Covariation among reproductive traits in flowering plants determine interactions with floral visitors

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ABSTRACT

Plant life-history strategies are constrained by cost-benefit trade-offs that determine plant form and function. However, despite recent advances in the understanding of plant trait variation, little is known about plant reproductive trade-offs and how these constrain life-history strategies and shape interactions with floral visitors. Here, we investigate plant reproductive trade-offs and how these drive interactions with floral visitors using a dataset of 16 reproductive traits for 1,506 plant species. We found that over half of all plant reproductive trait variation was explained by two independent axes. Specifically, the first axis indicated the presence of a trade-off between flower number and flower size, while the second axis indicated a pollinator dependency trade-off. In addition, plant reproductive trade-offs determined important differences in the interaction level among floral visitor guilds. Our study shows the main reproductive trade-offs of flowering plants and their relevance to understand plant-pollinator interactions in a global context.

INTRODUCTION

Flowering plants have an astonishing diversity of floral structures (Barrett, 2002; Schiestl & Johnson, 2013) that shape plant-pollinator associations (Dellinger, 2020; Fenster et al., 2004). However, not all reproductive trait combinations are possible due to evolutionary and ecological constraints (Stearns, 1989). Despite the recent advances in the theoretical and empirical understanding of the macroecological correlations between plant reproductive traits (Friedman, 2020; Roddy et al., 2021; Salguero-Gómez et al., 2016), their study is often limited to a handful number of reproductive traits that are rarely studied jointly. Thus, in order to progress towards a comprehensive understanding of the plant reproductive spectrum of trait variation as done recently for other vegetative and physiological plant traits (Chave et al., 2009; Díaz et al., 2016; Laughlin et al., 2021; Onoda et al., 2017; Wright et al., 2004), there is a need to acquire a multitrait perspective with broad geographical coverage. Importantly, the characterization of the reproductive trait covariation patterns can help to further understand the different plant ecological strategies (Agrawal, 2020) and improve our knowledge on plant-pollinator associations (Roddy et al., 2021).

Although there is an increasing number of macroecological studies that investigate plant reproductive traits (Baude et al., 2016; Grossenbacher et al., 2017; Moeller et al., 2017; Munoz et al., 2016), we still have poor understanding of how reproductive traits drive interactions with floral visitors at large ecological scales (Rech et al., 2016; Rüger et al., 2018; Salguero-Gómez et al., 2016; Sargent & Ackerly, 2008). In addition, the pollination system of a great number of plant species remains unexplored and is still unclear how specific key reproductive traits like mating or compatibility system influence plant-pollinator associations (Devaux et al., 2014; Tur et al., 2013). Interestingly, the use of trait-based approaches (Fenster et al., 2004; Rosas-Guerrero et al., 2014) and trait-matching analyses (Bartomeus et al., 2016; Stang et al., 2009) has shown to be of great importance when exploring the drivers of plant-pollinator interactions. For example, plant traits can define species' network roles (e.g., specialists vs generalists; Lázaro et al., 2013; Tur et al., 2013) and plant species that occupy reproductive trait space extremes are more likely to exhibit higher levels of specialisation and be more reliant on the trait-matching with pollinators (Coux et al., 2016; Junker et al., 2013). Indeed, morphological matching between plants and floral visitors often determines plant-pollinator interactions, and can thus strongly influence interaction network structure (Ibanez, 2012; Stang et al., 2009). Because the species' morphology can determine the species' functional role in the pollination network and the combination of traits has shown to increase the predictive power of the network interactions (Eklöf et al., 2013), an interesting novel approach is to investigate how traits in the multidimensional trait space determine species interaction patterns (see Dehling et al., 2016). Thus, by exploring the reproductive spectrum of trait variation is possible to delimit the different plant reproductive strategies and explore how these are associated with the different floral visitors.

With the recent availability of large trait databases (e.g., TRY Kattge et al., 2011; and COMPADRE Salguero-Gómez et al., 2015), plant ecological strategies are being increasingly examined, and are facilitating the identification of global patterns and constraints in plant form and function (Bruelheide et al., 2018; Carmona et al., 2021; Díaz et al., 2016; Salguero-Gómez et al., 2016). However, most studies with a multitrait perspective have focused on trait correlations from the leaf (Wright et al., 2004), wood (Chave et al., 2009), or root (Laughlin et al., 2021) related traits with little or no attention given to reproductive traits (E-Vojtkó et al., 2020; Roddy et al., 2021). Despite the lack of an holistic view that depict reproductive trait covariation patterns, there are widely recognized reproductive trait associations between pair of traits such as the negative correlation between flower size and flower number (Kettle et al., 2011; Sargent et al., 2007), the positive association between flower size and outcrossing rate (Goodwillie et al., 2010) or the association between outcrossing rate and lifespan where short lived versus perennial species tend to have low versus high levels of outcrossing (Barrett, 2003; Moeller et al., 2017), respectively. Although these different trait correlations (and others) have recently allowed to progress towards a conceptual framework that integrates the different floral trait relationships (Roddy et al., 2021), we still lack empirical evidence that investigates jointly these different reproductive trait associations.

