

Trade-offs among plant floral and reproductive traits determine interactions with floral visitors

Jose B. Lanuza^{1,2*}, Romina Rader¹, Jamie Stavert³, Liam K. Kendall⁴,
Manu E. Saunders¹ and Ignasi Bartomeus²

Plant life strategies are often delimited by vegetative and physiological traits but little is known about how floral and reproductive traits drive these strategies, and in turn shape plant interactions with floral visitors. Here, we compiled 13 floral, 4 reproductive and 3 vegetative traits for 1,506 plant species from 28 plant-pollinator network studies across 18 different countries. We investigated the associations among these traits, pollinator visitation and the functional role of plant species within the networks (interaction frequency, normalized degree and specialization). We found that 51.8% of trait variation was explained by two independent axes that encompassed plant form and function. Specifically, the first axis indicated the presence of a trade-off between flower number and flower size (PC1, 26.72%). The second axis indicated a trade-off for the level of pollinator dependency (PC2, 25.08%). Although the main axes of trait variation did not fully explain pollinator visitation rates, different plant life strategies were associated with visitation rates and pollinator functional groups. Overall, the main traits that determined plant species' functional roles were height, nectar concentration, pollen grains per flower, number of ovules, style length, selfing level and flower width. Our results highlight the need to consider plant reproductive and floral traits to improve understanding of plant life strategies and plant-pollinator interactions at broader spatial scales.

¹ School of Environmental and Rural Science, University of New England, Armidale, New South Wales 2350, Australia. ² Estación Biológica de Doñana (EBD-CSIC), E-41092 Seville, Spain. ³ Department of Conservation | Te Papa Atawhai, Auckland, New Zealand. ⁴ Centre for Environmental and Climate Science, Lund University, Sölvegatan 37, S-223 62 Lund, Sweden. * e-mail: barragansljose@gmail.com

There is an astonishing diversity of floral structures and plant reproductive strategies among flowering plants^{1,2}, which have long been of interest to pollination biologists in terms of their relevance to plant-pollinator interactions. However, most studies that have explored reproductive (e.g., mating and compatibility systems) and floral trait (e.g., flower size or nectar provision) variation have concentrated on the individual or community level and thus, broader macroecological patterns remain poorly

investigated³⁻⁷. Indeed, studies depicting species' life history strategies generally focus on vegetative traits and rarely consider reproductive traits⁸. As a consequence, a unified framework that explores the compromises among floral traits and their relevance to plant life strategies is currently lacking¹⁰. At the same time, there is growing interest in the determinants of plant-pollinator interactions via trait-based approaches¹¹ and trait-matching analyses¹². However, floral traits have been overlooked beyond highly specialised plant-pollinator systems^{10,13} and the role of plant reproductive biology remains little explored in plant-pollinator interactions (but see references^{14,15}).

With the recent availability of large trait databases, plant ecological strategies are increasingly being examined^{16,17}, and are facilitating the identification of global patterns and constraints of plant form and function^{8,18,19}. However, the main focus has been on vegetative traits such as leaf²⁰ or wood²¹ trade-offs with little or no attention given to reproductive and floral traits²², also critical to plant form and function. For instance, short lived versus perennial species tend to have low versus high levels of outcrossing, respectively^{6,23}. Further, outcrossing levels are positively correlated with flower size²⁴. In addition, the presence of costly rewards (e.g., pollen or nectar) and showy flowers or floral displays can only be understood through consideration of plant species' reliance upon animal pollination (pollinator dependence) and their role in attracting pollinators²⁵. Hence, exploring plant life strategies with reproductive and floral trade-offs, in conjunction with their pollinator dependence, is necessary for a balanced understanding of plant economics.

Several studies have identified links between plant traits and plant-pollinator network properties^{3,26,27}. Moreover, plant traits can also define species' network roles (e.g., specialists vs generalists). For example, species that occupy trait space extremes are more likely to exhibit higher specialization and be more reliant on trait-matching^{28,29}. This morphological matching between plant and floral visitors can determine plant-pollinator interactions, and thus shape their interaction network structure^{30,31}.

Despite the increasing knowledge of the relevance of traits on the species network roles, little is known about how plant reproductive and floral traits determine plant species' network roles at a macroecological scale.

Here, we explore the potential trade-offs among plant floral and reproductive traits and how these influence the structure of plant-pollinator networks. First, we identify the major axes of floral and reproductive trait variation and trade-offs that determine plant form and function. Second, we investigate how plant species' position in trait-space influences interaction strength with different guilds of floral visitors. Finally, we investigate how the main axes of trait variation and individual traits influence plant species roles within networks using complementary interaction network metrics (i.e., interaction strength, normalized degree and specialization).

RESULTS

Plant strategies. The phylogenetically informed principal component analysis (pPCA) captured by the first two and three axes 51.8% and 70.97% of trait variation, respectively (Fig. 1 and Supplementary Fig. S5) and had a phylogenetic correlation (λ) of 0.76. The first principal component (PC1) represented 26.72% of the trait variation and indicated a trade-off between flower number and flower size. We refer to this axis as the 'flower number - flower size trade-off' as already described in previous studies^{32,33}. Hence, one end of the spectrum comprised species with high investment in flower number and plant height but small flower size, short style length and low ovule number. The other end of this spectrum comprised species that were short in height and invested in large flowers, long styles, many ovules, but few flowers. The main contributing traits to PC1 were plant height, flower number, ovule number and flower size (loadings $> |0.5|$; Supplementary Table S3) but style length also contributed moderately on PC1 (loading = -0.33). The second principal component (PC2) represented 25.05% of the trait variation and indicated a trade-off between low

90 and high pollinator dependence. We refer to this axis as the 'pollinator dependence
91 trade-off'. The main driver of trait variation on PC2 was autonomous selfing (loading
92 = 0.85) but the other traits (except ovule number) also made moderate contributions
93 (loadings from 0.27 to 0.4; Supplementary Table S3). We found that high pollinator
94 dependence was associated with larger and a higher number of flowers, greater plant
95 height and longer styles. In contrast, species with high levels of autonomous selfing
96 tended to have fewer and smaller flowers, had shorter styles and were shorter in
97 height. Further, PC3 explained a considerable amount of trait variability (19.17%) and
98 the main contributors to this axis were style length (loading = -0.66) and the degree of
99 autonomous selfing (loading = -0.51). The remaining traits, apart from ovule number,
100 were moderately correlated to changes on PC3 (loadings from -0.23 to -0.46;
101 Supplementary Table S3). Thus, because style length was correlated with all traits on
102 PC3 and was the main driver of trait variation, we refer to this axis as the 'style length
103 trade-off'. Further, the pPCA with the subset of species that had nectar and pollen
104 quantity data showed that nectar quantity (microlitres of nectar per flower) was
105 positively associated with flower size, style length and ovule number (PC1, 23.40%);
106 and pollen quantity (pollen grains per flower) was positively correlated with flower
107 number and plant height and negatively associated with autonomous selfing (PC2,
108 21.67%; Supplementary Fig. S6). This pPCA explained similar variance with the first
109 two principal components (45.07%) and similar associations of traits despite some
110 variability in the loadings (Supplementary Table S4).



