effect covariates, and plant species, sampling year, and sampling site as random effects, revealed statistically significant heterogeneity across habitat types in both patch (χ^2 = 51.92, df = 8, P = 1.7 × 10^{-8}) and flower visitation probability (χ^2 = 48.89, df = 8, P = 6.7 × 10^{-8}). Flower patches and individual flowers on rock cliffs, forest interior and dolomitic outcrops had the lowest, and those in disturbances the highest, probabilities per time unit of being visited by pollinators (Fig. 6).
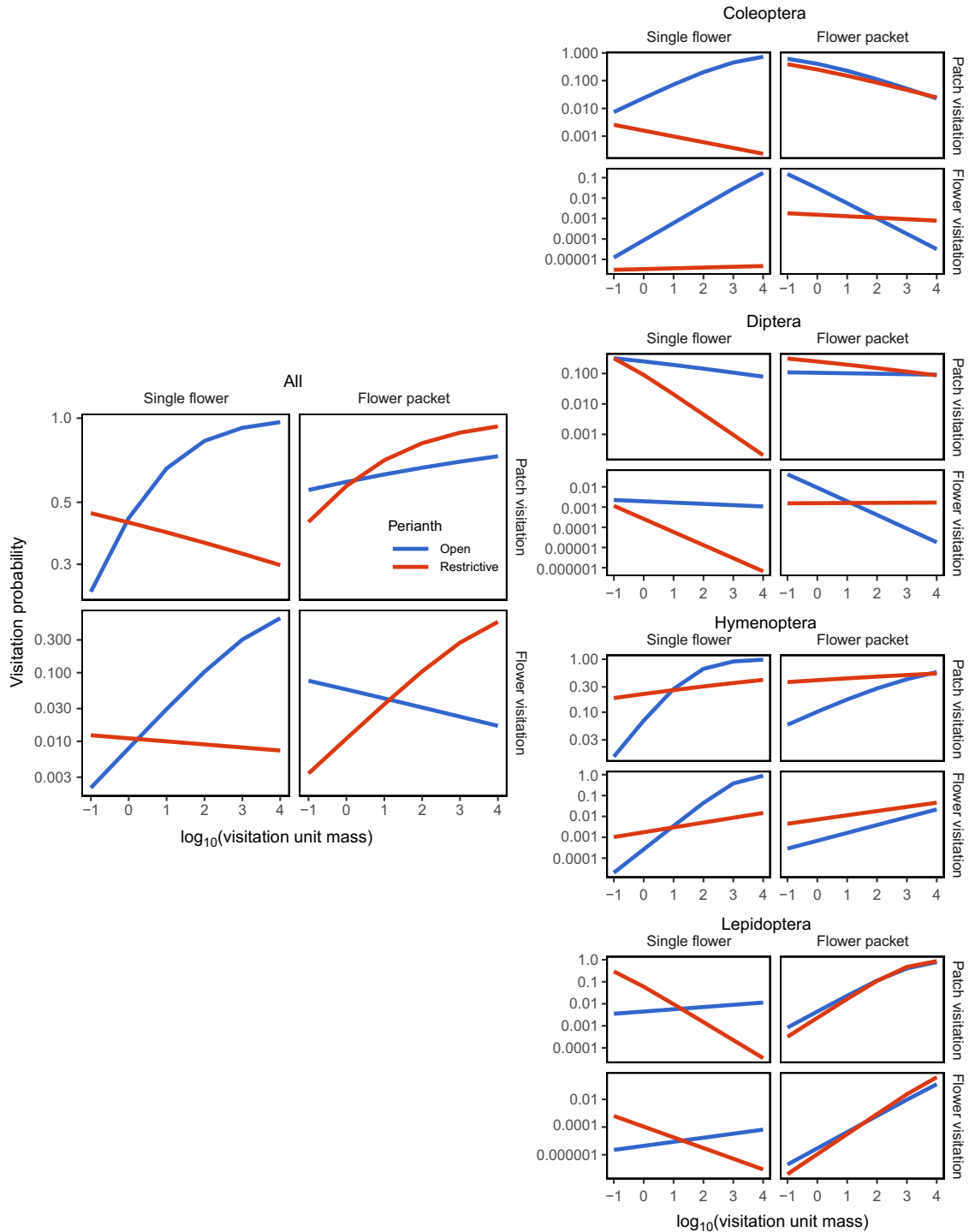
Fig. 4. Mean predicted marginal effects of visitation unit mass (measured as mg; $\log_{10}$-transformed) on patch and flower visitation probabilities (holding number of flowers per patch and day of year fixed), depicting interaction effects involving class of visitation unit (single flower vs. flower packet) and type of floral perianth (open vs. restrictive). Patch visitation probability is the probability that some flower in a focal flowering patch is probed in 3 minutes, and flower visitation probability is the probability that one individual flower is probed in 3 minutes. Graphs correspond to separate analyses conducted for all pollinators combined (left) and for each of the four major insect orders (right). Graphs were designed to emphasize differences between pollinator groups in the qualitative nature of interaction effects rather than quantitative differences in main effects, hence the different scales on vertical axes. See Appendix S5: Table S1 for statistical significance of main effects and interactions in models.