Here, we aim to progress knowledge on the reproductive trait covariation patterns and their association with the different floral visitor guilds by exploring at a broad geographical scale the reproductive spectrum of trait variation of entomophilous plant species from plant-pollination networks. First, we investigate what are the major axes of reproductive trait variation and trait correlations for the different plant species. Second, we investigate the association between the plant species' position in the multidimensional trait-space and the different floral visitor guilds with the help of qualitative (presence-absence of interaction) and quantitative (number of visits) information about plant-pollinator interactions. Finally, we investigate how both the main axes of trait variation, and individual traits, influence plant species' functional roles in the pollination network using a set of complementary interaction network metrics (i.e., number of visits, normalized degree and specialization).

MATERIALS AND METHODS

Plant-pollinator network studies

We selected 28 studies from 18 different countries that constituted a total of 64 plant-pollinator networks (see Table S1 and Fig. S1). These studies recorded plant-pollinator interactions in natural systems and were selected so that we had broad geographical representation across different biological communities. 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 (e.g., Carvalheiro et al., 2014; Fortuna et al., 2010; Olesen et al., 2007) or available in online archives (e.g., The Web of Life, Fortuna et al., 2010; and Mangal, Poisot et al., 2016). In total, our network dataset constituted 60 weighted (number of visits) 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* (Chamberlain et al., 2020). 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.

Plant traits

We selected a total of 19 different functional traits that comprised both reproductive and life history traits (see Table 1). From these, 16 were reproductive traits that consisted of 13 floral traits and 3 reproductive biology traits. Floral traits included morphological traits (e.g., style length) but also floral reward (e.g., pollen quantity) and floral display (e.g., number of flowers) related traits. Reproductive biology traits indicated the reproductive system of the plant and included breeding, mating and compatibility system. The 3 remaining traits were life history traits that are commonly used to characterize the fast-slow continuum of plant trait variation (i.e., plant height, lifespan and life form). For each plant species, we undertook an extensive literature and online search for all traits across a wide range of resources (plant databases, online floras, books, journals and images). From a total of 30,120 possible cells considering all traits and plant species (20 columns × 1,506 species), we were able to fill 24,341 cells (80.8% of the dataset, see Fig. S2 for missing values information for each trait). An extended description of each trait and how it was obtained can be found in Appendix S1.

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 (Jin & Qian, 2019; Smith & Brown, 2018).

Data Imputation

Trait missing values were imputed with the function *missForest* (Stekhoven & Bühlmann, 2012) 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* (Penone et al., 2014). To extract the eigenvectors, we used the function *PVRdecomp* from the package *PVR* (Chamberlain et al., 2018) based on a previous conceptual framework that considers phylogenetic eigenvectors (Diniz-Filho et al., 2012). We conducted two different imputations, one for the full set of species (1,506 species, 5.79% of missing values) excluding nectar and pollen traits because of the high percentage of missing values (Fig. S2) and a second one for the subset of species with data for pollen per flower and microliters of nectar (755 species, 8.01% of missing values).

Plant strategies

We explored the association between the different quantitative plant 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, $P < 0.01$), and thus we avoided overemphasizing flower size on the spectrum of trait variation. Prior to the analyses, we excluded outliers and standardized the data. Due to the high sensitivity of dimensionality reduction to outliers (Legendre & Legendre, 2012; Serneels & Verdonck, 2008), we excluded values outside the 2.5th–97.5th percentile range, 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 as indicated for principal component analysis (Legendre & Legendre, 2012). Although qualitative traits were not included in the dimensionality reduction analysis, we also investigated the statistical association of the different qualitative traits with the main axes of trait variation with the help of an Anova and a Tukey test. We performed the pPCA using the function *phyl.pca* from the package *phytools* (Revell, 2012) 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 transformation (Abdi & Williams, 2010). 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 (Fig. S3). 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

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* (Revell, 2012) 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).

Network analyses

First, we investigated how the different groups of floral visitors interacted along the main axes of reproductive trait variation (see below 'visitation patterns' section) with the help of qualitative and quantitative information of plant-pollinator interactions. For this, we used as qualitative information the binary version of the networks (presence-absence of interaction) that assumes equal weight across interactions and as quantitative information the number of visits of floral visitors to individual flowers that account for the intensity of the interaction. Although floral visitors are not always pollinators and number of visits does not consider each pollinator species efficiency (Ballantyne et al., 2015), the number of visits can provide valuable information of the contribution of floral visitors to pollination (Vázquez et al., 2005, 2012). Second, we investigated how the main axes of trait variation and individual traits influence plant species' functional roles in the pollination network using a set of complementary interaction network metrics: number of visits, normalized degree and specialization (see below 'plant species network roles' section).