Fig. 1 | Plant life-history strategies. Phylogenetically informed principal component analysis (pPCA) of 1,236 plant species from 28 plant-pollinator networks studies. The solid arrows indicate the direction of the different quantitative traits (flower number, plant height, style length, flower size, ovule number and level of autonomous selfing) across the two main axes of trait variation. The length of the arrows indicate the weight of the variables on each principal component and the labelled icons at their end represent the extreme form of the trait continuum. The dashed lines show the opposed direction of trait variation and the non-labelled icons at their end illustrate the opposing extreme of the continuum.

111 We found that most categorical traits were statistically associated with the first two
 112 axes of trait variation (Fig. 2 and Supplementary Table S2). Flower symmetry, which
 113 was only associated with PC2 (Sum of squares = 8.51, F-value = 14.72, $P < 0.01$), and

nectar provision, which was independent of PC1 and PC2 (PC1: Sum of squares = 0.37, F-value = 0.29, $P = 0.59$; PC2: Sum of squares = 0.83, F-value = 1.43, $P = 0.23$) showed lack of statistical association. In addition, we found with Tukey test statistical differences between the different levels of categorical traits in the trait space (Supplementary Fig. S7). Regarding self compatibility, we found larger differences on PC2 (i.e., species with unisexual flowers that were self incompatible were statistically differentiated from species with partial or full self compatibility; Supplementary Fig. S7a and Fig. S7b). Life forms differed statistically across both axes of trait variation and followed a gradient of larger life forms (trees and shrubs) with higher pollinator dependence to smaller ones (herbs) with lower pollinator dependence (Supplementary Fig. S7c and Fig. S7d). Consequently, lifespan also followed this gradient but perennial and short lived species only differed statistically on PC2 (Supplementary Fig. S7e and Fig. S7f). Species with unisexual flowers (monoecious and dioecious) were clustered on both extremes of the first two principal components and had the highest pollinator dependence and highest number of flowers (Supplementary Fig. S7g and Fig. S7h). Moreover, we found that the campanulate and capitulum flower shapes were differentiated from tube, papilionaceous, open and brush shapes in the trait space. The former morphologies had larger flowers and greater pollinator dependence, while the latter had higher flower number and greater autonomous selfing (Supplementary Fig. S7i and Fig. S7j). Regarding flower symmetry, zygomorphic flowers were associated with lower levels of pollinator dependence, whereas actinomorphic flowers had higher levels of pollinator dependence (Supplementary Fig. S7k and Fig. S7l).

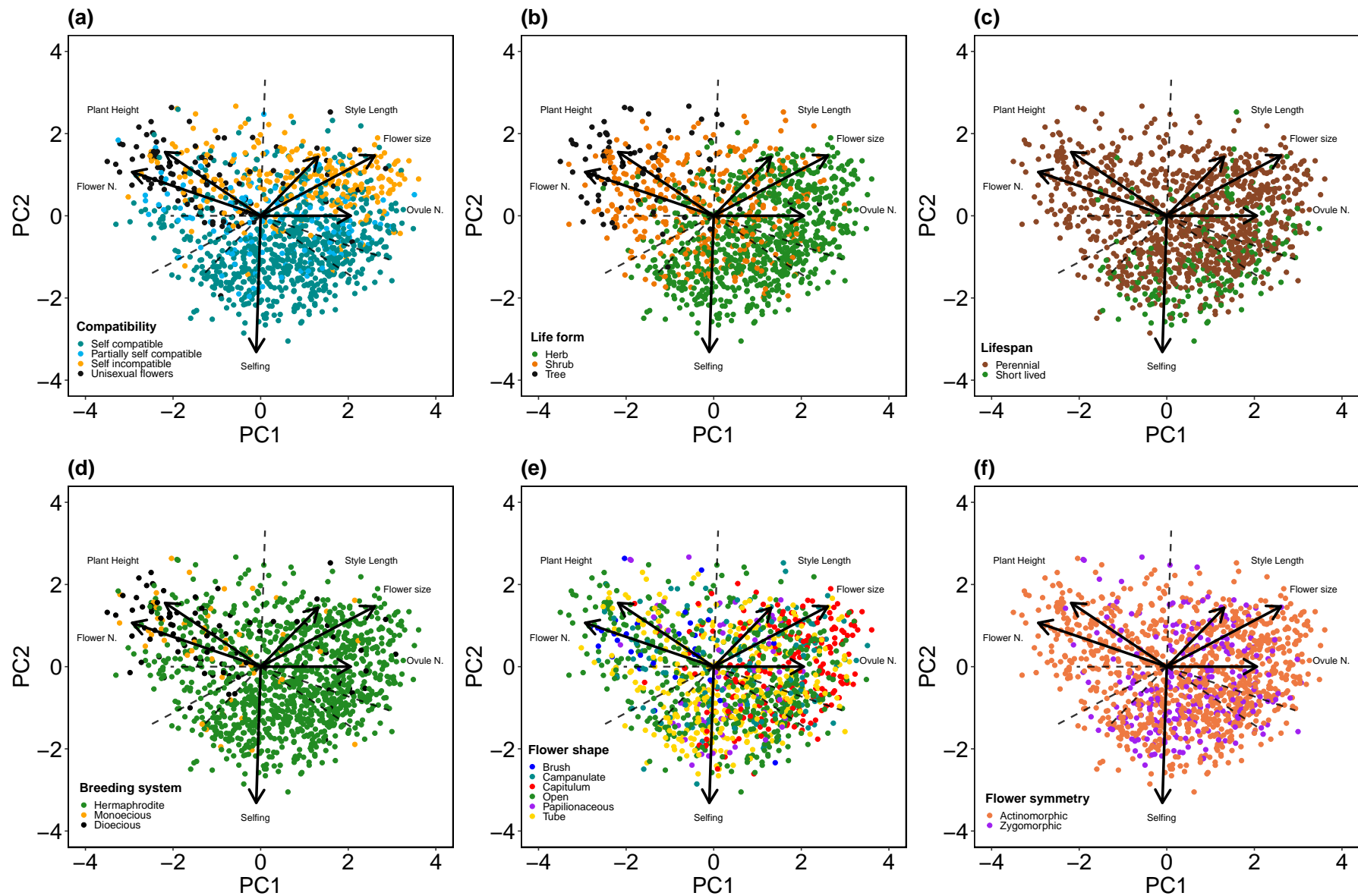


Fig. 2 | Location of the different qualitative traits on the trait space. The panel is composed by the traits that showed statistical association with the first two axes of trait variation: compatibility system (a), life form (b), lifespan (c), breeding system (d), flower shape (e) and flower symmetry (f).

