Unclusterable, underdispersed arrangement of plant species in pollinator niche space

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Abstract. Pollinators can mediate facilitative or competitive relationships between plant species, but the comparative importance of these two conflicting phenomena in shaping pollinator resource use in plant communities remains unexplored. This paper provides a case example and proof of concept of the idea that the arrangement in pollinator niche space of large species samples comprising complete or nearly complete plant communities can be instrumental to evaluate the importance of facilitation and competition as drivers of pollinator resource at the plant community level. Pollinator composition data for 221 plant species from the Sierra de Cazorla mountains (southeastern Spain), comprising 85% of families and ~95% of widely distributed species of entomophilous plants, were used to address the following questions: (1) Do objectively identifiable species clusters occur in pollinator niche space ? Three different pollinator niche spaces were considered whose axes were defined by insect orders (N = 7), families (N = 94) and genera (N = 346); and (2) If all plant species form a single, indivisible cluster in pollinator niche space, Are species overdispersed or underdispersed relative to a random arrangement ? "Clusterability" tests failed to reject the null hypothesis that there was only one pollinator-defined species cluster in pollinator niche space, irrespective of the space axes (insect orders, families or genera) or pollinator importance measurement (proportions of pollinator individuals or flowers visited by each pollinator type) considered. Randomly simulated species arrangements in each pollinator niche space showed that observed means of pairwise interspecific distances in pollinator composition were smaller than values from simulations, thus revealing significantly non-random, underdispersed arrangement of plant species within the single cluster existing in pollinator niche space. Arrangement of plant species in niche space in the montane plant community studied did not support a major role for interspecific competition as a force shaping pollinator resource use by plants, but rather a

situation closer to the facilitation-dominated extreme in a hypothetical competition-facilitation gradient. Results also illustrate the potential of investigations on complete or nearly complete entomophilous plant communities for addressing novel hypotheses and contributing insights to the understanding of the ecology and evolution of plant-pollinator systems.

Key words:clusterability; Mediterranean mountain habitats; plant community; pollinator composition; pollinator niche space; pollinator syndromes.

INTRODUCTION

The maturation of a full-fledged niche theory was a significant landmark in the trajectory of twentieth-century ecology (Vandermeer 1972, Chase and Leibold 2003, Ricklefs 2012). Originally aimed at investigating how many and how similar coexisting species could be in a community, niche theory was predominantly concerned with animal communities and rested on the overarching assumption that interspecific competition for limiting resources is a major driving force in shaping community composition and resource use by individual species (Chase and Leibold 2003). Notions derived from niche theory sometimes also made their way into plant community studies. In particular, the niche theory framework is behind investigations of plant-pollinator interactions that have envisaged animal pollinators as “resources” exploited by entomophilous plants to ensure sexual reproduction. In this context, pollinator partitioning over daily or seasonal gradients (Heinrich 1975, Herrera 1990, Stone et al. 1998, de Souza et al. 2017), generalization *vs.* specialization on pollinators as alternative strategies of resource use (Herrera 1996, 2005, Waser et al. 1996, Gómez and Zamora 1999, Armbruster 2017), or divergence in pollinator composition in response to interspecific competition (Moldenke 1975,

Kephart 1983, Johnson 2010, Bouman et al. 2016, Johnson and Bronstein 2019), are all notions rooted in niche theory and share its canonical assumption of competition as major driving force.

One insufficiently acknowledged limitation of the application of competition-laden niche theory to plant-pollinator systems is that, under certain circumstances, pollinator sharing by different plant species can result in facilitation rather than competition (Thomson 1978, Rathcke 1983, Callaway 1995). This possibility has been verified experimentally many times (see Braun and Lortie 2019 for review). Proximate mechanisms leading to pollinator-mediated interspecific facilitation include the "magnet species effect", whereby species highly attractive to pollinators can benefit co-flowering ones in the neighborhood that are visited less often (Feinsinger et al. 1986, Laverty 1992, Johnson et al. 2003, Hansen et al. 2007, Molina-Montenegro et al. 2008, Pellegrino et al. 2016); sequential facilitation, whereby earlier-flowering species benefit later-flowering ones at the same location by sustaining populations of site-faithful, shared pollinators (Waser and Real 1979, Ogilvie and Thomson 2016); floral mimicry, in which species can derive reproductive success when the colour, shape or scent of their flowers resemble those of a co-blooming plant (Gumbert and Kunze 2001, Johnson et al. 2003, Pellegrino et al. 2008); and diffuse beneficial effects of floral diversity at the plant community level on the pollination success of individual species (Ghazoul 2006, Seifan et al. 2014, Norfolk et al. 2016).

While the reality of both facilitative and competitive phenomena in plant-pollinator systems is well established, their comparative importance as drivers of pollinator resource use in natural communities remain essentially unexplored to date (but see, e.g., Tur et al. 2016). The deleterious effects of pollinator sharing and interspecific pollen transfer have been traditionally interpreted as supporting the role of competition in organizing multispecies plant-pollinator interactions by favoring pollinator partitioning (Stebbins 1970, Waser 1978, Wilson and

Thomson 1996, Morales and Traveset 2008, Mitchell et al. 2009). The hitherto little-explored possibility remains, however, that facilitative interactions among animal-pollinated plants could also be significant drivers of plant-pollinator interactions at the community level, since benefits of pollinator sharing can sometimes outweigh its costs (Tur et al. 2016) and the net outcome of opposing facilitation and competition might depend on environmental context (Moragues and Traveset 2005, Ghazoul 2006, Ye et al. 2014, Fitch 2017). I propose here that the comparative importance of competition *vs.* facilitation in shaping community-wide plant-pollinator systems could be evaluated by examining the arrangement of plant species in the pollinator niche space, as outlined in the next section.