Table 3. Tests for the presence of phylogenetic signal in species means for patch visitation and flower visitation probabilities.

Response variable and pollinator group	Pagel's λ	
	statistic	*P*
Patch visitation probability		
All pollinators	0.491	0.00001
Coleoptera	0.651	0.00001
Diptera	0.316	0.050
Hymenoptera	0.376	0.00002
Lepidoptera	0.208	0.00001
Flower visitation probability		
All pollinators	0.422	0.00001
Coleoptera	0.879	0.00001
Diptera	0.125	0.12
Hymenoptera	0.293	0.00033
Lepidoptera	0.167	0.0013

Notes: Mean values for patch visitation and flower visitation probabilities were computed for plant species, associated with the corresponding tips in the phylogenetic tree (Appendix S6: Fig. S1), and tested for phylogenetic signal. Statistical significance was obtained by randomization with 10^5 repetitions. Patch visitation probability is the probability of at least one flower in a patch being probed during a 3-minute period. Flower visitation probability is the probability of visitation of an individual flower during a 3-minute period.

Major insect orders.—Patch and flower visitation probabilities by major insect orders considered separately varied significantly among habitat types ($P < 0.0001$ in all cases), but the four groups did not vary in unison across habitats. A generalized linear mixed model similar to the one described in the preceding paragraph but whose main fixed effects were habitat type, insect order, and their interaction, revealed strong habitat × insect order interactions on both patch visitation ($\chi^2 = 1,461.6$, df = 24, $P < 2.2 \times 10^{-16}$) and flower visitation probability ($\chi^2 = 9,848.8$, df = 24, $P < 2.2 \times 10^{-16}$). Mean predicted marginal effects of habitat type on patch and flower visitation probabilities (holding census date and number of flowers per patch fixed) for each insect order are shown in Fig. 7. In general, patch and flower visitation by Hymenoptera varied relatively little across habitat types, experiencing only minor reductions in dolomitic outcrops, forest interior, and rock cliffs. The rest of insect orders did exhibit broad variations among habitat types in patch and flower visitation. Coleoptera and Lepidoptera were the two groups exhibiting the most marked changes in patch and flower visitation probabilities across habitat types. Coleoptera had particularly low visitation probabilities in disturbances, dolomitic outcrops, forest interior, and rock cliffs, and high visitations in dwarf mountain scrub, grasslands and meadows, and tall sclerophyllous scrub. Lepidoptera visitation probabilities were highest in disturbances, forest clearings and edges, grasslands and meadows, and springs/streams, and lowest in forest interior and rock cliffs. Diptera had fairly constant, moderate-to-low-visitation probabilities in all habitat types except forest interior and rock cliffs, where they reached minimum values (Fig. 7).

There was a fairly predictable, habitat-dependent variation in proportional pollinator composition as a consequence of the decoupling across habitat types of patch and flower visitation probabilities by the different insect orders. Dwarf mountain scrub, grasslands and meadows, and forest clearings and edges, for example, were characterized by pollinator assemblages in which the four insect orders had roughly similar patch and flower visitation probabilities (Fig. 7). In dolomitic outcrops and rock cliffs the pollinator assemblages tended to be dominated by Hymenoptera and Diptera, while combinations of Hymenoptera, Diptera, and Lepidoptera were characteristic of disturbances and streams/springs.

Phylogenetic regressions on habitat type.—Results of phylogenetic regressions of mean patch and flower visitation probability per species on habitat type differed in some respects from those obtained from models ignoring phylogenetic correlations underlying pollinator visitation. For all pollinators combined, statistically significant effects of habitat type on patch and flower visitation probabilities persisted after controlling for phylogenetic correlations (Table 4). Patterns of variation among habitats were also closely similar to those depicted in Fig. 6, with rock cliffs, forest interior, and dolomitic outcrops exhibiting lower overall visitation probabilities than other habitat types (results not shown). Separate phylogenetic regressions for insect orders revealed statistically significant relationships between visitation probabilities and habitat type only for Hymenoptera. The visitation–habitat relationships were statistically nonsignificant for Coleoptera and Diptera, and significant for patch visitation only in the case of Lepidoptera (Table 4).

