Complex long-term dynamics of pollinator abundance in undisturbed Mediterranean montane habitats over two decades

Carlos M. Herrera[1]

Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas, Avenida Americo Vespucio 26, E-41092 Sevilla, Spain

Abstract. Current notions of "pollinator decline" and "pollination crisis" mainly arose from studies on pollinators of economic value in anthropogenic ecosystems of mid-latitude temperate regions. Comprehensive long-term pollinator data from biologically diverse, undisturbed communities are needed to evaluate the actual extent of the so-called "global pollination crisis." This paper analyzes the long-term dynamics of pollinator abundance in undisturbed Mediterranean montane habitats using pollinator visitation data for 65 plant species collected over two decades. Objectives are (1) to elucidate patterns of long-term changes in pollinator abundance from the perspectives of individual plant species, major pollinator groups, and the whole plant community and (2) to propose a novel methodological implementation based on combining a planned missing data design with the analytical strength of mixed effects models, which allows one to draw community-wide inferences on long-term pollinator trends in species-rich natural habitats. Probabilistic measurements ("patch visitation probability" and "flower visitation probability" per time unit) were used to assess pollinator functional abundance for each plant species on two separate, randomly chosen years. A total of 13,054 pollinator censuses accounting for a total watching effort of 2,877,039 flower-min were carried out on 299 different dates. Supra-annual unstability in pollinator functional abundance was the rule, with visitation probability to flowering patches and/or individual flowers exhibiting significant heterogeneity between years in the majority of plant species (83%). At the plant-community level, there was a significant linear increase in pollinator functional abundance over the study period. Probability of pollinator visitation to flowering patches and individual flowers increased due to increasing visitation by small solitary bees and, to a lesser extent, small beetles. Visitation to different plant species exhibited contrasting changes, and insect orders and genera differed widely in sign and magnitude of linear abundance trends, thus exemplifying the complex dynamics of community-wide changes in pollinator functional abundance. Results of this investigation indicate that pollinator declines are not universal beyond anthropogenic ecosystems; stress the need for considering broader ecological scenarios and comprehensive samples of plants and pollinators; and illustrate the crucial importance of combining ambitious sampling designs with powerful analytical schemes to draw reliable inferences on pollinator trends at the plant community level.

Key words: *annual variation; bee abundance; climate change; generalized linear mixed models; long-term variation; Mediterranean habitats; mountain habitats; planned missing data design; plant community; pollinator community; pollinator functional abundance; pollinator visitation probability.*

Introduction

Environmental parameters that influence the dynamics of populations, communities, and ecosystems vary at hierarchically nested temporal scales, from daily through annual up to extremely long-term, geological time scales (Bennett 1990, Roy et al. 1996). On the lowermost segment of this gradient, ecological studies have traditionally concentrated on daily or seasonal dynamics, and investigations spanning more than a few years were scarce until relatively recent years (Weatherhead 1986, Magnuson 1990, Swanson and Sparks 1990, Herrera 1998). This situation has changed over the last two decades, following increased recognition of the importance of long-term data for gaining a better understanding of ecological processes, and also as a consequence of raised societal concerns about the magnitude and future impact of accelerating anthropogenic changes (Knapp et al. 2012, Robertson et al. 2012, Kominoski et al. 2018,

Kuebbing et al. 2018). Reports on long-term ecological data have proliferated in recent years, mostly aimed at detecting directional trends in population, community or ecosystem features in response to current environmental changes. These include, for example, studies on size and dynamics of populations (Meserve et al. 2003, Hallmann et al. 2017), community phenology and composition (Inouye et al. 2002, Stefanescu et al. 2003, CaraDonna et al. 2014, Zamora and Barea-Azcón 2015), plant life history (Linares and Tíscar 2011, Anderson et al. 2012), and plant–animal interactions (Herrera 1998, Thompson 1998, Koenig and Knops 2001, Hódar et al. 2012). Prominent among the latter are investigations on trends in pollinator populations, which have attracted considerable attention from ecologists because of the importance of animal pollination for sexual reproduction of wild and crop plants (Kremen et al. 2002, Klein et al. 2007, Ollerton et al. 2011, 2014, Senapathi et al. 2015, Breeze et al. 2016, Ollerton 2017). These investigations have frequently supported the notions of "pollinator decline" and "pollination crisis" (Bloch et al. 2006, Bommarco et al. 2012, Scheper et al. 2014, Breeze et al. 2016, Klein et al. 2017, Ollerton 2017). Nevertheless, evidence for these widely

held views mostly comes from studies carried out at impoverished human-managed ecosystems from mid-latitude regions in western Europe and North America, and is mostly related to a subset of pollinators of immediate economic value, typically bees (Ghazoul 2005, Winfree et al. 2009, Potts et al. 2010a, Archer et al. 2014, Tucker and Rehan 2018, but see Morales et al. 2013, Ollerton 2017, for examples from other regions or pollinator groups). Even for well-studied social bees, the data supporting their decline are geographically biased (Archer et al. 2014, Ollerton 2017). For example, the number of managed honey bee colonies has declined in North America and central Europe, but not in the Mediterranean Basin (Potts et al. 2010b). Studies on European bee diversity mostly come from regions where bee communities are not particularly diverse, rather than from areas where bee diversity reaches the highest continental values (Westphal et al. 2008). Geographic biases in research intensity imply that there are substantial gaps in our current understanding of pollinator losses, as discussed in detail by Archer et al. (2014).

Long-term, comprehensive pollinator data from biologically diverse, reasonably undisturbed pollinator and plant communities are urgently needed. First, to evaluate how global the postulated "global pollination crisis" and "global pollinator decline" (Potts et al. 2010a, Scheper et al. 2014) are, i.e., determining whether the alleged phenomenon is also taking place away from agroecosystems and other heavily human-managed habitats. Critical information on pollinator trends in non-anthropogenic habitats is still largely missing nearly 20 yr after its importance was first stressed by, e.g., Cane and Tepedino (2001) and Ghazoul (2005). Second, there are ecological reasons to suspect that the long-term dynamics of pollinators and pollination can follow different courses in species-poor and species-rich environments, as indicated in the next section. Third, environmental factors driving long-term changes in pollinator abundance will most likely differ among geographical regions (Potts et al. 2010b) and between natural and anthropogenic, or at least highly human-modified habitats. For example, pollinator populations in undisturbed habitats will be relatively safe from habitat destruction, land cover changes, or pesticides (Kremen et al. 2002, Potts et al. 2010a, Ollerton et al. 2014, Senapathi et al. 2015), but long-term changes could still occur driven by other environmental factors such as climate change (Memmott et al. 2007, Scaven and Rafferty 2013, Hofmann et al. 2018). And fourth, detailed long-term pollinator data from undisturbed, diverse plant and pollinator assemblages are uniquely suited to dissect the natural unfolding of environmentally driven alterations in pollinator abundance at the levels of plant species, plant community, and major pollinator groups. Identifying differences among pollinator groups in their temporal dynamics can help to clarify the ecological mechanisms responsible for directional trends in pollinator abundance at the community level (Balfour et al. 2018).

This paper presents a thorough analysis of the long-term dynamics of pollinator abundance in well-preserved habitats located well away from major anthropogenic disturbances. Using pollinator visitation data for 65 plant species collected over a 21-yr period in southeastern Spanish montane habitats, this study's primary aim is to elucidate how long-term changes in natural pollinator abundance unfold from the perspectives of individual plant species, major pollinator groups, and the regional plant community as a whole. As noted above, considerable information is currently available on the process of pollination deterioration in highly human-modified habitats and adjacent areas (Kremen et al. 2002, Magrach et al. 2017, Tucker and Rehan 2018), but remarkably little is known about how/whether such deterioration is taking place in large expanses of reasonably natural habitats. Documenting long-term, community-level, directional trends in pollinator abundance in species-rich natural communities is a difficult task that requires regional sampling strategies involving the collection of data over many years (Ghazoul 2005). This demands a formidable sampling effort and raises non-trivial practical constraints. The second aim of this paper is to make the case for a biologically meaningful, standardized methodological scheme universally applicable in natural habitats to obtain community-level information on long-term pollinator trends comparable across biomes, regions, or habitat types. General principles, conceptual underpinnings and motivation for this methodological framework are elaborated in the next section.

POLLINATOR TRENDS IN NATURAL HABITATS: A METHODOLOGICAL FRAMEWORK

Decline in the populations of insects that are associated with pollination has been sometimes taken as prima facie evidence for impairment of pollination services (Conrad et al. 2006, Goulson et al. 2008, Ollerton et al. 2014, Hallmann et al. 2017). "Pollinator decline," however, is not necessarily synonymous with "pollination decline" (Thomson 2001). Failure of keystone pollinators may not cause a decay in pollination success if it is followed by shifts in the composition and abundance of remaining pollinators that eventually compensate for the loss (Pauw 2007, Hudewenz and Klein 2015, Hallett et al. 2017). Pollinator and pollination declines are expected to be tightly correlated in depauperate habitats with low overall diversity such as agroecosystems, where compensatory shifts by other species are unlikely to follow the decay of key pollinators (Kremen et al. 2002). In wild habitats still harboring diverse pollinator communities, however, compensatory shifts and complementarity effects (Albrecht et al. 2012, Fründ et al. 2013) are likely to occur, and failure of some pollinators should be followed by pollination decline less often than in depauperate habitats (Pauw 2007, Hallett et al. 2017). In habitats with diverse pollinator communities, therefore, indices of pollinator abundance that are not directly linked to their pollinating activity at flowers (e.g., pan trap or Malaise trap captures; Nielsen et al. 2011, Hallmann et al. 2017, Hall 2018) are prone to be weakly correlated across years with measurements of pollinator service based on flower visitation or pollination success. Variable trapping biases and dissimilarity of results obtained with different passive pollinator sampling methods (Cane et al. 2000, Westphal et al. 2008, Hall 2018) are yet another reasons why these methods should be avoided in studies aiming to elucidate long-term trends in pollination service to plants. Implementation of pollinator abundance indices based on their activity at flowers, i.e., *functional abundance* as "perceived" by plants (Herrera 2005), is a minimum

requisite for testing hypotheses of long-term pollination trends in species-rich natural communities.

Unless data for the whole taxonomic spectrum of pollinators are collected, directional trends in pollinator functional abundance are susceptible to distortions and biases, since compensatory shifts following the possible decline of focal pollinators can remain unnoticed. For example, the decline of bumble bees in regions of western Europe and North America is well established (Goulson et al. 2008, Cameron et al. 2011, Bommarco et al. 2012, Kerr et al. 2015), yet temporal trends of other pollinator taxa that could be silently compensating for such decline remain largely unstudied. Wasps, for example, have been shown experimentally to replace bumble bees as efficient pollinators of *Asclepias* flowers (Hallett et al. 2017), and invasive bumble bees may replace advantageously the pollination services of declining native species (Madjidian et al. 2008). Substantial evidence shows that pollinator groups infrequently considered by recent research on pollinator trends are efficacious pollinators of many plants (Herrera 1987, Larson et al. 2001, Jauker and Wolters 2008, Orford et al. 2015, Rader et al. 2016, Tiusanen et al. 2016). Pollinator sampling designs should therefore be taxonomically unprejudiced to allow for the detection of possible compensatory shifts and directional population trends among pollinators other than bees. Unprejudiced taxonomic composition should also hold for the set of plant species chosen for study. These should ideally approach a random draw from the community of entomophilous plants, avoiding biases favoring species blooming at convenient times of year, yielding high data/sampling effort ratios, or having certain favorite pollinator types. For example, only about one-third of the $N = 397$ European entomophilous species surveyed by Müller (1883) had their flowers visited by bumble bees (37.3%). Inferences drawn from European studies of pollinator decline that focus exclusively on bumble bees and bumble bee-pollinated plants will therefore apply only to a relatively modest fraction of the continental entomophilous flora.

Pollinator abundance indices used in studies of temporal trends often represent ad hoc measurements designed to cope with the limitations of the particular data at hand (Cameron et al. 2011, Bommarco et al. 2012, Ollerton et al. 2014). Furthermore, studies on pollinator temporal trends have often conflated, or treated interchangeably, pollinator abundance and pollinator diversity (see, e.g., Ollerton 2017), two distinct properties of pollinator communities whose functional relationship remains largely unknown. The lack of a standardized, biologically meaningful pollinator abundance currency applicable to any plant species in any ecological scenario remains a serious hindrance for formulating and testing even the simplest ecologically motivated comparisons among habitats or pollinator groups such as, e.g., Do pollinator types differ in abundance trends? Do temporal trends of pollinator functional abundance differ between habitats or plant species? For functional abundance analyses, the relationship between plants and pollinators can be reduced to two simple binary outcome variables depicting the probability of a flowering patch or an individual flower being visited by a pollinator during a pre-defined time frame (named "patch visitation probability" and "flower visitation probability," respectively, in this paper). This probabilistic approach to measuring pollinator functional abundance has

one requisite with two derived advantages. The requisite is that data must be collected following explicitly defined sampling units that are easily applicable to any plant species and amenable to extensive replication. The first advantage is that the biological meaning of these two probabilistic measurements is quite straightforward: their reciprocals estimate the mean length of time that flowering patches or individual flowers have to wait between consecutive pollinator visits, expressed in number of pre-established time frame units. The second advantage of the probabilistic approach is that statistical methods specifically tailored for binomial processes (generalized linear models; McCullagh and Nelder 1989) can be applied for obtaining standardized, comparable estimates of temporal trends in pollinator abundance, and all their analytical power harnessed for quantifying the rate of change, evaluating the uncertainty of estimates, and conducting formal statistical tests of explicit hypotheses.

