ECOGRAPHY

Research article

Untangling the plant reproductive success of changing community composition and pollinator foraging choices

Alfonso Allen-Perkins[1,2], Maddi Artamendi[3,4], Daniel Montoya[3,5], Encarnación Rubio[6] and Ainhoa Magrach[3,5]

[1]Grupo de Sistemas Complejos (GSC), ETSIDI, Universidad Politécnica de Madrid, Madrid, Spain
[2]Grupo Interdisciplinar de Sistemas Complejos (GISC), Madrid, Spain
[3]Basque Centre for Climate Change-BC3, Leioa, Spain
[4]University of the Basque Country, UPV-EHU, Leioa, Spain
[5]Ikerbasque, Basque Foundation for Science, Bilbao, Spain
[6]Departamento de Biología Vegetal y Ecología, Universidad de Sevilla, Seville, Spain

Correspondence: Alfonso Allen-Perkins (alfonso.allen.perkins@gmail.com)

Pollinator choices when selecting flowers for nectar or pollen collection are crucial in determining the effectiveness of pollination services provided to plants. From the plant's perspective, this effectiveness is a phenomenon shaped by factors at both the species- (e.g. pollinator density and flower morphology) and community-level, including pollinator diversity and plant competition for pollinators. At the species level, individual pollinator effectiveness is influenced by foraging choices, plant identity, and the resulting pollen flow within and between plant species. In natural ecosystems, these species coexist within a complex community, where various interactions can modify foraging choices and alter pollen flows, giving rise to community-level effectiveness, a less explored aspect of pollinator effectiveness. This study investigates the drivers of individual pollinator foraging choices across two study areas and two flowering seasons. It also assesses the community-level effectiveness of pollination services received by different plant species, considering indirect interactions between plants through shared pollinators and evaluating their impact on plant reproductive success. Our results show that the determinants of pollinator foraging choices are consistent across different habitats, with floral constancy and flower abundance playing pivotal roles across all species and sites. Foraging choices can shift throughout the flowering season as plant and pollinator composition changes, significantly impacting pollination effectiveness. The overlap in pollination service use by individuals of the same plant species decreases their fruit set, whereas sharing pollinator services with individuals of other plant species increases fruit set. Our results support significant, positive biodiversity–ecosystem functioning associations driven by both plant and pollinator species richness, suggesting that the overlap in pollination service use by different plant species fosters facilitative interactions rather than competition. This is likely influenced by more stable pollination supplies under high plant species diversity conditions and the existence of mechanisms to mitigate the negative impacts of heterospecific pollen deposition.

Introduction

The outcome and effectiveness of the interactions between plants and their pollinators is largely determined by the movement trajectories and visitation sequences that pollinators follow (Kortsch et al. 2023). The foraging decisions that underlie these different trajectories can be determined by aspects such as the diversity and abundance of different plant species (Potts et al. 2003), their spatial arrangement (Kortsch et al. 2023), or the composition, abundance, and characteristics of the rest of the pollinator community (Brosi and Briggs 2013). The order in which specific plant individuals are visited is an important determinant of pollinator effectiveness, with a more faithful sequence of visitation to individuals of the same plant species reducing the probability of heterospecific pollen deposition, and generally improving plant reproductive success (Arceo-Gómez and Ashman 2011). While the preferences of different pollinator species for specific plant species are often considered static attributes – leading species to be classified as generalists or specialists (Larsson 2005) – there is actually a dynamic interplay between short-term specialization for conspecific pollen transfer and long-term generalization existing at various biological levels (from individuals to populations, to species or communities), which is critical for ecological functioning, plant speciation, and the evolution of plant mating systems (Brosi 2016). The plant preferences shown by the same pollinator species can change through space and time, with individuals of the species more frequently visiting plant individuals belonging to the same species at different moments throughout the flowering season or across different sites (Brosi 2016, Magrach et al. 2021). However, this dynamism has been underemphasized in the literature when analysing pollinator foraging choices and their consequences for pollinator effectiveness and plant reproductive success (although see Morse 1977, Inouye 1978, Brosi and Briggs 2013, Cervantes-Loreto et al. 2021). Particularly, significant knowledge gaps persist concerning the combined impacts of shifts in floral resource availability and the composition of pollinator communities and how these affect the behavior of pollinators and, consequently, the pollination functions they perform when viewed from a community-wide perspective.

The pollination effectiveness observed at the species level represents only a fraction of the overall effectiveness experienced by individual plants. This broader perspective encompasses interactions with various individuals from different species, thereby constituting a community-level effectiveness (Willcox et al. 2017). Although this part of the pollinator effectiveness has received much less attention, recent research contributes to further our understanding of pollinator effectiveness at the community level. For example, a recent synthesis (Artamendi et al. unpubl.) demonstrates that pollinator species diversity is positively related to plant reproductive success. Although the specific mechanisms by which this positive biodiversity–ecosystem functioning relationship arises are yet to be determined, with complementarity and selection effects appearing as probable causes (Loreau and Hector 2001), this research suggests that a more diverse pollinator community is also a more effective one. Moreover, our attention has shifted beyond species richness alone, and we are now exploring how the interactions among species contribute to shaping community structure and plant reproductive success. Previous findings (Magrach et al. 2021) indicate that a specific balance of redundancy and complementarity in the functions carried out by various pollinator species plays a crucial role in determining plant reproductive success. However, a major caveat in this research is that it adopts a static perspective and analyses community structure of the aggregated plant–pollinator community through time. This overlooks the dynamics in plant and pollinator community composition which potentially affect structure–function relationships through time (Magrach et al. 2023).

Understanding how pollinator foraging choices ultimately influence plant reproductive success requires recognizing potential direct and indirect interactions between co-occurring plant and pollinator species (Moeller 2004, Flanagan et al. 2010, Carvalheiro et al. 2014, Willcox et al. 2017). To systematically analyze these interactions, plant–pollinator communities are commonly modeled as bipartite networks that illustrate the interactions between plants and their pollinators (Olesen et al. 2006, Bascompte and Jordano 2013). In these networks, individuals or groups of individuals from plant and pollinator species, or the species themselves, are depicted as nodes, with their direct observed interactions represented as links connecting these nodes. This network representation enables the inference of system properties at multiple structural scales, from local (node-level) to global (the entire network) (Guimarães 2020). It also encompasses the meso-scale, an intermediate structural scale between local and global, which focuses on analyzing the structural characteristics of subgraphs, the interaction patterns among subsets of nodes, and how these interactions contribute to the overall architecture and functionality of the system. For instance, this multi-scale network approach allows us to elucidate properties such as the degree at the local level, represented by the count of direct connections a node has; modularity at the global level, which reflects the network's division into distinct subgroups; and motif configurations at the meso-scale, characterized by recurring interconnection patterns among node subsets (Guimarães 2020). Specifically, the analysis of three-node subgraphs, or triplets, involving two plant species and their shared pollinator species exemplifies how meso-scale motifs can reveal the existence of indirect interactions between these two plant species that might be overlooked if analysis were limited to only community or individual approaches (Simmons et al. 2018). Given the ability of subgraphs (such

as triplets) to simultaneously capture both direct and indirect interactions, there is growing interest in meso-scale analysis (Simmons et al. 2018). However, this scale has been less explored compared to studies at the local (node) level (Tur et al. 2013, Gómez et al. 2020, Arroyo-Correa et al. 2021) and the community (global) level (Lázaro et al. 2020, Magrach et al. 2021). While interest in subgraph analyses has grown significantly in recent years, especially in studies of mutualistic interaction networks (Simmons et al. 2018, 2020, Lanuza et al. 2023, Allen-Perkins et al. 2024a), knowing how much detail on the network structure is needed to understand the system's ecological functioning remains an open question and will depend on the specific research question being addressed (Guimarães 2020). Nonetheless, recent empirical findings indicate that meso-scale analysis is the most effective descriptor for quantifying the structure of ecological networks and their links to vital ecological rates, such as plant reproduction success (Allen-Perkins et al. 2024a). Moreover, by concentrating on this intermediate scale, we can reintroduce a measure of effectiveness into analyses of community structure–function. In particular, three-node subgraphs can be a proxy for conspecific or heterospecific pollen deposition, depending on whether the two plants involved in the triplet belong to the same or different species, respectively (Allen-Perkins et al. 2024a).