A hypothesis on species arrangement in pollinator niche space

Pollinator-mediated interspecific facilitation and competition can be envisaged as exerting opposite forces on pollinator resource use, tending to favor pollinator sharing and divergence, respectively. Insights into the relative importance of these two conflicting forces could thus be gained by examining how *the whole set* of animal-pollinated species in a plant community are arranged in the multidimensional niche space whose axes are biologically distinct pollinator "types". Such types should include all objectively recognizable pollinators types that are sufficiently different in size, morphology, behavior and/or pollinating features as to represent different resources from the plants' perspective. A simple sketch of this idea referred to just two pollinator niche axes is shown in Fig. 1. Divergence in pollinator resource use, denoted by two or more distinct species clusters in pollinator space (Fig. 1A), would be consistent with competition playing a prevailing role in the organization of plant-pollinator interactions. On the opposite extreme, a single cluster of densely packed (underdispersed relative to a random distribution) species in the pollinator niche space (Fig. 1C) would be suggestive of predominant

facilitation having promoted convergence in pollinator resource use by the different plant species. The intermediate situation, in which species form a single cluster of uniformly distributed species (overdispersed relative to a random distribution) in pollinator niche space (Fig. 1B) would point to a sort of balance between facilitation (favoring a single cluster) and competition (driving species repulsion in niche space via limiting similarity effects).

The main objective of this paper is to provide a case example and proof of concept for the preceding framework by examining the arrangement in the pollinator niche space of a very large sample of entomophilous plant species from a hyperdiverse community. A secondary objective is to highlight the importance of adopting "zooming out" approaches in the study of the ecology of plant-pollinator interactions (Herrera 2020). Current knowledge of pollination system niches has been mostly obtained from studies dealing with small species samples (usually < 25 species), or focusing on specific pollination guilds associated with particular pollinators. While irreplaceable for other purposes, these investigations lack the biological amplitude needed to address broad-scale questions and warrant generalizations on the overall organization of plant-pollinator systems (Johnson 2010, Herrera 2019, 2020). Only a comprehensive coverage of the ecological and phylogenetic range of the insect-pollinated plants in a region and their whole set of pollinators could help to discriminate among the scenarios hypothesized in Fig. 1. The species sample examined here virtually encompasses the whole community of entomophilous plants in a southeastern Spanish biodiversity hotspot (see *Study area and plant species sample* below) and the whole spectrum of their insect pollinators.

The following two specific questions will be addressed: (1) Are there distinct, objectively identifiable plant species clusters in the pollinator niche space ? Three different pollinator niche spaces with broadly different dimensionalities will be considered, with axes defined by insect

orders, families and genera; and (2) If plant species form a single indivisible cluster in the pollinator niche space, Is there evidence for either overdispersed or underdispersed arrangement of species within the cluster ? Two simplifications in the scheme of Fig. 1 must be acknowledged. First, the sign and magnitude of the hypothesized competition-facilitation balance mediated by pollinators may depend on the spatial scale considered (Tur et al. 2016, Braun and Lortie 2019). And second, the scheme does not incorporate the possibility that even if divergence in pollinator composition can not be detected, pollinator partitioning associated with differential blooming time or habitat segregation could still reflect the effect of competition. The possible relationships between interspecific differences in habitat type and flowering time, and interspecific divergence in pollinator composition, will also be addressed.

MATERIALS AND METHODS

Study area and plant species sample

Pollinator composition data considered in this paper were collected during February-December 1997-2019 (with a gap in 2000-2002) in the Sierras de Cazorla-Segura-Las Villas Natural Park (Jaén Province, southeastern Spain), a region characterized by outstanding biological diversity and well-preserved mountain habitats. Sampling sites were the same as in Herrera (2019, 2020), where details on locations can be found. Quantitative data on pollinator composition were obtained for 221 plant species in 48 families (Appendix S1: Table S1). This sample comprises 85% of families and ~95% of widely distributed species of entomophilous plants in the study area (Gómez Mercado 2011, C. M. Herrera, *unpublished data*), and is a superset of the 191 species in 43 families studied by Herrera (2020: Table 1). Asteraceae (41 species), Lamiaceae (24), Fabaceae (14), Brassicaceae (12), Rosaceae (11) and Ranunculaceae (9) contributed most species to the sample. About two thirds of species (N = 156) were sampled

for pollinators only one year, and the rest were sampled ≥ 2 years. In the vast majority of species (N = 211) pollinator sampling was conducted on a single site. Data for the same species obtained in more than one site or year were combined into a single sample for the analyses. Pollinators of some of the species considered here vary among sites or years, but such intraspecific variation is always small in comparison to the broad interspecific range occurring in the large species sample considered here (e.g., Herrera 1988, 2019, C. M. Herrera, *unpublished data*), which justifies characterizing each plant species by the combined sample of pollinator data from different sites and years.