In most natural communities, it will be impractical to quantify pollinator abundance for many plant species every year during a period long enough to be commensurate with the scale of environmental change. Reducing the temporal scope and the number of plant species down to feasible numbers comes at the cost of reduced generality. This study exemplifies a pragmatic strategy to alleviate the feasibility vs. generalizability conflict in the design of long-term ecological studies through the application of a "planned missing data design," in which strict completeness of species-year combinations was relaxed. Under this incomplete sampling strategy (Graham et al. 2006, Noble and Nakagawa 2018), many species–year combinations were randomly and deliberately missed during data collection, and only a random fraction of the total sample universe (i.e., all possible plant species–year combinations) was sampled for pollinator abundance. Planned missing data designs are usually used when researchers incorporate missing data with the intention of later using data imputation to recover such missing data (Enders 2010, Noble and Nakagawa 2018). In the present instance, however, this approach was not chosen for later making imputations of the missing data, but rather as a feasible way for detecting temporal trends even without complete temporal series of pollinator abundance data for every plant species. This was achieved by directly applying linear mixed models to the sparse species–year data matrix. In addition to tolerating sparseness in the data, linear mixed models allow drawing conclusions with reference to a broad inference space, which makes them particularly well suited to answer ecological questions whose scope transcends the limits of the specific samples studied (McLean et al. 1991, Bolker et al. 2009, Bolker 2015). The combination of planned missing data design with linear mixed models is the core element in the methodological framework of the present study, which will permit inferences on pollinator linear trends at the plant community level despite incomplete sampling of the species–year universe.

MATERIALS AND METHODS

Study area

Pollinator visitation data analyzed in this paper were obtained during February–September 1997–2017 (with a

TABLE 1. Plant species (*N* = 65) sampled for pollinator visitation on two or more years during 1997–2017 in the Sierra de Cazorla, southeastern Spain.

Species (Family)†	Life form‡	Flowering time§	Sampling site¶	Years sampled	No. sampling dates	No. pollinator censuses#	Flowering units × min
Achillea odorata (Asteraceae)	Hem	175	NC	2011, 2016	8	147	11,013‖
Allium roseum (Alliaceae)	Geo	140	CV	2011, 2016	4	205	35,592
Allium scorodoprasum (Alliaceae)	Geo	212	NC	2014, 2016	7	215	27,336‖
Anthyllis vulneraria (Fabaceae)	Hem	149	BJ	2008, 2015	7	140	148,290
Aphyllanthes monspeliensis (Aphyllanthaceae)	Hem	157	NC	2009, 2017	6	200	28,518
Armeria filicaulis (Plumbaginaceae)	Cha	153	NC	2010, 2016	7	161	21,795‖
Asphodelus cerasiferus (Asphodelaceae)	Geo	145	PP	2004, 2015	2	136	17,316
Berberis hispanica (Berberidaceae)	Pha	159	NT	2011, 2017	4	175	90,336
Campanula dieckii (Campanulaceae)	The	176	NC	2007, 2016	6	130	24,222
Carlina hispanica (Asteraceae)	Hem	228	VC	2010, 2015	6	145	10,080‖
Catananche caerulea (Asteraceae)	Hem	172	NZ	2006, 2017	6	150	5,214‖
Centaurea calcitrapa (Asteraceae)	Hem	189	RH	2005, 2015	4	126	9,249‖
Chondrilla juncea (Asteraceae)	Hem	229	NC	2014, 2017	7	175	8,871‖
Cirsium pyrenaicum (Asteraceae)	Hem	224	VC	2010, 2015	6	140	8,982‖
Cistus monspeliensis (Cistaceae)	Pha	152	HM	2007, 2016	4	154	7,569
Digitalis obscura (Veronicaceae)	Cha	161	PO	2004, 2014	4	140	18,201
Echium flavum (Boraginaceae)	Hem	146	BJ	2008, 2015	4	160	39,180
Erinacea anthyllis (Fabaceae)	Cha	145	CA	2004, 2015	2	136	99,420
Eryngium campestre (Apiaceae)	Hem	223	NC	2014, 2017	9	250	35,964‖
Eryngium dilatatum (Apiaceae)	Hem	198	NC, RM	2009, 2015	7	200	38,841‖
Fumana baetica (Cistaceae)	Cha	169	NC	2011, 2017	8	160	15,054
Gladiolus illyricus (Iridaceae)	Geo	175	NC	2004, 2014, 2015	7	190	15,216
Helianthemum apenninum (Cistaceae)	Cha	150	VC	2007, 2016	5	165	10,593
Helianthemum oelandicum (Cistaceae)	Cha	145	NC	2010, 2017	6	167	20,445
Helleborus foetidus (Ranunculaceae)	Cha	63	RH, NA	1998, 1999, 2012, 2013	21	1786	54,921
Hypericum perforatum (Clusiaceae)	Hem	193	NC	2010, 2016	9	140	27,825
Inula montana (Asteraceae)	Hem	170	NC	2015, 2017	6	155	6,669‖
Klasea pinnatifida (Asteraceae)	Hem	169	NC	2015, 2017	5	165	9,480‖
Knautia subscaposa (Dipsacaceae)	Hem	167	BJ	2007, 2015	4	177	12,687‖
Lavandula latifolia (Lamiaceae)	Cha	220	AU, CB, CC, NA, RT	1997, 2014, 2015, 2016	19	753	383,496
Linum bienne (Linaceae)	The	177	NC	2007, 2016	7	172	36,426
Linum tenue (Linaceae)	The	171	NA	2014, 2017	6	190	10,941
Lithodora fruticosa (Boraginaceae)	Cha	154	NC	2009, 2016	7	185	72,195
Lysimachia ephemerum (Primulaceae)	Geo	183	CV	2009, 2017	5	200	39,603
Mantisalca salmantica (Asteraceae)	Hem	199	NC	2010, 2016	6	160	8,535‖
Marrubium supinum (Lamiaceae)	Cha	164	NE	2004, 2014	7	160	72,465
Narcissus bujei (Amaryllidaceae)	Geo	65	CZ	2008, 2017	4	205	11,889
Narcissus cuatrecasasii (Amaryllidaceae)	Geo	113	FB	2010, 2011	5	214	34,080
Narcissus hedraeanthus (Amaryllidaceae)	Geo	86	NZ	2013, 2017	5	205	20,703
Narcissus longispathus (Amaryllidaceae)	Geo	90	GU, LC	2006, 2015	8	295	32,859
Orchis coriophora (Orchidaceae)	Geo	175	NC	2004, 2015	2	120	29,514
Ornithogalum umbellatum (Hyacinthaceae)	Geo	142	BJ	2010, 2016	6	160	24,837
Phlomis herba-venti (Lamiaceae)	Hem	183	PM	2005, 2014	4	150	74,397
Phlomis lychnitis (Lamiaceae)	Cha	178	EC	2004, 2014	2	151	18,546
Pistorinia hispanica (Crassulaceae)	The	170	LT	2004, 2014	5	161	133,569
Plumbago europaea (Plumbaginaceae)	Cha	226	NC	2014, 2017	8	205	64,245
Primula acaulis (Primulaceae)	Hem	111	FB, LC	2010, 2011	5	153	26,256
Rosa micrantha (Rosaceae)	Pha	181	NC	2010, 2017	7	145	10,422
Rosmarinus officinalis (Lamiaceae)	Pha	140	GU	2004, 2017	4	166	88,515
Santolina rosmarinifolia (Asteraceae)	Cha	192	NC	2010, 2015	8	130	29,889‖
Saponaria ocymoides (Caryophyllaceae)	Hem	153	VC	2004, 2017	2	141	70,680
Satureja intricata (Lamiaceae)	Cha	193	NC	2010, 2015	6	147	68,655
Sedum album (Crassulaceae)	Cha	185	NC	2010, 2017	5	165	7,305‖

TABLE 1. (Continued)

Species (Family)†	Life form‡	Flowering time§	Sampling site¶	Years sampled	No. sampling dates	No. pollinator censuses#	Flowering units × min
Sideritis incana (Lamiaceae)	Cha	178	RM	2008, 2014	6	130	54,819
Silene psammitis (Caryophyllaceae)	The	149	GU	2004, 2016	4	132	21,645
Sisymbrella aspera (Brassicaceae)	Hel	171	NC	2010, 2016	8	180	39,942
Stachys officinalis (Lamiaceae)	Hem	190	NC	2010, 2015	8	138	49,356
Teucrium aureum (Lamiaceae)	Cha	180	NC	2006, 2014	4	142	106,956
Teucrium rotundifolium (Lamiaceae)	Cha	176	NC	2007, 2016	6	181	49,818
Thymus mastichina (Lamiaceae)	Cha	169	NA	2004, 2014	5	160	80,343
Thymus orospedanus (Lamiaceae)	Cha	153	VC	2004, 2016	4	163	172,485
Urginea maritima (Hyacinthaceae)	Geo	236	VA	2014, 2017	10	219	14,787
Valeriana tuberosa (Valerianaceae)	Hem	136	BJ	2010, 2015	6	165	8,412‖
Viola cazorlensis (Violaceae)	Cha	151	AG, BC, PT	2005, 2007, 2015	6	123	26,625
Viola odorata (Violaceae)	Hem	112	FB	2010, 2011	5	198	22,950

Notes: Information on life form, flowering time, sampling sites, and total sampling effort are also shown for each species. See Appendix S1 for details and photographs of sampling sites.

†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.

¶Codes for the 29 sampling sites are shown in Appendix S1: Table S1, where location details and photographs are also included.

#Each "pollinator census," the basic sampling unit used in this study, consisted of a 3-min watch of all insects probing flowers in a flowering patch of the focal plant species.

‖Species for which the densely packed inflorescences, rather than individual flowers, were considered as the individual flowering unit in pollinator censuses.

gap in 2000–2003) in the Sierras de Cazorla-Segura-Las Villas Natural Park (Jaén Province, southeastern Spain). This region is characterized by large expanses of well-preserved habitats and outstanding plant diversity (Médail and Diadema 2009, Gómez Mercado 2011, Molina-Venegas et al. 2015). Sampling sites (*N* = 29) encompassed an elevational range of 850–1750 m above sea level and were all located in undisturbed habitats (Appendix S1: Table S1, Fig. S1). Criteria for selecting sites for pollinator sampling at the beginning of the study were that (1) signs of recent disturbances to vegetation were not apparent; (2) disturbances in the near future (e.g., by logging) were deemed unlikely; (3) all major regional habitat types were represented; and (4) the local abundance and distribution of one or more of focal insect-pollinated plant species (see *Plant species sample*) permitted the pre-established replication requirements (see *Pollinator visitation*). Major vegetation types at sampling sites included evergreen *Quercus*-dominated Mediterranean forest and tall scrubland; *Pinus nigra* or *P. pinaster* forest with deciduous *Quercus*; and several types of mature *Pinus nigra* forest. Representative photographs of all sites are shown in Appendix S1: Figs. S2–S30.

Recent trends in precipitation and temperature have been documented for the eastern Iberian Peninsula including the Sierra de Cazorla area (Linares and Tíscar 2010, Dorado Liñán et al. 2015, Coll et al. 2017). Meteorological data from two weather stations located within (Vadillo-Castril, elevation 960 m) or close (Pozo Alcón, elevation 893 m) to my study area were analyzed to corroborate these climatic trends for the 1997–2017 period. Daily precipitation data from Vadillo-Castril were provided by Centro de Capacitación y Experimentación Forestal. This station lacked temperature data and daily maximum and minimum temperature records for the Pozo Alcón station were taken from Red de Información Agroclimática de Andalucía.[2]

Plant species sample

Pollinator visitation to flowers was assessed for 65 plant species belonging to 28 different families (Table 1). Mean pollinator sampling dates for the species studied (Table 1) closely coincided in each case with peak or near peak flowering dates, and fell in March (3 species), April (4 species), May (11 species), June (28 species), July (11 species) and August (8 species). Seasonal distribution of peak flowering times in the species sample closely reflected the seasonal pattern of flowering times at the plant community level in the region (C. M. Herrera, *unpublished observations*). The majority of species chosen for study were widely distributed and/or locally abundant in the study area, and most of them (85%) were considered "very frequent" or "frequent" in the region by Gómez Mercado (2011). Lamiaceae (12 species), Asteraceae (10 species), Amaryllidaceae (4 species), and Cistaceae (4 species) contributed about one-half of species to the sample. Hemicryptophytes (22 species), chamaephytes (21 species), and geophytes (12 species) were the predominant life forms in the species sample (Table 1).

Supra-annual sampling scheme

It was impractical to assess pollinator abundance for each of the 65 plant species every year of the study period, hence

a planned missing data design was adopted as noted above. For each plant species studied, pollinator abundance was assessed in the same site for two separate years (Table 1). Exceptions were five species that were sampled more than two years and/or more than one site because they were part of other investigations (*Gladiolus illyricus*, *Helleborus foetidus*, *Lavandula latifolia*, *Narcissus longispathus*, *Viola cazorlensis*; Table 1). Particular care was taken to conduct pollinator censuses (see *Pollinator visitation* for definition) on the same flowering patches in different sampling years. For long-lived perennials, censuses in different years were generally performed on the same individuals. Due to the extremely slow pace of successional changes in the structure and composition of vegetation in the study region (Herrera 1998; *personal observations*), changes in vegetation during the temporal span of this study were imperceptible at all pollinator sampling sites. For a given plant species, the same number of pollinator censuses were conducted in different years, done in the same number of sampling dates during the local flowering peak. Species–year combinations for the second sampling were chosen randomly, subject to constraints set by time availability, sampling site accessibility, and random variation of the number of years elapsing between the earliest and latest sampling for each species ("supra-annual span"). Each year, species to be resampled were chosen a priori, the choice being thus uninformed by, e.g., phenology or flowering intensity. Average supra-annual span $\pm$ SE (means will be reported $\pm$ SE throughout this paper) was 7.3 ± 0.4 yr, ranging between 1 and 19 yr ($N = 65$ species), and its frequency distribution did not depart significantly from normality ($W = 0.970$, $P = 0.12$, Shapiro–Wilk normality test; Appendix S2: Fig. S1). The 136 species–year combinations actually sampled, out of the 65 species $\times$ 21 yr sample universe, are shown in Appendix S2: Fig. S2.