Our aim here is threefold: 1) to investigate how floral resource composition and configuration, and pollinator community composition, simultaneously determine individual pollinator foraging choices and pollinator effectiveness (measured as floral constancy) through time, 2) to assess the overall community-level pollination services received by different plant species, and 3) to understand the functional consequences of these changing pollinator preference patterns through time and space from the plant's perspective. To this end, we characterize the potential determinants of pollinator foraging choices across a flowering season for nine different pollinator species in two different habitats. We then combine this information with a meso-scale analysis of individual foraging networks that depicts observed flying sequences of the different pollinator species and shows potential indirect interactions between plant individuals through pollen deposition. We expect that species-level pollinator effectiveness, defined as a pollinator species-level trait that describes the amount of pollen transferred to a floral stigma in a single visit (Willcox et al. 2017) (measured here in terms of floral constancy), will change throughout the flowering season, following changes in floral resource availability through time, and increasing intra- and inter-specific competition as more pollinator species and individuals emerge. We also expect that the overall pollination service received across the different individuals of the same plant species will vary. However, we expect that these variations will be smaller within more pollinator-diverse communities, as complementarity and redundancy in pollinator roles will buffer any changes in pollinator preferences. Finally, we expect that plant individuals visited by more efficient pollinators (those that show greater floral constancy) and those that are involved in less indirect interactions with other plant species (fewer heterospecific subgraphs and hence subject to less heterospecific pollen deposition) will have greater reproductive success. However, heterospecific pollen deposition is not necessarily detrimental to plant reproductive success (Gavini et al. 2021, Lopes et al. 2021). Alternatively, the sharing of pollinator species between plant species could lead to facilitative interactions rather than competitive ones, and heterospecific pollen deposition could be positively related to plant reproductive success. The analytical framework we present here provides essential information to understand how spatial and temporal dynamics in plant and pollinator communities shape pollinator foraging choices and their effectiveness, and the consequences of this for plant reproductive success.

Material and methods

Overview

To understand the mechanisms underlying pollinator visitation sequences, and the impacts these have for plant reproductive success, we gathered data on the identity of plant species visited by different pollinator species across different foraging bouts at 10 sites located in two different ecosystems (below). First, we used these data to model and compare the floral selection process for the five most frequent pollinators in each ecosystem by using integrated step-selection functions (iSSFs, Avgar et al. 2016), while also assessing their floral constancy (Fig. 1a), and whether this proxy for species-level pollination effectiveness changed through space and time (Fig. 1b). Second, we characterized the community-level pollination effectiveness received by the individuals of the different plant species in our communities, using a spatially explicit approach. In doing this, we combined the foraging decisions of the different pollinator species that visit each plant species together with the probability that these plant individuals were visited immediately after an individual of the same plant species (subsection Community-level effectiveness, Fig. 1c, e). Finally, we assessed the overall general structure of indirect interactions between plants (through shared pollinator species, subsection Structural analysis, Fig. 1d, f), and related all of these variables to the reproductive success of the different plants (subsection Reproductive success analysis, Fig. 1).

Pollinator sequences, resource availability and seed production

We collected data from five mountain meadows within Gorbeia National Park (northern Spain), and five stone pine forest fragments located near Doñana National Park (southwestern Spain, 10 sites in total). Sites were separated from each other by at least 1 km to ensure independence of the pollinator community. Sites in Gorbeia were located within relatively steep areas to prevent grazing. Within each site, we established one square plot (25 × 25 m in Gorbeia and 10 × 10 m in Doñana, due to COVID pandemic limitations and team constraints in Doñana), which we subdivided into 1 ×
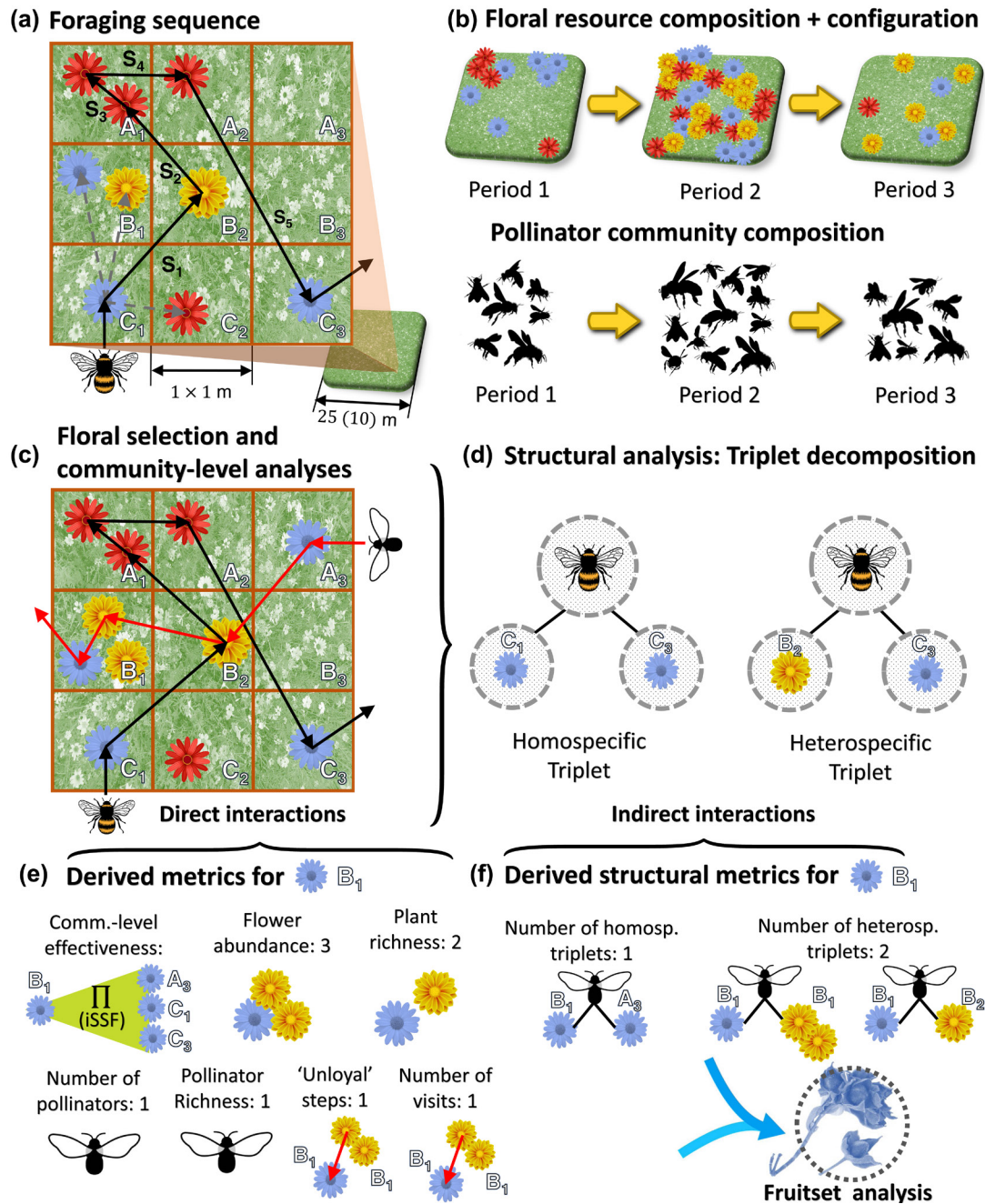
Figure 1. (a) Diagram of a visitation sequence made by a pollinator to plants within a plot. The black arrows represent each step of the actual sequence, whereas the dashed grey arrows show three examples of alternative (or potential) random steps for the step S_1. (b) Representation of changes over time in floral resources and pollinator communities. Examples of the direct (c) and indirect interactions (d) recorded per plot and flowering period, along with the metrics to characterize them (panels e and f, respectively) per plant species and subplot. We display all metrics for a blue flower in panel c (subplot B_1), except for community-level effectiveness, where only relevant calculation elements are highlighted. With those metrics we modeled plants' fruit set (reproduction success analysis).

1 m subplots (625 and 100 m² for each plot in Gorbeia and Doñana, respectively, summing across five locations 3125 and 500 m², respectively).

During two flowering seasons in Gorbeia (2020 and 2021) and one in Doñana (2021 due to COVID-related limitations in 2020), we recorded the sequence of flowering plants visited by different pollinator species as follows. From March to July, we surveyed each plot bi-weekly, at least six times each year in Gorbeia and eight times in Doñana. Each time we visited a particular site, we walked around the plot and whenever we spotted a floral visitor (hereafter pollinator) visiting a plant species, we followed the sequence of plant individuals it visited (Fig. 1a), recording the identity of the plant species each time as well as the spatial coordinates of the subplot in

which the plant individual was located. We considered a visit to be successful whenever the pollinator touched the reproductive parts of the flower. Sequences were recorded when we had at least two consecutive records of successful visits by the same pollinator individual. Individual pollinators were not marked to avoid any interference with their normal behavior. As a result, the same individual could have been recorded in multiple foraging bouts, but we treated them as distinct individuals in our analysis. The plot survey order was randomized between weeks to avoid sampling effects. We repeated this process at different times throughout the same day, between 10:00 and 18:00, under similar weather conditions, no rain or wind. All plots were surveyed for at least 3 h each week. Overall, this procedure rendered approximately 90 (120) h of pollinator sampling over 6 (8) weeks per plot and year in Gorbeia (Doñana), and an estimated sampling coverage of subplot plant–pollinator interactions in each plot of ~ 90% (see the Supporting information for further details).