Pollinator sampling dates for each species roughly matched its peak flowering date. The mean date of pollinator censuses for each species, expressed as days from 1 January, was used in analyses relating differences in pollinator composition to variation in flowering phenology. Mean census dates for the species studied ranged between 39–364 days from 1 January, and most species flowered during May-July (interquartile range = 145-190 days from 1 January) (Appendix S1: Table S1). For analyses relating differences in pollinator composition to dissimilarity in habitat type, each plant species was classed into one of the following nine major habitat categories (total species per habitat in parentheses; see also Herrera 2020): banks of permanent streams or flooded/damp areas around springs (18); dwarf mountain scrub dominated by cushion plants (27); forest edges and large clearings (34); forest interior (20); patches of grasslands and meadows on deep soils in relatively flat terrain (40); local disturbances caused by humans, large mammals or natural abiotic processes (24); sandy or rocky dolomitic outcrops (29); tall, dense Mediterranean sclerophyllous forest and scrub (17); vertical rock cliffs (12 species). Individual species' assignments to habitat types are shown in Appendix S1: Table S1.

Pollinator composition

Data on pollinator composition were obtained for every species as described in Herrera (2019, 2020). The elemental sampling unit was the "pollinator census", consisting of a 3-min watch of a flowering patch whose total number of open flowers was also counted. All pollinators visiting some flower in the focal patch during the 3-min period were identified, and total number of flowers probed by each individual was recorded. Detailed information on sampling effort is shown in Appendix S1: Table S1. For all plant species combined, a total of 28,128 censuses were conducted on 575 different dates. Assessing the number of flowers visited by pollinators was impractical in the case of species with tiny flowers densely packed into compact inflorescences (e.g., Apiaceae, Asteraceae). In these species the number of inflorescences available per patch and visited per census were counted rather than individual flowers, although for simplicity I will always refer to "flower visitation". Close-up photographs of pollinators visiting flowers were taken routinely during censuses, which were used for identification, keeping photographic vouchers, and ascertaining the pollinating status of different insect taxa. Only taxa whose individuals contacted anthers or stigmas, or with discernible pollen grains on their bodies, were considered as pollinators.

Data analysis

Two measurements of pollinator importance and three different pollinator niche spaces will be considered throughout the analyses. Pollinator composition for each plant species will be assessed using the proportion of pollinator individuals recorded and the proportion of flowers visited for each pollinator type, which will be termed "proportion of visitors" and "proportion of visits", respectively. Three distinct, taxonomically-defined classifications of pollinators will be considered in the analyses, based respectively on their affiliation to insect orders, families and

genera. These classifications defined three pollinator niche spaces that differed in their dimensionality and the biological meaning of their axes (n = 7, 94 and 346 dimensions for the spaces defined by orders, families and genera, respectively). Out of a total of 33,835 individual pollinators recorded in censuses, 100% were identified to order and family, and 98.3% to genus, but only 80.3% to species. Analyses on a possible fourth pollinator niche space defined by species were not undertaken because excluding data with missing species-level identifications would have led to severe taxonomic biases and distortion of species arrangements in pollinator niche space. For instance, about half (46%) of all individual pollinators that remained unidentified at the species level belonged to just four bee genera (*Andrena*, *Ceratina*, *Lasioglossum*, *Panurgus*).

The question of whether species clusters could be recognized in each of the three pollinator niche spaces considered (defined by insect orders, families and genera) was first addressed informally by comparing the distribution of species in a reduced bidimensional space with the various scenarios envisaged in Fig. 1. For each pollinator niche space, nonmetric multidimensional scaling (NMDS) was performed on the matrix of interspecific pairwise distances in relative importance of pollinator types (proportion of visitors and proportion of visits). Computations were performed with the function metaMDS in the package vegan (Oksanen et al. 2019) for the R computing environment (R Core Team 2018; all statistical analyses in this paper were carried out using R). In metaMDS the ordination is followed by a rotation via principal components analysis, which consistently ensures that the first axis reflects the principal source of variation in the data and thus enhances the possibility of revealing clusters. Unless otherwise stated the Manhattan distance metric (also known as L1 norm, city block or taxicab metric; Deza and Deza 2013) was used to compute interspecific distances

matrices for NMDS and rest of analyses involving distance matrices. The Manhattan metric is better suited than the widely used Euclidean metric for analyses of high dimensionality data as those done here (Hinneburg et al. 2000, Aggarwal et al. 2001, Houle et al. 2010).

Formal statistical analyses of "clusterability", or whether a meaningful clustered structure can be objectively established in a multidimensional data set (Ackerman and Ben-David 2009, Nowakowska et al. 2015, Simovici and Hua 2019), were conducted on the set of species coordinates in each of the three pollinator niche spaces considered (each defined by either proportion of visitors or proportion of visits). Dip multimodality tests (Hartigan and Hartigan 1985) were applied to distributions of pairwise distances between species, a method particularly robust to outliers, anomalous topologies and high dimensionality (Adolfsson et al. 2019). These tests evaluated the null hypothesis that the distribution of interspecific distances in pollinator space was unimodal, denoting a single species cluster, against the alternative hypothesis that the distribution had two or more modes, denoting the existence of at least two clusters (Adolfsson et al. 2019; see Brownstein et al. 2019, Simovici and Hua 2019, for examples of applications). The clusterabilitytest function in the clusterability package (Neville and Brownstein 2019) was used for computations, and statistical significance was determined by Monte Carlo simulations with 10^5 repetitions. Since results of clusterability tests did not support the Fig. 1A scenario, it was important to assess whether the failure to identify species clusters in the pollinator niche spaces considered was an spurious outcome of pooling species from different habitats and with different flowering phenologies, which could be partitioning pollinators in time or space. This possibility was examined by simultaneously regressing each matrix of interspecific distance in pollinator composition against corresponding pairwise matrices of distances in blooming time (absolute difference between mean pollinator census dates) and habitat type dissimilarity

(simple mismatching coefficient), using the multi.mantel function in the phytools package (Revell 2012). Statistical significance was evaluated using permutations with 10^5 repetitions.