Pollinator visitation

Pollinator visitation to flowering patches and individual flowers was assessed by conducting observations according to the same standardized sampling design for all plant species studied. The basic sampling unit, termed "pollinator census" hereafter, consisted of a 3-min watch of a flowering patch whose total number of open flowers was also counted. All pollinators visiting flowers in the patch during the 3-min period were identified (see *Pollinator identification*), and the total number of flowers probed by each pollinator recorded. The areal extent and number of open flowers in monitored patches varied among plant species. Depending on flower density it was adjusted to permit confident monitoring of all pollinator activity in the patches from a distance of 1.5–2.0 m. It was impractical to assess the number of individual florets visited by pollinators when tiny flowers were densely packed into compact inflorescences (e.g., Asteraceae, Dipsacaceae). In these cases ($N = 16$ species, Table 1) the number of flower heads per patch and visited per census were counted rather than flowers, and visitation probabilities thus actually refer to inflorescences. For simplicity, I will refer hereafter to both individual flowers and flower heads as "flowers."

For each species–year combination, the following census replication rules were followed as strictly as possible. A minimum of 60 censuses should be conducted on ≥20 different, widely spaced flowering patches with roughly similar flower numbers. Censuses should be spread over three different, non-consecutive dates. On each date, censuses should be evenly 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. As found elsewhere (Fijen and Kleijn 2017, Knop et al. 2017), prior studies in the study area have shown that abundance and diversity of insect pollinators declined considerably in the afternoon (Herrera 1990, 1995; *personal observations*), and there was no evidence of crepuscular or nocturnal pollination for any of the plant species studied here. In addition, flowers of about one-third of the species studied are not available to pollinators in the afternoon, since their corollas whither (e.g., *Asphodelus*, *Hypericum*, *Urginea*), close (e.g., *Campanula*, *Catananche*, *Chondrilla*), or fall (e.g., *Cistus*, *Helianthemum*, *Linum*) shortly after noon. Several factors precluded fulfilling all the preceding rules for some species in some years. Since pollinator censuses were undertaken only on sunny windless days, long spells of poor weather sometimes limited the number of censuses and/or sampling days per year for species that flowered in winter–early spring. Other factors occasionally preventing fulfillment of replication rules included logistic problems (e.g., temporarily inaccessible sampling sites) and destruction of flowering patches by herbivorous mammals. Number of distinct sampling dates, number of censuses, and flower-min observational effort for every species, are summarized in Table 1. This study is based on pollinator visitation data acquired during a total of 13,054 pollinator censuses carried out on 299 different dates and accounting for a total watching effort of 2,877,039 flower-min. With the single exception of *Helleborus foetidus* (see *Acknowledgments*), I single-handedly conducted all censuses throughout the study, thus results are free from inter-observer heterogeneity.

Pollinator identification

Pollinators recorded during censuses were identified using one or more of the following methods, mentioned in decreasing order of frequency: (1) my familiarity with insect pollinators in the study region; (2) comparisons of close-up photographs taken during censuses with a reference collection of identified specimens; (3) identification by specialists on the basis of supplied close-up photographs taken during censuses; and (4) collection of specimens that were sent to specialists. Insect taxonomists that contributed identifications for this study are listed in *Acknowledgments*. Out of a total of 18,305 pollinators recorded in censuses (all plant species and years combined), 77.2% were identified down to species, 4.3% were assigned to cryptic pairs of congeneric species (e.g., *Polyommatus celina/icarus*, *Orphilus beali/niger*), and 17.7% were identified to genus. The remaining 0.8% was identified only to family, which, in nearly all cases, involved flies of the family Anthomyiidae. Orders and genera will be the only taxonomic levels considered in this paper. Subgenera of *Lasioglossum* (subgenera *Dialictus*, *Evylaeus*, *Lasioglossum*) and *Halictus* (subgenera *Halictus*, *Seladonia*, *Vestitohalictus*) bees (Halictidae), and some

subgenera of *Empis* flies (subgenera *Euempis*, *Xanthempis*; Empididae), were afforded consideration of genera due to distinctiveness in size and foraging behavior at flowers.

Close-up photographs of pollinators visiting flowers were routinely taken during censuses using a DSLR digital camera and 105 mm macro lens. In addition to being used for identification purposes and keeping photographic vouchers of pollinators, these photographs also helped to ascertain the pollinator status of the different taxa, particularly those with small body sizes. Only taxa whose individuals contacted anthers or stigmas and had pollen grains on body surfaces, as verified by naked eye observations or close-up photographs, are considered as pollinators in this study.

Data analysis

Analytical approach.—Two measurements of pollinator functional abundance ("pollinator abundance" hereafter) were considered: (1) *patch visitation probability*, defined as per-time-unit probability that at least one pollinator entered the flowering patch under observation and probed at least one flower, and (2) *flower visitation probability*, or per-time-unit probability that one individual flower in the patch was visited per census, estimated as the ratio of number of flowers visited to those available in the patch. These two measurements will always refer to a 3-min time frame, which was the duration of each census. Patch visitation probability provides a rough measurement of the operational abundance of pollinators from the perspective of the local flowering plant population. Flower visitation probability reflects the frequency with which individual flowers are expected to receive pollinator service. Patch visitation and flower visitation probabilities are not entirely independent of each other, because average patch visitation probability sets an upper limit on average flower visitation probability. This statistical nonindependence did not affect results because both parameters were analyzed separately.

Each pollinator census provided point estimates of patch visitation and flower visitation probabilities. Replication of pollinator censuses across sites and plant species, and over two or more years within species, allowed calculation of population estimates and associated uncertainty measurements for pollinator abundance measurements. Tests performed in this study and their logical relationships are summarized in Table 2. Pollinator abundance measurements were tested at three different taxonomic resolution levels (all pollinator taxa combined, the four major insect orders separately, and selected genera separately) and two different inference spaces, namely at a local scale within individual plant species and at the regional plant community level. "Year" was the predictor variable in all analyses. It was treated as a categorical predictor when testing for significance of supra-annual *heterogeneity* within plant species (i.e., the dependent variable of interest varies significantly among years), or as a continuous predictor when testing for supra-annual *trends* at the plant community level (i.e., the dependent variable of interest increased or decreased linearly in the plant community as a whole from the beginning to the end of the study period). It must be stressed that by distributing the sampling years for all plant species over the 1997–2017 period (Appendix S2), sampling each species two or more times, and treating species as random effects, linear trends at the plant community level can effectively be estimated by generalized linear mixed models despite data for individual species coming from just two sampling years. In each of the Tests 5–10 (Table 2), the model parameter estimate for the year term represents the common linear slope obtained from information from all years and plant species. Tests of curvilinearity, obtained by including a year quadratic term in models, were conducted in preliminary analyses but never resulted in statistically significant improvements of linear fits. For simplicity, these tests will be omitted from the analyses reported here.

Linear mixed models were applied for testing the plant community-wide hypothesis of linear trends in pollinator

TABLE 2. Summary of the different tests of supra-annual variation in pollinator abundance conducted in this study, identified as numbered entries in the table.

Pollinator functional abundance measurement (response variable) and taxonomic level (class of pollinators considered)	Inference space (domain of applicability of results)	
	Individual plant species. Predictor: Year as categorical variable (tests for fluctuations)†	Regional plant community. Predictor: Year as continuous variable (tests for linear trends)†
Patch visitation probability		
All taxa	1 (Fig. 3)	5 (Table 4)
Orders	2 (Appendix S5: Fig. S1)	6 (Table 5)
Selected genera		7 (Fig. 10)
Flower visitation probability		
All taxa	3 (Fig. 4)	8 (Table 4)
Orders	4 (Appendix S5: Fig. S2)	9 (Table 5)
Selected genera		10 (Fig. 10)

Notes: Tests differ with regard to the pollinator abundance measurement used as response variable, the taxonomic category of pollinators considered, whether supra-annual fluctuations or linear trends are tested, and the domain of applicability of results. The figure or table holding the results for each test is shown in parentheses beside each entry.

†Synopsis of linear models used in the different tests, expressed in R language syntax. See *Data analysis: Statistical procedures* for additional details. Tests 1 and 2: glm(formula = patch.visitation ~ factor(year) + scale(flowers.in.patch), family = "binomial" (link = "logit"), data=.). Tests 3 and 4: glm(formula = flowers.visited/flowers.in.patch ~ factor(year) + scale(flowers.in.patch), family = "binomial" (link = "logit"), weights = flowers.in.patch, data=.). Tests 5, 6 and 7: glmer(patch.visitation ~ scale(as.numeric(year)) + scale(flowers.in.patch) + (1| species) + (1|site), family = "binomial" (link = "logit"), data=.). Tests 8, 9 and 10: glmer(flowers.visited/flowers.in.patch ~ scale(as.numeric (year)) + scale(flowers.in.patch) + (1|species) + (1|site), family = "binomial" (link = "logit"), weights = flowers.in.patch, data=.)

abundance (Table 2). Justification for applying mixed models to the pollinator census data included (1) information was obtained according to a planned missing data design where the grouping variables (plant species and sampling site) were a random subset from larger populations; (2) there were many levels per grouping variable (plant species and sampling sites), relatively few data on each level (only one or a few species were sampled in most sites; Appendix S1: Table S1), and uneven sampling across levels; and (3) the central objective of analyses was to make predictions about unobserved levels of grouping variables (Bolker 2015).

Statistical procedures.—Statistical significance of within-species, supra-annual changes in patch (Tests 1 and 2, Table 2) and flower visitation probabilities (Tests 3 and 4, Table 2) was evaluated by fitting generalized linear models to pollinator census data separately for each plant species. Binomial error distribution and logit link function were used in these models, and the predictor was year as a categorical variable. Between-year comparisons for individual plant species may be affected to an unknown extent by unaccounted sources of variance other than year itself (e.g., delayed effects on pollinator activity of weather during the days immediately preceding censuses). The possible influence of such effects on results was tested indirectly by looking for associations between statistical significance of between-year fluctuations in patch and flower visitation, and total number of sampling dates for each species, on the assumption that more sampling dates could have produced more accurate estimates of between-year differences and better buffering against short-term stochastic effects. Furthermore, since the number of flowers per patch could influence pollinator behavior and visitation probability, it was included as a covariate in all models. Number of flowers was centered to mean zero and scaled to standard deviation unity to circumvent model convergence problems due to large eigenvalues and eigenvalue ratios. A detailed analysis of the effects of variation in patch flower numbers on pollinator visitation probabilities fall beyond the scope of this study and only results that are relevant to the interpretation of supra-annual variation will be presented. Syntax of models fitted is shown in footnotes to Table 2. In patch visitation analyses the response was a binary variable, 1–0 for visited and unvisited patch, respectively. In flower visitation analyses, the response was a continuous variable ranging between 0 and 1, the quotient of flowers visited during the census to flowers available in the patch. In analyses consisting of arrays of concurrent statistical tests addressing a common null hypothesis, significance levels were adjusted using the Benjamini-Hochberg procedure (Benjamini and Hochberg 1995) to account for increased type I error rates.

Generalized linear mixed models were applied for testing linear trends in aspects of pollinator abundance at the regional plant community level. Binomial error distribution and logit link function were used in all instances. Either patch visitation (visited/unvisited patch; Tests 5, 6, and 7, Table 2) or flower visitation (flowers visited/flowers available; Tests 8, 9, and 10, Table 2) were the response variables, and year was the continuous, primary fixed effect (predictor). Year was centered to mean zero and scaled to standard deviation unity to avoid problems of convergence in model fitting due

to large eigenvalue ratios. Number of flowers in the patch (scaled and centered) were included as a fixed-effect covariate to control for its influence on pollinator visitation. Plant species and sampling sites were included as random intercepts effects ("scalar random effects"; Bolker 2015). Syntax of models fitted is shown in footnotes to Table 2. The sampling structure inherent to the data, with many missing species–year–site combinations, precluded the incorporation of more complex random effects (e.g., year × species or year × site non-scalar random effects). Elucidating patterns of variation among plant species or sampling sites in pollinator visitation measurements fall beyond the scope of this paper, and presentation of random effect parameter estimates will be limited to variance estimates.

All statistical analyses were carried out using the R environment (R Core Team 2017). The p.adjust function from the stats library was used for Benjamini-Hochberg adjustments of statistical significance levels. Generalized linear models were fitted with function glm from the R stats library, and generalized linear mixed models with the glmer function in the lme4 library (Bates et al. 2015). Functions from the sjPlot library (Lüdecke 2017) were used to check the assumptions of mixed-effects models (Pinheiro and Bates 2000, Bolker 2015). Fitted generalized linear mixed models were checked for overdispersion using function dispersion_glmer from the blmeco library (Korner-Nievergelt et al. 2015). Adding observation-level random effects to the data (a new grouping variable with a separate level for every observation; Bolker 2015) was sufficient to fix the weak overdispersion of some models. Statistical significance of the fixed effect in the models (year) was determined by ordinary log-likelihood ratio tests (Zuur et al. 2009) using the anova function from the R stats library. 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 predicted marginal effects of year on measurements of pollinator visitation holding number of flowers per patch fixed.

Results

The environment, 1997–2017

Total annual precipitation fluctuated widely over the 1997–2017 period, ranging between 567 and 1961 mm/yr (Appendix S3: Fig. S1), but this variation did not conform to a linear temporal trend (Appendix S3: Table S1). Semiannual precipitation did exhibit a linear trend. January–June precipitation tended to increase and July–December precipitation tended to decrease over the period considered (Appendix S3: Fig. S1). A shift in seasonal distribution of precipitation, which tended to be more concentrated on winter–spring, seemed to occur during the study period as denoted by the marginally significant year × half-year period interaction effect on precipitation (Appendix S3: Table S1).