Discussion

Many different approaches have been used over the years to quantify pollinator visitation to flowers, although few of these allow for proper statistical comparisons as noted in the *Introduction*. The method used here, whereby pollinator visitation rate is measured in terms of the probability of flowering patches or individual flowers being visited in a given length of time, overcomes these limitations and can be universally applied to any plant species (Herrera 2019). It must be stressed that this method, albeit without explicit recognition of its probabilistic connotations and analytical advantages, was proposed long ago and applied in community studies by Arroyo et al. (1985) and Inouye and Pyke (1988). These authors also emphasized its value for comparative purposes. Despite these advantages, however, not many studies have adopted this method for quantifying pollinator visitation in plant community contexts (e.g., Motten 1986, Totland 1993, Lázaro et al. 2013). This fact, in combination with the much larger, phylogenetically
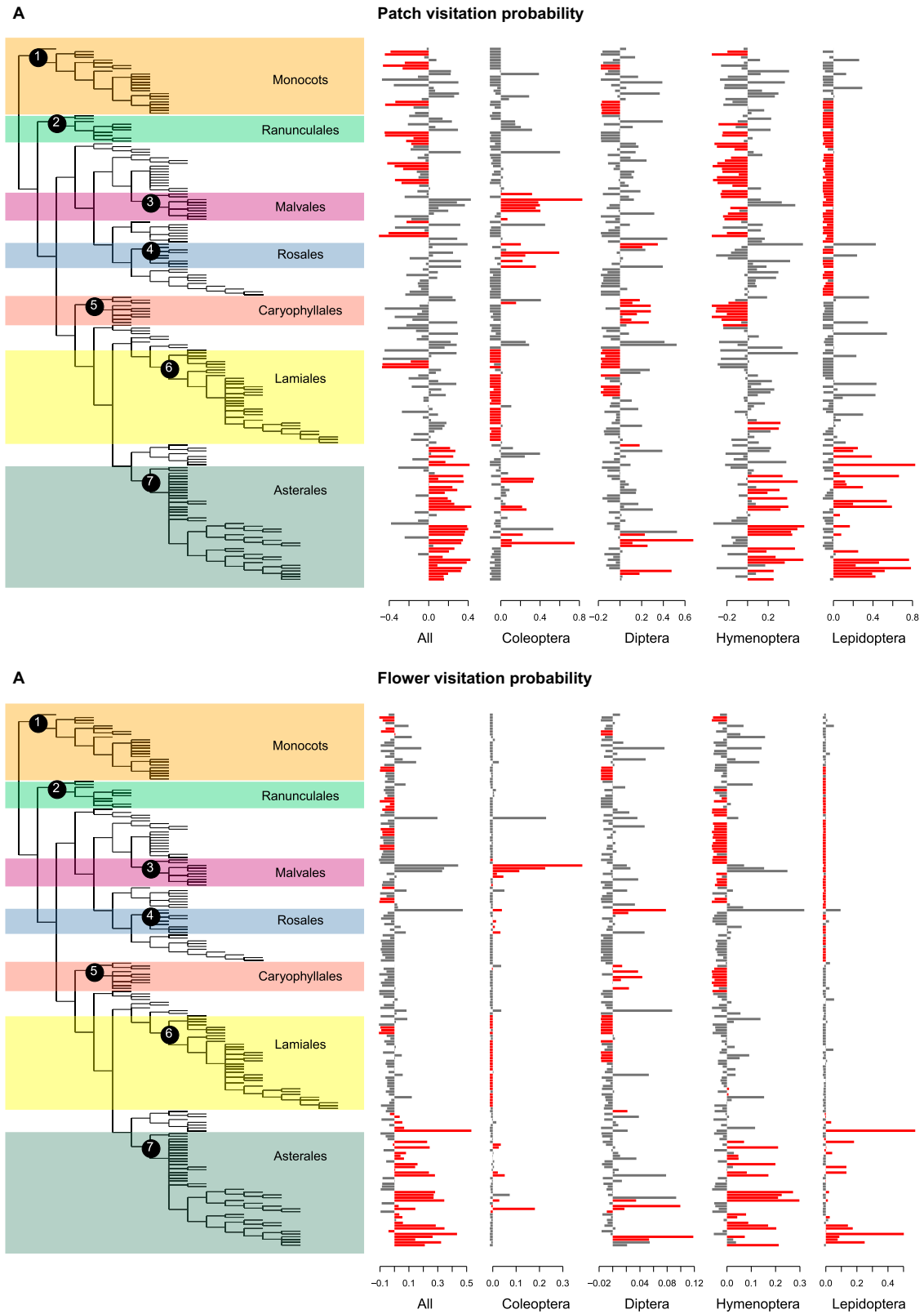
Fig. 5. Visualization of species means for (A) patch visitation probability and (B) flower visitation probability for the set of $N = 191$ plant species studied in relation to the phylogenetic tree depicting their evolutionary relationships (see Appendix S6:

Fig. 5. (*Continued*)