Simulations were performed to elucidate whether the arrangement of species in pollinator niche space matched any of the scenarios depicted in Figs. 1B and 1C. The observed mean pairwise distance between species in each pollinator space was compared with a distribution of means obtained from simulated pollinator composition data. Each simulation consisted of permuting the values in each column of the raw plant species x pollinator type data matrix (number of pollinator individuals or number of flower visits contributed by each pollinator type); computing for each plant species the proportional importance of each pollinator type in the simulated data; obtaining the pairwise distances matrix; and finally computing the mean pairwise distance between species. This simulation procedure created random configurations of proportional pollinator compositions for individual plant species, and thus random arrangements of plants in the corresponding pollinator niche space, but preserved exactly both the observed distributional properties of visitors or visits for every pollinator type, and the absolute and relative numerical importances of the different pollinator types for all plant species combined. A total of 10^5 simulated species arrangements were computed in each of the three pollinator niche spaces, using proportion of visitors and proportion of visits as measurements of pollinator type importance. To test whether the observed arrangement of species in the pollinator niche space departed significantly from the randomly simulated ones, the mean interspecific distance observed was compared with the 0.025 and 0.975 quantiles of the distribution of simulated means.

RESULTS

Most plant species in the sample studied (*N* = 221) had very taxonomically diverse arrays of insect pollinators. On average (± SE), individual plant species were pollinated by 3.3 ± 0.1 different insect orders (interquartile range, IQR = 3–4), 10.7 ± 0.4 insect families (IQR = 6–14) and 16.7 ± 0.8 insect genera (IQR = 7–22). The number of orders, families and genera of pollinators recorded for each plant species are summarized in Appendix S2: Table S1, and the complete list of taxonomic categories recorded is presented in Appendix S2: Table S2.

Neither the informal analysis based on nonmetric multidimensional scaling (NMDS) nor the formal one testing clusterability by means of dip tests supported the existence of objectively definable plant species clusters in any of the three pollinator niche spaces considered. Irrespective of whether pollinator composition was assessed using proportion of visitors or proportion of visits, the cloud of points in the reduced two-dimensional space obtained with NMDS was roughly centered on the bivariate origin (0, 0), and there was not any indication of clusters or discontinuities suggestive of species groups with contrasting, well-defined pollinator types (Fig. 2). Clusterability analyses using dip tests likewise failed to detect clustered structures underlying the data in any of the three pollinator niche spaces considered (Table 1).

Multiple Mantel regressions revealed no statistically significant effects of interspecific dissimilarity in flowering time or habitat type on interspecific distance in pollinator composition when the axes of the pollinator niche space were insect orders (Table 2). When niche spaces were defined by families and genera, in contrast, statistically significant relationships did exist between distance in pollinator composition and dissimilarities in flowering time and habitat type. In all these instances the relationships were positive, denoting that species pairs sharing the same habitat type or flowering at similar times of year tended to be significantly more similar in

pollinator composition at the family and genus levels of taxonomic resolution than species from different habitats or flowering at different times of year.

Simulations showed that plant species were significantly underdispersed in the pollinator niche space. Regardless of the niche space considered or the measurement of pollinator importance used, the observed mean of pairwise interspecific distances in pollinator composition was always significantly smaller than simulated values, falling well below the lower limit of the range defined by the 0.025–0975 quantiles (Fig. 3). The extent of underdispersion, as intuitively assessed by the disparity between the observed mean and the range of simulated ones, increased from order- through family- to genus-defined pollinator niche spaces.

DISCUSSION

Considerable effort has been invested to develop reliable methods for grouping sets of objects in multivariate space in such a way that objects falling in the same group are more similar among themselves than to objects in other groups, a technique known as "cluster analysis" (Hennig et al. 2016) widely used in ecological applications. Clustering techniques often focus on the problem of optimally splitting a multivariate data set into $k \geq 2$ clusters (Halkidi et al. 2016), yet the problem of elucidating whether cohesive and well-differentiated groups of objects actually exist in the data, i.e., testing the null hypothesis that $k = 1$ against the alternative $k \geq 2$, has been rarely investigated due to computational difficulties (the so-called "clusterability problem"; Ackerman and Ben-David 2009, Nowakowska et al. 2015, Simovici and Hua 2019). Following recent technical developments, it has been advised that a prior study of clusterability should become an integral part of any cluster analysis (Adolfsson 2016, Adolfsson et al. 2019, Simovici and Hua 2019). Clusterability tests could be profitably

incorporated as a first step in analyses of ecological questions traditionally addressed by means of cluster analysis, so that the existence in multivariate spaces of objectively recognizable clusters of objects (e.g., species, plots, communities) can be rigorously evaluated before proceeding to clustering. This applies also to pollination studies, which have sometimes used clustering to identify plant groupings in multivariate spaces defined by floral traits or pollinator composition (Ollerton et al. 2009, de Jager et al. 2011, Abrahamczyk et al. 2017, Schurr et al. 2019, Vandelook et al. 2019). As exemplified by this study, clusterability analysis allows tests of hypotheses in pollination ecology by providing an objective means of ascertaining whether groups of plants defined by pollinators actually exist in a given species sample.