Monthly means of daily maximum temperature tended to increase significantly over 2000–2017 (Appendix S3: Table S1). This trend affected all months similarly, as denoted by nonsignificance of the year × month interaction

effect and the roughly parallel temperature × year regressions (Appendix S3: Fig. S2). On average, mean daily maximum temperatures increased 0.05 ± 0.11°C/yr, or ~1°C from the beginning to the end of this study. Monthly means of daily minimum temperature did not increase significantly over the same period (Appendix S3: Table S1, Fig. S2).

The pollinators

For all plant species and years combined, Hymenoptera (46.0% of individuals), Diptera (19.7%), Coleoptera (17.5%), and Lepidoptera (16.5%) accounted for the vast majority of individual pollinators recorded (N = 18,305). Three additional insect orders (Hemiptera, Neuroptera, Orthoptera) contributed altogether a negligible fraction of total pollinators (0.3%) and will not be considered further in this paper.

With few exceptions, most plant species studied had taxonomically diverse pollinator assemblages at the insect order level (Fig. 1). Only five species (7.7% of total) had pollinators belonging exclusively (>99% individuals) to one insect order (Hymenoptera: *Digitalis obscura*, *Helleborus foetidus*, *Phlomis lychnitis*, *Viola odorata*; Diptera: *Saponaria ocymoides*; Appendix S4: Table S1). Hymenoptera were the dominant pollinators (>50% of individuals) in 30 species, while Diptera, Lepidoptera, and Coleoptera predominated in 8, 6, and 5 species, respectively (Fig. 1). Two or more orders had roughly similar proportional importances in the remaining 16 species (Fig. 1; see also Appendix S4: Table S1, for sample sizes and summaries of pollinator composition for each plant species).

Pollinators that were identified at least to genus (N = 18,129) belonged to 245 genera, all plants and years combined. Diptera (83 genera) and Hymenoptera (69) exhibited the highest generic diversities, and Lepidoptera (52) and Coleoptera (38) the lowest ones. Truncated genus abundance curves for these four major orders including genera contributing >1% of pollinators are shown in Fig. 2. Curves denoted similar dominance in all orders, with a few abundant genera accounting for a large proportion of individuals. Within the Hymenoptera, bees of the genera *Bombus*, *Andrena*, *Evylaeus*, *Hylaeus*, and *Ceratina*, mentioned in decreasing order of frequency, were most frequent and accounted collectively for 50.7% of individuals. Within the Diptera, *Sphaerophoria*, *Bombylius*, *Eristalis*, *Rhyncomyia*, and *Nowickia* were most frequent, accounting altogether for 42.8% of individuals. The genera *Anthrenus*, *Lobonyx*, *Anthaxia*, *Dasytes*, and *Pseudovadonia* accounted collectively for 56.6% of individuals in the Coleoptera. Within the Lepidoptera, species of *Argynnis*, *Thymelicus*, *Melanargia*, *Aricia*, and *Lasiommata* accounted for 57.6% of individuals.

Individual plant species: patch visitation

Average patch visitation probabilities (probability of at least one flower in a patch being probed during a 3-min period) from different sampling years, all pollinators combined, are plotted in Fig. 3 for every plant species studied (Test 1, Table 2). Heterogeneity among years was statistically significant in 24 species (37% of total). Among these latter, the number of species with temporal increases (positive slopes in Fig. 3) doubled the number of species with decreases (16 vs.

8 species, respectively; Fig. 3). Statistical significance of supra-annual variation for individual plant species was not related to the number of different days on which censuses were performed (Table 1; 6.1 ± 0.8 d and 6.0 ± 0.4 d for species with and without significant supra-annual variation, respectively; χ^2 = 0.25, df = 1, P = 0.61, Kruskal-Wallis rank sum test).

Supra-annual variation in patch visitation probabilities for the four main orders (Test 2, Table 2) is summarized in Appendix S5: Fig. S1, separately for each plant species. The corresponding statistical significance levels are shown in Appendix S5: Table S1. All orders exhibited significant supra-annual fluctuation in patch visitation probabilities in a substantial number of the plant species studied. Coleoptera patch visitation fluctuated significantly in 15 plant species (23% of total; 4 declines, 11 increases), Diptera in 17 species (26%; 8 declines, 9 increases), Hymenoptera in 26 species (40%; 7 declines, 19 increases), and Lepidoptera in 8 species (12%; 2 declines, 6 increases). In those plant species where statistically significant supra-annual changes occurred there was thus a prevailing trend for all major insect orders to increase in patch visitation probabilities (Appendix S5: Fig. S1).

Individual plant species: flower visitation

Mean flower visitation probabilities (probability of visitation of an individual flower during a 3-min period) on different sampling years, all pollinators combined, are shown in Fig. 4 for all the plant species studied (Test 3, Table 2). Species differed by more than two orders of magnitude in mean flower visitation probability, which ranged between 0.0043 ± 0.0038/3 min in *Viola cazorlensis* and 0.552 ± 0.164/3 min in *Cistus monspeliensis* (interquartile range = 0.050–0.177). Statistically significant supra-annual fluctuations in flower visitation probability occurred in 54 species (83% of total). Among these latter, species with increases in flower visitation probabilities predominated over those with decreases (33 vs. 21 species, respectively; Fig. 4). Statistical significance of supra-annual variation was not related to the number of different days on which censuses were performed (6.1 ± 0.5 d and 5.9 ± 0.4 d for species with and without significant supra-annual variation, respectively; χ^2 = 0.22, df = 1, P = 0.64, Kruskal-Wallis rank sum test).

Flower visitation probabilities by the four main orders (Test 4, Table 2), separately by plant species and year, are summarized in Appendix S5: Fig. S2, and associated statistical significance levels are shown in Appendix S5: Table S2. One or more orders exhibited significant supra-annual variation in flower visitation probabilities in the vast majority of the plant species studied (62 out of 65 species). Coleoptera flower visitation probability varied significantly among years in 21 plant species (32% of total; 5 declines, 16 increases), Diptera in 35 plant species (54%; 15 declines, 20 increases), Hymenoptera in 49 plant species (75%; 16 declines, 33 increases), and Lepidoptera in 31 plant species (48%; 14 declines, 17 increases). In those plant species where some statistically significant fluctuation occurred, the prevailing trend across years was thus one of increased flower visitation probabilities by one or more orders (Appendix S5: Fig. S1).
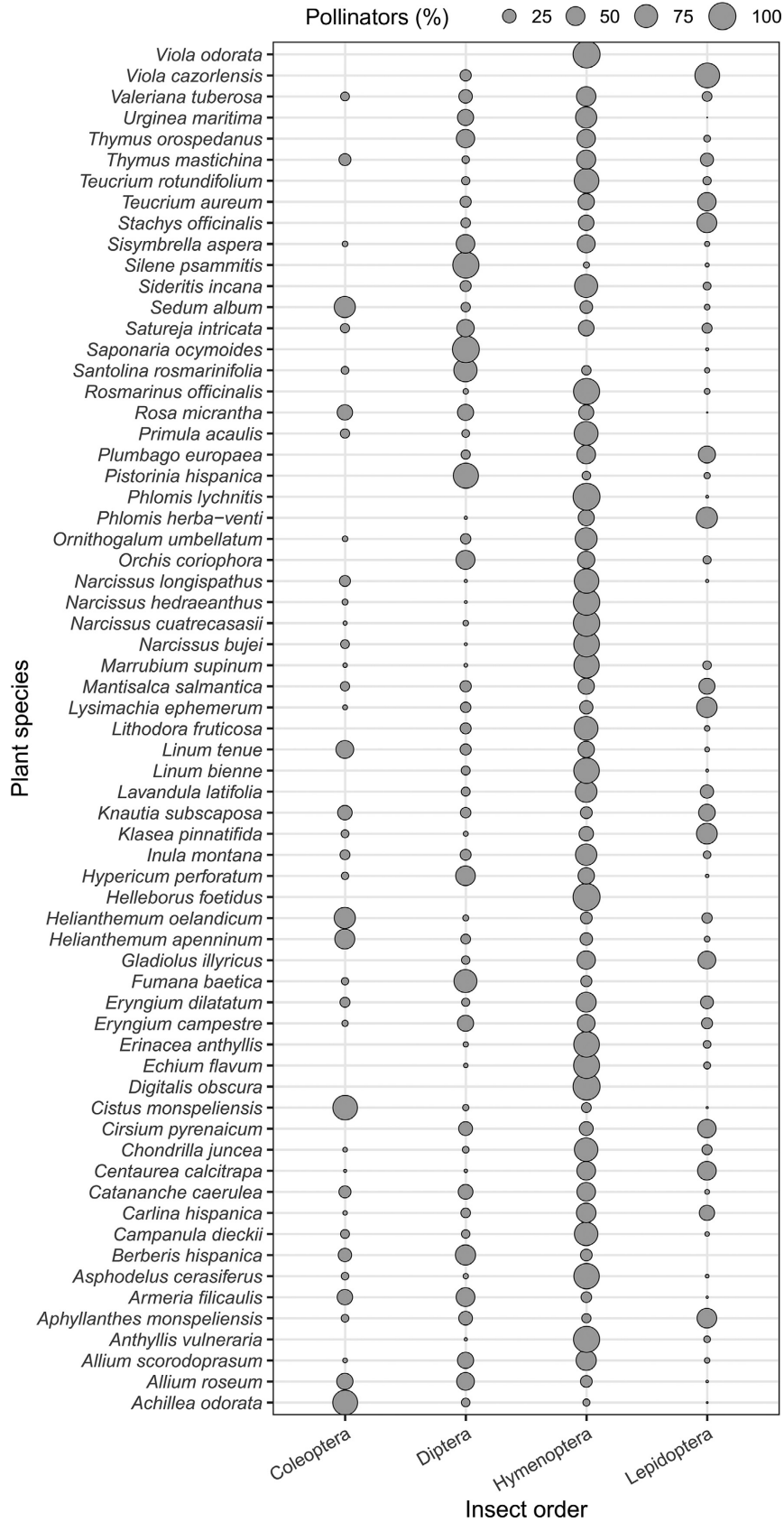
FIG. 1. Proportional importance of the four main insect orders as pollinators of the 65 plant species considered in this study, all years combined. Raw data and sample sizes shown in Appendix S4: Table S1.
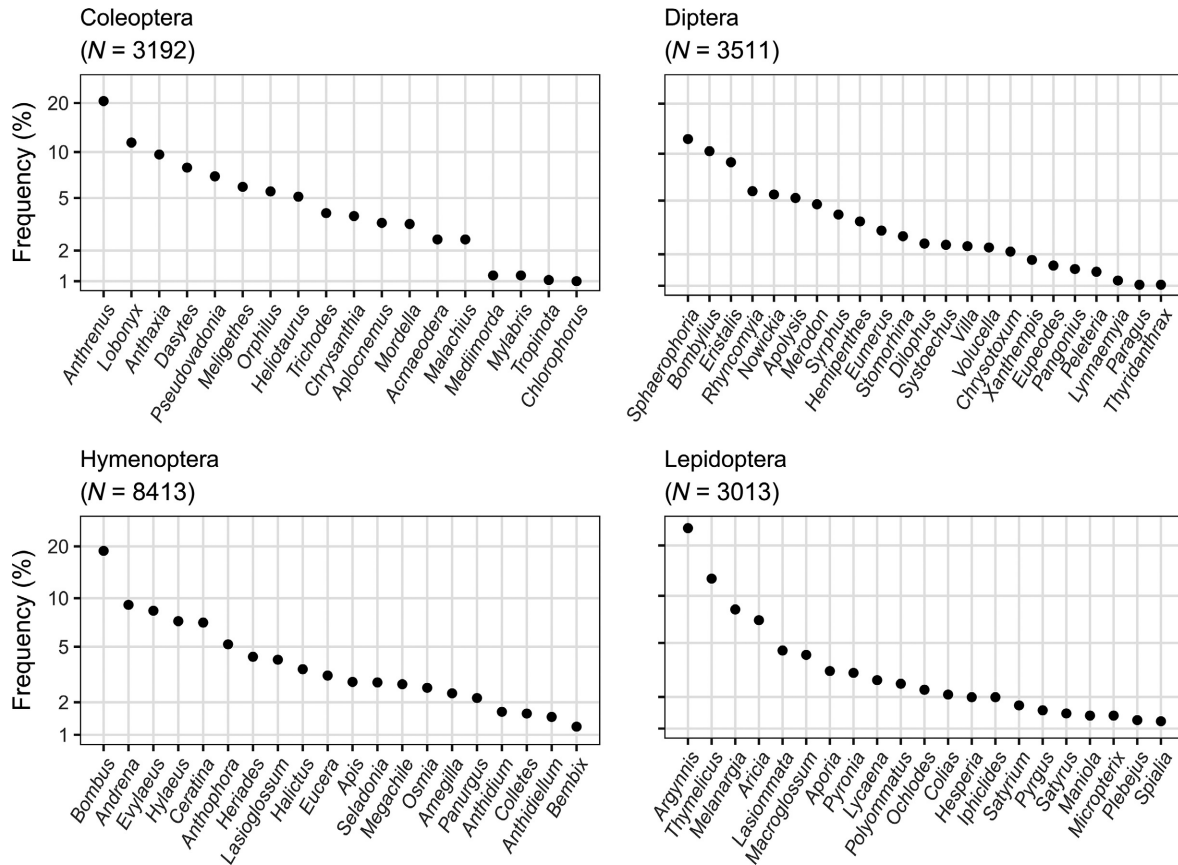
FIG. 2. Truncated genus abundance curves for the four major orders of pollinators, all years and plant species combined. Each graph shows only those taxa contributing >1% of total individuals recorded for the order (*N*). Note logarithmic scale on vertical axes.