To monitor changes in the composition of the flowering plant community, the availability of resources at each site, and the niche overlap among plant species, we also recorded the number of flowers available for all flowering plants within each subplot, at three different points in time (from now on referred to as periods), during the flowering season of each year. The periods considered were 1) from mid-March to early-May (period 1), 2) from early-May to mid-June (period 2), and 3) from mid-June to July (period 3). However, due to mobility restrictions associated with the COVID-19 pandemic, in 2020 the team did not conduct fieldwork at period 1.

Finally, to obtain a measure of pollination function per subplot, we estimated the average number of fruits per flower in Doñana's sites during 2021. The pandemic impacted our data collection on plant reproductive success in Gorbeia, making it unrepresentative. In Doñana, we focused on the reproductive success for a subset of plant species in the community. Specifically, we focused on abundant species that are also highly self-incompatible and whose flowers only last a few hours, opening in the morning and dropping their petals in the afternoon (mostly genus *Cistus*) (Bosch 1992). This allowed us to link individual plant reproductive success to the specific spatial and temporal conditions present during the day in which that specific plant individual received a pollinator visit. The selected subset includes six species of the Cistaceae family: *C. salviifolius*, *C. crispus*, *C. ladanifer*, *C. libanotis*, *Halimium halimifolium*, and *H.calcynum*. We estimated the average number of fruits per flower within 1853 individual flowers throughout the flowering season (Supporting information).

Foraging movement analysis

To compare movement patterns and assess the generality of the subplot-selection processes of pollinators from Gorbeia and Doñana, we adapted integrated step-selection functions (iSSFs, Avgar et al. 2016), a common modeling approach used for telemetry data. iSSFs compare environmental attributes of observed steps (the linear segment between two consecutive plant individuals located in different subplots within a visitation sequence) with alternative random steps

taken from the same starting point (Thurfjell et al. 2014) (Fig. 1a for an example), using conditional logistic regression (Gail et al. 1981, Thurfjell et al. 2014, Fieberg et al. 2021).

Because our pollinator visitation dataset consisted of a large number of pollinator species (> 100), most of them appearing just a few times, we focused on the five species with the largest number of steps at each of the two study areas, which accounted for ~ 72.42% of the total steps in Gorbeia and ~ 65.45% in Doñana. The species selected were mainly bees (*Apis mellifera*, which appeared in both rankings, *Bombus pascuorum*, *B. lapidarius*, *B. terrestris*, *Xylocopa cantabrita*, *Dasypoda cingulata*, and *D. albimana*), and two species of syrphid flies of the genus *Sphaerophoria* and *Eristalis* (Supporting information), totalling nine species for both study areas. For those pollinator species, we studied the probability of observing a step as a function of 1) the difference in plant richness between the ending and starting subplots of a given step (Δrichness); 2) the change in the total number of flowers (Δtotal flowers); 3) the step length (Supporting information), and 4) whether the pollinator individual was consistently visiting plant individuals of the same species or not, from now on referred to as exhibiting floral constancy (Brosi and Briggs (2013); which we consider a proxy for species-level pollinator effectiveness as it is related to a higher plant reproductive success (Brosi and Briggs 2013, Willcox et al. 2017).

To assess whether the probability of observing a step changed through space (i.e. across the different sites) or time (i.e. across the different periods, times of day or years) we evaluated whether the mean values of the different explanatory variables (i.e. step length, floral constancy, Δrichness, and Δtotal flowers; Supporting information) significantly differed when changing such conditions. To avoid an increased number of false positives, we used the framework introduced by Hothorn et al. (2008) – along with the procedure proposed by Herberich et al. (2010) – for multiple comparisons when neither homoscedasticity nor normality nor balanced group sizes can be assumed. In addition, we also tested if pollinators are impeded from visiting any plant species due to trait mismatches. To do so, we compared the observed visitation patterns to those expected under a scenario where pollinators interact randomly with all the available flower resources present at a given location and flowering period (Supporting information).

Our foraging movement analyses were conducted in R ver. 4.3.0 (www.r-project.org), with the package 'survival' ver. 3.3-1 (Therneau and Grambsch 2000, Therneau 2022). We found no multicollinearity among covariates when we checked their variance inflation factors with the package 'performance' ver. 0.10.4 (Lüdecke et al. 2020). The comparisons of multiple means were performed with the package 'multcomp' ver. 1.4-19 (Hothorn et al. 2008).

Community-level effectiveness

Following our analyses of the determinants of foraging choices and pollinator effectiveness of individual pollinator species, we then assessed the overall pollination service received by the individuals of the different plant species located in each

of the subplots by the whole pollinator community. Here, we used successful visitation to plant individuals as a proxy for overall effectiveness, due to challenges in measuring factors like adequate pollen deposition at the community level. However, our emphasis is particularly justified in our study context, where there appears to be limited trait matching within our studied communities.

To estimate community-level effectiveness of the pollination service received by an individual of plant species S at subplot (x,y) within a given plot from any pollinator species (hereafter community-level effectiveness), we calculated the probability that a step started in a plant individual at location (x_0,y_0) would end in an individual of the same plant species at (x,y), during a given flowering period F, and denoted as $p^F_{(x_0,y_0)\rightarrow(x,y)}$. To do so, we fitted the iSSF (Supporting information), combining the data collected for all pollinator species seen to visit that specific plant species and recorded during period F. Then, we averaged the value of $p^F_{(x_0,y_0)\rightarrow(x,y)}$ across all subplots (x_0,y_0) where plant species S was recorded during period F:

$$\Pi^F_{(x,y)} = \frac{1}{\ell} \sum_{(x_0,y_0)\in\mathcal{L}(S,F))} p^F_{(x_0,y_0)\rightarrow(x,y)}, \tag{1}$$

where $\mathcal{L}(S, F)$ represents the set of ℓ locations (subplots) in which we recorded flowers of species S in period F.

Finally, to test our hypothesis that variations in the community-level effectiveness experienced by individuals of the same plant species will be smaller in communities with higher pollinator diversity, for each group of conspecific plant individuals in a given subplot, we estimated their average pollination efficiency and the total number of pollinators that visited those individuals, per flowering period. Then, we used a generalized linear mixed model (GLMM) with a beta function, to study the relationship between the average community-level effectiveness and pollinator richness. The model also included the following fixed factors: 1) plant species identity, 2) time period, and 3) year. We included plot identity as a random factor.

Our estimates of the community-level effectiveness were conducted with R ver. 4.3.0 (www.r-project.org) using the above-mentioned packages plus the 'glmmTMB' ver. 1.1.3 package (Brooks et al. 2017) for model fitting.

Structural analysis

In addition to the overall community-level effectiveness received by different plant individuals, we also characterized potential flows between plant individuals of the same or different species by analysing the meso-scale structure of the network of interactions between plant and pollinator individuals. To this end, we built bipartite, individual-based plant–pollinator interaction networks for each site and sampling week. To build the networks, and given that we lack individual spatial coordinates for the individuals of the same plant species, we defined all conspecific individuals within a

subplot as a plant node and individual pollinators as pollinator nodes. Then, we established a connection between plant and pollinator nodes if we had recorded an interaction within our visitation sequence data (Fig. 2).

To characterize the network's meso-scale, we counted the total number of homospecific and heterospecific triplets within our networks (Allen-Perkins et al. 2024a). Here, triplets are patterns of connections that consist of one pollinator node (individual) linked to two plant nodes. When both plant nodes belong to the same species, the triplet is homospecific, and if the two plant nodes belong to two different species, it is considered heterospecific (examples in Fig. 2). Note that triplets can only be built among co-flowering plants that have been observed within the same visitation sequence in the field. From a plant individual's perspective, the number of homospecific and heterospecific triplets it is involved in is a proxy for the amount of conspecific and heterospecific pollen it is receiving at different points in time. Further, it provides us information of the identity of the plant nodes that contribute to the diet of the different pollinator species. Thus, the number of triplets also reflects the potential of each plant individual to indirectly influence (via apparent competition or facilitation) all co-flowering individuals through shared pollinators (Carvalheiro et al. 2014). We then calculated the total number of homospecific and heterospecific triplets in which a specific plant node is involved at a given date by adding the number of subgraphs containing that node during the weeks
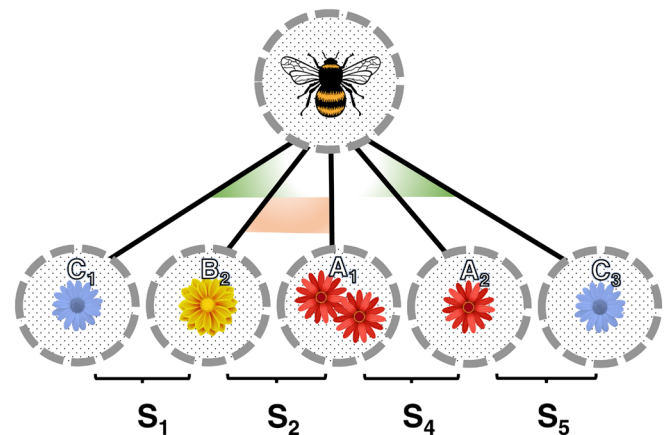