Analyses were conducted on the subset of 60 weighted networks sampled in a unique flowering season and site, which included 556 plant and 1,126 pollinator species. In total, our network dataset (excluding meta-webs and non-weighted networks) included 2,256 interactions of bees with plants, 1,768 non-syrphid-Diptera interactions, 845 syrphids interactions, 437 Lepidoptera interactions, 432 Coleoptera interactions and 362 non-bee-Hymenoptera interactions. 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 visitor groups and the main axes of trait variation (pPCA with imputed dataset) on both qualitative and quantitative floral interactions 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) bees (Hymenoptera-Anthophila), (ii) non-bee-Hymenoptera (Hymenoptera-non-Anthophila), (iii) syrphids (Diptera-Syrphidae), (iv) non-syrphid-Diptera (Diptera-non-Syrphidae), (v) Lepidoptera and (vi) Coleoptera. Moreover, because the guild of bees was the most represented group with 2,256 records and had the highest frequency of visits, we also explored presence-absence of the interaction and number of visits of the main bee 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 ecosystems (Hung et al., 2018). Hence, to control for the effect of *A. mellifera* on the observed visitation patterns of bees, we conducted an analogous analysis with presence-absence of the interaction and number of visits excluding *A. mellifera*. We found that *A. mellifera*, was partly driving some of the observed trends on PC1 (Fig. S4). However, we did not detect major differences on PC2 and PC3.

We implemented Bayesian generalized linear mixed models using the R package *brms* (Bürkner, 2017). We modelled presence-absence of observed interactions and number of visits as a function of the main axes of plant trait variation and their interactions with floral visitor guilds (e.g., number of 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 different floral visitor guilds. 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 for presence-absence of interaction and number of visits a Bernoulli and a zero inflated negative binomial distribution, respectively. The models were run with non or very weakly informative informative priors from the brm function so they have neglible influence on the results (Bürkner, 2017), 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* package (Gabry et al., 2019).

Plant species network roles

We investigated whether different quantitative traits determined different plant species' functional roles in the pollination network using Bayesian modelling and regression trees. For this, we selected simple and complementary species-level network metrics commonly applied in bipartite network studies (Dormann et al., 2008) 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) specialization (d') (Blüthgen et al., 2006), 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* (Dormann et al., 2008).

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 ~ 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 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 explaining species roles within the network of interaction. We focused exclusively on quantitative traits because almost all categorical traits were statistically associated with the first two axes of trait variation (Table S2). We conducted this analysis using the *rpart* function from the *rtrees* package (Therneau et al., 2015) with method *'anova'* with a minimum of 50 observations per terminal node and we used the *rpart.plot* package (Milborrow, 2015) to plot the regression trees. We considered the species level indices as response variables (number of visits, 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 (Fig. S5).

RESULTS

Plant strategies

The phylogenetically informed principal component analysis captured by the first two and three axes 51.8% and 70.97% of the reproductive trait variation, respectively (Fig. 1 and Fig. S6). The first principal component (PC1) represented 26.72% of the trait variation and indicated a negative correlation between flower number and flower size ('flower number - flower size'). The main contributing traits to PC1 were plant height, flower number, ovule number and flower size (loadings > $|0.5|$; Table S3) but style length also contributed moderately to PC1 (loading = -0.33). One end of this axis comprised species with high investment in flower number and plant height but small flower size, short style length and low ovule number. For instance, on this end of the spectrum we find the species *Cornus florida* which has approximately a total of 10.000 flowers, an average height of 7.5m, flowers of 3mm wide, a style length of 3.5mm and a total of 2 ovules per flower. 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. For instance, on this side of the axis we find the species *Petunia axillaris* that has approximately 10 flowers per plant, a height of 0.5m, flowers over 50mm wide, styles of 25mm and over 200 ovules per flower. The second principal component (PC2) represented 25.05% of the trait variation and indicated the variation from low to high autonomous selfing, or in other words, high to low pollinator dependence, respectively.

The main driver of trait variation on PC2 was autonomous selfing (loading = 0.85) but the other traits (except ovule number) also made moderate contributions (loadings from 0.27 to 0.4; Table S3). In general terms, species with high pollinator dependence were associated with larger and a higher number of flowers, greater plant height and longer styles. A species example of this side of the spectrum is *Zuccagnia punctata* that is a self incompatible shrub which depends totally on floral visitors, it has approximately 1500 flowers per plant, 3m height and a style length of 20mm. In contrast, species with low pollinator dependence tended to have fewer and smaller flowers, shorter plant height and shorter styles. For instance, on this side of the spectrum we find the species *Veronica peregrina* which is a self compatible herb that is thought to be almost a complete selfer, it has around 20 flowers per plant, a height of 0.2m and a style length of 0.25mm. Further, PC3 explained a considerable amount of trait variability (19.17%) and the main contributors to this axis were style length (loading = -0.66) and the degree of autonomous selfing (loading = -0.51). The remaining traits, apart from ovule number, were moderately correlated to changes on PC3 (loadings from -0.23 to -0.46; Table S3). In addition, the pPCA with the subset of species that had nectar and pollen quantity data showed that nectar quantity (microlitres of nectar per flower) and pollen grains per flower were positively associated with flower size, style length and ovule number but negatively associated with flower number (PC1, 26.82%; Fig. S7). This pPCA explained similar variance with the first two principal components (45.52%) and similar associations of traits despite some variability in the loadings (Table S4).