Phylogenetic signal of traits. We found a strong phylogenetic signal ($P < 0.01$) in all quantitative traits (Supplementary Table S5). The traits that showed the highest phylogenetic signal were ovule number ($\lambda = 1$), pollen grains per flower ($\lambda = 1$) and plant height ($\lambda = 0.96$), followed by flower length ($\lambda = 0.75$), flower width ($\lambda = 0.73$), number of flowers per plant ($\lambda = 0.69$) and nectar concentration ($\lambda = 0.65$). The traits that showed a moderate phylogenetic signal were inflorescence width ($\lambda = 0.57$), style length ($\lambda = 0.49$) and autonomous selfing ($\lambda = 0.34$). Finally, microliters of nectar per flower showed the lowest phylogenetic signal of all traits ($\lambda = 0.14$).

Visitation patterns. The main axes of trait variation explained little of the overall visitation rates ($conditionalR2 = 0.31$; $marginalR2 = 0.06$) but showed relevant trends when we explored the interaction with the different floral visitors guilds (Fig. 3). All floral visitors guilds visited plant species with higher pollinator dependence more frequently (PC2; Fig. 3b and Fig. 3e). In addition, all guilds other than Syrphids and Lepidoptera (i.e., all Hymenoptera, non-Syrphidae-Diptera and Coleoptera) showed greater visitation rates on species with small numerous flowers (PC1; Fig. 3a and Fig. 3d). On the style length trade-off (PC3), Anthophila-Hymenoptera, Lepidoptera and Non-Anthophila-Hymenoptera showed greater visitation rates on plant species with larger styles and higher levels of selfing; while Syrphidae, Non-Syrphidae-Diptera and Coleoptera showed higher visitation rates on species with shorter styles and lower selfing (Fig. 3c and Fig. 3f). Furthermore, when running an additional model that separates the most represented families of Anthophila-Hymenoptera (bees; $marginalR2 = 0.30$; $conditionalR2 = 0.03$) showed that the family Apidae was the main driver of the observed patterns (Supplementary Fig. S8).

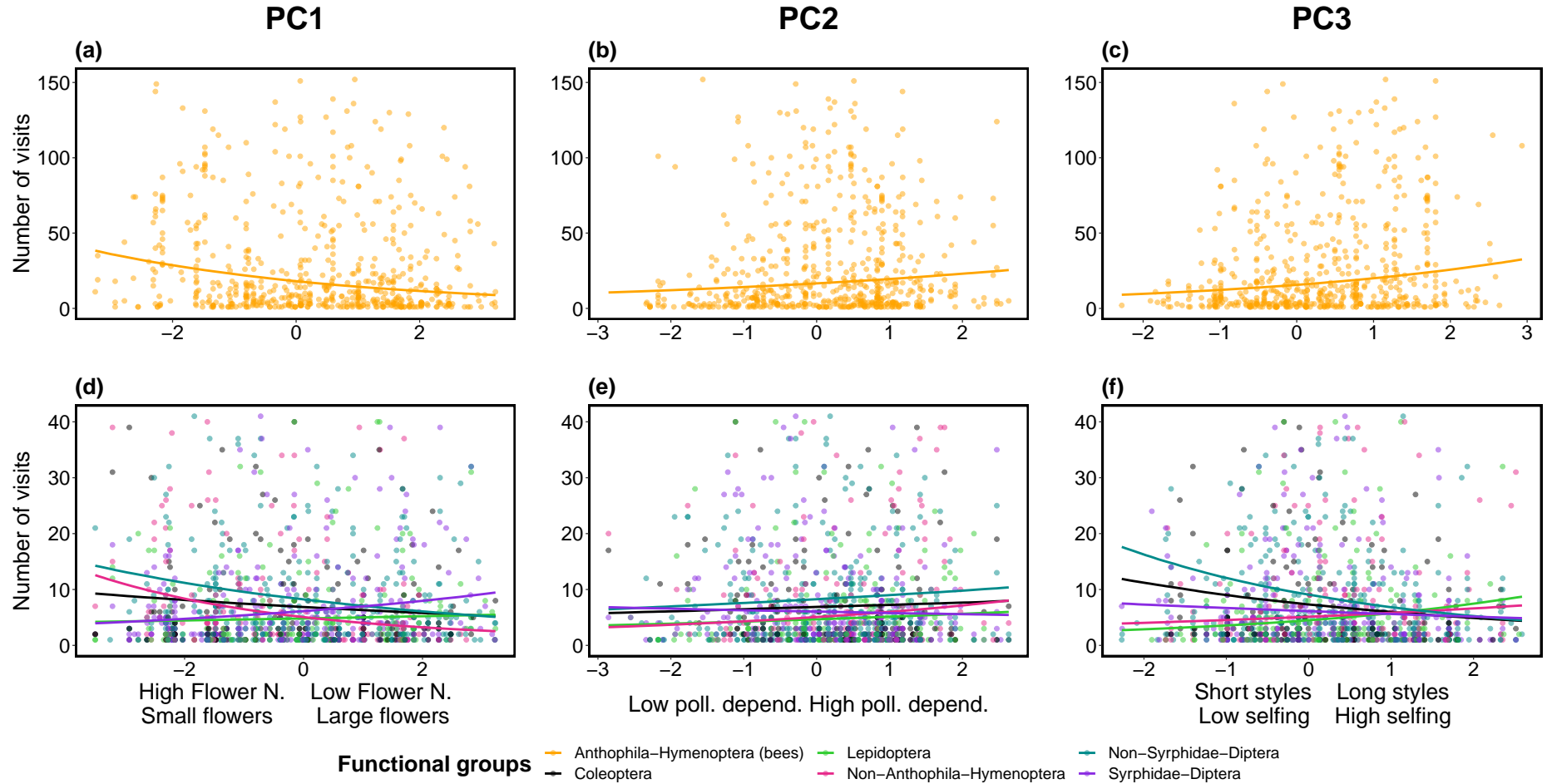


Fig. 3 | Visitation rates across the three main axes of trait variation. Fitted posterior estimates of the number of visits made by the different floral visitors guilds in relation to PC1, PC2 and PC3. Bees (a, b and c) and the rest of guilds (d, e and f) were plotted separately for visualization purposes. In addition, we trimmed the plotting area that was over the 95th percentile to improve visualisation. PC1 represents the flower number - flower size trade-off, PC2 represents the pollinator dependence trade-off and PC3, the style length trade-off.