Figure 2. Examples of a bipartite, individual-based plant–pollinator for the foraging sequence in Fig. 1a. Plant nodes represent groups of conspecific plant individuals within a given subplot, whereas pollinator nodes depict an individual floral visitor. Interactions (continuous lines) illustrate the existence of an observed visit between the counterparts of the plant and pollinator nodes in a visitation sequence. Each plant node shows the subplot position modeled by the node (for example, C_1 at the leftmost node), as well as the plant species (represented with different types of flower), and the number of plant individuals of that species within the subplot. Within that network, we highlight the structure of a homospecific (green, between plant nodes at C_1 and C_3) and heterospecific triplets (orange, between plant nodes at B_2 and A_1). Note that homospecific triplets also appear between plant nodes that have not been visited sequentially, as in the example highlighted here.

leading up to that date. In our reproductive success analysis (below), to estimate the number of triplets, we used the date on which the fruit set of the plant node was measured.

Our estimates of the subgraph descriptors were conducted with R ver. 4.3.0 (www.r-project.org) and the packages 'bipartite' ver. 2.16 (Dormann et al. (2008), 'matlib' ver. 0.9.5 (Friendly et al. 2021), and 'igraph' ver. 1.2.6 (Csardi and Nepusz 2006).

Reproductive success analysis

Finally, we assessed how foraging decision processes, indirect interactions, and resource availability affected plant reproductive success, by fitting a GLMM to the plant nodes (subsection Structural analysis) of the Doñana dataset. We used the average fruit set as our response variable, and fitted a Gaussian model with a log link function (Supporting information). As explanatory variables, the model included the following covariates estimated during the flowering periods in which the pollinator visit was recorded: 1) the average community-level effectiveness of the pollination service received by plant nodes, estimated as the mean values obtained from the iSSF models in the Community-level effectiveness subsection and weighted according to Eq. (1); 2) the number of steps received that started in plant species other than that of the focal plant node; 3) the number of indirect interactions (triplets), both homospecific and heterospecific, in which a specific plant node was involved; 4) plant and pollinator richness at the subplot level; 5) the total number of flowers and pollinators observed in the subplot, 6) the total number of pollinator visits received by a plant individual, 7) plant species identity; and 8) the flowering period. We used 'plot' as a random intercept to account for multiple individuals of the same plant species measured at each plot.

To keep the regression variables on similar scales and use the fitted parameters of the models as (within-study) effect sizes; that is, measures of variable importance (Schielzeth 2010), all numeric explanatory variables were centered and scaled during the analysis.

Our analyses were conducted in R ver. 4.3.0 (www.r-project.org), with the 'glmmTMB' ver. 1.1.3 package (Brooks et al. 2017). We found no high collinearity among explanatory variables when we checked their variance inflation factors with the R-package 'performance' ver. 0.8.0 (Lüdecke et al. 2020). We also checked model assumptions with the R-package 'DHARMa' ver. 0.4.5 (Hartig 2020), and performed a power analysis with 'pwr' ver. 1.3-0 (Champely 2020) to assess the probability of rejecting a false null hypothesis.

Results

Over the full length of our field experiment we surveyed a total of 85 flowering plant species in Gorbeia and 24 in Doñana (25.0 ± 13.4 and 9.2 ± 2.5 per plot, respectively), accounting for 185 916 and 49 666 flowers, respectively.

Plant richness and flower abundance were highly variable among plots, flowering periods, and years (Supporting information). We documented 5901 and 10 026 distinct plant–pollinator interactions in Gorbeia and Doñana, distributed among 1206 and 557 independent flower visitation sequences by 135 and 68 different pollinator species, respectively (Supporting information). Pollinator richness and pollinator interactions were also highly variable among plots, flowering periods, and years (Supporting information). The five most abundant species (the ones actually used for the analyses) in Gorbeia took part in at least 3985 interactions, grouped in 524 sequences with 4.5 ± 4.7 steps on average; whereas the five most abundant species in Doñana performed 5973 interactions, distributed in 239 sequences with 24.0 ± 30.8 steps on average. For all the flying sequences recorded, 9.1 ± 5.7 flowers from 2.3 ± 0.9 plant species were visited in Gorbeia, and 18.0 ± 23.5 flowers from 1.1 ± 0.3 plant species in Doñana. Most of the steps in those sequences were loyal (88.5 and 99.4% in Gorbeia and Doñana, respectively).

Foraging movement analysis

In both study areas, pollinator foraging choices were determined by floral constancy (Fig. 3a–b), plant species richness (Fig. 3c–d), and floral abundance (Fig. 3e–f), with most species tending to execute loyal movements towards less diverse plots with greater floral abundance. As opposed to Gorbeia, where step length did not influence most foraging decisions (Fig. 3g), all species preferred to move towards plots located further away in Doñana (Fig. 3f). Foraging choices for *A. mellifera*, the only shared species between both sites, seemed to respond to the same variables in both study areas, except in the case of step length, with individuals in Doñana preferring to move to more distant subplots.

Our analysis shows that environmental conditions (i.e. the combinations of site location, flowering period, time of the day, and year) influence the probability of observing a step (Supporting information). Further, environmental conditions affected floral constancy of the main pollinators in Gorbeia (Supporting information) but not in Doñana, where more than 99% of observed steps were loyal. For example, the probability that *B. pascuorum* will be faithful to a plant species changes significantly throughout the flowering season, with more faithful movements at the beginning and at the end of the season, and less constancy in the middle of the season. This partially confirms our hypothesis that the average pollinator effectiveness will change throughout the flowering season. Finally, although we found no significant differences in the mean values of plant richness and floral abundance due to changes in environmental conditions, fluctuations in those variables modulate the results obtained from our foraging movement models (see next subsection for an example).

Finally, our analysis of pollinator visitation frequencies shows these are mostly based on plant relative abundances rather than on trait-matching between plant and pollinator species (Supporting information).
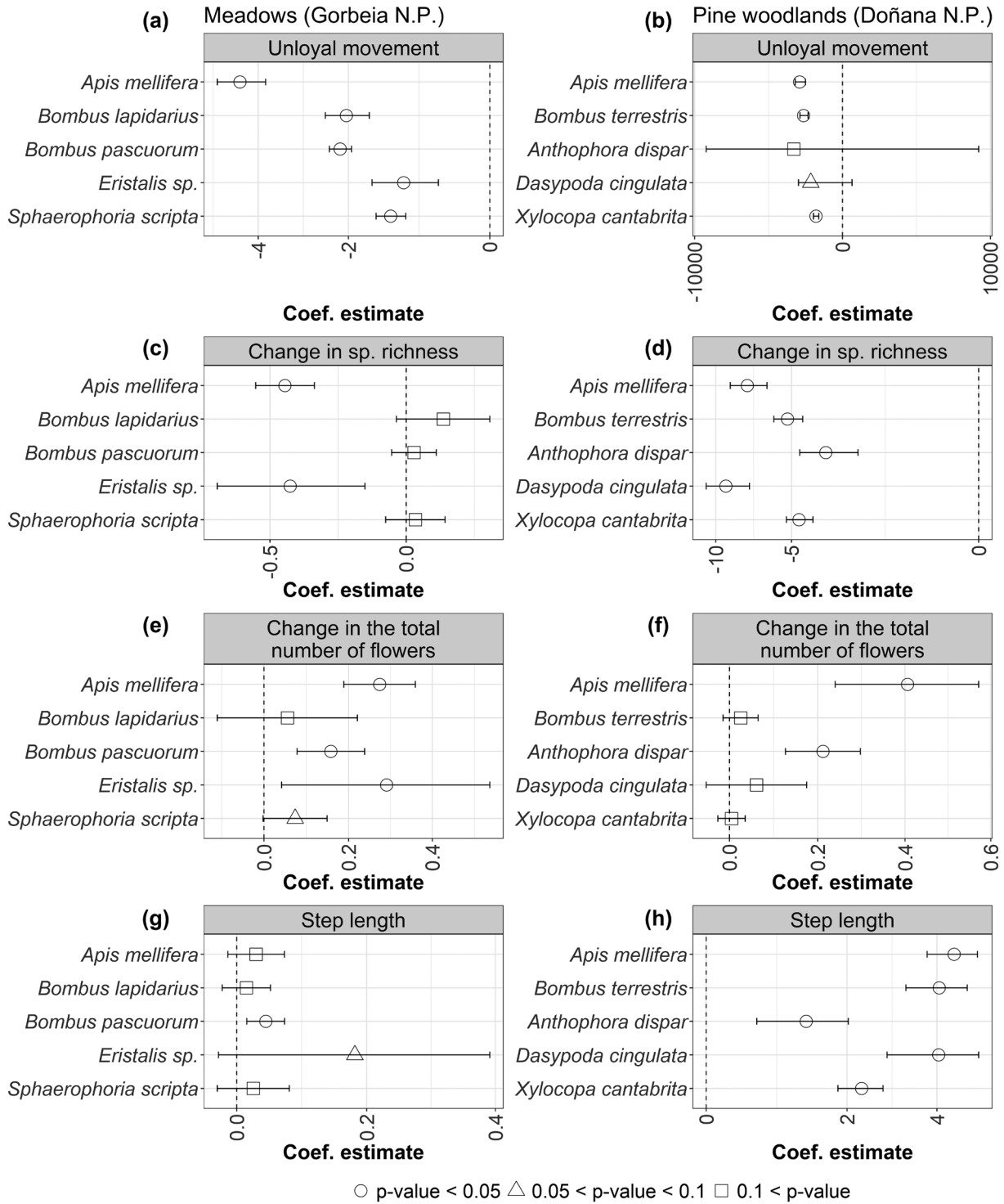
Figure 3. Coefficients estimated from the foraging choice model in the Supporting information for the five floral visitors that have the largest number of recorded steps within our study sites (in pseudo-logarithmic scale): results for unloyal movement (panels a–b), change in plant species richness (c–d), change in flower abundance (e–f), and step length (g–h). Left panels (a, c, e, g) show the results for the pollinator species in Gorbeia National Park (N.P.), whereas right panels (b, d, f, h) show those for the pine woodlands within Doñana N.P. Dashed lines indicate no effect. Markers show the mean value of the corresponding coefficients and error bars depict their 95% confidence intervals. The shape of the markers classifies the coefficient's p-value in the following categories: p-value < 0.05 (circle), 0.05 < p-value < 0.10 (triangle), and 0.10 < p-value (square).