We found that most categorical traits were statistically associated with the first two axes of trait variation (Fig. 2 and Table S2). Flower symmetry, which 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 a Tukey test) statistical differences between the different levels of categorical traits in the trait space (Fig. S8). 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; Fig. S8a and Fig. S8b). 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 (Fig. S8c and Fig. S8d). Consequently, lifespan also followed this gradient but perennial and short lived species only differed statistically on PC2 (Fig. S8e and Fig. S8f). 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 (Fig. S8g and Fig. S8h). 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 (Fig. S8i and Fig. S8j). Regarding flower symmetry, zygomorphic flowers were associated with lower levels of pollinator dependence, whereas actinomorphic flowers had higher levels of pollinator dependence (Fig. S8k and Fig. S8l).

Phylogenetic signal

We found a strong phylogenetic signal ($P < 0.01$) for most quantitative traits (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 partly presence-absence of interaction partners (conditional $R^2 = 0.26$; marginal $R^2 = 0.20$) but little of the overall number of visits (conditional R^2 = 0.31; marginal R^2 = 0.06). However, we found relevant differences across the different floral visitor guilds on both presence-absence of interactions and number of visits (Fig. 3). We found that plants with high flower number and small flowers had higher interaction partners of Coleoptera, non-bee-Hymenoptera and all Diptera guilds but plants with low flower number but large flowers had higher interaction partners of bees and Lepidoptera guilds (flower number - flower size trade-off, PC1; Fig. 3a). However, plant species with high flower number but small flowers had higher number of visits of bees and syrphids guilds (PC1; Fig. 3d). Remarkably, all plant species with higher pollinator dependence had higher number of interacting partners and number of visits for all floral visitor guilds (PC2; Fig. 3b and Fig. 3e). Finally, plant species with short styles and low selfing had higher interaction partners of all guilds but bees that interacted clearly more with plant species with long styles and high selfing (style length trade-off; Fig. 3c). However, for number of visits, we found that plants with long styles and high selfing interacted more frequently with Lepidoptera and non-bee-Hymenoptera guilds (Fig. 3f).

The additional model for both presence-absence of interaction (marginal R^2 = 0.29; conditional R^2 = 0.19) and number of visits (marginal R^2 = 0.30; conditional R^2 = 0.03) for the most represented families of bees showed that the family Apidae was the main driver of the observed patterns. The contrasting differences between presence-absence of interaction and number of visits for bees on PC1 (Fig. 3a and Fig. 3d) were driven by the family Andrenidae that had higher number of interacting partners but lower number of visits on plant species with low number of large flowers (Fig. S9).

Plant species network roles

The variance of the different plant species-level network metrics was poorly explained by the three main axes of trait variation (Fig. S10; number of visits ~ PCs, conditional R^2 = 0.11, marginal R^2 = 0.02; normalized degree ~ PCs, conditional R^2 = 0.24, marginal R^2 = 0.02; and, specialization ~ PCs, conditional R^2 = 0.37, marginalR^2 = 0.03). Overall, the most notable trends were found on PC1 and PC3 for number of visits and specialization.

On the flower number - flower size trade-off (PC1), number of visits was higher for plant species with more flowers but was lower for plant species with larger flowers (Fig. S10a). On PC1, specialization showed the opposite trend (Fig. S10g). On the style length trade-off (PC3), number of visits was lower for plants with shorter styles and lower autonomous selfing and higher for species with longer styles and higher autonomous selfing (Fig. S10c). Again, specialization showed the opposite trend to number of visits (Fig. S10i).

When we further investigated the combination of traits that drive plant network roles, we found that the regression tree for number of visits was best explained by plant height, nectar concentration and style length (Fig. 4a; root node error = 1%). Specifically, species taller than 3.9m had the highest number of visits, while species that were shorter than 3.9m and had a nectar concentration lower than 16% had the lowest number of visits. Normalized degree was best explained by nectar concentration, pollen grains per flower, plant height, flower width and autonomous selfing (Fig. 4b; root node error = 2%). 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 0.78m had the lowest normalized degree. Finally, specialization was best explained by plant height, ovule number, pollen grains per flower and autonomous selfing (Fig. 4c; root node error = 7%). Overall, plant species with the highest specialization were shorter than 1.3m, 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 5.1m and with lower than 14 ovules per flower had the lowest specialization values.

DISCUSSION

This study demonstrates that plant species exhibit clear trade-offs among their vegetative and reproductive traits and that these trade-offs determine interactions with floral visitors. These trade-offs are differentiated along three axes of trait variation: (i) flower number - flower size, (ii) pollinator dependence and (iii) style length. These reproductive trade-offs helped partly explain the presence of floral visitor interactions, but not their number of visits. However, floral visitor guilds formed distinct relationships with the main axes of trait variation. Moreover, we found that the plant species network roles were best explained by plant size and floral reward related traits.