Fig. S1 for a tree with labeled tips). For each visitation measurement, separate panels are shown for all pollinators combined and for each major insect order (Coleoptera, Diptera, Hymenoptera, Lepidoptera). Each horizontal bar corresponds to one plant species, and its length and direction denote the mean visitation probability relative to the overall zero-centered sample mean, i.e., left- and right-facing bars correspond to values that are smaller and larger than the overall sample mean, respectively. Shown in red are species with statistically significant local Moran's I_i ($P < 0.05$), denoting instances of local phylogenetic associations. Clusters of red-colored bars are indicative of "local hotspots" of phylogenetic autocorrelation for the particular group of pollinators and visitation measurement involved. Numbered clades correspond to phylogenetically and taxonomically defined groups of species mentioned in the text: 1, Monocots: all monocots in the sample; 2, Ranunculales: species of Berberidaceae, Ranunculaceae, and Papaveraceae; 3, Malvales: Thymelaeaceae and Cistaceae; 4, Rosales: Rosaceae; 5, Caryophyllales: Plumbaginaceae and Caryophyllaceae; 6, Lamiales: Scrophulariaceae, Lamiaceae, and Orobanchaceae; and 7, Asterales: Campanulaceae and Asteraceae.

more diverse sample considered here in comparison to most earlier community studies, will limit opportunities for discussing the results of this study in the context of earlier investigations.

Pollinator visitation rate: a species-specific feature

It has been shown many times that pollinator visitation rates vary among plant species and, within species, among locations and years (Husband and Barrett 1992, McCall and Primack 1992, Herrera et al. 2001, Price et al. 2005, Herrera 2019). I am not aware, however, of any previous attempt at explicitly partitioning the overall variance in pollinator visitation at the regional plant community level into components attributable to interspecific, spatial, and suprannual variation. By sampling many species in many years and sites, this study has been able to show that variation among species was by far the largest source of variance in total pollinator visitation (i.e., all pollinators combined) in the Sierra de Cazorla region. Variance components due to differences among years and sites, although significantly greater than zero, were much less important quantitatively than variance due to interspecific differences. Since most species were sampled at single sites and years, this result could be a spurious consequence of limited sampling in time and space. Nevertheless, the result was similar after computing variance components only for subsets of species that were sampled on more than one year or more than one site, which tends to rule out the possibility that the variance structure of the whole species sample was a spurious consequence of having sampled most species on single years and sites. Taken together, results of variance partitions point to the conclusion that, in the region and species sample studied, visitation rate by all pollinators was largely a species-specific attribute, and that
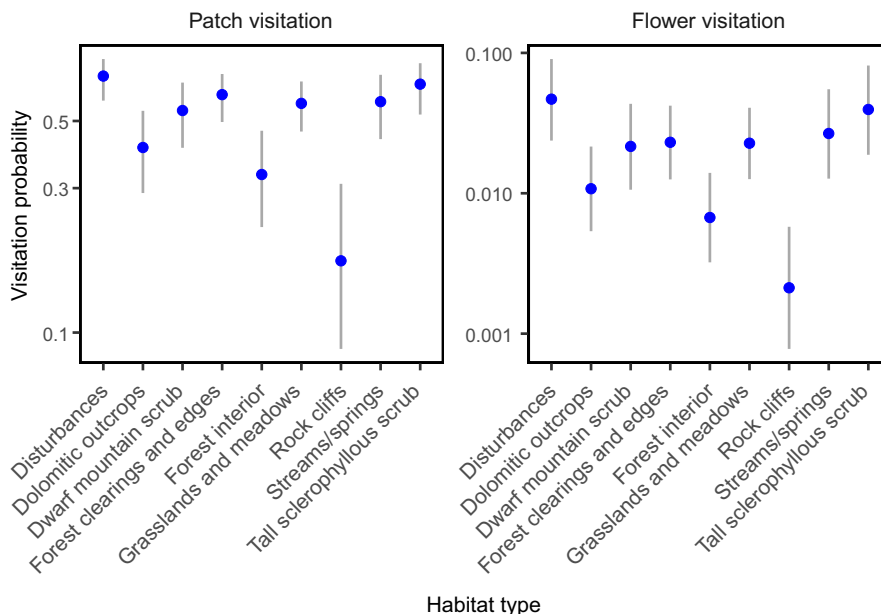