Community-level effectiveness

We found that the community-level effectiveness of the pollination service received by the ten most abundant plants in our census (Supporting information) depends simultaneously on the composition of the pollinator community at a given site, the spatial distribution of the plant individuals within the site (step length), and the differences in plant richness and flower abundance of the corresponding subplots (Supporting information), which change substantially through space and time (Fig. 4a). As a consequence, we observed substantial variation in the community-level effectiveness experienced by different plant individuals. This variation is evident not only among individuals of different species, but also among individuals of the same species situated in different subplots within the same site, and across the different periods of time and sites (Supporting information). Despite such variation, community-level effectiveness consistently increases with pollinator richness, particularly in Gorbeia (Fig. 4b). This observation aligns with our hypothesis that communities with greater pollinator diversity have lower variation in the community-level effectiveness experienced by individuals of the same plant species.

Structural analysis

In our communities, the number of homospecific subgraphs is moderately correlated with the total number of visits per week (Spearman's $\rho = 0.61$, p-value < 0.05), whereas the number of heterospecific subgraphs is not (Spearman's $\rho = 0.14$, p-value < 0.05). Overall, homospecific subgraphs are much more abundant than heterospecific ones (paired Wilcoxon-test: p-value < 0.05 for all plant species), except in most individuals of *Rosmarinus officinalis* where they are comparable (paired Wilcoxon-test: p-value $= 0.44$) (Supporting information). In general, subplots with several plant species and higher number of visits contain one plant species that is much more abundant than the others and takes part in most of the subplot's triplets, both homospecific and heterospecific (Supporting information). Therefore, plant individuals belonging to the most visited and abundant plant species tend to share visits by each individual pollinator species with their conspecifics, unlike what happens with rare or rarely visited individuals.

Reproductive success

Overall, the major drivers of fruit set are plant species identity (effect-size of plant species between -2.10 and 0.28, Fig. 5) and pollinator richness at a given subplot and period of time (effect-size ~ 0.18, Fig. 5f) (Supporting information). However, our power analysis also indicates that we should not rule out the potential significance of other explanatory variables: the probability of rejecting a false null hypothesis is less than 8% with our sample size (n $= 187$ observations). Thus, foraging choices can also influence fruit production of individual plants, albeit to a lesser extent. Specifically, we found that fruit set increases with the average community-level effectiveness of the pollination service received by plants (effect-size ~ 0.05, Fig. 5a), whereas it decreases with increasing numbers of unloyal steps involving sequential visits to individuals of different plant species (effect-size ~ -0.03, Fig. 5b). These results support our hypothesis that plant individuals visited by more efficient pollinators (showing greater floral constancy) have greater reproductive success.

Contrary to our expectations, an increase in the number of homospecific triplets in which a plant node is involved (a proxy for conspecific pollen flow) reduces fruit set (effect-size for homospecific triplets ~ -0.04, Fig. 5c), whereas an increase in the number of heterospecific triplets in which plant individuals are involved (a proxy for heterospecific pollen flow) enhances it (effect-size for heterospecific triplets ~ 0.05, Fig. 5d). Further, we find a negative relationship between both pollinator abundance and the number of pollinator visits received by a plant individual and its fruit set (effect-sizes ~ -0.09 and ~ -0.03, respectively, Fig. 5h–i).

Finally, our model shows that plant community composition also affects fruit set, with greater plant richness and flower abundance resulting in plant individuals with greater fruit sets (effect-sizes ~ 0.04 and ~ 0.02, respectively, Fig. 5e–g). This can be observed for example at the beginning of the flowering season (period 1), when plant richness and flower abundance are smaller (Supporting information) fruit set is also smaller (effect-size for flowering period 1 ~ -0.06).

Discussion

Our results show that the determinants of pollinator foraging choices can be quite general across habitats, with floral constancy and flower abundance playing important roles for all species and sites. The foraging choices of different pollinator species can shift throughout the flowering season in response to changes in the composition of plant and pollinator communities, with important implications for pollination effectiveness and the pollination services that plants receive. We find that while intra-specific overlap in the use of pollination services decreases fruit set, inter-specific overlap increases it, despite the potential increase in heterospecific pollen deposition. We also find that areas with greater plant and pollinator species exhibit larger values of plant reproductive success.

Our findings add to the burgeoning body of research that shows that plant and pollinator communities are dynamic and spatially heterogeneous (Olesen et al. 2007, 2011, Magrach et al. 2020, Fründ 2021). Interactions between plants and their pollinators are determined by pollinator foraging movements, which in turn depend on factors that vary in space and time (e.g. floral constancy and abundance (Goulson et al. 1997). Pollinator effectiveness also varies through time (Ivey et al. 2003), leading to a change in the average pollination service received by plants and ultimately affecting their reproductive success. Our results thus point to a strong relationship between pollinator foraging and fruit set, our proxy for plant reproductive success. Such scaling-up