Over half of all plant trait variation was captured by the flower number - flower size and pollinator dependence trade-offs. Trait variation on these two axes was associated with the 'fast-slow continuum' in plant (Salguero-Gómez et al., 2016) and animal (Healy et al., 2019) life-history strategies, as indicated by the different floral and reproductive biology traits associated with plant height, life form and lifespan. The 'slow' part of this continuum (i.e., tall trees and shrubs) included plant species with many flowers, few ovules, higher pollinator dependence, frequent occurrence of self-incompatibility and more complex breeding systems (e.g., monoecious and dioecious species). In contrast, plant species that employed the 'fast' strategy (i.e., short herbs), had fewer flowers, more ovules, frequent occurrence of self-compatibility and lower pollinator dependence. Further, on the first two axes of trait variation, we found additional support for the previously described positive association between higher outcrossing rate and larger floral display (Goodwillie et al., 2010). The positive correlation between larger floral display and higher pollinator dependence in our dataset further confirmed this trend (Fig. S11).

Despite the low predictive power of the main trait variation axes for broad-level interaction patterns (number of interaction partners and number of visits), we found changes in the interaction patterns among and within floral visitor guilds across these axes that suggest plant life-history strategies influence plant-pollinator interactions. For example, all floral visitor guilds visited plant species with higher pollinator dependence more frequently, and high pollinator dependence was associated with large floral displays and greater pollen quantities (Fig. 1 and Fig. S6). This trend is consistent with previous studies that show plant species with higher reproductive investment tend to be visited by pollinators more frequently (Hegland & Totland, 2005; Kaiser-Bunbury et al., 2014; Lázaro et al., 2013). In regard to the flower number - flower size and style length trade-offs, different pollinator guilds showed contrasting visitation patterns across the continuum of trait variation, which could be associated with different pollination syndromes at a macroecological scale. For instance, bees and syrphid flies were clearly associated with opposing life-strategies on PC1 and PC3 (Fig. 3) suggesting possible niche partitioning (Palmer et al., 2003; Phillips et al., 2020) between these two guilds. However, despite floral rewards not being included in the main analysis because there was insufficient data available, floral reward related traits were among the best at characterising species network roles (Fig. 4). More detailed exploration of reproductive trade-offs in conjunction with floral rewards is needed to help elucidate plant-pollinator associations. In any case, it is worth noting that other local factors such as species relative abundances, surely explain part of the observed variability (Bartomeus et al., 2016; Encinas-Viso et al., 2012; Vázquez et al., 2007) that reproductive trade-offs do not.

To conclude, we provide a robust description of plant reproductive trade-offs using a large global dataset of plant traits. We identified the major reproductive strategies of flowering plants and how these strategies influence interactions with different floral visitor guilds. Although the explained variation that we found in the first two axes is lower than previous studies of vegetative traits (Carmona et al., 2021; Díaz et al., 2016) it is consistent with the largest and most recent study that has characterised plant life strategies with vegetative and reproductive traits (Salguero-Gómez et al., 2016). Future work needs to integrate the reproductive compromises that we have identified with vegetative and physiological trade-offs to create a more comprehensive spectrum of plant trait variation. 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 (Gervasi & Schiestl, 2017; Mackin et al., 2021). Finally, including plant-pollinator networks from unrepresented areas of the world and a more complete description of plant reproductive trade-offs is essential for a better understanding of the global patterns in plant-pollinator interactions.

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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 biology**	Compatibility system	Self-incomp. Part. self-comp. Self-comp.
Floral	Flowers per plant	**Reproductive biology**	Breeding system	Hermaphrodite Monoecious Dioecious
Floral	Nectar (μl)			
Floral	Nectar (mg)			
Floral	Nectar concentration (%)			
Floral	Pollen grains per flower			
Reproductive biology	Autonomous selfing (fruit set)			