Visitation probabilities and number of flowers per patch

The number of flowers per censused patch was included as a covariate in models fitted to test the effect of year on patch and flower visitation probabilities for each plant species, whose results have been presented in the preceding two sections (Tests #1 and #3 in Table 2; Figs. 3 and 4). A graphical summary of estimated model parameters for the year (as a factor) and flowers-per-patch (scaled) terms in the models for all insect orders combined is shown in Fig. 5. After statistically controlling for annual variation in flower or patch visitation, patch visitation probability was directly related to the number of flowers per patch in the majority of plant species, (i.e., model parameter estimates > 0), while flower visitation probability was inversely related in most species (model parameter estimates < 0). Estimates of supra-annual variation, however, were unrelated to these patterns. Interspecific variation in model parameters estimating supra-annual variation in patch and flower visitation probabilities (vertical axes in Fig. 5) was independent of pollinator visitation responses to number of flowers per patch ($r_s = -0.086$ and -0.060, $P = 0.52$ and 0.64, for patch and flower visitation, respectively; Spearman rank correlation coefficients).

Supra-annual fluctuations in pollinator composition

As shown in the preceding sections, between-year variation in pollinator abundance experienced by individual plant

species reflected fluctuations in patch and flower visitation probabilities by one or more major insect orders. Composition of pollinator assemblages at the order level varied considerably among years in many species (see, e.g., *Aphyllanthes monspeliensis*, *Armeria filicaulis*, *Cistus monspeliensis*, or *Marrubium supinum*; Appendix S5: Figs. S1, S2). This section examines the relationships between interspecific differences in long-term unstability of pollinator composition and factors related to sampling design, ecological conditions, and species-specific traits.

The number of insect orders whose patch or flower visitation probabilities varied significantly among years ("fluctuating orders" hereafter) provides a rough index of the magnitude of supra-annual changes in pollinator composition for a particular plant species. Frequency distributions of the number of fluctuating orders are shown in Fig. 6. Irrespective of whether patch or flower visitation data are considered, plant species differed widely in number of fluctuating orders and therefore in the magnitude of supra-annual changes in pollinator composition (Fig. 6). A measurement of supra-annual pollinator composition dissimilarity was obtained by computing for each species the Euclidean distance between sampling years in the four-dimensional space defined by visitation probabilities of the four major orders (Appendix S5: Table S3). Interspecific variation in pollinator composition dissimilarity was not significantly related to either the number of years elapsing between earliest and latest sampling occasions or the total number of distinct sampling
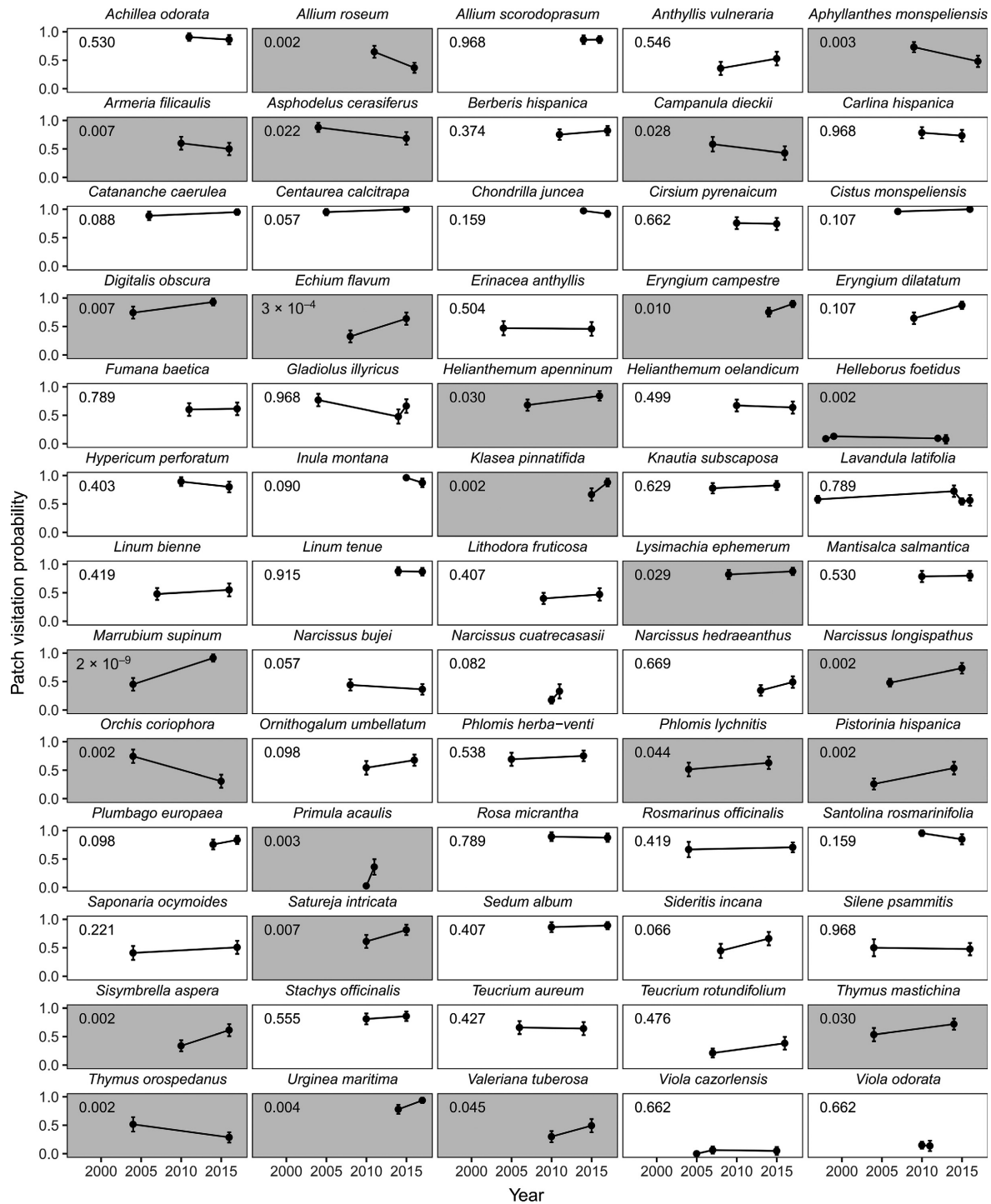
Fig. 3. Pollinator patch visitation probabilities (the probability that at least one flower in a focal flowering patch is probed in 3 min) for the 65 plant species studied on different study years, all insect taxa combined. Dots represent means, and vertical segments extend over ± 2 SE. Figures inside panels are P values for the effect of year (corrected with the Benjamini-Hochberg procedure), which were obtained for each species from separate generalized linear models that included the number of flowers per patch as a covariate (models for Test 1 in Table 2). Panels with a gray background highlight species with $P < 0.05$.

dates for each species (Table 3). These results tend to dismiss the possibility that observed variation between plant species in the magnitude of supra-annual pollinator dissimilarity was a spurious consequence of interspecific differences in supra-annual sampling span and the number of distinct sampling dates. Supra-annual dissimilarity in composition was not

significantly related to elevation of sampling site (a proxy for ecological conditions), flower corolla type (open vs. restrictive), or plant life form (Table 3). In contrast, there were highly significant positive relationships between supra-annual dissimilarity in patch visitation and flower visitation, and flowering phenology (mean pollinator census date, days from
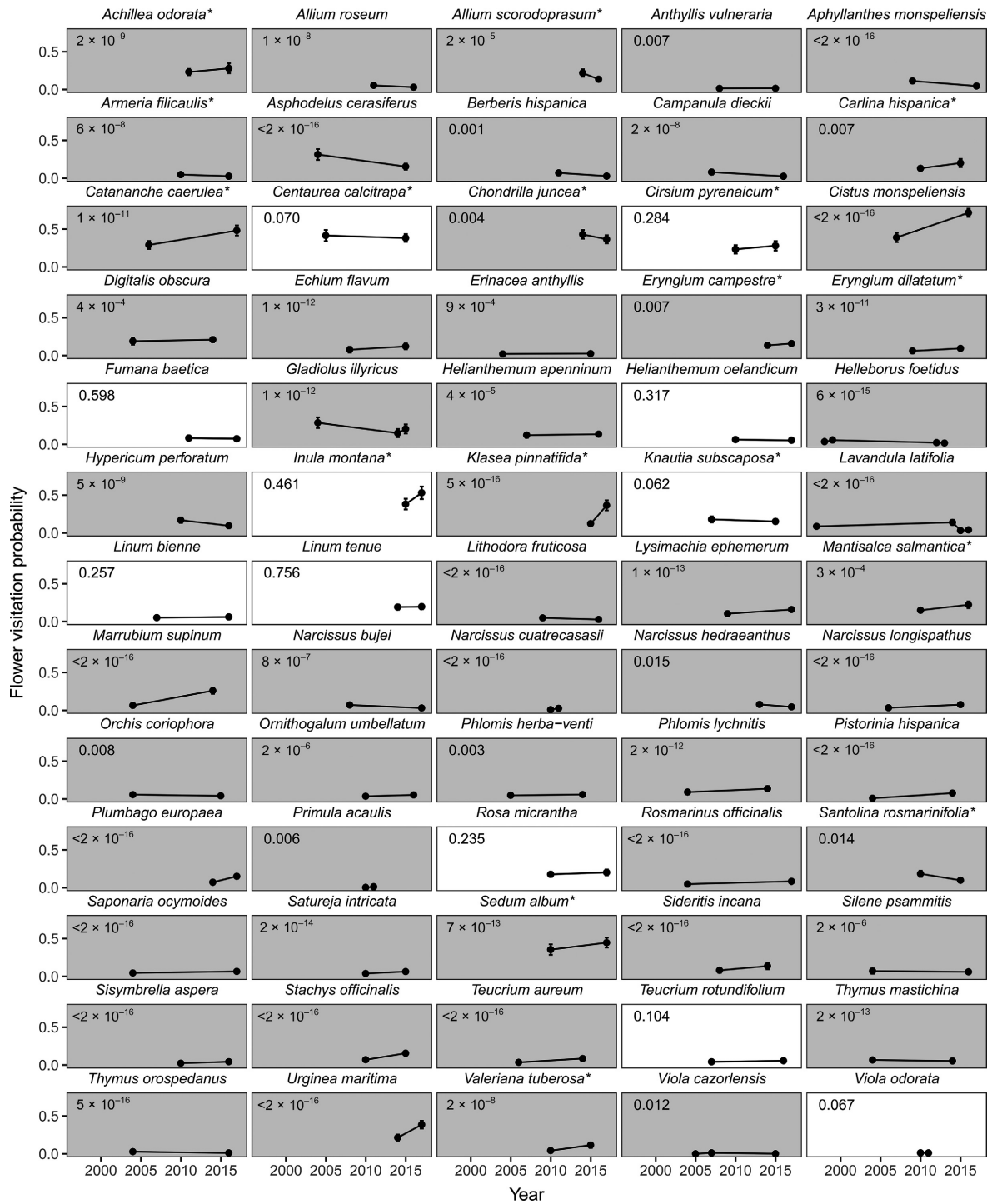
FIG. 4. Pollinator flower visitation probability (probability of individual flowers in a focal flowering patch being probed in 3 min) for the 65 plant species studied in different years, all insect taxa combined. Dots represent means, and vertical segments extend over ±2 SE. Figures inside panels are *P* values for the effect of year (corrected with the Benjamini-Hochberg procedure), which were obtained for each species from separate generalized linear models that included the number of flowers per patch as a covariate (models for Test 2 in Table 2). Panels with a gray background highlight species with *P* < 0.05. Species in which visitation rate refers to inflorescences rather than single flowers are marked with asterisks.

1 January; Table 3). On average, pollinator assemblages of species that flowered in winter and early spring (February–April; e.g., *Helleborus foetidus*, *Narcissus cuatrecasasii*, *Primula acaulis*, *Viola odorata*) were the least supra-annually variable, while those of summer flowering species (June–August; e.g., *Centaurea calcitrapa*, *Chondrilla juncea*, *Eryngium campestre*, *Urginea maritima*) were the most variable (Fig. 7).
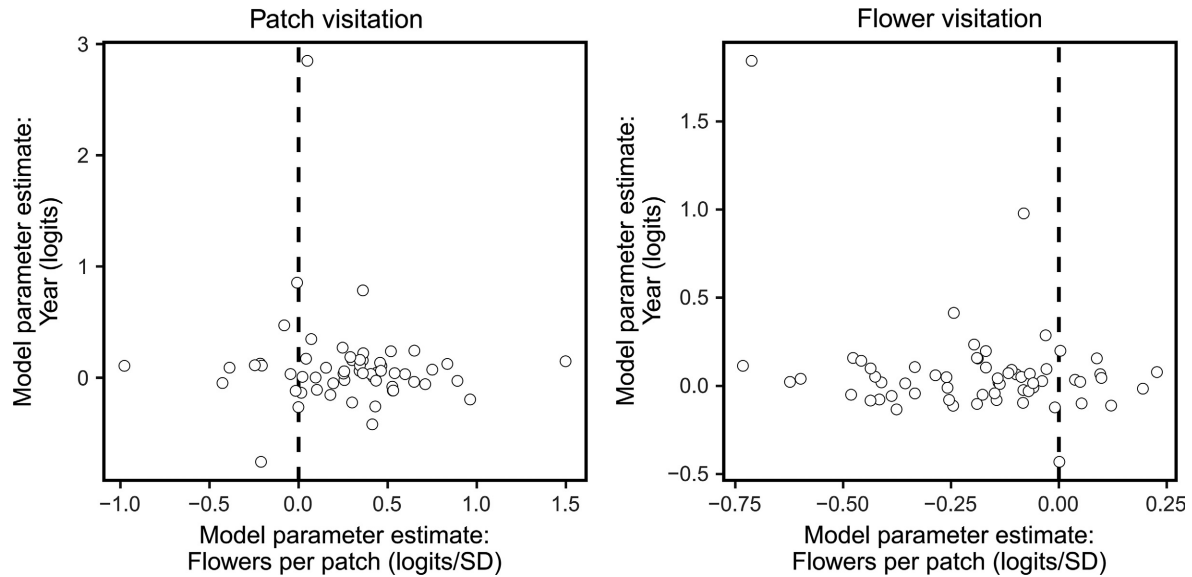
FIG. 5. Estimated model parameters for the year (as factor) and flowers-per-patch (centered to mean zero and scaled to standard deviation unity) terms in the models relating patch and flower visitation probabilities to year fitted separately for each plant species, all insect orders combined (Tests 1 and 3 in Table 2). Each symbol corresponds to one species ($N = 61$). Four species that were sampled in more than two years (Table 1) were excluded since, in these instances, the year factor did not have a unique model parameter. Vertical dashed lines are drawn at $x = 0$ and mark the boundary between positive (right) and negative (left) responses of pollinator visitation to number of flowers per patch.
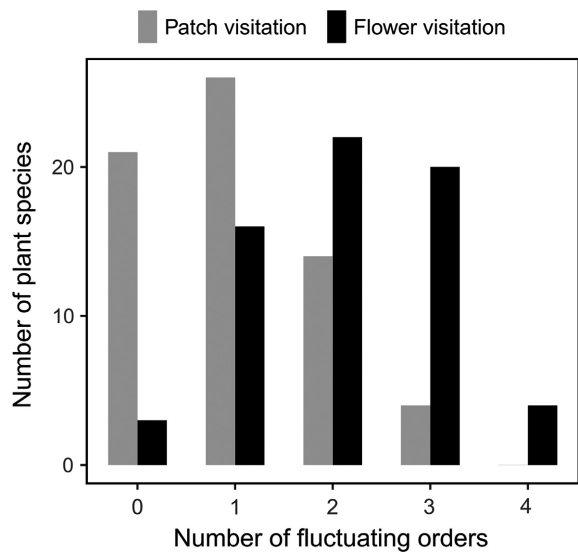
FIG. 6. Frequency distributions of the number of pollinator insect orders (out of the four possible: Coleoptera, Diptera, Hymenoptera, Lepidoptera) that exhibited statistically significant supra-annual changes in visitation probabilities (fluctuating orders) for each plant species. Changes refer to the particular set of years on which each species was sampled. Separate distributions are shown for figures obtained from patch visitation and flower visitation data (Appendix S5: Tables S1, S2, respectively).