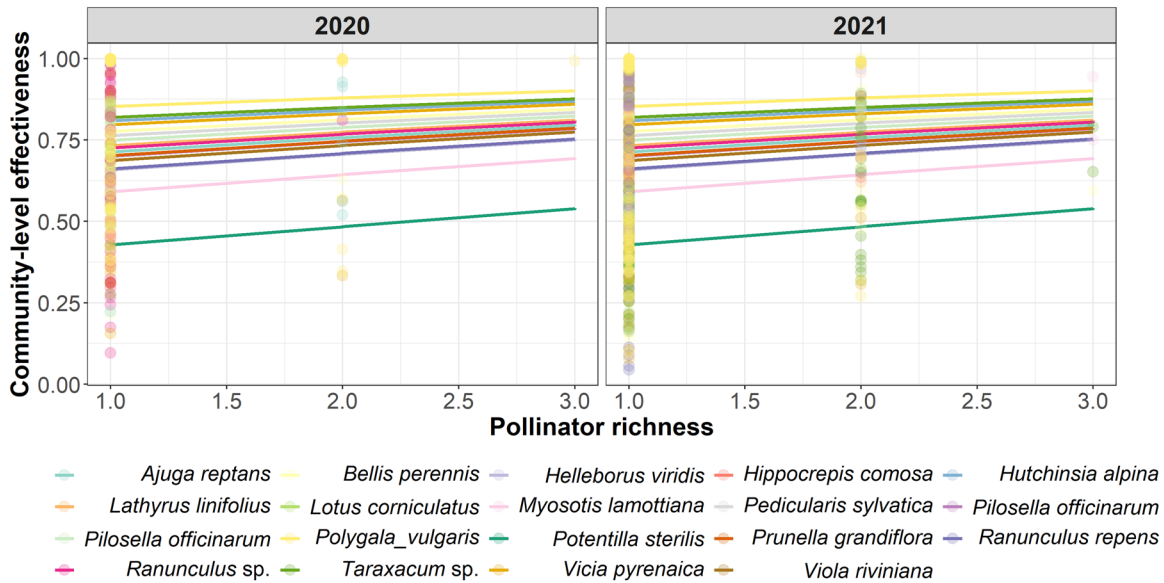**(a) Polygala vulgaris**
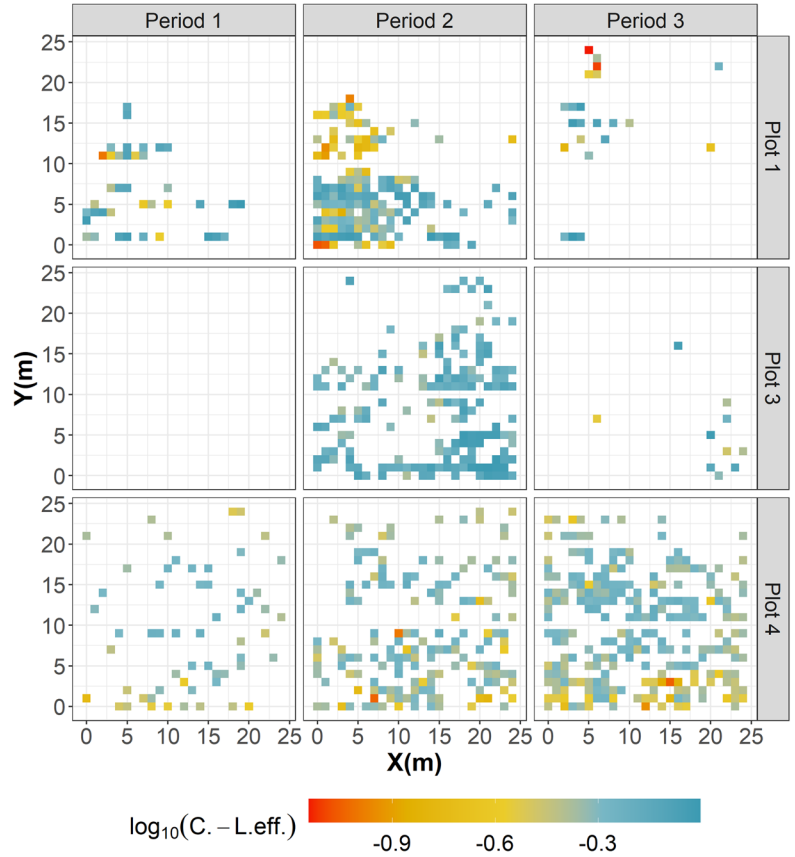
(b) Gorbeia N.P.

Figure 4. (a) Community-level effectiveness of the pollination service received by the individuals of *Polygala vulgaris* (in log-scale). Each panel represents a 25 × 25 m plot in Gorbeia National Park (N.P.) in 2021. Rows display the information for a given site, whereas columns show information by flowering period. (b) Results for pollinator richness in the community-level effectiveness GLMM (R-package 'ggef-fects' ver. 1.3.1; Lüdecke 2018) per plant species and year in Gorbeia N.P. Dots represent the response dependence on the explanatory variable, whereas lines show their expected values.
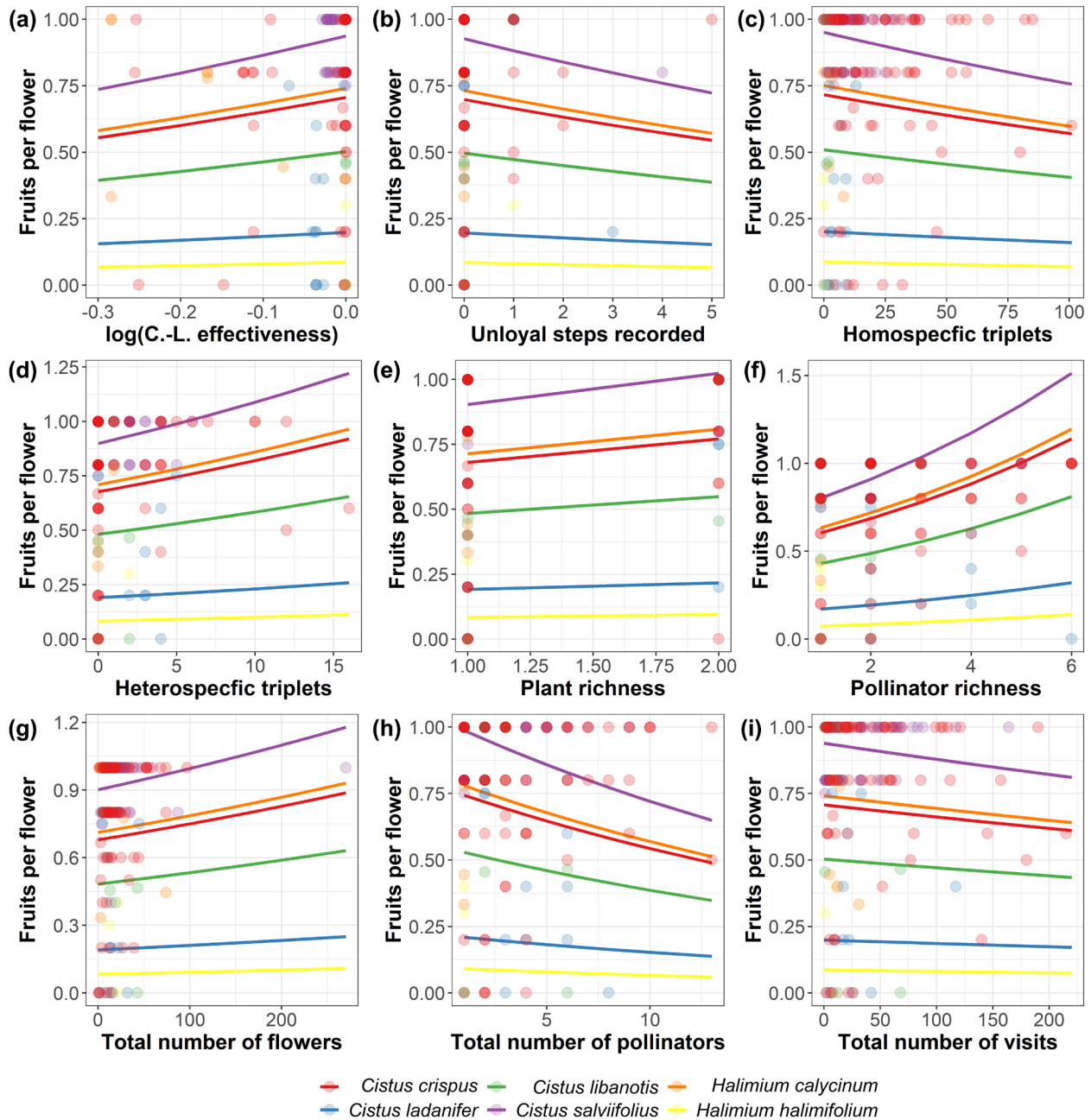
Figure 5. Results for plant explanatory variables in the seed production GLMM (R-package 'ggeffects' ver. 1.3.1 (Lüdecke (2018)): community-level effectiveness (panel a) and number of unloyal steps (b), number of homospecific and heterospecific triplets (c–d, respectively), plant and pollinator richness (e–f, respectively), total number of flowers and pollinators (g–h, respectively), and total number of pollinator visits recorded (i). Each panel shows the results for each plant species: *Cistus crispus* (red), *C. ladanifer* (blue), *C. libanotis* (green), *C. salviifolius* (purple), *Halimium calycinum* (orange) and *H. halimifolium* (yellow). Dots represent the fruit set dependence on the explanatory variable, whereas lines show their expected values.

of the effects of individual movement patterns to higher-level community properties has been observed elsewhere (McWilliams et al. 2019), but this study provides new empirical evidence from the context of plant–pollinator communities. In addition, the dynamic nature of plant and pollinator communities leads to important questions regarding our static classification of species within the specialist–generalist spectrum (Brosi 2016) or how we define their effectiveness. Changes in pollinator effectiveness through time suggest that different plant species maximize the pollination services they receive under different conditions, leading to a certain asynchrony in reproductive success (Wang et al. 2021) among different plant species, which could be one of the mechanisms that allows plant diversity to be maintained. For example,

although we have data for a small number of species, we find that while *C. ladanifer* and *H. calycium* show similar floral abundances throughout the flowering season (Supporting information), their reproductive success is maximized at different points following variations in community composition through time (Supporting information; e.g. shifting complementarity and redundancy in pollinator roles through time, Magrach et al. 2021).