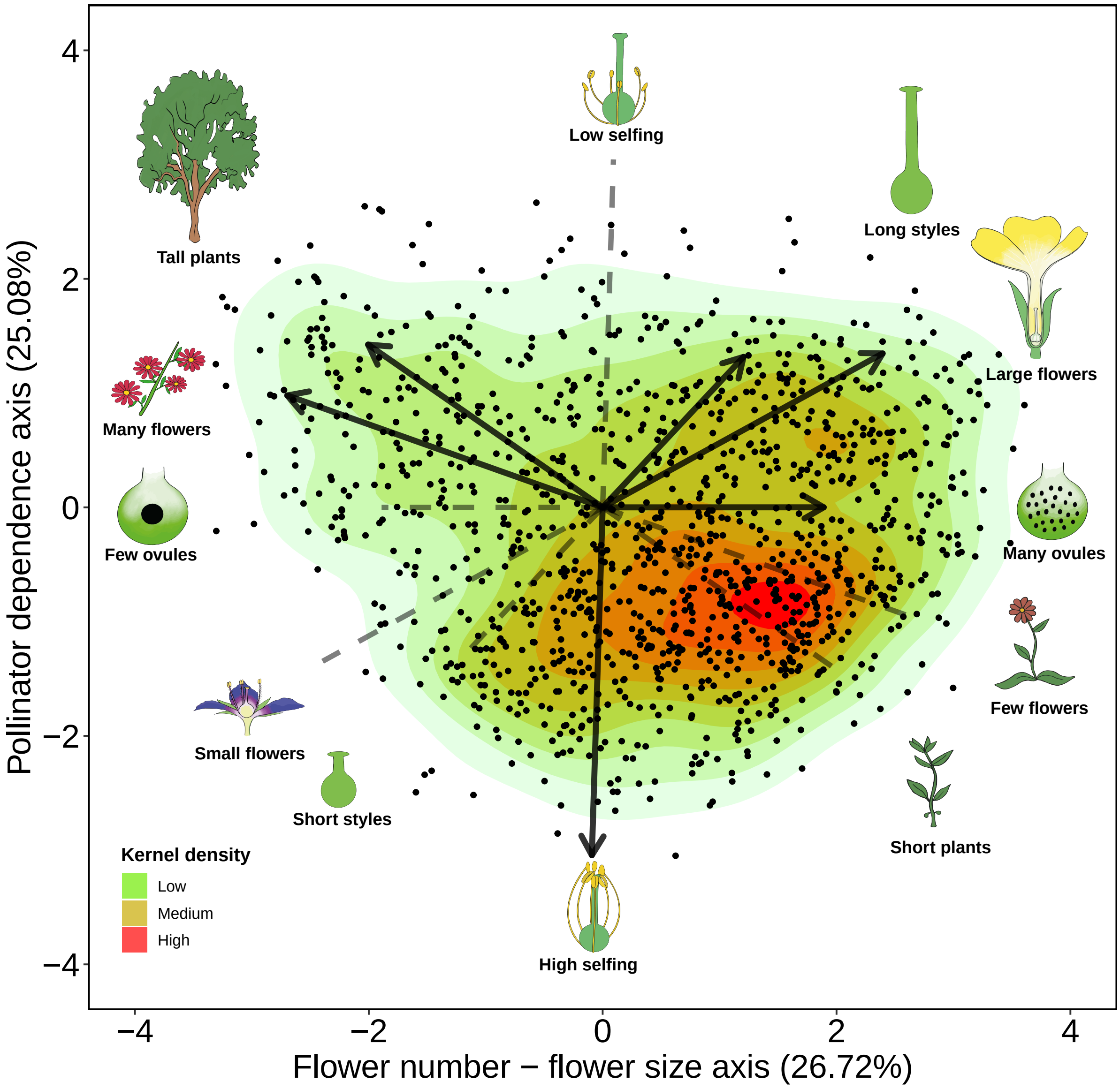

Figure 1 Phylogenetically informed principal component analysis (pPCA) of 1,236 plant species from 28 plant-pollinator network studies. The solid arrows indicate the direction of the different quantitative traits (flower number, plant height, style length, flower size, ovule number and level of autonomous 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 dashed lines show the opposed direction of trait variation. The icons at both ends of arrows and dashed lines illustrate the extreme form of the trait continuum.