Community-level trends: all pollinators

Generalized linear mixed models fitted to patch and flower visitation data, all pollinator taxa combined (Tests 5 and 8, Table 2), revealed statistically significant, positive linear trends in pollinator abundance at the regional plant

community level over 1997–2017 (Table 4). Community-level trends were discernible despite large variances in visitation probabilities associated with plant species and, to a lesser extent, sampling sites, the two random effects included in models (Table 4). Parameter estimates for the year fixed effect were closely similar for patch and flower visitation data, and their confidence intervals overlapped extensively. Log odds for patch and flower visitation events, all pollinators combined, increased by 0.108 and 0.095 per time standard deviation unit (6.0 yr in the sample), respectively (Table 4). Exponentiation of these figures produced odds ratios of 1.113 and 1.100 for patch and flower visitation events, respectively. The odds of a randomly chosen flowering patch or flower being visited during the three-minute duration of a pollinator census thus increased by about 10% every six years. From 1997 to 2017, the predicted marginal effect of year on patch visitation probability increased from 0.55 to 0.64, and the marginal effect on single flower visitation probability increased from 0.019 to 0.026 (Fig. 8). As shown in the next two sections, different groups of pollinators contributed differently to these long-term linear trends of increasing pollinator visitation.

Community-level trends: insect orders

Results of generalized linear mixed models testing linear trends at the plant community level in patch and flower visitation probability by the four major orders (Tests 6 and 9, Table 2) are summarized in Table 5. Coleoptera and Hymenoptera exhibited statistically significant, increasing linear trends in patch visitation probability, while Diptera and Lepidoptera did not show significant trends. Results for flower visitation probability were similar, except that Diptera showed a significant, albeit weak increasing trend.

TABLE 3. Relationships across plant species ($N = 65$) between supra-annual dissimilarity in composition of the pollinator assemblage (Euclidean distance among sampling years in the multivariate space defined by visitation probabilities of the four major insect orders) and several putative correlates associated with sampling design, ecological features, and plant intrinsic traits.

	Patch visitation data†			Flower visitation data†		
Putative correlate	r_s	χ^2	P	r_s	χ^2	P
Sampling design						
Supra-annual span‡	−0.074		0.56	−0.081		0.52
Number of sampling dates§	0.162		0.20	0.161		0.20
Ecological features						
Sampling site elevation	0.036		0.78	−0.059		0.64
Mean pollinator census date (days from 1 January)	0.499		0.00003	0.488		0.00005
Plant intrinsic traits						
Life form		7.05	0.22		5.68	0.34
Corolla type (open vs. closed)¶		2.11	0.15		0.031	0.86

Notes: †Results of Spearman rank correlations (r_s) and Kruskal–Wallis analyses of variance (χ^2).
‡Length of interval in years between the earliest and latest pollinator sampling for a given species (Appendix S2).
§Number of distinct sampling dates on which censuses were conducted (Table 1).
¶Species with bowl-shaped, non-restrictive, dialypetalous corollas vs. those with tubular, sympetalous, or otherwise restrictive corollas (e.g., papilionaceous corollas).
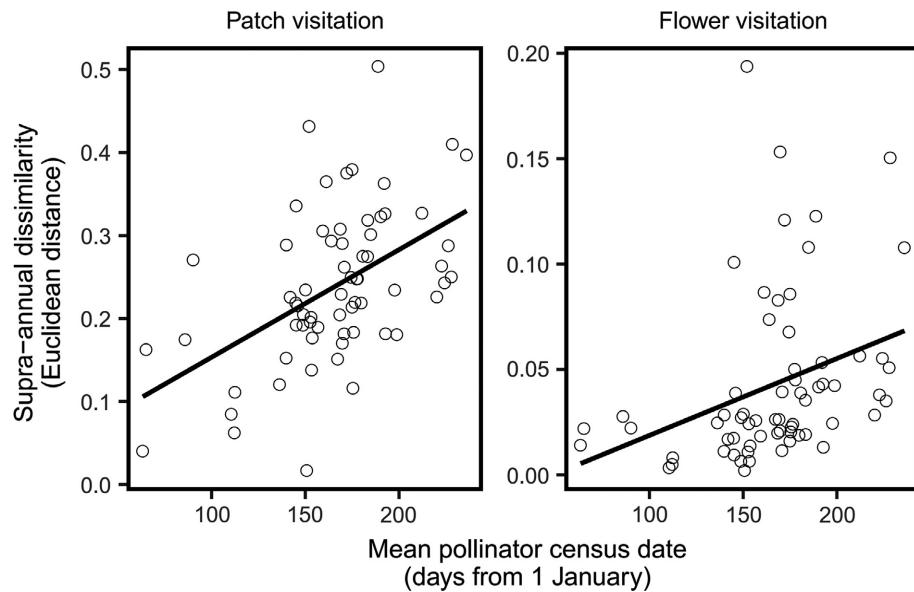

FIG. 7. Relationships across species ($N = 65$) between time of flowering (mean date of pollinator censuses) and supra-annual dissimilarity in pollinator composition, as measured with the Euclidean distance between sampling years in the space defined by patch (left) or flower (right) visitation probabilities of the four major insect orders. Lines are least-squares fitted regressions.

Coleoptera had the steepest temporal increases in patch and flower visitation probabilities (odds ratios = 1.694 and 1.611, respectively; computed by exponentiating log odds in Table 5), followed by Hymenoptera (odds ratios = 1.264 and 1.255, respectively).

Predicted marginal effects of year on patch and flower visitation probabilities computed separately for the four major insect orders are plotted in Fig. 9. Patterns for the two visitation-related parameters are closely similar. The most important result is that, at the plant community level, the predicted probability per time unit of flowering patches or individual flowers being visited by hymenopterans increased considerably over the study period. This led to a substantial increase in the dominance of this group over the rest of orders in terms of patch and flower visitation. Visitation probabilities

increased significantly with year also for Coleoptera and Diptera (only for flower visitation; Table 5), but these increasing trends actually had negligible impacts on predicted marginal effects, because of the lower quantitative importance of these two orders for most plant species (Fig 1; Appendix S4: Table S1). In general, therefore, predicted visitation probabilities of Coleoptera, Diptera and Lepidoptera remained roughly constant in absolute terms between 1997 and 2017, although their relative importance declined steadily because of the steep increase of Hymenoptera (Fig. 9).

Community-level trends: selected genera

Long-term linear trends in patch and flower visitation documented in the preceding sections are the composite

TABLE 4. Results of generalized linear mixed models testing supra-annual linear trends in total pollinator visitation, all taxa combined, at the regional plant community level (N = 13,054 pollinator censuses; Tests 5 and 8 in Table 2).

| | Fixed effect, year† | | | | Random effects | | | |
| | | | | | Plant species (N = 65) | | Sampling site (N = 29) | |
Response variable	Parameter estimate‡	95% confidence interval§	χ^2¶	P	Variance#	ICC‖	Variance#	ICC‖
Patch visitation probability	0.108	0.047–0.168	12.25	0.00047	1.481	0.289	0.346	0.068
Flower visitation probability	0.095	0.040–0.155	11.10	0.00086	2.038	0.224	0.511	0.056

Notes: †Number of flowers per patch was included as a fixed-effect covariate in models. This was done exclusively for statistically controlling its influence on pollinator visitation, and results for this covariate are omitted.

‡Year was centered to mean zero and scaled to standard deviation unity. Parameter estimates shown are thus standardized coefficients that represent the expected change in log odds for an increase of one standard deviation on the predictor axis (= 6.0 yr in the data), holding fixed the number of flowers per patch (fixed-effect covariate).

§Obtained using the profile likelihood method.

¶From likelihood ratio tests.

#Between-group variance, i.e., variation between individual intercepts and average intercept.

‖Intraclass correlation coefficient, a measurement of the correlation among observations within the same group of data (species or sampling site), which equals the ratio of the among-group variance to the total variance.
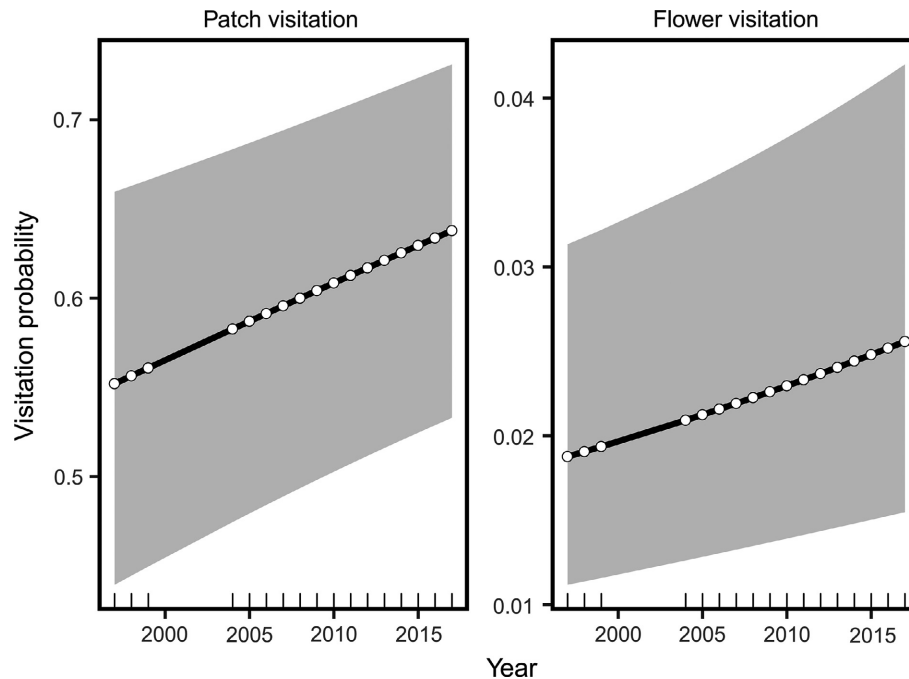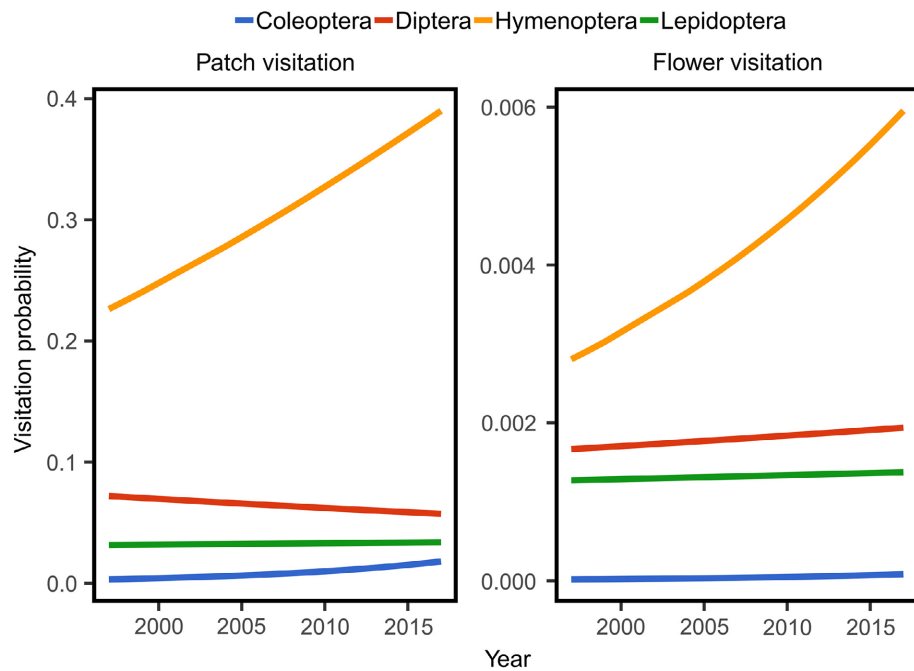

FIG. 8. Mean predicted marginal effects of year (holding the number of flowers per patch fixed) on patch and single flower visitation probabilities, all pollinators combined. Confidence intervals (95%) of prediction shown as shaded areas, computed without taking into account the uncertainty of the random effects parameters. See Table 4 for analytical results, statistical significance levels, and additional details.

outcome of trends at lower taxonomic levels, and more specifically of the proportion of lower-level taxa whose visitation probabilities declined, remained stable, or increased over the years. This section analyses long-term trends in patch and flower visitation probabilities for the 20 most frequent genera in each major insect order (19 in Coleoptera; Tests 7 and 10, Table 2). The insect genera included in these analyses accounted for 98.5%, 84.1%, 92.6%, and 90.3% of all Coleoptera, Diptera, Hymenoptera, and Lepidoptera individuals recorded in censuses, respectively. Results of analyses, including model parameter estimates and statistical significance levels, are presented in Appendix S6:

Table S1. Graphical summaries of model parameter estimates are shown in Fig. 10.