By following individual pollinator movement trajectories for different pollinator species across the whole flowering season within two contrasting habitat types and for two consecutive years, we are able to show a number of general patterns across different species. Specifically, our models describing the foraging choices for the nine most frequently observed pollinator species (including both bees and syrphid flies) reveal that the visits they perform are strongly coupled with floral cover and highly variable through space and time (Hervías-Parejo et al. 2023). Further, we find that pollinator species tend to consistently show floral constancy, although this again changes through time (Supporting information; Yourstone et al. 2023). Although these results apparently contradict that interaction patterns in plantâ–pollinator systems are neutral (Parra et al. 2022), we can not rule out the existence of neutral mechanisms since both the visited plants and the pollinators considered here were very abundant.

In line with recent research (Artamendi et al. unpubl.), our results show that pollinator species richness has a positive effect on plant reproductive success, showing one of the largest effect sizes. This adds to the large body of evidence supporting the positive role of biodiversity for ecosystem functioning (Hong et al. 2021). The positive relationship between diversity and function is well documented in models and experiments where the number of species is controlled for and other sources of variation of biodiversity are prevented (e.g. dispersal, environmental heterogeneity). Results based on field observations, where biodiversity and its drivers were not controlled for, show that biodiversity to ecosystem functioning relationships can be more variable (Hagan et al. 2021). Despite this variability, our field-based results from a largely independent plant–pollinator system show that the effect of pollinator richness on plant fruit-set is clear and positive.

We find that intra-specific overlap in the use of pollination services leads to lower reproductive success, while it increases under conditions of higher inter-specific overlap, and in areas with greater plant and pollinator species diversity. This shows that despite the increase in heterospecific pollen deposition that results from these conditions, at least some plant species thrive under more diverse conditions, and suggests that rather than competitive interactions, this sharing of pollinator resources seems to foster facilitative interactions between plant species (Moeller 2004). Further, these results suggest the plant species have strong mechanisms to avoid the negative consequences of heterospecific pollen deposition (Arceo-Gómez and Ashman 2011), including differences in flower morphology and position of stigmas which enable various pollinator species to carry the pollen in different parts of their bodies (Armbruster et al. 1994) (e.g. disc flowers depositing pollen in ventral parts of pollinators and labiate flowers depositing in dorsal areas).

While greater pollinator diversity increases reproductive success, an increase in the number of visits received by plant individuals reduces it. This is in line with previous research that describes the cost–benefit curves for different plant–pollinator interactions, for many of which the relationship between the number of pollinator visits and reproductive success saturates rather than showing a linear trend (Morris et al. 2010), or even reverses, becoming detrimental (Aizen et al. 2014, Garibaldi et al. 2020). The mechanisms to explain these non-linear trends include the removal of previously deposited pollen by new visitors, floral damage, or clogging of stigmas by excess pollen, among others (Morris et al. 2010).

This study has several limitations. For example, the findings reported here should be confirmed by more precise measures of plant reproductive success, such as viable seed set, as proposed by Mendes et al. (2021). Also, the extension of facilitative interactions between plant species to the broader plant community, including self-compatible plants or those less abundant, needs further exploration. In addition, future research should make use of longer time scales and assess whether these patterns are consistent across several years or whether they change under varying environmental conditions. Specifically, it would be interesting to investigate how declining pollinator diversities might affect the existence of facilitative interactions between species. Despite these limitations, our research takes us closer to understanding biodiversity–ecosystem function within plant and pollinator communities, and how sharing pollinator resources between plant species in more diverse communities can actually result in facilitative interactions. This is probably related to a greater stability in the pollination services received that overrides any potential negative effects of increasing heterospecific pollen deposition.

Author contributions

Alfonso Allen-Perkins: Conceptualization (equal); Data curation (supporting); Formal analysis (equal); Methodology (equal); Software (lead); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Maddi Artamendi**: Data curation (lead); Methodology (supporting); Writing – review and editing (equal). **Daniel Montoya**: Conceptualization (equal); Formal analysis (supporting); Methodology (equal); Validation (equal); Visualization (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Encarnación Rubio**: Data curation (lead); Methodology (supporting); Writing – review and editing (equal). **Ainhoa Magrach**: Conceptualization (equal); Data curation (supporting); Formal analysis (equal); Funding acquisition (lead); Methodology (equal); Project administration (lead); Resources (lead); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ecog.07240.

Data availability statement

Data are available from the Zenodo Repository: https://zenodo.org/records/11396556 (Allen-Perkins et al. 2024b).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Aizen, M. A., Morales, C. L., Vázquez, D. P., Garibaldi, L. A., Sáez, A. and Harder, L. D. 2014. When mutualism goes bad: density-dependent impacts of introduced bees on plant reproduction. – New Phytol. 204: 322–328.

Allen-Perkins, A., Hurtado, M., García-Callejas, D., Godoy, O. and Bartomeus, I. 2024a. Multilayer diffusion networks as a tool to assess the structure and functioning of fine grain sub-specific plant–pollinator networks. – Oikos 2024: e10168 10.1111/oik.10168.

Allen-Perkins, A., Artamendi, M., Montoya, D., Rubio, E. and Magrach, A. 2024b. Data from: Untangling the plant reproduc-tive success of changing community composition and pollinator foraging choices. – Dryad Digital Repository, https://zenodo.org/records/11396556.

Arceo-Gómez, G. and Ashman, T.-L. 2011. Heterospecific pollen deposition: does diversity alter the consequences? – New Phytol. 192: 738–746.

Armbruster, W. S., Edwards, M. E. and Debevec, E. M. 1994. Floral character displacement generates assemblage structure of western Australian triggerplants (*Stylidium*). – Ecology 75: 315–329.

Arroyo-Correa, B., Bartomeus, I. and Jordano, P. 2021. Individual-based plant–pollinator networks are structured by phenotypic and microsite plant traits. – J. Ecol. 109: 2832–2844.

Avgar, T., Potts, J. R., Lewis, M. A. and Boyce, M. S. 2016. Integrated step selection analysis: bridging the gap between resource selection and animal movement. – Methods Ecol. Evol. 7: 619–630.

Bascompte, J. and Jordano, P. 2013. Mutualistic networks. Monographs in population biology. – Princeton Univ. Press.

Bosch, J. 1992. Floral biology and pollinators of three co-occurring cistus species (Cistaceae). – Bot. J. Linn. Soc. 109: 39–55.

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M. and Bolker, B. M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. – R J. 9: 378–400.

Brosi, B. J. 2016. Pollinator specialization: from the individual to the community. – New Phytol. 210: 1190–1194.

Brosi, B. J. and Briggs, H. M. 2013. Single pollinator species losses reduce floral fidelity and plant reproductive function. – Proc. Natl Acad. Sci. USA 110: 13044–13048.

Carvalheiro, L. G. et al. 2014. The potential for indirect effects between co-flowering plants via shared pollinators depends on resource abundance, accessibility and relatedness. – Ecol. Lett. 17: 1389–1399.

Cervantes-Loreto, A., Ayers, C. A., Dobbs, E. K., Brosi, B. J. and Stouffer, D. B. 2021. The context dependency of pollinator interference: how environmental conditions and co-foraging species impact floral visitation. – Ecol. Lett. 24: 1443–1454.

Champely, S. 2020. pwr: basic functions for power analysis. – R package ver. 1.3-0, https://CRAN.R-project.org/package=pwr.

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K. and Ellison, A. M. 2014. Rarefaction and extrapolation with hill numbers: a framework for sampling and estimation in species diversity studies. – Ecol. Monogr. 84: 45–67.

Csardi, G. and Nepusz, T. 2006. The igraph software package for complex network research. – InterJ. Complex Syst. 1695.

Dormann, C. F., Gruber, B. and Fruend, J. 2008. Introducing the bipartite package: analysing ecological networks. – R News 8: 8–11.

Fieberg, J., Signer, J., Smith, B. and Avgar, T. 2021. A 'how to' guide for interpreting parameters in habitat-selection analyses. – J. Anim. Ecol. 90: 1027–1043.

Flanagan, R. J., Mitchell, R. J. and Karron, J. D. 2010. Effects of multiple competitors for pollination on bumblebee foraging patterns and *Mimulus ringens* reproductive success. – Oikos 120: 200–207.

Friendly, M., Fox, J. and Chalmers, P. 2021. matlib: matrix functions for teaching and learning linear algebra and multivariate statistics. – R package ver. 0.9.5, https://CRAN.R-project.org/package=matlib.

Fründ, J. 2021. Dissimilarity of species interaction networks: how to partition rewiring and species turnover components. – Ecosphere 12: e03653.

Gail, M. H., Lubin, J. H. and Rubinstein, L. V. 1981. Likelihood calculations for matched case-control studies and survival studies with tied death times. – Biometrika 68: 703–707.

Garibaldi, L. A., Sáez, A., Aizen, M. A., Fijen, T. and Bartomeus, I. 2020. Crop pollination management needs flower-visitor monitoring and target values. – J. Appl. Ecol. 57: 664–670.