The present study failed to identify distinct clusters of plant species in the pollinator niche space. Groups with species more similar to each other in pollinator composition than to species in other groups were not statistically recognizable in the very large species sample of entomophilous plants considered. This conclusion emerges as a particularly robust one, since it was consistently attained regardless of the particular taxonomic resolution adopted to define the axes of the pollinator niche space (insect orders, families or genera) or the measurement of pollinator importance (proportion of visitors or proportion of visits). Variation in pollinator composition across the large species sample was essentially continuous. This was largely a consequence of the generalized pollination systems exhibited by the vast majority of plant species considered, each of which had pollinators belonging to a substantial number of different insect orders and families. Similar predominance of generalized pollination systems has been reported by other community studies (McCall and Primack 1992, Waser et al. 1996, Bosch et al. 1997), but I am not aware of any previous investigation evaluating the reality of species clusters in multidimensional pollinator spaces using objective statistical methods. Studies of plant-

pollinator networks have often looked for, and sometimes found, “modules” consisting of subsets of plant and animal species that are closely linked internally but weakly linked to other modules (Olesen et al. 2007, Dormann and Strauss 2014), which would suggest some parallels with the concept of species clusters in pollinator space considered in this study. The concepts are not strictly comparable, however, because plant-pollinator network data usually contain a blend of information on plant species abundances, pollinator visitation rates and pollinator composition (C. M. Herrera, *unpublished information*). As a matter of fact, “modular” plant-pollinator networks can fail to pass the clusterability test after information on plant species abundance and pollinator visitation rates is purged from the data by computing for each plant species the proportions of different pollinator types. For instance, the set of $N = 25$ plant species in Memmott’s (1999) plant-pollinator network, which was presented as an example of modular structure by Dormann and Strauss (2014; see also Olesen et al. 2007), is unclusterable in the pollinator niche space defined by the 79 insect taxa involved using the methods applied in the present study (C. M. Herrera, *unpublished information*). This contrast between plant-pollinator network modularity and plant clusterability in pollinator niche space seems another factor contributing to the disconnection between community ecology and network approaches pointed out by Blüthgen (2010).

Pollinators from different insect orders, families or genera generally have contrasting morphological and behavioral attributes, and these differences can eventually lead to variation in important pollinating features such as, e.g., ability to access floral rewards, daily or seasonal activity rhythm, flower visitation rate, frequency of pollen removal or deposition, or flight distance between flowers. On this basis, taxonomically-defined groupings of insects have been often treated as distinct “functional pollinator groups” and related to distinct plant “pollination

syndromes", or suites of floral features that are associated to particular pollinator groups (Fægri and van der Pijl 1979, Fenster et al. 2004, Ollerton et al. 2007, 2009, Gómez et al. 2008). The relationship between insect taxonomic affiliation and pollination attributes lends biological justification to using taxonomic categories to define the axes of multidimensional pollinator niche spaces. This study has shown that the arrangement of plant species in pollinator niche space did not match any of the scenarios postulated on the assumption that interspecific competition is an important force shaping pollinator resource use by plants. Not only there were no discernible species clusters that could reflect a prevalence of pollinator niche partitioning, but also (1) the arrangement of species was significantly more dense than expected by chance given the observed abundances of the different pollinator types considered; and (2) Mantel multiple regressions revealed that species sharing the same habitats or blooming at the same time of year were more similar to each other in pollinator composition than species that segregated temporally or spatially.

Results of this study suggest that concepts quintessential to competition-laden niche theory, such as limiting similarity, character displacement and competitive exclusion (Chase and Leibold 2003, Johnson and Bronstein 2019), do not generally apply to entomophilous plants in my study region in relation to their exploitation of insect pollinator resources. In addition, the absence in my plant species sample of objectively recognizable clusters linked to particular pollinator groups does not support the generality of plant pollination syndromes associated to specialization on particular insect functional groups (see also Ollerton et al. 2009, 2015). Observed patterns, consisting of plants not showing objectively-definable partitioning of pollinators and being underdispersed in pollinator niche space, would fall close to the facilitation-dominated extreme in a hypothetical competition-facilitation gradient. The

competition-facilitation balance in plant-pollinator systems can depend on particularities of the ecological scenario under consideration (Moragues and Traveset 2005, Ghazoul 2006, Ye et al. 2014, Fitch 2017), and results of the present study can be tentatively related to features of plant-pollinator interactions in the study region. On one side, insect pollinators probably are not a limiting resource for the majority of entomophilous plants in the region, as shown by the high flower visitation rates in most habitat types (Herrera 2020), generally weak or inexistent pollen limitation even in plants blooming at the most adverse periods of year (Herrera 1995, 2002, Alonso 2005, Alonso et al. 2012, 2013), and increased pollinator abundance in recent times in parallel to the long-term warming trend exhibited by the regional climate (Herrera 2019). And on the other, sharing of individual pollinators by different plant species seems a widespread phenomenon, as denoted by the frequent occurrence of heterospecific pollen grains in the stigmas of most species (Arceo-Gómez et al. 2018), common field observations of insect individuals interspersing visits to flowers of different species in the same foraging bout, and close-up photographs often revealing conspicuous mixed pollen loads on pollinator bodies (C. M. Herrera, *unpublished observations*). Taken together, all these observation are in accordance with the interpretation that the unclusterable, underdispersed arrangement of plant species in pollinator niche space found in this study reflects a prevailing role of interspecific facilitation as the organizing driver of plant-pollinator systems in the montane habitats studied.