A considerable number of genera exhibited statistically significant linear trends in patch visitation probability (34 genera, 43.0% of total, all orders combined), the sign of which was predominantly positive (21 genera). Even more genera showed statistically significant linear trends in flower visitation probability (58 genera, 73.4%), the sign being positive in 28 genera (Appendix S6: Table S1). All orders had genera with positive and negative linear trends, but their relative proportions varied (Fig. 10). In Coleoptera and Hymenoptera genera with positive trends in both patch and flower

TABLE 5. Results of generalized linear mixed models testing supra-annual linear trends in patch and flower visitation probabilities by the four major pollinator groups at the regional plant community level ($N = 13,054$ pollinator censuses; Tests 6 and 9 in Table 2).

| | Fixed effect, year | | | | Random effects | | | |
| | | | | | Plant species ($N = 65$) | | Sampling site ($N = 29$) | |
Response variable and pollinator group	Parameter estimate	95% confidence interval	χ^2	P	Variance	ICC	Variance	ICC
Patch visitation probability								
Coleoptera	0.527	0.393–0.663	61.15	5.3×10^{-15}	10.856	0.754	0.250	0.017
Diptera	−0.074	−0.154 to 0.006	3.28	0.070	2.434	0.367	0.913	0.138
Hymenoptera	0.234	0.172–0.295	55.67	8.6×10^{-14}	1.526	0.296	0.337	0.065
Lepidoptera	0.021	−0.075 to 0.119	0.18	0.67	5.044	0.561	0.663	0.074
Flower visitation probability								
Coleoptera	0.477	0.413–0.541	223.16	2.2×10^{-16}	11.911	0.758	0.511	0.033
Diptera	0.045	0.018–0.073	10.55	0.0012	3.078	0.390	1.516	0.192
Hymenoptera	0.227	0.147–0.307	30.87	2.8×10^{-8}	3.864	0.295	0.613	0.047
Lepidoptera	0.023	−0.010 to 0.057	1.87	0.17	6.270	0.581	1.228	0.114

Note: All footnotes to Table 4 apply also here.

FIG. 9. Mean predicted marginal effects of year (holding the number of flowers per patch fixed) on patch and single flower visitation probability by the four major insect orders. See Table 5 for analytical results, statistical significance levels, and additional details.

visitation probabilities prevailed (upper right quadrants in plots, Fig. 10), and genera with negative trends (lower left quadrant, Fig. 10) were comparatively scarce. In Diptera and Lepidoptera, in contrast, the numbers of genera with increasing and decreasing long-term trends were roughly similar (Fig. 10). As denoted by the size of confidence ellipses, Hymenopteran genera were the least variable in sign and magnitude of linear trends, Coleopteran and Lepidopteran genera were intermediate, and Dipteran genera fell at the opposite extreme and had characteristically heterogeneous supra-annual patterns (Fig. 10).

In the Coleoptera, the genera *Acmaeodera* (Buprestidae), *Dasytes* (Dasytidae), *Tropinota* (Scarabaeidae), and

Mylabris (Meloidae) stood apart from the rest by their particularly steep increases in patch and flower visitation probabilities over the study period. Within the Diptera, the genera *Syrphus* (Syrphidae), *Dilophus* (Bibionidae), and *Xanthempis* (Empididae) had the most steep declining trends, while *Peleteria* (Tachinidae), *Eumerus* (Syrphidae), and *Hemipenthes* (Bombyliidae) had very steep increasing trends. In the Lepidoptera, the genus *Iphiclides* (Papilionidae) stood alone by its strong increasing trend in patch and flower visitation, while on the opposite extreme some genera of Hesperiidae (*Pyrgus*, *Thymelicus*) and Nymphalidae (*Maniola*) had declining trends. In the Hymenoptera (all bees except *Bembix*), patch and flower visitation
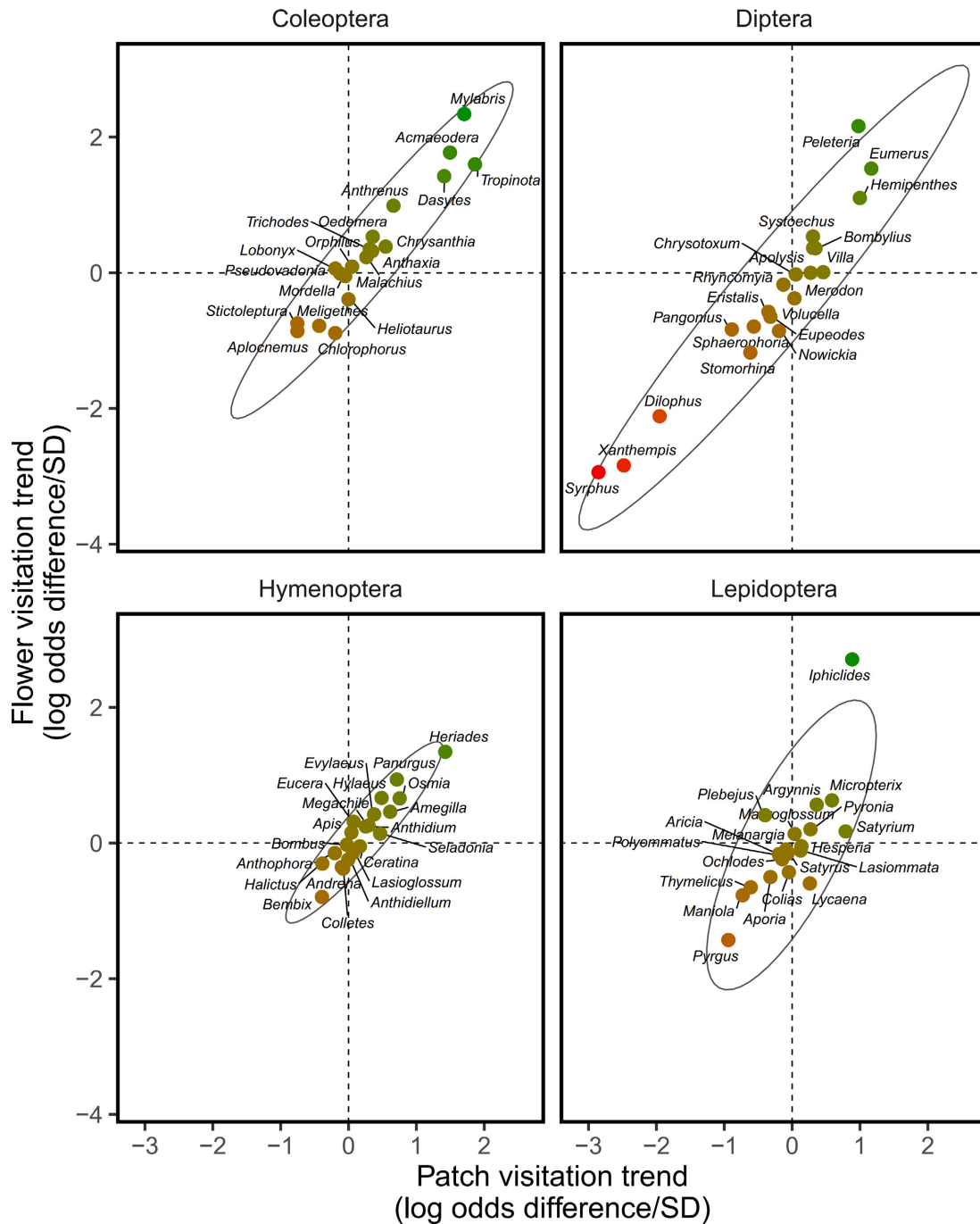
Fig. 10. Long-term, community-wide trends in patch and flower visitation probability by the most frequent genera in each of the four major insect orders (Tests 7 and 10 in Table 2). Generalized linear mixed models were fitted separately for each genus, with either patch or flower visitation probability as the binomial response variable. Plotted are parameter estimates obtained for each genus for the fixed effect in the model (year). These values represent the expected change in log odds for an increase of one standard deviation in year (6.0 yr in the data). Genera in the upper right quadrants show positive trends in both patch and flower visitation probabilities, while those in lower left quadrants are characterized by negative trends in both magnitudes. Points on or close to the origin correspond to genera without long-term trends. Ellipses represent the 95% confidence intervals around the bivariate means. Dots are coded using a color gradient running from strongly declining (red) to strongly increasing trends (green), colors being mapped to the geometric distance of each point to the origin. Detailed results of analyses, including model parameter estimates used in this figure and their associated statistical significance levels, are presented in Appendix S6: Table S1.

probabilities by the genera *Heriades*, *Osmia* (Megachilidae), *Panurgus* (Andrenidae), and *Hylaeus* (Colletidae) tended to increase most markedly over the study period. Long-term

trends for the two genera of social bees (*Apis*, *Bombus*) were either statistically nonsignificant or, if significant, quantitatively negligible (Appendix S6: Table S1).

DISCUSSION

The changing montane environment

Dendroclimatological reconstructions and temporal series of instrumental meteorological data show that the southeastern quarter of the Iberian Peninsula, where the Sierra de Cazorla is located, is experiencing significant warming in combination with a weak decline in total annual precipitation, shifts in its seasonal distribution, and increased drought index (precipitation minus evapotranspiration; Martín-Benito et al. 2008, Linares and Tíscar 2010, Vicente-Serrano et al. 2014, Dorado Liñán et al. 2015, Coll et al. 2017). Data from the Vadillo-Castril and Pozo Alcón weather stations for the period 1997–2017 presented in this paper conform closely to these regional patterns. Average trend values of up to +0.7°C per decade in summer daily maximum temperature reported previously (Acero et al. 2014) closely match the estimated mean increase of +0.05°C per year found in this study for the Pozo Alzón weather station over 2000–2017.

Current environmental changes have been linked to a variety of structural and functional variations in the Mediterranean climate ecosystems of the Iberian Peninsula, including phenological shifts in plants and pollinators (Gordo and Sanz 2005), accelerated shrubland degradation (Vicente-Serrano et al. 2012), and decline in tree growth (Martín-Benito et al. 2008, Linares and Tíscar 2010, Dorado Liñán et al. 2015). Climate change might also directly or indirectly influence the size of pollinator populations and their interactions with plants (Memmott et al. 2007, Hegland et al. 2009, Thomson 2010), and climate-mediated detrimental effects on pollination success have been implicated to explain declines in seed regeneration of animal-pollinated plants in natural Mediterranean habitats (Giménez-Benavides et al. 2018). I am not aware, however, of any prior investigation addressing changes in pollinator abundance in natural Mediterranean habitats of the Iberian Peninsula on a time scale commensurate with that of ongoing climatic change.

The changing pollinators

The negligible frequency of honey bees (*Apis mellifera*) and the high taxonomic diversity of insect pollinators found in this study underscore the ecological integrity of pollinator assemblages in the undisturbed montane habitats studied. In number of individuals, *Apis mellifera* ranked 21st and accounted for only 1.3% of all insects recorded in pollinator censuses. The species was recorded from flowers of only 18 plant species (27% of total). Managed beehives have been absent from my core study area at least since 1987, and honey bees recorded in my censuses most likely originated from small feral colonies living in tree hollows in mature forests or from managed beehives several kilometers away (C. M. Herrera, *unpublished data*). Regardless of their origin, patch and flower visitation probabilities by honey bees remained stable throughout this study (*Apis* data point in Fig. 10 located close to the origin). They represented a negligible fraction (2.9%) of all individual bees recorded, which contrasts with the much higher values reported by pollination community studies in Mediterranean-climate areas of the Iberian Peninsula (range = 50–83% of all bees; Herrera 1988*b*, Bosch et al. 1997, Magrach et al. 2017) or elsewhere in the Mediterranean Basin (32–65%; Potts et al. 2003, 2006). The harmful effect of honey bees on the size and diversity of native pollinator populations (Shavit et al. 2009, Lindström et al. 2016, Torné-Noguera et al. 2016) has probably been insignificant in these montane habitats during at least three decades, which provides an unique opportunity to gain insights on long-term trends of natural pollinators in an unusually honey-bee-free environment.

The insect pollinator assemblage of the 65 plant species considered in this study consisted of 260 genera and at least 615 species (C. M. Herrera, *unpublished data*). These figures amply exceed all published estimates for plant communities in the Mediterranean Basin, the only exception being the 666 species reported from 133 plant species from a phrygana ecosystem in Greece (J. Herrera 1988, Petanidou and Ellis 1993, Petanidou et al. 2008, Bosch et al. 2009, Magrach et al. 2017). Coleoptera, Diptera, and Lepidoptera accounted collectively for a substantial fraction of the genera (73.5%), species (49.8%; C. M. Herrera, *unpublished data*), and individuals (54%) recorded, and the dominant pollinators of 19 plant species (29% of total) belonged to one of these three orders. These results stress the important contribution of non-hymenopterans to the regional pollinator assemblage, and strongly support the view highlighted in *Introduction* that biologically realistic assessments of long-term pollinator dynamics, particularly in species-rich, natural habitats require an unprejudiced consideration of all taxonomic groups of pollinators, not just hymenopterans as frequently done in studies of highly human-modified habitats (Winfree et al. 2009, Bommarco et al. 2012, Ollerton et al. 2014, Senapathi et al. 2015, 2017).