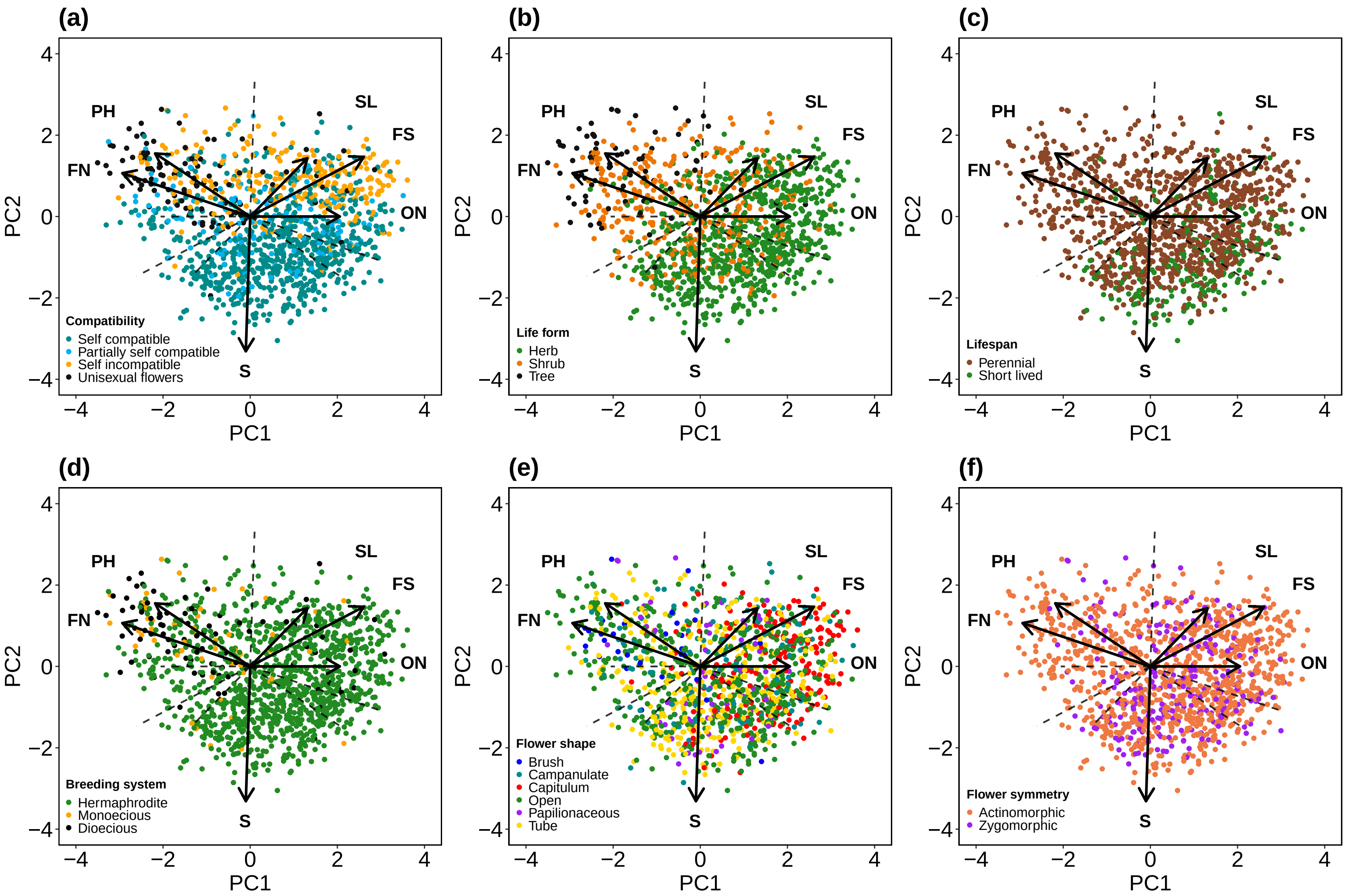

Figure 2 Location of the different qualitative traits on the trait space. The panel is composed by the traits that showed statistical association with the first two axes of trait variation: compatibility system (a), life form (b), lifespan (c), breeding system (d), flower shape (e) and flower symmetry (f). The solid arrows indicate the direction of variation of the different quantitative traits showed in figure 1: flower number (FN), plant height (PH), style length (SL), flower size (FS), ovule number (ON) and the level of autonomous selfing (S).