Fig. 6. Mean predicted marginal effects of habitat type on patch and flower visitation probabilities (dots), all pollinators combined (holding day of year and number of flowers per patch fixed). Vertical segments denote 95% confidence intervals. Note logarithmic scale on vertical axes.
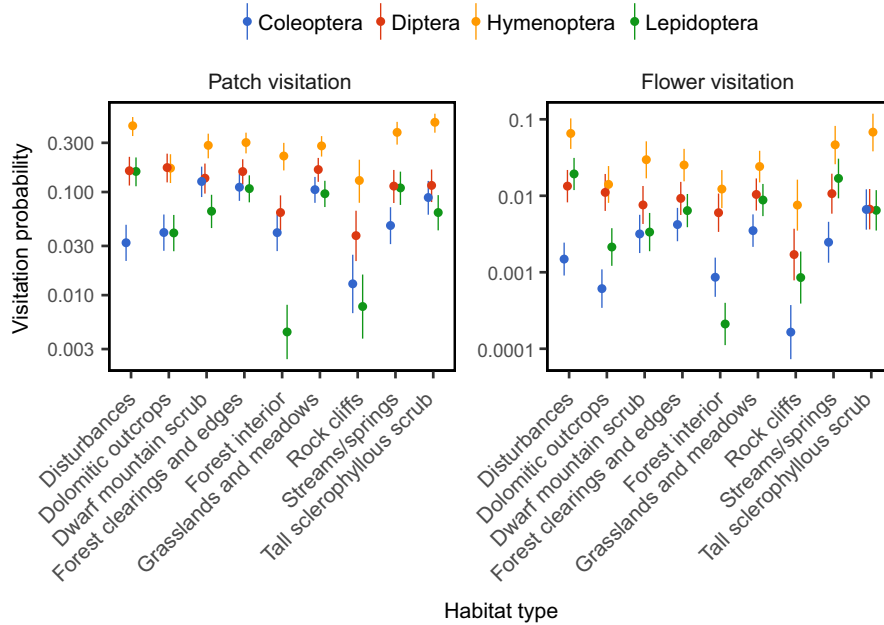
FIG. 7. Mean predicted marginal effects of habitat type on patch and flower visitation probabilities (dots), computed separately for each of the four major insect orders (holding day of year and number of flowers per patch fixed). Vertical segments denote 95% confidence intervals. Note logarithmic scale on vertical axes.

interspecific differences should be expected to be robust to the blurring effects of temporal and spatial intraspecific variations. Visual inspection of Figs. 3 and 4 in Herrera (2019) further adds to the view that, in the large species sample examined here, interspecific differences in visitation rates by all pollinators combined are likely to persist in the face of long-term suprannual changes experienced by individual plant species.

The large species sample examined in this study allowed estimation of both the range and the shape of the

TABLE 4. Results of phylogenetic regressions testing for the effect of habitat type on patch and flower visitation probabilities after statistically accounting for the significant phylogenetic correlations underlying pollinator visitation data.

	Response variable			
	Patch visitation probability		Flower visitation probability	
Pollinator group	χ^2	P	χ^2	P
All pollinators	71.22	2.8×10^{-12}	19.62	0.012
Coleoptera	11.12	0.19	8.25	0.41
Diptera	12.42	0.13	14.62	0.067
Hymenoptera	48.53	7.8×10^{-8}	24.68	0.0017
Lepidoptera	17.44	0.026	5.23	0.73

Notes: For each response variable, analyses were performed for all pollinators combined and for each major insect order separately. Patch visitation probability is the probability of at least one flower in a patch being probed during a 3-minute period. Flower visitation probability is the probability of visitation of an individual flower during a 3-minute period.

distributions of species means for patch and flower visitation probabilities. Interspecific differences in these two parameters were very broad, encompassing nearly three orders of magnitude and 200-fold ranges. This substantial variation, in addition to revealing extensive interspecific differences in pollinator service, enhanced the statistical power for identifying predictors of pollinator visitation, which could perhaps have remained undetected in a smaller species sample with narrower range of variation. The scarce comparative evidence available suggests that broad interspecific variation in pollinator service is probably the rule in most plant communities. Mean flower visitation probabilities for individual species obtained in this study are compared in Table 5 to published data from other community studies in different continents and vegetation types, after converting pollinator visitation figures to a common measurement unit. Community means and ranges of flower visitation probability were remarkably homogeneous across continents and vegetation types. For instance, the mean for Mediterranean montane species studied here was virtually identical to those from distant and ecologically dissimilar communities, such as boreal and alpine habitats in Norway or meadow–forest habitats in Massachusetts (Table 5). This suggests the intriguing possibility of ecological invariance in community-level descriptors of per-flower pollinator visitation, a hypothesis deserving further study.

Pollinator visitation rate: intrinsic and extrinsic predictors

All plant intrinsic and extrinsic predictors contributed to explain variation in patch and flower visitation

Table 5. Pollinator visitation rates (all pollinators combined) from community studies conducted in different regions and vegetation types.

Vegetation type and region	No. plant species	Flower visitation probability (visits/minute)		Reference
		Mean ± SE	Range	
Mediterranean montane, Spain	191	0.037 ± 0.003	0.0011–0.2146	this study
Alpine and boreal, Norway	41†	0.037 ± 0.012	0.0003–0.4050	Totland (1993, 1994, 2001), Totland and Schulte-Herbrüggen (2003), Hansen and Totland (2006), Totland et al. (2006), Lundemo and Totland (2007), Lázaro et al. (2013); A. Lázaro (*personal communication*)
Alpine, Australia	36†	0.016 ± 0.003	0.0002–0.0742	Inouye and Pyke (1988)
Alpine tundra, New Hampshire, USA	35	0.022 ± 0.057	‡	McCall and Primack (1992)
Deciduous forest, USA	6	0.026 ± 0.007	0.0050–0.0453	Motten (1986)
Woodland-meadow (1982), Massachusetts, USA	124	0.035 ± 0.101	‡	McCall and Primack (1992)
Woodland-meadow (1983), Massachusetts, USA	108	0.034 ± 0.069	‡	McCall and Primack (1992)
Tropical forest, Central America	11	0.028 ± 0.015	0.0027–0.1610	Kay and Schemske (2003)
Mountain fynbos, South Africa	92	0.018 ± 0.058	‡	McCall and Primack (1992)