Plant species functional roles. The variance of the different plant species level metrics was poorly explained by the three main axes of trait variation (Supplementary Fig. S9; interaction frequency ~ PCs, *conditionalR2* = 0.11, *marginalR2* = 0.02; normalized degree ~ PCs, *conditionalR2* = 0.24, *marginalR2* = 0.02; and, specialization ~ PCs, *conditionalR2* = 0.37, *marginalR2* = 0.03). Overall, the most notable trends were found on PC1 and PC3 for interaction frequency and specialization. On the flower number - flower size trade-off (PC1), interaction frequency was higher for plant species with more flowers but was lower for plant species with larger flowers. On PC1, specialization showed the opposite trend. On the style length trade-off (PC3), interaction frequency was lower for plants with shorter styles and lower autonomous selfing and higher for species with longer styles and higher autonomous selfing. Again, specialization showed the opposite trend to interaction frequency.

When we further investigate which combination of traits drive plant network roles, we show that the regression tree for visitation frequency was best explained by plant height, nectar concentration and style length (Fig. 4a). Specifically, species taller than 3.9 m had the highest interaction frequency, while species that were shorter than 3.9 m and had a nectar concentration lower than 16% had the lowest interaction frequency. Normalized degree was best explained by nectar concentration, pollen grains per flower, plant height, flower width and autonomous selfing (Fig. 4b). Species with a nectar concentration over 49% had the highest levels of normalized degree, whereas species with nectar concentration lower than 49%, more than 21,000 pollen grains per flower and height less than 0.78 m had the lowest normalized degree. Finally, specialization was best explained by plant height, ovule number, pollen grains per flower and autonomous selfing (Fig. 4c). Overall, plant species with the highest specialization were shorter than 1.3 m, had more than 14,000 pollen grains per flower and autonomously self-pollinated less than 11% of their fruits. In contrast, species taller or equal than 5.1 m and with lower than 14 ovules per flower had the lowest specialization values.

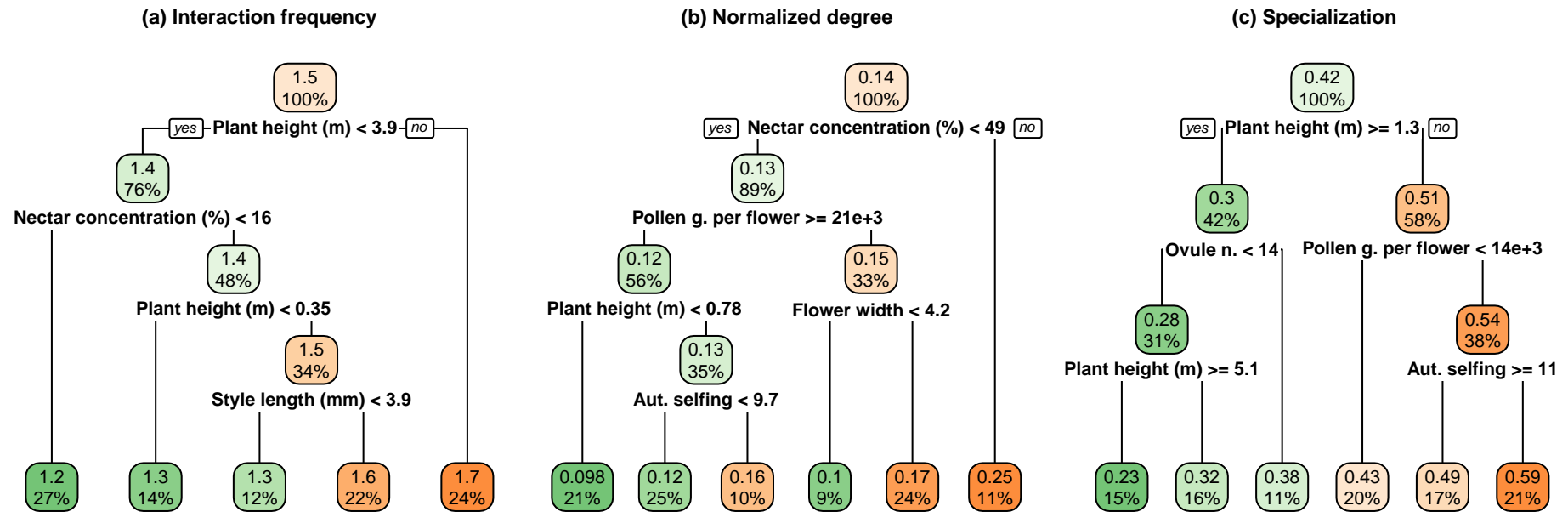


Fig. 4 | contribution of traits in plant's network roles. Regression tree analysis of interaction frequency (log-transformed), normalized degree and specialization for the subset of species with quantitative data for pollen and nectar traits. The superior value inside the node indicates the mean value of the different species-level metric and the lower value, the percentage of species that are considered in each node. Thus, the top node has the mean value of the named trait for the 100% of species. Each node has a yes/no question and when the condition is fulfilled, the branch turns to the 'yes' direction and when not, to the 'no' direction. This rationale is followed in all the regression trees as indicated in the first branch division of the topmost node of each tree.

DISCUSSION

Here, we show that plant species exhibit clear trade-offs in their floral, reproductive and vegetative traits. These trade-offs are differentiated on three main axes of trait variation: (i) flower number - flower size, (ii) pollinator dependence and (iii) style length. Although these axes of trait variation did not explain overall visitation rates, we found that plant life strategies were clearly associated with different floral visitors guilds. Interestingly, pollen and nectar related traits were better than all other traits for characterizing plant species functional roles within their interaction networks.

Over 50% of plant trait variation was captured by the flower number - flower size and pollinator dependence trade-offs. Variation in these two axes of trait variation appears to be associated with the commonly described 'fast-slow continuum' in plant⁸ and animal³⁴ life-history strategies as indicated by the different floral and reproductive traits associated with plant height, life form and lifespan. The 'slow' part of the continuum (i.e., tall trees and shrubs) had plant species with many flowers, few ovules, higher pollinator dependence, greater occurrence of self-incompatibility and more complex breeding systems (e.g., monoecious and dioecious species). In contrast, species that employed the 'fast' strategy (i.e., short herbs), had fewer flowers, more ovules, greater occurrence of self compatibility and lower pollinator dependence. Further, on the first two axes of trait variation, we found additional support for the positive association already described in a previous study between outcrossing rate and floral display²⁴. This trend was further confirmed when looking at the specific correlation between floral display and autonomous selfing for our dataset (see Supplementary Fig. S10).