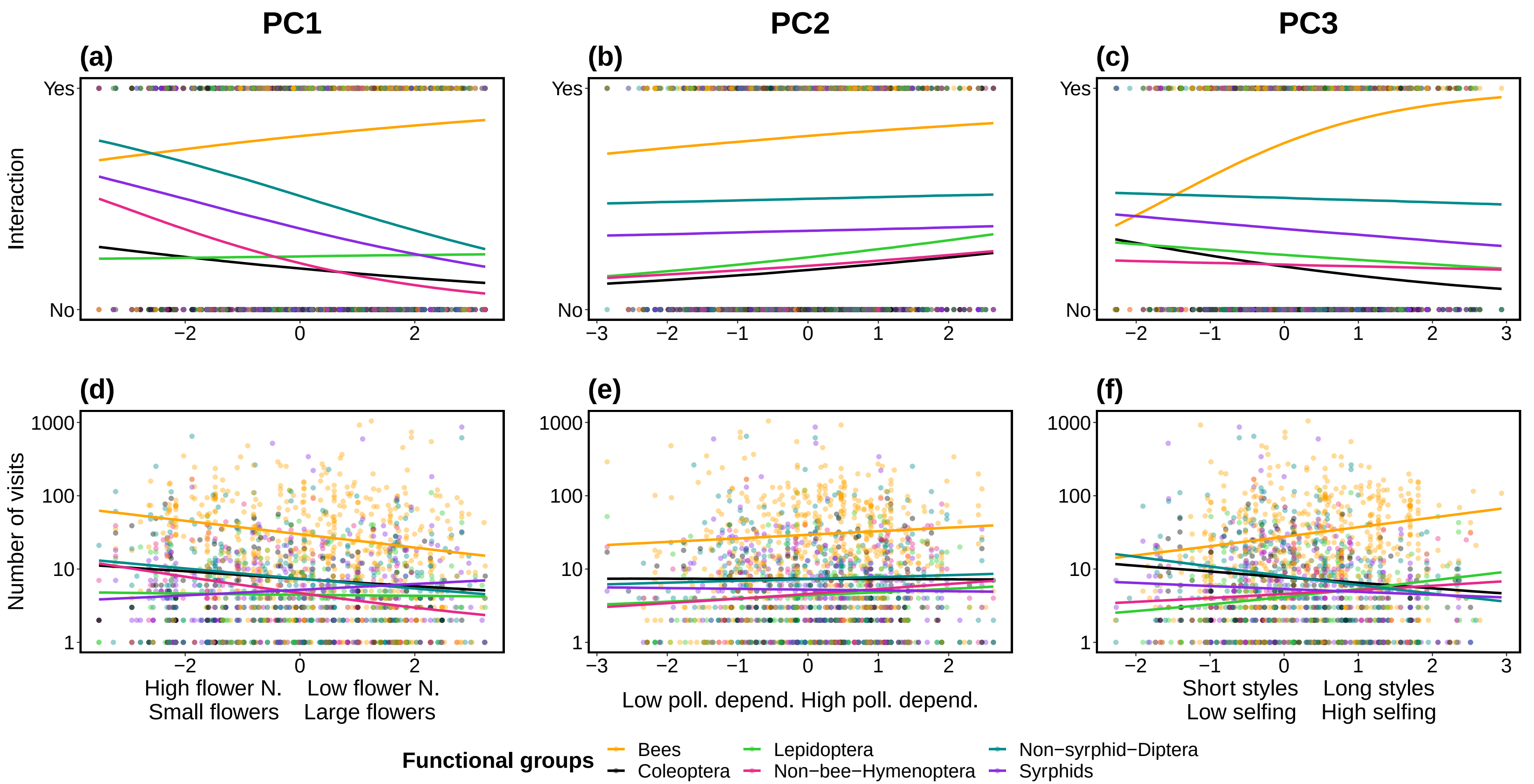

Figure 3 Fitted posterior estimates of the presence-absence of interaction (a, b and c) and number of visits (d, e and f) of the different floral visitor guilds in relation to the main axes of trait variation (PC1, PC2 and PC3). PC1 represents the flower number - flower size axis, PC2 represents the pollinator dependence axis and PC3, the style length - pollinator dependence axis. For visualization purposes, due to large differences between number of visits of bees and the rest of guilds, the number of visits was log-transformed (Y-axis of lower panel).

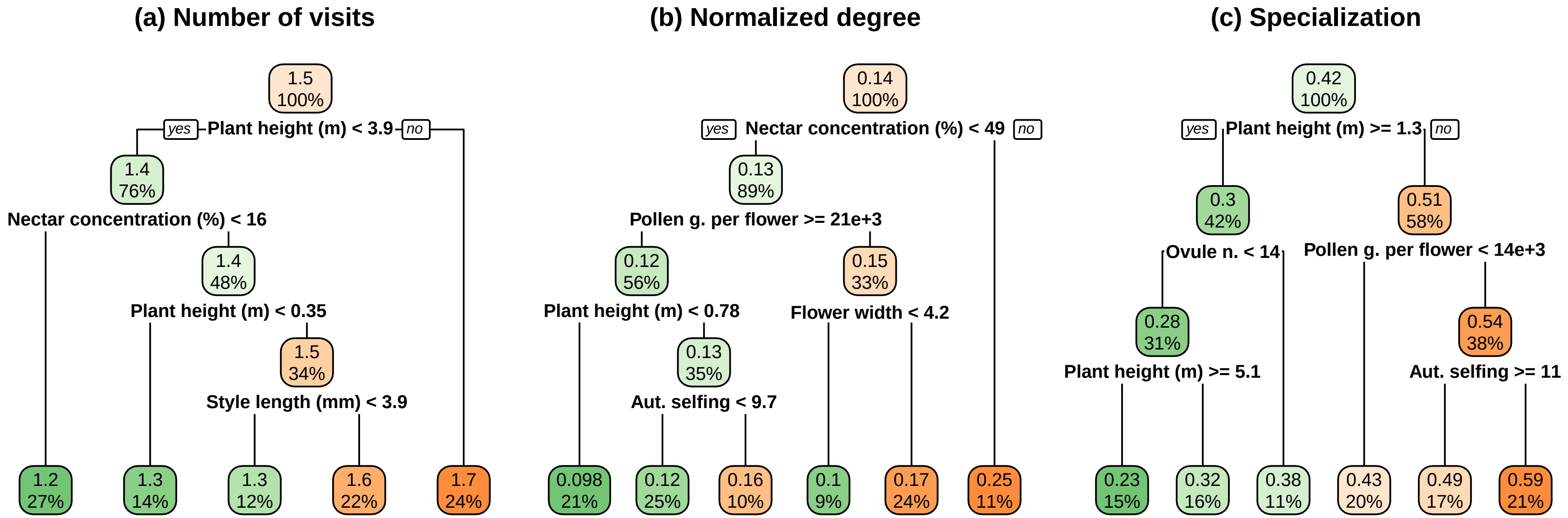

Figure 4 Contribution of traits in plant's network roles. Regression tree analysis of number of visits (log-transformed), normalized degree and specialization for the subset of species with quantitative data for pollen and nectar traits. The superior value inside the node indicates the mean value of 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.