Notes: Original figures were transformed to common units. In each region, multiple data for the same species were averaged.
† Only species with nonzero visitation records are included.
‡ Visitation probabilities estimates for individual species were not available in the original publication.

probabilities, all pollinators combined. Among intrinsic predictors, the simple floral traits considered, namely perianth type, mass of visitation unit, and type of visitation unit, were all related to pollinator visitation. Simple functional relationships, however, could not be inferred due to interactions between predictors. For example, pollinator visitation increased steadily with increasing log mass of visitation unit, a surrogate for its size, but this relationship only held for species with single flowers with open perianths, or those with flower packets and restrictive perianths, but not for species possessing other trait combinations. Single flowers with open perianths tended to have higher visitation rates than those with restrictive perianth, but these relationships did not held for flower packets. Comparable relationships have been reported previously by the few studies that have examined interspecific relationship between floral traits and pollinator visitation at the plant community level (McCall and Primack 1992, Hegland and Totland 2005, Lázaro et al. 2013). In the present instance, positive relationships between pollinator visitation rates and log mass of visitation unit may be parsimoniously explained as a consequence of the direct relationship between per-flower sugar secretion and flower log mass reported for southern Spanish plants (Herrera 1985), on the plausible assumption that consistently greater floral rewards should favor greater average visitation rates.

Another species-specific, intrinsic predictor having an effect on patch and flower visitation probabilities was the evolutionary history of each species as represented by its phylogenetic relationships. There was, on one side, a global phylogenetic trend in the sample roughly reflecting an increasing trend in visitation probabilities from basal through more derived clades. In addition, there were phylogenetic correlation hotspots characterized by either similarly low (Monocots, some Ranunculales, some Lamiales) or similarly high (most Asterales) pollinator visitation probabilities. To my knowledge, no previous study has examined variations in pollinator visitation rates in a broad phylogenetic framework, thus it is not possible to know whether phylogenetic patterns found here are representative for the angiosperms as a whole or apply only to my species sample. In addition, an even more phylogenetically encompassing species sample would be needed to ascertain whether phylogenetic patterns occurring in my sample are linked to the evolutionary trajectories of floral traits considered here or depend on other factors. Keeping these caveats in mind, two implications of the phylogenetic analyses shown here deserve consideration. First, the well-known differences between taxonomic groups and evolutionary lineages in incidence of pollen limitation (Larson and Barrett 2000, Knight et al. 2005, Alonso et al. 2010, Vamosi et al. 2013, Bennett et al. 2018) could reflect underlying, insufficiently recognized phylogenetic effects on pollinator visitation rates. It is worth noting in this regard that the ubiquitous pollen limitation occurring within the plant order Asparagales (Bennett et al. 2018: Fig. 3) is consistent with the low pollinator visitation rates found here for Monocots, most of which belong to Asparagales. And second, because of the overall phylogenetic signal and local hotspots of phylogenetic correlations in pollinator visitation, the taxonomic affiliation of species chosen for pollination investigations can sometimes predefine those conclusions of research that depend on pollinator visitation rates. This adds one

more instance to the growing list of challenges to pollination studies due to unacknowledged geographic or taxonomic biases (Rodger et al. 2004, Archer et al. 2014, Ollerton et al. 2015, Herrera 2019).

Habitat type was a significant predictor of pollinator visitation rate. Among the nine habitat types recognized, dolomitic outcrops, forest interior, and, particularly, rock cliffs were characterized by comparatively low pollinator visitation at both the flowering patch and individual flower levels. These patterns could arise from habitat-specific ecological factors influencing pollinator visitation but, given the strong phylogenetic signal characterizing pollinator visitation rates in the sample, could also reflect possible phylogenetic niche conservatism if plant species that are closely related phylogenetically tended to occur in similar environments (Losos 2008, Münkemüller et al. 2015). The second possibility is not consistent with the results of phylogenetic regressions, which showed that the value of habitat type as a predictor of pollinator visitation persisted after statistically accounting for the phylogenetic relationships among species. Instead, habitat-specific ecological factors seem to account for the reduced pollinator service in dolomitic outcrops, forest interior and rock cliffs. In these three habitats, low attractiveness of flowering plants to pollinators due to scarcity of flowers in their immediate vicinity may have contributed to the low-visitation rates, since previous studies have often found that floral neighborhood characteristics are important determinants of pollinator visitation to individual plants or flowering patches (Laverty 1992, Molina-Montenegro et al. 2008, Montero-Castaño and Vilà 2015). In dolomitic outcrops, low pollinator visitation probably was also a consequence of strong interspecific competition for pollinator service arising from high diversity of sympatric entomophilous plants (Alonso et al. 2013) in combination with small size of local insect populations derived from aridity, low plant productivity and sparse vegetation. In the case of forest interior and rock cliffs, energetic constraints on foraging due to low density of flowering plants and thermal limitations on ectothermic pollinators set by the low solar irradiance available in these shady environments (Beattie 1971, Herrera 1995a, b, 1997, Zamora 1999) can also have reduced pollinator visitation.