Despite the low predictive power of the main axes of trait variation on overall visitation patterns, we found commonalities among and within floral visitors guilds across these axes that indicate the influence of life-history strategies on floral visitation

rate. For example, all guilds showed an increasing trend of visitation on plant species with higher pollinator dependence, which were also associated with larger floral displays and greater pollen quantities (Fig. 1 and Supplementary Fig. S6). This trend is consistent with previous plant-pollinator studies that show higher visitation rates on species that make greater reproductive investment^{35–37}. In regard to the flower number - flower size and style length trade-offs, different guilds showed contrasting visitation rates, which could be associated with different pollination syndromes at a macroecological scale. For instance, the guilds of bees and syrphids were clearly associated with opposing life-strategies on PC1 and PC3 (Fig. 3) indicating a possible niche partitioning among these two guilds^{38,39}. However, these plant-pollinator associations do not account for some of the traits (i.e., pollen and nectar quantity) that had greater relevance on the species network roles (Fig. 4) because of insufficient data availability and lack of pollinator efficiency measurements for more complete descriptions of the pollination syndromes¹³. In any case, it is worth noting that this general pattern emerges in field-measured plant-pollinator networks, where other local factors such as species relative abundances, will surely explain part of the observed variability^{12,40,41}.

To conclude, we provide the first description of plant floral and reproductive trade-offs using a large global dataset of plant traits and interactions with floral visitors. This allowed us to identify the major reproductive strategies of flowering plants and how plant life strategies determine their interaction with floral visitor guilds. Although the percentage of explained variation found with the first two axes (~50%) is lower than other studies that have evaluated life histories with vegetative traits^{18,19}, this percentage is consistent with the largest and most recent study that have characterized life strategies with both vegetative and reproductive (i.e., semelparity and iteroparity) traits⁸. Future work needs to integrate these floral and reproductive compromises with the already described vegetative and physiological trade-offs¹⁸ to create a more comprehensive spectra of trait variation¹⁰. Further, the varying level of phylogenetic signal among traits deserves further attention to understand evolutionary changes on

mating and flower morphology in response to pollinators^{42,43}. Finally, a more complete description of the macroecological patterns of plant-pollinator interactions including unrepresented areas of the world⁴⁴ and traits that have been largely ignored (e.g., floral rewards and plant mating system) are needed to progress in our understanding of the global patterns in plant-pollinator interactions.

MATERIALS AND METHODS

Plant-pollinator network studies. We selected 28 studies from 18 different countries that constituted a total of 64 plant-pollinator networks. These studies recorded plant-pollinator interactions in natural systems and were selected so that we had broad geographical representation. Although these studies differ in sampling effort and methodology, all studies provided information about plant-pollinator interactions (weighted and non-weighted), which we used to build a database of plant species that are likely to be animal pollinated. Many of these networks are freely available either as published studies^{3,45} or available in online archives (e.g., ‘The Web of Life’⁴⁵ and ‘Mangal’⁴⁶). In total, our network dataset (see Supplementary Table S1) constituted 60 weighted (interaction frequency) and 4 unweighted (presence/absence of the interaction) networks, each sampled at a unique location and year, as well as eight meta-webs where interactions were pooled across several locations and multiple years.

Taxonomy of plants and pollinators. All species names, genera, families and orders were retrieved and standardized from the taxonomy data sources NCBI (<https://www.ncbi.nlm.nih.gov/taxonomy>) for plants and ITIS (<https://www.itis.gov/>) for pollinators, using the R package *taxize*⁴⁷. We filled the ‘not found’ searches manually using <http://www.theplantlist.org/> and <http://www.mobot.org/> for plants and <http://www.catalogueoflife.org/> for floral visitors.

Functional traits. We selected 20 different functional traits based on their relevance to plant reproduction and data availability (Table 1). These included twelve quantitative and eight categorical traits belonging to three broader trait groupings (13 floral, 4 reproductive and 3 vegetative). For each plant species, we undertook an extensive literature and online search across a wide range of resources (plant databases, online floras, books, journals and images). From a total of 30,120 cells (20 columns \times 1,506 species) we were able to fill 24,341 cells (80.8% of the dataset, see Supplementary Fig. S1 for missing values information for each trait).

Phylogenetic Distance. We calculated the phylogenetic distance between different plant species using the function *get_tree* from the package *rtrees* (<https://github.com/daijiang/rtrees>), which downloads phylogenetic distances from the extended R implementation of the Open Tree of Life^{48,49}.

Data Imputation. Trait missing values were imputed with the function *missForest*⁵⁰ which allows imputation of data sets with continuous and categorical variables. We accounted for the phylogenetic distance among species on the imputation process by including the eigenvectors of a principal component analysis of the phylogenetic distance (PCoA) which has been shown to improve the performance of *missForest*⁵¹. To extract the eigenvectors, we used the function *PVRdecomp* from the package *PVR*⁵² based on a previous conceptual framework that considers phylogenetic eigenvectors⁵³. Although the variable of autonomous selfing had a high percentage of missing values (68%), we were able to solve this by back transforming the qualitative column of autonomous selfing to numerical. The categories of ‘none’, ‘low’, ‘medium’ and ‘high’ were converted to representative percentages of each category 0%, 13%, 50.5% and 88% respectively. This reduced the percentage of missing values for this column from 68% to 35% and allowed the imputation of this variable. However, we were unable to include nectar and pollen traits on the imputation process because of the high percentage of missing values (Supplementary Fig. S1). Hence, the imputed dataset had

Table 1 | Quantitative and categorical traits used in this study.

| Quantitative traits | | Categorical traits | | |
|---------------------|--------------------------------|---------------------|----------------------|---|
| Type | Traits | Type | Traits | Categories |
| Vegetative | Plant height (m) | Vegetative | Lifepan | Short-lived Perennial |
| Floral | Flower width (mm) | Vegetative | Life form | Herb Shrub Tree |
| Floral | Flower length (mm) | Floral | Flower shape | Brush Campanulate Capitulum Open Papilionaceous Tube |
| Floral | Inflorescence width (mm) | Floral | Flower symmetry | Actinomorphic Zygomorphic |
| Floral | Style length (mm) | Floral | Nectar | Presence Absence |
| Floral | Ovules per flower | Reproductive | Autonomous selfing | None Low Medium High |
| Floral | Flowers per plant | Reproductive | Compatibility system | Self-incomp. Part. self-comp. Self-comp. |
| Floral | Nectar (μ l) | Reproductive | Breeding system | Hermaphrodite Monoecious Dioecious |
| Floral | Nectar (mg) | | | |
| Floral | Nectar concentration (%) | | | |
| Floral | Pollen grains per flower | | | |
| Reproductive | Autonomous selfing (fruit set) | | | |

1,506 species, seven categorical and eight numerical variables and 5.79% of missing values. Further, we conducted an additional imputation on the filtered raw data by filled cells of either pollen grains per flower or microlitres of nectar. This subset comprised 755 species, 8.01% missing values and all traits but milligrams of nectar (~50% of missing values) were included in the imputation process.