Gavini, S. S., Sáez, A., Tur, C. and Aizen, M. A. 2021. Pollination success increases with plant diversity in high-Andean communities. – Sci. Rep. 11: 22107.

Gómez, J. M., Perfectti, F., Armas, C., Narbona, E., González-Megías, A., Navarro, L., DeSoto, L. and Torices, R. 2020. Within-individual phenotypic plasticity in flowers fosters pollination niche shift. – Nat. Commun. 11: 4019.

Goulson, D., Ollerton, J. and Sluman, C. 1997. Foraging strategies in the small skipper butterfly, *Thymelicus flavus*: when to switch? – Anim. Behav. 53: 1009–1016.

Guimarães, P. R. 2020. The structure of ecological networks across levels of organization. – Annu. Rev. Ecol. Evol. Syst. 51: 433–460.

Hagan, J. G., Vanschoenwinkel, B. and Gamfeldt, L. 2021. We should not necessarily expect positive relationships between biodiversity and ecosystem functioning in observational field data. – Ecol. Lett. 24: 2537–2548.

Hartig, F. 2020. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. – R package ver. 0.3.0, https://CRAN.R-project.org/package=DHARMa.

Herberich, E., Sikorski, J. and Hothorn, T. 2010. A robust procedure for comparing multiple means under heteroscedasticity in unbalanced designs. – PLoS One 5: e9788.

Hervías-Parejo, S., Colom, P., Beltran Mas, R., Serra, E., Pons, S., Mesquida, V. and Traveset, A. 2023. Spatio-temporal variation in plant–pollinator interactions: a multilayer network approach. – Oikos 2023: e09818.

Hong, P., Schmid, B., Laender, F. D., Eisenhauer, N., Zhang, X., Chen, H., Craven, D., Boeck, H. J. D., Hautier, Y., Petchey, O. L., Reich, P. B., Steudel, B., Striebel, M., Thakur, M. P. and Wang, S. 2021. Biodiversity promotes ecosystem functioning despite environmental change. – Ecol. Lett. 25: 555–569.

Hothorn, T., Bretz, F. and Westfall, P. 2008. Simultaneous inference in general parametric models. – Biom. J. 50: 346–363.

Hsieh, T. C., Ma, K. H. and Chao, A. 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). – Methods Ecol. Evol. 7: 1451–1456.

Inouye, D. W. 1978. Resource partitioning in bumblebees: experimental studies of foraging behavior. – Ecology 59: 672–678.

Ivey, C. T., Martinez, P. and Wyatt, R. 2003. Variation in pollinator effectiveness in swamp milkweed, *Asclepias incarnata* (Apocynaceae). – Am. J. Bot. 90: 214–225.

Jordano, P. 2016. Sampling networks of ecological interactions. – Funct. Ecol. 30: 1883–1893.

Kortsch, S., Saravia, L., Cirtwill, A. R., Timberlake, T., Memmott, J., Kendall, L., Roslin, T. and Strona, G. 2023. Landscape composition and pollinator traits interact to influence pollination success in an individual-based model. – Funct. Ecol. 37: 2056–2071.

Lanuza, J. B., Allen-Perkins, A. and Bartomeus, I. 2023. The non-random assembly of network motifs in plant–pollinator networks. – J. Anim. Ecol. 92: 760–773.

Larsson, M. 2005. Higher pollinator effectiveness by specialist than generalist flower-visitors of unspecialized *Knautia arvensis* (Dipsacaceae). – Oecologia 146: 394–403.

Lázaro, A., Gómez-Martínez, C., Alomar, D., González-Estévez, M. A. and Traveset, A. 2020. Linking species-level network metrics to flower traits and plant fitness. – J. Ecol. 108: 1287–1298.

Lopes, S. A., Bergamo, P. J., Najara Pinho Queiroz, S., Ollerton, J., Santos, T. and Rech, A. R. 2021. Heterospecific pollen deposition is positively associated with reproductive success in a diverse hummingbird-pollinated plant community. – Oikos 2022: e08714. https://doi.org/10.1111/oik.08714.

Loreau, M. and Hector, A. 2001. Partitioning selection and complementarity in biodiversity experiments. – Nature 412: 72–76.

Lüdecke, D. 2018. ggeffects: Tidy data frames of marginal effects from regression models. – J. Open Source Softw. 3: 772.

Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P. and Makowski, D. 2020. performance: An R package for assessment, comparison and testing of statistical models. – J. Open Source Softw. 6: 3139. https://doi.org/10.21105/joss.03139

Magrach, A., Lara, C., Luna, U. M., Díaz-Infante, S. and Parker, I. 2020. Community-level reorganizations following migratory pollinator dynamics along a latitudinal gradient. – Proc. R. Soc. B 287: 20200649.

Magrach, A., Molina, F. P. and Bartomeus, I. 2021. Niche complementarity among pollinators increases community-level plant reproductive success. – Peer Commun. J. 1.

Magrach, A., Artamendi, M., Lapido, P. D., Parejo, C. and Rubio, E. 2023. Indirect interactions between pollinators drive interaction rewiring through space. – Ecosphere 14: e4521.

McWilliams, C., Lurgi, M., Montoya, J. M., Sauve, A. and Montoya, D. 2019. The stability of multitrophic communities under habitat loss. – Nat. Commun. 10: 2322.

Mendes, S. B., Timóteo, S., Loureiro, J. and Castro, S. 2021. The impact of habitat loss on pollination services for a threatened dune endemic plant. – Oecologia 198: 279–293.

Moeller, D. A. 2004. Facilitative interactions among plants via shared pollinators. – Ecology 85: 3289–3301.

Morris, W. F., Vázquez, D. P. and Chacoff, N. P. 2010. Benefit and cost curves for typical pollination mutualisms. – Ecology 91: 1276–1285.

Morse, D. H. 1977. Resource partitioning in bumble bees: the role of behavioral factors. – Science 197: 678–680.

Olesen, J. M., Bascompte, J., Dupont, Y. L. and Jordano, P. 2006. The smallest of all worlds: pollination networks. – J. Theor. Biol. 240: 270–276.

Olesen, J. M., Bascompte, J., Dupont, Y. L. and Jordano, P. 2007. The modularity of pollination networks. – Proc. Natl Acad. Sci. USA 104: 19891–19896.

Olesen, J. M., Stefanescu, C. and Traveset, A. 2011. Strong, long-term temporal dynamics of an ecological network. – PLoS One 6: e26455.

Parra, S. A., Thébault, E., Fontaine, C. and Dakos, V. 2022. Interaction fidelity is less common than expected in plant–pollinator communities. – J. Anim. Ecol. 91: 1842–1854.

Potts, S. G., Vulliamy, B., Dafni, A., Ne'eman, G. and Willmer, P. 2003. Linking bees and flowers: how do floral communities structure pollinator communities? – Ecology 84: 2628–2642.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. – Methods Ecol. Evol. 1: 103–113.

Signer, J., Fieberg, J. and Avgar, T. 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. – Ecol. Evol. 9: 880–890.

Simmons, B. I., Cirtwill, A. R., Baker, N. J., Wauchope, H. S., Dicks, L. V., Stouffer, D. B. and Sutherland, W. J. 2018. Motifs

in bipartite ecological networks: uncovering indirect interactions. – Oikos 128: 154–170.

Simmons, B. I., Beckerman, A. P., Hansen, K., Maruyama, P. K., Televantos, C., Vizentin-Bugoni, J. and Dalsgaard, B. 2020. Niche and neutral processes leave distinct structural imprints on indirect interactions in mutualistic networks. – Funct. Ecol. 35: 753–763.

Therneau, T. M. 2022. A package for survival analysis in R. – R package ver. 3.3-1. https://CRAN.R-project.org/package=survival.

Therneau, T. M. and Grambsch, P. M. 2000. Modeling survival data: extending the Cox model. – Springer.

Thurfjell, H., Ciuti, S. and Boyce, M. S. 2014. Applications of step-selection functions in ecology and conservation. – Movem. Ecol. 2: 4.

Tur, C., Vigalondo, B., Trøjelsgaard, K., Olesen, J. M. and Traveset, A. 2013. Downscaling pollen-transport networks to the level of individuals. – J. Anim. Ecol. 83: 306–317.

Wang, S. et al. 2021. Biotic homogenization destabilizes ecosystem functioning by decreasing spatial asynchrony. – Ecology 102: doi:10.1002/ecy.3332.

Willcox, B. K., Aizen, M. A., Cunningham, S. A., Mayfield, M. M. and Rader, R. 2017. Deconstructing pollinator community effectiveness. – Curr. Opin. Insect Sci. 21: 98–104.

Yourstone, J., Varadarajan, V. and Olsson, O. 2023. Bumblebee flower constancy and pollen diversity over time. – Behav. Ecol. 34: 602–612.

Zhang, J. 2021. Spaa: species association analysis. – R package ver. 0.5.3, https://github.com/helixcn/spaa.