Pollinator composition: community-wide patterns

Pollinator composition is an important component of pollinator service, since different pollinators vary in per-visit pollen transfer efficacy and quality of transferred pollen (Herrera 1987, Sahli and Conner 2007, King et al. 2013). Coleoptera, Diptera, Hymenoptera, and Lepidoptera, the main groups of insect pollinators in the species sample studied here, generally differ in quantity and/or quality of their pollination service. As a general trend, per-visit pollen removal or deposition tend to decline in the direction

Hymenoptera-Lepidoptera-Diptera-Coleoptera, although broad variations can occur within orders and exceptions to this ranking are frequent, depending on the particular plant and insect species concerned (Schemske and Horvitz 1984, Herrera 1987, Larsson 2005, Sahli and Conner 2007, Theiss et al. 2007, Koski et al. 2018). These four insect orders have also been traditionally related to distinct plant "pollination syndromes," or suites of floral characteristics that are associated to particular pollinator groups (Fægri and van der Pijl 1979, Fenster et al. 2004).

Pollinator composition, in terms of relative contributions of Coleoptera, Diptera, Hymenoptera, and Lepidoptera, varied extensively among species in the sample studied. The variation was essentially continuous, as revealed by the ordination analysis of the between-species dissimilarity matrix. Discontinuities in pollinator composition over the bivariate ordination plane did not exist, and discrete groups with species more similar to each other than to species in other groups were not recognizable. All possible combinations of relative pollinator importance of the four major insect orders were represented in the species sample, and the frequency distributions of relative importance were essentially unimodal in all cases. These results indicate, on one side, that the vast majority of plants in the montane habitats studied had generalized pollination systems, each species depending for pollination on two or more insect orders with disparate morphology and behavior. Similar pervasiveness of generalized pollination systems has been previously emphasized in other community studies (McCall and Primack 1992, Herrera 1996, Waser et al. 1996). And on the other side, the absence of distinct species clusters associated with particular pollinators falsifies expectations from "pollination syndromes" views postulating that plants partition the range of available pollinators by specializing on particular groups, a result that corroborates those of Ollerton et al. (2009; see also Ollerton et al. 2015). Consideration of the 10 species (5.2% of total) exclusively or predominantly pollinated by single insect orders, and falling around the periphery of the species cluster obtained by the ordination analysis, further adds to the failure to support pollinator syndromes linked to distinct pollinator groups. Species that depended entirely or predominantly on the same insect order for pollination were conspicuously heterogeneous in their floral characteristics (Appendix S7: Fig. S1). It must be stressed, however, that the current state of pollinator visitation does not necessarily imply that certain pollinator groups did not drive the evolution of certain plant species toward certain morphologies, in which case there may have been true partitioning of pollinators in the plant species' evolutionary history.

Pollinator composition: responses to predictors

The continuous interspecific variation in pollinator composition occurring in the species sample studied can be parsimoniously explained in terms of the heterogeneous

visitation responses of major insect groups to variation in floral traits, phylogeny, and habitat type. Insect orders differed in the specific flower trait combinations to which they were responsive and in the shape of the relationships. For example, visitation rates by Coleoptera increased with increasing visitation unit mass in species with single flowers, but declined in species with flower packets. Lepidoptera responded positively to increasing mass of visitation unit in species with flowers packets, but negatively in species with single flowers and restrictive perianths. Hymenoptera stood alone from the rest by responding positively to increasing mass of visitation unit in all instances, and their visitation rates were not impaired by restrictive perianths.

Pollinator composition of individual plant species depended strongly on phylogeny. Patch and flower visitation probabilities by all insect orders except Diptera exhibited strong phylogenetic signals, thus showing that evolutionarily related plant species were more similar to each other in visitation probabilities by the different insect orders than to species more distant phylogenetically. Phylogenetic signal, however, was not homogeneously distributed across the plant phylogeny, and the distribution of significant hotspots of local phylogenetic autocorrelation was specific to each insect order. These hotspots indistinctly arose from local similarity in either above- or under-average visitation rates, as illustrated by the high-visitation hotspots of Coleoptera and Lepidoptera associated with Malvales and Asterales, respectively; the low-visitation hotspots of Hymenoptera characterizing Caryophyllales; and the low-visitation hotspots of both Diptera and Coleoptera associated with Lamiales. There were some instances of complementarity between insect orders in their phylogenetic hotspots. For example, the Caryophyllales simultaneously exhibited a low-visitation hotspot for Hymenoptera and a high-visitation hotspot for Diptera. Even acknowledging that my species sample falls short at achieving a complete phylogenetic coverage of entomophilous angiosperms in the study region, these results provide compelling evidence that plant phylogeny alone is an important predictor of pollinator composition in terms of major insect groups. This relationship is not necessarily mediated by similarity of phylogenetically related taxa in macroscopic floral traits of the sort traditionally considered in studies focusing on pollination syndromes (Fægri and van der Pijl 1979, Fenster et al. 2004, Ollerton et al. 2009). This is illustrated in my sample by the high-Coleoptera hotspot associated with species of Malvales, which belong to families with disparate macroscopic floral traits (Cistaceae and Thymelaeaceae; compare *Cistus* and *Daphne* in Appendix S7: Fig. S1), or by species in the high-Diptera and low-Hymenoptera hotspot associated with Caryophyllales (compare *Arenaria* and *Saponaria* in Appendix S7: Fig. S1).