Plant strategies. We explored the trade-offs between different quantitative plant functional traits with a phylogenetically informed Principal Component Analysis (pPCA). We did not include the quantitative variables of flower length and inflorescence width because they were highly and moderately correlated to flower width respectively (Pearson's correlation = 0.72, $P < 0.01$ and Pearson's correlation = 0.36, $P < 0.01$ respectively), and thus we avoided overemphasizing flower size on the spectrum of trait variation. Although qualitative traits were not included in the dimensionality reduction analysis, we also investigated the association of the different qualitative traits with the main axes of trait variation. Prior to the analyses, we excluded outliers and standardized the data. Due to the high sensitivity of dimensionality reduction to outliers, we excluded values within the 2.5th–97.5th percentile range⁵⁴, and thus our final dataset had 1,236 species. Then, we log transformed the variables to reduce the influence of outliers and z-transformed ($X = 0$, $SD = 1$) so that all variables were within the same numerical range. We performed the pPCA using the function *phyl.pca* from the package *phytools*⁵⁵ with the method lambda (λ) that calculates the phylogenetic correlation between 0 (phylogenetic independence) and 1 (shared evolutionary history) and we implemented the mode covariance because values for each variables were on the same scale following transformation⁵⁶. Moreover, to corroborate that our imputation of missing values did not affect our results, we conducted a pPCA on the full dataset without missing values (see Supplementary Fig. S2). We found little difference between the explained variance with the imputed dataset (51.08%) and the dataset without missing values (52.87%). In addition, the loadings on each principal component had a similar contribution and correlation patterns, with the exception of plant height which showed slight variations between

the imputed and non-imputed dataset. Finally, we conducted an additional phylogenetic informed principal component analysis for the subset of species with pollen and nectar quantity. For this, we included all quantitative traits considered in the main pPCA plus pollen grains and microlitres of nectar per flower.

Phylogenetic signal of traits. We calculated the phylogenetic signal of the different quantitative traits on the imputed dataset with the full set of species (N = 1,506) with the package *phytools* version 0.7-70⁵⁵ and we used Pagel's λ as a measurement of the phylogenetic signal. However, for pollen and nectar traits, phylogenetic signal was calculated only on the subset of species that had quantitative information for these traits (N = 755).

Networks analyses. Analyses were conducted on the subset of 60 weighted networks with interaction frequency sampled in a unique flowering season and site, which included 556 plant and 1,126 pollinator species. In total, our weighted network dataset (excluding meta-webs) included 2,256 interactions of Anthophila-Hymenoptera (i.e., bees) with plants, 1,768 non-Syrphidae-Diptera interactions, 845 Syrphidae interactions, 437 Lepidoptera interactions, 432 Coleoptera interactions and 362 non-Anthophila-Hymenoptera interactions. Although floral visitors are not always pollinators and the frequency of visits does not consider each pollinator species efficiency⁵⁷, visitation rate provides valuable information of the contribution of floral visitors to pollination^{58,59}. Sampling methods varied across networks but this was accounted for in analyses by considering them in the random effects of the modelling process. All analyses were conducted in R version 4.0.3.

Visitation patterns. We used Bayesian modelling (see below for details) to explore the effect of floral visitors groups and the main axes of trait variation (pPCA with imputed dataset) on floral visits per plant species. For this, we divided floral visitors into six main guilds that differ in life form, behaviour and are likely to play a similar ecological role: (i) Hymenoptera-Anthophila (bees), (ii) Hymenoptera-non-Anthophila (non-bee

Hymenoptera), (iii) Syrphidae-Diptera, (iv) non-Syrphidae-Diptera, (v) Lepidoptera and (vi) Coleoptera. Moreover, because Hymenoptera-Anthophila was the most represented group with 2,256 records and had the highest frequency of visits of all groups, we also explored the visitation rate of the main Hymenoptera-Anthophila families (Andrenidae, Apidae, Colletidae, Halictidae and Megachilidae) on the trait space. In addition, we found that *Apis mellifera* was the floral visitor with the largest proportion of records counted (7.55% of the total). This finding is consistent with previous research showing that *A. mellifera* was the most frequent floral visitor in a similar dataset of 80 plant-pollinator networks in natural ecosystems⁶⁰. Hence, to control for the effect of *A. mellifera* on the observed visitation patterns of bees, we conducted an analogous analysis excluding *A. mellifera*. We found that *A. mellifera* was partly driving some of the observed trends on PC1 (Supplementary Fig. S3). However, we did not detect major differences on PC2 and PC3.

We implemented Bayesian generalized linear mixed models using the R package *brms*⁶¹. We modelled the frequency of visits as a function of the main axes of plant trait variation and their interactions with floral visitor functional groups (Visits ~ PC1 x FGs + PC2 x FGs + PC3 x FGs). Because we were interested in possible differences in the visitation patterns among floral visitors groups to plants with different strategies, we included interactions between the main axes of trait variation (PC1, PC2 and PC3) and the floral visitor guilds. In this model, we added a nested random effect of networks nested within the study system to capture the variation in networks among studies and within networks. Moreover, we included the phylogenetic covariance matrix as a random factor due to the possible shared evolutionary histories of species and therefore lack of independence across them. We specified this model with a zero inflated negative binomial distribution and weakly informative priors from the *brms* function. We run this model for 3,000 iterations and with previous 1,000 warm up iterations. We set delta (Δ) to 0.99 to avoid divergent transitions and visualized the posterior predictive checks with the function *pp_check* using the *bayesplot* package⁶².

Plant species functional roles. We investigated whether different quantitative traits determined plant species functional roles using Bayesian modelling and regression trees. For this, we selected simple and complementary species-level network metrics commonly applied in bipartite network studies⁶³ with a straightforward ecological interpretation relevant to our research goals. The different plant species-level metrics were: (i) sum of visits per plant species; (ii) normalized degree, calculated as the number of links per plant species divided by the total possible number of partners; and (iii) specialization⁶⁴, which measures the deviation of an expected random choice of the available interaction partners and ranges between 0 (maximum generalization) and 1 (maximum specialization). Normalized degree and specialization were calculated with the *specieslevel* function from the R package *bipartite*⁶³.

First, we modelled the distinct plant species metrics (sum of visits, normalized degree and plant specialization) as a function of the three main axes of trait variation (plant species level metric \sim PC1 + PC2 + PC3). For each response variable (i.e., each plant species level metric), we used different distribution families (zero inflated negative binomial for the sum of visits, weibull for normalized degree and zero one inflated beta for specialization). Finally, we used the same random factors, model settings and conducted the same posterior predictive checks for each model as detailed above in the ‘visitation patterns section’.