CONCLUDING REMARKS

Excepting a few classical monographs considering complete or nearly complete regional plant–pollinator assemblages (Müller 1883, Robertson 1928, Moldenke 1976), the vast majority of pollination community studies have examined only small numbers of plant species at a time (e.g., Ollerton 2017:Appendix 2, and datasets included in the bipartite package for R, Dormann

et al. 2008). Small species sets drawn from much larger pools of entomophilous species provide suitable systems for investigating whether a particular phenomenon occurs or not (e.g., testing for pollinator-mediated competition or facilitation in a well-chosen group of species; see references in *Introduction*), but are intrisically unable to address more ambitious, broadly-encompassing questions bearing on the strength or frequency with which the phenomenon of interest operates in a particular ecological context. In addition, unacknowledged biases in the selection of pollination study systems can lead to small plant species samples rarely representing truly scaled-down, taxonomically- and ecologically-unbiased versions of whole plant communities, possibly leading to distorted representations of natural patterns (Ollerton et al. 2015). Place-based ecological research pursuing "general understanding through the sort of detailed understanding of a particular place" (Price and Billick 2010, p. 4) has been only infrequently adopted by pollination studies. As exemplified by the present investigation (see also Herrera 2020), comprehensive studies of complete or nearly complete entomophilous plant communities possess an unexplored potential for testing novel hypotheses and contributing realistic insights to the understanding of the ecology and evolution of plant-pollinator systems.

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SUPPORTING INFORMATION

Appendix S1

Plant species studied, habitat types, flowering time and pollinator sampling effort.

Appendix S2

Orders, families and genera of insect pollinators recorded.

TABLE 1. Tests for multimodality of pairwise distances between plant species (*N* = 221) in three different pollinator niche spaces whose axes are defined by insect orders, families and genera.

Axes of pollinator niche space *	Pollinator importance measurement			
	Proportion of visitors		Proportion of visits	
	Dip statistic	*P* value	Dip statistic	*P* value
Orders (*n* = 7)	0.0067	0.96	0.0088	0.64
Families (*n* = 94)	0.0020	0.92	0.0016	0.99
Genera (*n* = 346)	0.0012	0.69	0.00089	0.98

Notes: Each test evaluates the null hypothesis that the distribution of interspecific pairwise distances in the given pollinator space is unimodal, denoting a single cluster of plant species, against the alternative hypothesis that the distribution has two or more modes, denoting the existence of at least two clusters. *P* values determined by Monte Carlo simulation with 10^5 repetitions. Computations were performed with the clusterabilitytest function of the clusterability package (Neville and Brownstein 2019), called with the following options: test="dip", distance_metric = “manhattan”, d_reps=1e5, d_simulatepvalue = TRUE, reduction="none", distance_standardize="none".

* *n* = dimensionality of the pollinator niche space.

TABLE 2. Results of multiple Mantel regressions simultaneously assessing the significance of dissimilarity between plant species in blooming date and habitat type as predictors of distance in pollinator composition, using three different pollinator niche spaces whose axes are defined by insect orders, families and genera.

	Pollinator importance measurement							
	Proportion of visitors				Proportion of visits			
	Predictor:				Predictor:			
	Blooming date		Habitat type		Blooming date		Habitat type	
Axes of pollinator niche space *	Parameter estimate	*P* value	Parameter estimate	*P* value	Parameter estimate	*P* value	Parameter estimate	*P* value
Orders (n = 7)	-0.0178	0.65	1.5353	0.21	-0.0456	0.32	0.9529	0.47
Families (n = 94)	0.1039	0.0003	1.5937	0.062	0.0912	0.0025	1.7140	0.076
Genera (n = 346)	0.1175	0.0001	1.9740	0.001	0.1152	0.0001	2.3612	0.0009

* n = dimensionality of the pollinator niche space.

Captions to figures

FIG. 1. Schematic depiction of three possible arrangements of 30 animal-pollinated plant species (black dots) in an imaginary pollinator niche space defined by two pollinator types (horizontal and vertical axes). The coordinates of each species on the axes are the relative contributions of pollinator types to its pollinator assemblage. It is proposed that the importance of interspecific competition for pollinators as a major driving force shaping the arrangement of plants in the pollinator niche space should decline from A to C (see text).

FIG. 2. Distribution of the N = 221 plant species studied on the plane defined by axes from Nonmetric Multidimensional Scaling applied to the matrices of pairwise distances in pollinator composition (MDS1, MDS2). Original pairwise distances were computed using two different measurements of relative pollinator importance (proportions of visitors recorded and proportion of flowers visited), and referred to three different pollinator niche spaces whose axes were defined by insect orders (n = 7 dimensions), families (n = 94) and genera (n = 346). Stress values, an inverse measurement of goodness of fit, are shown in graphs. Note that meanings of MDS1 and MDS2 axes are not comparable across graphs, since axis pairs were obtained from independent ordination analysis on different data.

FIG. 3. Observed (thick solid lines) and randomly simulated (grey histograms; $N = 10^5$ simulations) values for the mean pairwise distance between plant species in pollinator niche space. Distances were computed for two different measurements of relative pollinator importance (proportions of visitors recorded or proportions of flowers visited), and referred to three different pollinator niche spaces whose axes are defined by insect orders (n = 7 dimensions), families (n = 94) and genera (n = 346). The dashed lines denote the 0.025 and 0.975 quantiles of the distributions of simulated mean values.