In addition to floral traits and phylogenetic relationships, habitat type was another key predictor of pollinator composition, as shown by the decoupled variation across habitat types in visitation rates by different insect groups. Visitation rates by Hymenoptera (mostly bees) varied little among habitat types, a result that contrasts with published reports of between-habitat heterogeneity in bee abundance in other Mediterranean regions (Torné-Noguera et al. 2014). Visitation by the remaining three insect orders varied in contrasting ways across habitats. Variation among habitats in pollinator composition was in part the consequence of phylogenetically related plant species with their distinctive pollinator assemblages tending to occur in similar environments. This phylogenetic conservatism hypothesis was supported for Coleoptera, Diptera, and Lepidoptera, but not for Hymenoptera. Significant effects of habitat type on visitation probabilities by the former three orders vanished after statistically accounting for the phylogenetic correlations underlying pollinator visitation data. In contrast, habitat effects on Hymenoptera abundance remained significant after accounting for phylogeny. It can be speculated that the comparative stability of Hymenoptera across habitats could be the outcome of homogeneity among habitats in the abundance of their common larval and adult food (nectar plus pollen), while the broad variation in abundance of the rest of pollinator groups may reflect heterogeneity between habitats in the supply of their highly heterogeneous larval and adult foods. No data are available to evaluate this ecological hypothesis. In conclusion, therefore, between-habitat differences in pollinator composition occurring in my study region were the composite outcome of habitat-specific, phylogenetically independent responses in the case of Hymenoptera, in combination with significant phylogenetic niche conservatism in the case of Coleoptera, Diptera, and Lepidoptera.

Concluding Remarks

In the long run, local and regional plant communities are molded by the concerted, continued, intricate action of evolutionary, historical, and ecological events, and for this reason, they accumulate considerable amounts of biological information about the past and current operation of these building forces (Herrera 1992, Ackerly 2004, Donoghue 2008). Pollination community studies involving large species samples thus have considerable potential for understanding the present-day ecology and past evolution of plant–pollinator interactions (Arroyo et al. 1982, 1985, Inouye and Pyke 1988, Herrera 1992, McCall and Primack 1992, Totland 1993, Lázaro et al. 2013). In contrast, small or modest species sets drawn from a much larger regional pool represent artificially assembled samples often selected for practical convenience rather than biological motivations, but they provide suitable arenas for detailed study of specific questions or testing particular hypotheses. These two "zooming-out" and "zooming-in" approaches, respectively, to the study of the ecology and evolution of plant pollination are bound to contribute complementary

insights, since small or modest species samples will rarely represent truly scaled-down, phylogenetically and ecologically unbiased versions of whole plant communities. As noted in the *Introduction*, research relying on ambitious sampling efforts involving many plant species remains overly underrepresented in comparison to that focusing on single species or small samples. By examining a unusually large, phylogenetically and ecologically diverse sample of species, the present study has illustrated the hitherto underexploited potential of pollination community studies at the regional scale to (1) reveal the importance of interactions among species-specific floral traits as predictors of pollinator visitation and composition and also, possibly, pollen limitation; (2) shed new light on long-standing, controversial issues in pollination research such as, e.g., the reality of so-called "pollination syndromes" (Fenster et al. 2004, Ollerton et al. 2009); (3) identify potential avenues for future research, e.g., examining heterogeneity among habitats or geographical regions in pollinator service and pollen limitation in the context of the phylogenetic relationships among species; (4) formulate novel hypotheses and questions that could hardly have arisen from studies dealing with limited species samples, e.g., asking whether complementary phylogenetic hotspots exhibited by different pollinator groups reflect some relationships over an evolutionary time scale, or suggesting the possible ecological invariance of community-level descriptors of per-flower pollinator visitation; and (5) identify potential methodological cautions that should be taken into consideration by studies dealing with limited, phylogenetically biased species samples, e.g., the extent to which results of these studies can be tainted by phylogenetic signals in pollinator abundance and composition not being accounted for. More generally, results of this study have shown that, given sufficient ecological and phylogenetic diversity in a species sample, components of pollinator service can be predicted by considering a few simple flower features, habitat type and evolutionary history.

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