Second, to better understand these complex trait relationships, we used regression trees. Regression trees are recursive algorithms which can detect complex relationships among predictors and allow identification of the relevance of specific trait combinations on species functional roles. We focused exclusively on quantitative traits because almost all categorical traits were statistically associated with the first two axes of trait variation (Supplementary Table S2). We conducted this analysis using the *rpart* package⁶⁵ version 4.1-15 with method ‘*anova*’ with a minimum of 50 observations per terminal node and we used *rpart.plot*⁶⁶ version 3.0.9 to plot the regression trees. We considered the species level indices as response variables (interaction frequency,

normalized degree and specialization) and we performed one regression tree per metric using the different quantitative traits as predictors. We calculated two regression trees per plant species-level metric, one for the full set of species and another for the subset of species for which we had pollen and nectar traits. We focused on regression trees that included floral rewards because they consistently showed pollen and nectar traits as being the best for explaining the different species-level metrics (see Supplementary Fig. S4).

References

1. Barrett, S. C. H. The evolution of plant sexual diversity. *Nature Reviews Genetics* **3**, 274–284 (2002).
2. Schiestl, F. P. & Johnson, S. D. Pollinator-mediated evolution of floral signals. *Trends in Ecology & Evolution* **28**, 307–315 (2013).
3. Carvalheiro, L. G. *et al.* The potential for indirect effects between co-flowering plants via shared pollinators depends on resource abundance, accessibility and relatedness. *Ecology Letters* **17**, 1389–1399 (2014).
4. Baude, M. *et al.* Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature* **530**, 85–88 (2016).
5. Munoz, F., Violle, C. & Cheptou, P.-O. CSR ecological strategies and plant mating systems: Outcrossing increases with competitiveness but stress-tolerance is related to mixed mating. *Oikos* **125**, 1296–1303 (2016).
6. Moeller, D. A. *et al.* Global biogeography of mating system variation in seed plants. *Ecology Letters* **20**, 375–384 (2017).
7. Grossenbacher, D. L. *et al.* Self-compatibility is over-represented on islands. *New*

- 429 *Phytologist* **215**, 469–478 (2017).
- 430 8. Salguero-Gómez, R. *et al.* Fast-slow continuum and reproductive strategies structure
431 plant life-history variation worldwide. *Proceedings of the National Academy of Sciences of*
432 *the United States of America* **113**, 230–235 (2016).
- 433 9. Rüger, N. *et al.* Beyond the fastSlow continuum: Demographic dimensions
434 structuring a tropical tree community. *Ecology Letters* **21**, 1075–1084 (2018).
- 435 10. Roddy, A. B. *et al.* Towards the flower economics spectrum. *New Phytologist* **229**,
436 665–672 (2021).
- 437 11. Fenster, C. B., Armbruster, W. S., Wilson, P., Dudash, M. R. & Thomson, J. D.
438 Pollination Syndromes and Floral Specialization. *Annual Review of Ecology, Evolution,*
439 *and Systematics* **35**, 375–403 (2004).
- 440 12. Bartomeus, I. *et al.* A common framework for identifying linkage rules across
441 different types of interactions. *Functional Ecology* **30**, 1894–1903 (2016).
- 442 13. Dellinger, A. S. Pollination syndromes in the 21st century: Where do we stand and
443 where may we go? *New Phytologist* **228**, 1193–1213 (2020).
- 444 14. Tur, C., Castro-Urgal, R. & Traveset, A. Linking Plant Specialization to Dependence
445 in Interactions for Seed Set in Pollination Networks. *PLoS ONE* **8**, e78294 (2013).
- 446 15. Devaux, C., Lepers, C. & Porcher, E. Constraints imposed by pollinator behaviour
447 on the ecology and evolution of plant mating systems. *Journal of Evolutionary Biology* **27**,
448 1413–1430 (2014).
- 449 16. Kattge, J. *et al.* TRY a global database of plant traits. *Global Change Biology* **17**,
450 2905–2935 (2011).
- 451 17. Salguero-Gómez, R. *et al.* The compadre Plant Matrix Database: An open online

- 452 repository for plant demography. *Journal of Ecology* **103**, 202–218 (2015).
- 453 18. Díaz, S. *et al.* The global spectrum of plant form and function. *Nature* **529**, 167–171
454 (2016).
- 455 19. Carmona, C. P. *et al.* Erosion of global functional diversity across the tree of life.
456 *Science Advances* **7**, eabf2675 (2021).
- 457 20. Wright, I. J. *et al.* The worldwide leaf economics spectrum. *Nature* **428**, 821–827
458 (2004).
- 459 21. Chave, J. *et al.* Towards a worldwide wood economics spectrum. *Ecology letters* **12**,
460 351–366 (2009).
- 461 22. E-Vojtkó, A., Bello, F. de, Durka, W., Kühn, I. & Götzenberger, L. The neglected
462 importance of floral traits in trait-based plant community assembly. *Journal of*
463 *Vegetation Science* **31**, 529–539 (2020).
- 464 23. Barrett, S. C. H. Mating strategies in flowering plants: The outcrossing-selfing
465 paradigm and beyond. *Philosophical Transactions of the Royal Society B: Biological Sciences*
466 **358**, 991–1004 (2003).
- 467 24. Goodwillie, C. *et al.* Correlated evolution of mating system and floral display traits
468 in flowering plants and its implications for the distribution of mating system variation.
469 *The New Phytologist* **185**, 311–321 (2010).
- 470 25. Ollerton, J., Winfree, R. & Tarrant, S. How many flowering plants are pollinated by
471 animals? *Oikos* **120**, 321–326 (2011).
- 472 26. Lázaro, A., Hegland, S. J. & Totland, Ø. The relationships between floral traits and
473 specificity of pollination systems in three Scandinavian plant communities. *Oecologia*

- 474 157, 249–257 (2008).
- 475 27. Bartomeus, I. Understanding Linkage Rules in Plant-Pollinator Networks by Using
476 Hierarchical Models That Incorporate Pollinator Detectability and Plant Traits. *PLOS*
477 *ONE* **8**, e69200 (2013).
- 478 28. Junker, R. R. *et al.* Specialization on traits as basis for the niche-breadth of flower
479 visitors and as structuring mechanism of ecological networks. *Functional Ecology* **27**,
480 329–341 (2013).
- 481 29. Coux, C., Rader, R., Bartomeus, I. & Tylianakis, J. M. Linking species functional
482 roles to their network roles. *Ecology Letters* **19**, 762–770 (2016).
- 483 30. Stang, M., Klinkhamer, P. G. L., Waser, N. M., Stang, I. & van der Meijden, E.
484 Size-specific interaction patterns and size matching in a plantPollinator interaction
485 web. *Annals of Botany* **103**, 1459–1469 (2009).
- 486 31. Ibanez, S. Optimizing size thresholds in a plant-pollinator interaction web: Towards
487 a mechanistic understanding of ecological networks. *Oecologia* **170**, 233–242 (2012).
- 488 32. Sargent, R. D., Goodwillie, C., Kalisz, S. & Ree, R. H. Phylogenetic evidence for a
489 flower size and number trade-off. *American Journal of Botany* **94**, 2059–2062 (2007).
- 490 33. Kettle, C. J. *et al.* Ecological Implications of a Flower Size/Number Trade-Off in
491 Tropical Forest Trees. *PLOS ONE* **6**, e16111 (2011).
- 492 34. Healy, K., Ezard, T. H. G., Jones, O. R., Salguero-Gómez, R. & Buckley, Y. M. Animal
493 life history is shaped by the pace of life and the distribution of age-specific mortality
494 and reproduction. *Nature Ecology & Evolution* **3**, 1217–1224 (2019).
- 495 35. Hegland, S. J. & Totland, Ø. Relationships between species' floral traits and