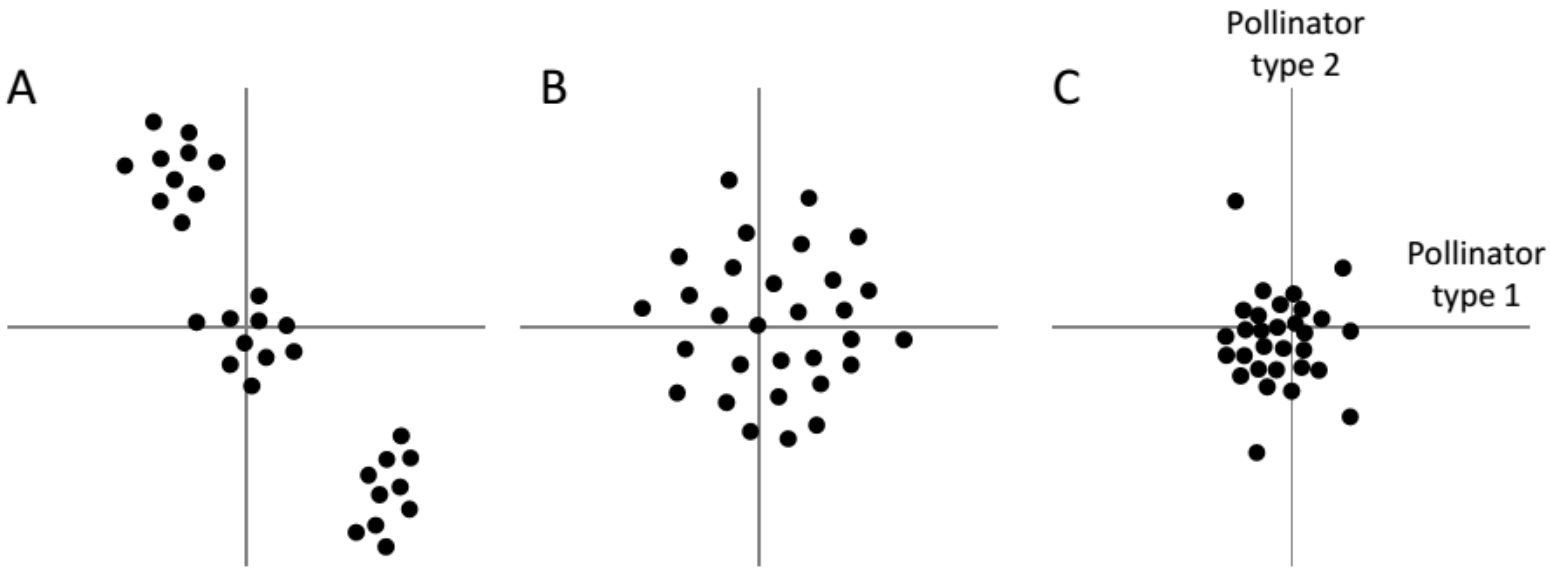

Fig. 1.

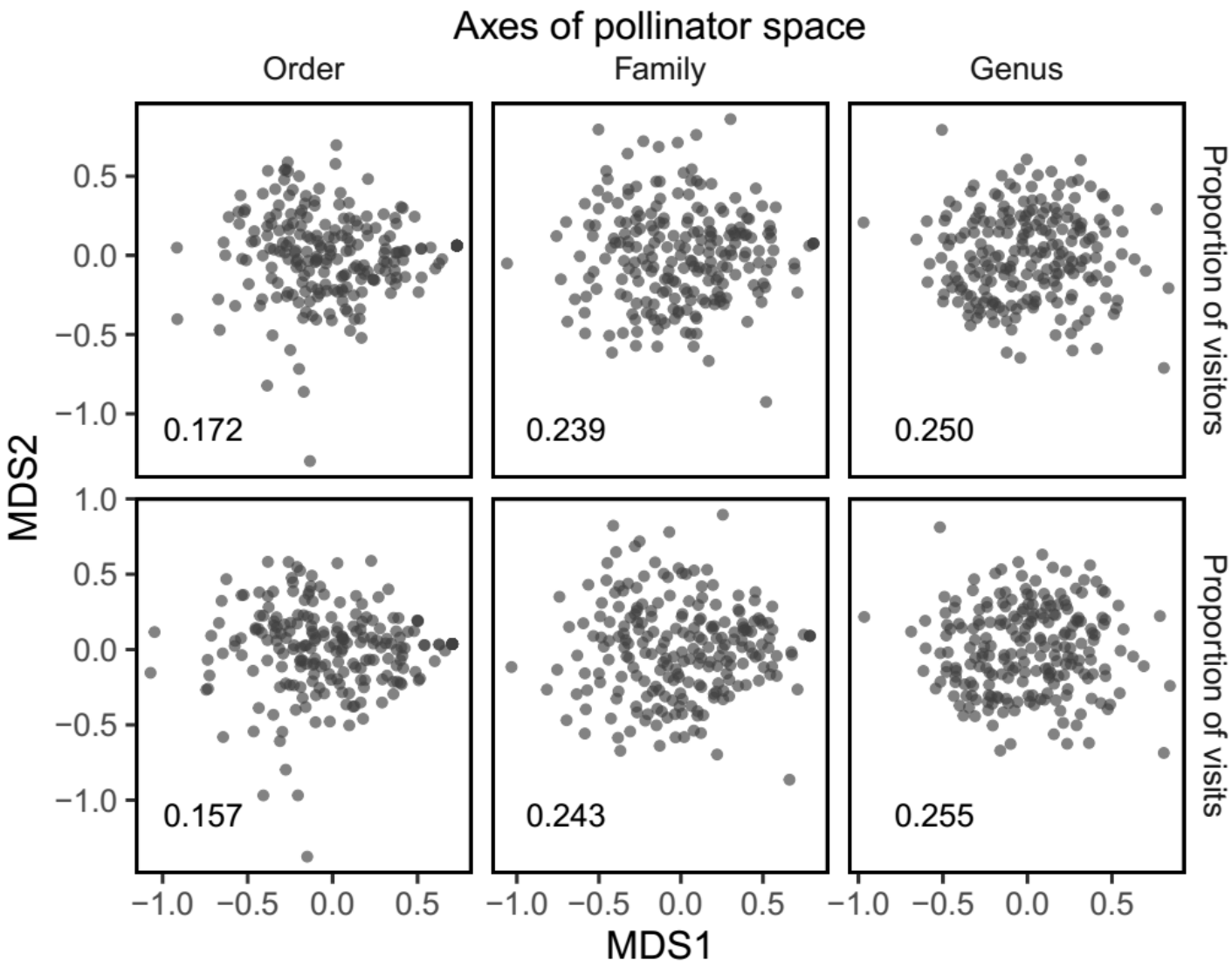
Axes of pollinator space
Order
Family
Genus
Proportion of visitors
Proportion of visits
MDS2
MDS1
0.172
0.239
0.250
0.157
0.243
0.255
1.0
0.5
0.0
−0.5
−1.0