Rather than revealing a decline in pollinator abundance associated with current climatic trends in the Sierra de Cazorla mountains, the present investigation has documented significant long-term increases in pollinator visitation probability to flowering patches and individual flowers. In most plant species, patch visitation probability was directly related, and flower visitation probability inversely related, to the number of flowers per patch. Nevertheless, the possibility that long-term trends in patch and flower visitation are a spurious consequence of supra-annual variations in the number of flowers in censused patches can be safely rejected. Including in all analyses the number of flowers per patch as a covariate efficaciously controlled for the influence of its variation on pollinator visitation, as clearly shown by the statistical independence of model parameter estimates for year and flowers per patch. Circumstantial evidence supports instead the view that major trends in pollinator abundance are the result of increasing ambient temperature favoring the activity, and perhaps also population size and elevational distribution range, of certain sun-loving, ectothermic pollinators. In general, positive relationships between ambient temperature and pollinator abundance are to be expected in alpine and montane habitats where the thermal environment often constrains the activity of ectothermic pollinators (Kalin Arroyo et al. 1985, Totland 1994, Herrera 1995). In the present study, this applies

particularly to bees, whose positive linear trend in abundance was the main factor responsible for the community-wide increase in patch and flower visitation. Small-sized solitary bees that exhibited some of the strongest positive trends over 1997–2017 (*Evylaeus, Heriades, Hylaeus, Panurgus, Seladonia*; Fig. 10) typically select the hottest period of daytime for foraging, fly preferentially in late spring-summer, avoid flowers at shady locations, and depend exclusively on solar irradiance for warming up (Herrera 1990, 1997, Shmida and Dukas 1990, Osorio-Canadas et al. 2016; C. M. Herrera, *unpublished data*). Increasing ambient temperatures during the study period may therefore have broadened the seasonal duration and spatial extent of their favorable microhabitats, leading to greater flower visitation by these abundant bees (Fig. 2). This provides support to earlier predictions on the possible beneficial impact of climatic warming on Mediterranean bees (Osorio-Canadas et al. 2016) and, more generally, on the body-size-dependent effects of climate warming on populations of ectothermic animals (Lindmark et al. 2018). Similar mechanisms might also explain the long-term changes in activity at flowers of some small- and medium-sized ectothermic beetles (e.g., *Anthrenus, Dasytes, Mylabris, Tropinota*; Fig. 10), the other insect group along with bees that contributed to increasing patch and flower visitation probabilities. Although detailed information on the thermal ecology of these beetles is not available, they generally forage at sunny places during the hottest period of daytime, and increasing ambient temperatures may have broadened their favorable microhabitats.

Increasing temperature and rainfall reduction may have accounted for the decline in abundance of some pollinator groups via detrimental effects on larval life stages. This most likely applies to all declining genera of hoverflies (Syrphidae) with aphidophagous larvae (*Syrphus, Sphaerophoria, Eupeodes*; Fig. 10), for which the warming trend may have reduced their larval food supply (Adler et al. 2007). The decline of hoverflies with aquatic larvae (*Eristalis*; Fig. 10) might be related to the progressive narrowing of the rainfall period. Natural history information on the species involved is insufficient to interpret several conspicuous declining trends in abundance in relation to climate change, such as those of some genera in the butterfly family Hesperiidae (*Thymelicus, Pyrgus*), or some Bibionid (*Dilophus*) and Empidid flies (*Xanthempis*; Fig. 10).

More than a few pollinator genera showed nonsignificant or, if significant, quantitatively minor long-term trends in abundance despite changes in precipitation and temperature (i.e., those located on or close to the origin in the graphs of Fig. 10). Prominent among these are the two genera of social bees, *Bombus* and *Apis*, which elsewhere are the focus of current concerns on pollinator declines (see references in *Introduction*). All *Bombus* species that are widely distributed in the Sierra de Cazorla region were recorded in this study (*pascuorum, pratorum, sylvestris, terrestris, vestalis*; Castro 1989; C. M. Herrera, *unpublished data*). The long-term stability shown collectively by this group is at odds with sharp reductions in the size of *Bombus* populations around their southern range limits in North America and western Europe (Kerr et al. 2015), and with the declines predicted by species distribution models for the Mediterranean region (Rasmont et al. 2015).

Between-year fluctuations: the plants' perspective

Broad between-year fluctuations in abundance and composition of animal pollinator assemblages seem the rule in nature, as documented for innumerable plant species from diverse habitats and geographical regions (Herrera 1988*a*, Eckhart 1992, Brunet 2009, Lázaro et al. 2010, Smith-Ramírez et al. 2014, Fisogni et al. 2016). With few exceptions, however, the small number of plant species considered in earlier studies and their narrow temporal scopes have precluded interspecific comparisons of the sign and magnitude of annual changes, as well as exploring possible correlates of interspecific variation (but see, e.g., Lázaro et al. 2010). One major result of the present study is thus the finding that as many as 54 of the 65 plant species studied (83%) exhibited statistically significant fluctuations between sampling years in flowering patch visitation probability, flower visitation probability, or both (Figs. 3, 4). As found in other plant diversity hotspots (Alonso et al. 2010), seed production by many of the species studied here is frequently pollen limited (Herrera 1995, 2002, 2004, Alonso et al. 2013). It may thus be tentatively concluded that (1) widespread supra-annual fluctuations in pollinator visitation are likely to translate into parallel oscillations and uncertainties in the sexual reproduction of many species (Herrera 1995, 2002) and (2) positive linear trends in pollinator visitation at the plant community level may in the long run result in a predictable reduction in pollen limitation and improved sexual reproduction in some species. The possible impact of these effects on the persistence and dynamics of these mountain plants will depend on differences among pollinator taxa in quantitative and qualitative aspects of pollinating effectiveness (Herrera 1987, Larsson 2005, Fisogni et al. 2016), and also on the degree to which seed production is actually limiting the recruitment of their populations (Giménez-Benavides et al. 2018).

For a given plant species fluctuations in pollinator visitation probabilities often did not occur in unison across insect orders, which led to broad supra-annual variations in the relative importance of major pollinator groups as previously reported for other plant communities (Lázaro et al. 2010). Plant species varied widely in supra-annual instability of pollinator composition, as measured by the Euclidean distance between years in the four-dimensional space defined by visitation probabilities of major orders. In some instances, fluctuations in pollinator composition were extreme, as in species where pollinator assemblages were alternatively dominated by Lepidoptera or Hymenoptera (e.g., *Phlomis herba-venti, Teucrium aureum*; Appendix S5). In the opposite extreme, there were species whose relative pollinator composition remained essentially constant across years (e.g., *Achillea odorata, Fumana baetica, Helianthemum apenninum, Lysimachia ephemerum*). Interspecific differences in supra-annual stability of pollinator composition were unrelated to variation in length of sampling interval, location along the elevational gradient, life form, or corolla type, but were closely correlated with time of flowering. Winter- and early-spring-flowering species had pollinator assemblages whose composition changed little between years, while summer-flowering ones tended to have the most variable ones. This seasonal gradient in the supra-annual stability of pollinator composition runs parallel to the seasonal gradient in overall

pollinator diversity occurring in the study region (C. M. Herrera, *unpublished data*), which indicates that the most taxonomically diverse pollinator assemblages were also those with the most intensely fluctuating compositions. These results suggest that, in the montane habitats studied, the generalist pollination system of many summer-flowering species (e.g., *Lavandula latifolia*, Herrera 1988*a*) is intrinsically associated with extreme supra-annual fluctuations in composition. Furthermore, unrecognized seasonal biases in the selection of plant species for pollinator community studies are likely to result in biased conclusions with regard to the long-term stability in pollinator assemblage composition. For example, had the present study focused on a narrower seasonal window by considering only summer flowering species, then supra-annual unstability in pollinator composition at the plant community level would have been overestimated.

Community-wide inferences

At mid latitudes, species richness of regional plant communities often numbers in the hundreds, roughly three-quarters of which are expected to be biotically pollinated (Ollerton et al. 2011). Leaving aside some classical monographs that dealt with complete or nearly complete regional plant–pollinator assemblages (Müller [1883], 397 plant species; Robertson [1928], 453 species; Moldenke [1976], 133 genera), pollination community studies have been customarily confined to a sample, generally small, of all biotically pollinated species occurring in a given region (the species sample universe). The present investigation is not an exception to the incompleteness of pollination community studies imposed by practical limitations. The set of 65 plant species considered here, although more numerous than in many previous community studies, still represents only about 15% of biotically pollinated species occurring in the study area (C. M. Herrera, *unpublished data*). In contrast to previous research, however, explicit recognition here that the set of species studied was just a sample drawn from the broader universe to which conclusions on pollinator abundance trends should ideally apply, combined with the application of mixed effects models to data collected using a planned missing data design, have allowed for the first time reaching conclusions on pollinator abundance trends that are applicable to the entire plant community.

Generalized linear mixed models "are still part of the statistical frontier" (Bolker 2015:309). Application of generalized linear mixed models and treatment of plant species and sampling sites as random effects are two innovative aspects of the analytical scheme adopted in this study. A key property of mixed effects models is their potential for making inferences that apply to different populations of effects, or "inference spaces," some of which have no counterpart in conventional fixed effects models (McLean et al. 1991, Schabenberger and Pierce 2001, Littell et al. 2006). In the context of the present study, the regional plant community represents the "broad inference space" (sensu McLean et al. 1991), or the universe of all possible plant species and sites that could have been chosen for sampling pollinators for this study (Schabenberger and Pierce 2001). Conclusions of this study on community-wide linear trends in pollinator abundance refer to that broad inference space. This means that model parameter estimates for the year fixed effect and their associated uncertainties (Tables 4, 5) refer to the entire regional plant community including unobserved levels of random variables, and do not depend on the random effects, i.e., the particular sample of species and sites studied insofar as these are representative of the population one wishes to generalize to (Littell et al. 2006, Bolker 2015). In summary, therefore, it is the analytical properties of mixed effects models that made possible to state the conclusion that over the period 1997–2017 a randomly chosen flowering patch or flower, from any randomly chosen species of the plant community, located in any randomly chosen site of the study region, experienced a significantly increasing probability per time unit of being visited by some insect pollinator, and more specifically by some bee.

Concluding Remarks

As stressed in *Introduction*, claims of "pollinator decline" and "pollination crisis" repeatedly echoed in recent ecological literature have been often motivated by pollinator data from biologically impoverished, anthropogenic or highly human-modified ecosystems in a few European and North American regions. Results of this study from undisturbed montane habitats of the Sierra de Cazorla in southeastern Spain do not show a decline of overall pollinator functional abundance over the 1997–2017 period despite significant climatic changes involving rainfall and temperature. Instead, average probability of pollinator visitation per time unit to flowering patches and individual flowers tended to increase significantly over the two decades covered by this investigation, mostly as a consequence of increasing visitation by bees and, to a smaller extent, also by beetles. From 1997 to 2017, the estimated probability of patch visitation by bees (per 3-min) at the plant community level increased from 0.226 to 0.390, and the probability of bee visitation to individual flower from 0.0028 to 0.0059 (Fig. 9). Reciprocals of these figures indicate that the estimated time between consecutive bee visits to patches shortened from 13 to 8 min over the study period, and the estimated time between consecutive bee visits to individual flowers from 17 to 8 h. These results denote a notable improvement of the pollinating environment for plants in terms of a shortening of their "waiting times" for bee pollinators.

Results of the present study militate against the universality of pollinator declines apart from heavily human-altered ecosystems and their immediate surroundings. In addition, this investigation has shown that, in natural habitats, the unfolding of community-wide changes in pollinator abundance presumably induced by climatic change can obey extremely complex dynamics that defy naïve generalizations based on modest sampling. Although increasing trends in pollinator abundance prevailed at the plant and pollinator community levels, not all plant species experienced similar changes over time in pollinator abundance or composition. Likewise, temporal trends in pollinator abundance were far from homogeneous across the different orders and genera of insect pollinators, which caused substantial alterations in the taxonomic composition of the pollinators of many plant species. On one hand, these findings highlight the critical importance of analyzing taxonomically comprehensive samples of plants and pollinators when looking for temporal

trends in pollinator abundance in natural habitats. And on the other, they raise some reasonable skepticism about earlier generalizations on long-term pollinator trends that are based on data from just a few plant species or taxonomically limited subset of pollinators. In general, the contrasting thermal niches and foraging responses to temperature variation of different pollinator groups are expected to generate heterogeneous responses to climate warming, and facilitate compensatory shifts in abundance that could ultimately contribute to the thermal resilience of plant–pollinator communities (Herrera 1997, Kühsel and Blüthgen 2015). Such effects may eventually prove to be widespread. For example, an increase over a 20-yr period in the proportional importance of "warm-loving" bee species similar to that found in the present study was recently reported by Hofmann et al. (2018) for a botanical garden in Germany. Furthermore, the disparate trophic resources exploited by the larval stages of major insect pollinator groups (i.e., orders, families) are likely to be affected differentially by climate change. Consequently, plant-pollinator communities in biologically diverse, large protected areas are more likely to withstand the impact of climate change than biologically depauperated areas. Combining powerful analytical schemes with ambitious sampling designs that are not limited to particular groups of pollinators or plants thus seems essential to draw reliable inferences on pollinator trends at the regional plant community level in biologically diverse environments.

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