- 496 pollinator visitation in a temperate grassland. *Oecologia* **145**, 586–594 (2005).
- 497 36. Lázaro, A., Jakobsson, A. & Totland, Ø. How do pollinator visitation rate and seed
498 set relate to species' floral traits and community context? *Oecologia* **173**, 881–893 (2013).
- 499 37. Kaiser-Bunbury, C. N., Vázquez, D. P., Stang, M. & Ghazoul, J. Determinants of the
500 microstructure of plantPollinator networks. *Ecology* **95**, 3314–3324 (2014).
- 501 38. Palmer, T. M., Stanton, M. L. & Young, T. P. Competition and coexistence: Exploring
502 mechanisms that restrict and maintain diversity within mutualist guilds. *the american*
503 *naturalist* **162**, S63–S79 (2003).
- 504 39. Phillips, R. D., Peakall, R., van der Niet, T. & Johnson, S. D. Niche perspectives on
505 plantPollinator interactions. *Trends in Plant Science* **25**, 779–793 (2020).
- 506 40. Vázquez, D. P. *et al.* Species abundance and asymmetric interaction strength in
507 ecological networks. *Oikos* **116**, 1120–1127 (2007).
- 508 41. Encinas-Viso, F., Revilla, T. A. & Etienne, R. S. Phenology drives mutualistic
509 network structure and diversity. *Ecology letters* **15**, 198–208 (2012).
- 510 42. Gervasi, D. D. L. & Schiestl, F. P. Real-time divergent evolution in plants driven by
511 pollinators. *Nature Communications* **8**, 14691 (2017).
- 512 43. Mackin, C. R., Peña, J. F., Blanco, M. A., Balfour, N. J. & Castellanos, M. C. Rapid
513 evolution of a floral trait following acquisition of novel pollinators. *Journal of Ecology*
514 **109**, 2234–2246 (2021).
- 515 44. Poisot, T. *et al.* Global knowledge gaps in species interaction networks data. *Journal*
516 *of Biogeography* **48**, 1552–1563 (2021).
- 517 45. Fortuna, M. A. *et al.* Nestedness versus modularity in ecological networks: Two

- sides of the same coin? *Journal of Animal Ecology* **79**, 811–817 (2010).
46. Poisot, T. *et al.* Mangal making ecological network analysis simple. *Ecography* **39**, 384–390 (2016).
47. Chamberlain, S. *et al.* Taxize: Taxonomic information from around the web. (2020).
48. Smith, S. A. & Brown, J. W. Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany* **105**, 302–314 (2018).
49. Jin, Y. & Qian, H. V. PhyloMaker: An R package that can generate very large phylogenies for vascular plants. *Ecography* **42**, 1353–1359 (2019).
50. Stekhoven, D. J. & Bühlmann, P. MissForestNon-parametric missing value imputation for mixed-type data. *Bioinformatics* **28**, 112–118 (2012).
51. Penone, C. *et al.* Imputation of missing data in life-history trait datasets: Which approach performs the best? *Methods in Ecology and Evolution* **5**, 961–970 (2014).
52. Santos, T., Diniz-Filho, J. A., e Luis, T. R., Bini, M. & Santos, M. T. Package ‘PVR’. (2018).
53. Diniz-Filho, J. A. F. *et al.* On the selection of phylogenetic eigenvectors for ecological analyses. *Ecography* **35**, 239–249 (2012).
54. Legendre, P. & Legendre, L. *Numerical ecology*. (Elsevier, 2012).
55. Revell, L. J. Phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**, 217–223 (2012).
56. Abdi, H. & Williams, L. J. Principal component analysis. *WIREs Computational Statistics* **2**, 433–459 (2010).
57. Ballantyne, G., Baldock, K. C. R. & Willmer, P. G. Constructing more informative

- 540 plantPollinator networks: Visitation and pollen deposition networks in a heathland
 541 plant community. *Proceedings of the Royal Society B: Biological Sciences* **282**, 20151130
 542 (2015).
- 543 58. Vázquez, D. P., Morris, W. F. & Jordano, P. Interaction frequency as a surrogate for
 544 the total effect of animal mutualists on plants. *Ecology Letters* **8**, 1088–1094 (2005).
- 545 59. Vázquez, D. P. *et al.* The strength of plantPollinator interactions. *Ecology* **93**, 719–725
 546 (2012).
- 547 60. Hung, K.-L. J., Kingston, J. M., Albrecht, M., Holway, D. A. & Kohn, J. R. The
 548 worldwide importance of honey bees as pollinators in natural habitats. *Proceedings of*
 549 *the Royal Society B: Biological Sciences* **285**, 20172140 (2018).
- 550 61. Bürkner, P.-C. Brms: An R package for Bayesian multilevel models using Stan.
 551 *Journal of statistical software* **80**, 1–28 (2017).
- 552 62. Gabry, J., Simpson, D., Vehtari, A., Betancourt, M. & Gelman, A. Visualization in
 553 Bayesian workflow. *Journal of the Royal Statistical Society: Series A (Statistics in Society)*
 554 **182**, 389–402 (2019).
- 555 63. Dormann, C. F., Gruber, B. & Fründ, J. Introducing the bipartite package: Analysing
 556 ecological networks. *interaction* **1**, (2008).
- 557 64. Blüthgen, N., Menzel, F. & Blüthgen, N. Measuring specialization in species
 558 interaction networks. *BMC Ecology* **6**, 9 (2006).
- 559 65. Therneau, T., Atkinson, B., Ripley, B. & Ripley, M. B. Package ‘rpart’. Available
 560 online: [cran. ma. ic. ac. uk/web/packages/rpart/rpart. pdf](http://cran.ma.ic.ac.uk/web/packages/rpart/rpart.pdf) (accessed on 20 April 2016) (2015).
- 561 66. Milborrow, S. Rpart. plot: Plot rpart Models. An Enhanced Version of plot. rpart. R
 562 package version **1**, (2015).