Fig. 2

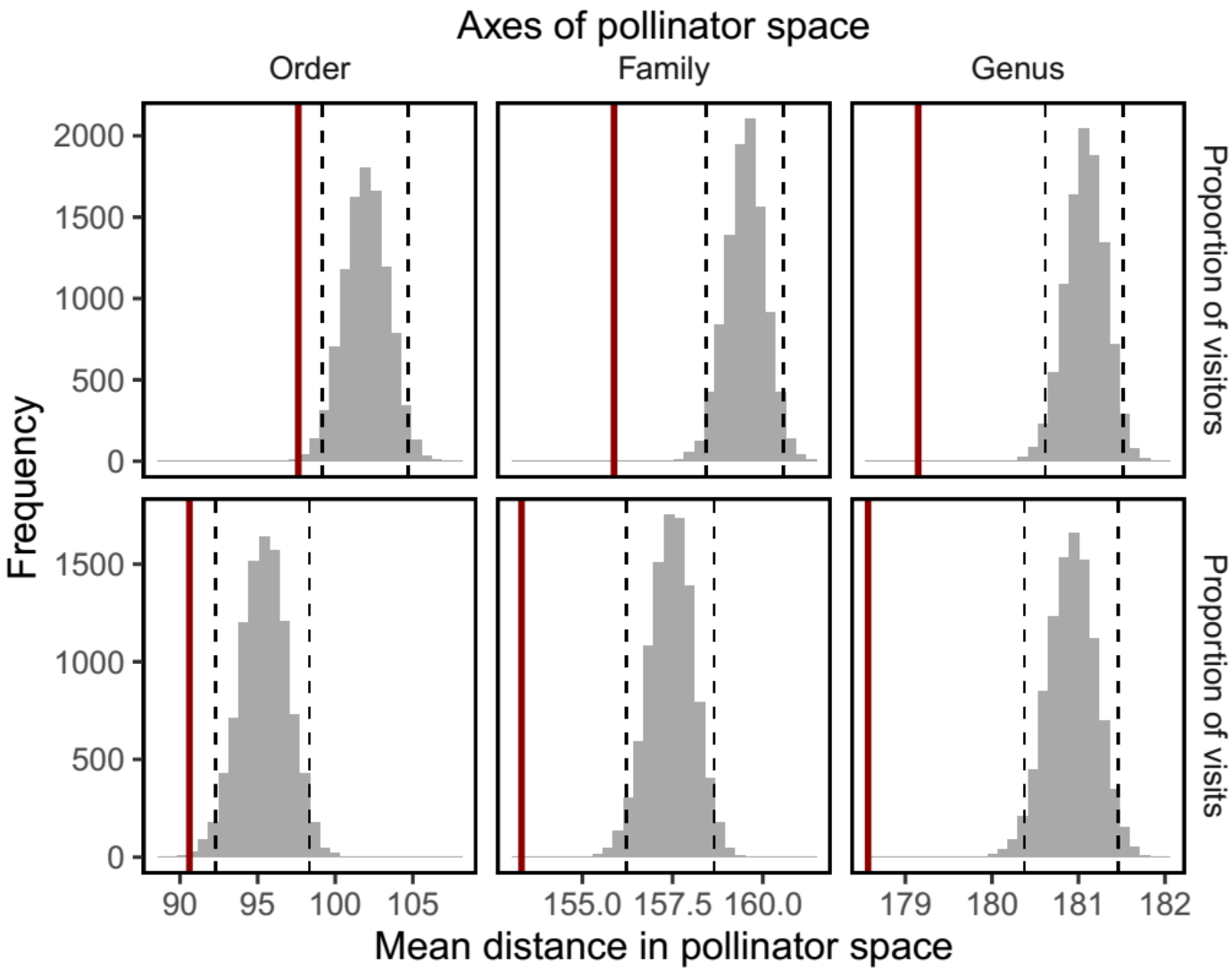
Axes of pollinator space
Order
Family
Genus
Frequency
2000
1500
1000
500
0
Proportion of visitors
Proportion of visits
90
95
100
105
155.0
157.5
160.0
179
180
181
182
Mean distance in pollinator space

Fig. 3