Plant reproductive strategies structure plant-pollinator networks

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Abstract

Increasing availability of large datasets have improved our understanding of organismal life history and pollination biology. However, most attention has focused on vegetative traits when delimiting plant life strategies and overlooked key floral and reproductive traits. In addition, plant-pollinator research rarely considers the reproductive biology of the species and has overemphasized the study of highly specialized interactions. Greater knowledge of the

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plant reproductive trade-offs between these traits can shed light on the macroecological patterns and help our understanding of life strategies.

Here, we compiled 20 reproductive traits for 1,506 plant species from 28 plant-pollinator network studies and 18 different countries that constitute a total of 64 unique networks and 8 meta-webs. We explore the different trade-offs of floral, reproductive, and vegetative traits of the main quantitative traits in the trait space. Then, we evaluate whether the frequency of pollinator visits within networks change across the primary axes of trait variation and pollinator functional groups and how individual traits contribute to the overall visitation patterns. Finally, we investigate if the functional role of the plant species (interaction frequency, normalized degree and specialization) in the network is associated with the primary axes of trait variation and the different plant traits.

We found that 51.8% of the trait variation was explained by two independent axes that determined plant form and function. The first axis showed the flower number versus flower size compromise (PC1, 26.72%) where species were divided in two opposed strategies with high investment in flower number and plant height on one extreme or high investment in flower size, style length and larger number of ovules on the other. The second axis showed the pollinator dependence trade-off (PC2, 25.08%) between species with high pollinator dependence with greater plant height and higher investment in floral traits on one end and low pollinator dependence with smaller height and lower investment in floral traits on the other. An additional principal component analysis with the subset of species with quantitative data of pollen and nectar showed that nectar quantity was positively associated with flower size, style length and ovule number (PC1, 24.70%) and pollen quantity was positively correlated with flower number and plant height and negatively associated with autonomous selfing (PC2, 20.59%). The main axes of trait variation with the full set of species did not explain the overall visitation patterns but showed marked trends for the different functional groups. For instance, all pollinator functional

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groups had higher frequency of visits on plant species with high pollinator dependence (PC2); and bees (Anthophila), the most abundant functional group, had higher frequency of visits on species with high number of flowers and tall plant height (PC1); and, on species with longer styles and higher levels of autonomous selfing (PC3). Overall, plant species with small size, low nectar concentration and short styles showed lower visitation rates than plant species with the opposed traits; species with small amounts of floral rewards (pollen and nectar), low number of flowers and small flowers had in general lower number of visiting species (normalized degree); and species under 1.3 m, with high rewards of pollen and nectar showed the highest levels of specialization. This work highlights the need to consider essential plant reproductive and floral traits to improve understanding of plant life strategies and plant-pollinator interactions at large scales.

INTRODUCTION

Among flowering plants there is an astonishing diversity of floral structures and plant reproductive strategies (Barrett 2002, Schiestl and Johnson 2013). Subsequently, pollination biologists have long studied their relevance on plant-pollinator interactions. However, despite recent efforts exploring reproductive (e.g., mating and compatibility system) and floral traits (e.g., flower size or nectar provision) with large sets of species (Carvalheiro et al. 2014, Baude et al. 2016, Munoz et al. 2016, Grossenbacher et al. 2017, Moeller et al. 2017), most studies focus on the individual, community level or specific taxa and macroecological patterns remain poorly investigated. For instance, studies depicting species' life history strategies generally focus on vegetative traits and rarely consider reproductive traits on the main axes of trait variation (Díaz et al. 2016, Salguero-Gómez et al. 2016). In addition, there is not a unified framework that explores the compromises of floral traits and their relevance on plant life strategies (Roddy et al. 2021). Similarly, there is growing interest in understanding what determines plant-pollinator network structure. Approaches with traits range from the description of pollination syndromes (e.g., Dellinger 2020), to more specific trait-matching analysis (Bartomeus et al. 2016), but again the reproductive biology of the species has received little attention (but see Tur et al. 2013 and @devaux2014) and floral traits have been overlooked beyond highly specialised plant-pollinator interactions (Dellinger 2020, Roddy et al. 2021).

With increased availability of large trait databases, plant ecological strategies have begun to be examined more frequently (e.g., TRY, Kattge et al. 2011 and COMPADRE, Salguero-Gómez et al. 2015), highlighting global patterns and constraints of plant form and function (Díaz et al. 2016, Salguero-Gómez et al. 2016, Carmona et al. 2021). However, these resources and their research have mainly focused on vegetative traits such as the leaf (Wright et al. 2004) or wood (Chave et al. 2009) trade-offs and neglected reproductive and floral traits that also can influence the

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spectrum of trait variation. For instance, short lived and perennial species tend to have high

and low levels of outcrossing respectively (Barrett 2003, Moeller et al. 2017) and outcrossing

levels have been shown to be positively correlated with flower size (Goodwillie et al. 2010). In

addition, the presence of costly rewards (e.g., pollen or nectar) and showy flowers or floral

displays cannot be understood without considering pollinators that are thought to be

responsible for approximately 87.5% of the pollination of flowering plants (Ollerton et al. 2011).

Hence, exploring plant life strategies with reproductive and floral trade-offs, in conjunction

with their known pollinators seems necessary for a correct understanding of the plant

economics.

Several key studies have progressed knowledge of the link between traits and network

properties (Lázaro et al. 2008, Bartomeus 2013, Carvalheiro et al. 2014, Klumpers et al. 2019).

Functional traits can determine whether species interact, and thus define the species network

role (e.g., specialist vs generalist). For instance, species with high investment in floral display

tend to have higher visitation rates (Stang et al. 2006, Novella-Fernandez et al. 2019) and greater

specialization is generally associated with occupation of the trait space extremes (Junker et al.

2013, Coux et al. 2016). In addition, the structure of the pollination network highly depends on

the degree of trait-matching between plants and pollinators (Stang et al. 2009, Ibanez 2012,

Peralta et al. 2020). However, little is known about the consequences of reproductive traits and

floral rewards on plant species roles. In addition, although some attempts have been made to

evaluate trait relationships in plant-pollinator interactions at a global scale (Carvalheiro et al.

2014, Rech et al. 2016), macroecological patterns have been little explored.

Here, we explore the major axes of plant reproductive trait variation. We investigate how these

traits influence the structure of plant-pollinator networks by compiling a unique dataset

comprising 20 plant functional traits for 1,506 species from 64 unique networks and 8

metawebs. First, we evaluate the major axes of reproductive trait variation and tradeoffs that

determine plant form and function. Second, we investigate how plant species' position in trait-space influences interaction strength with different pollinator functional groups. Finally, we assess the relevance of the main axes of trait variation and traits in understanding the plant species role within the networks with complementary species level metrics (i.e., interaction strength, normalized degree and specialization).

METHODS

Plant-pollinator network studies

We selected 28 studies from 18 different countries that constituted a total of 64 plant-pollinator networks. All these studies censored plant-pollinator interactions in natural systems and were selected in order to have a wide representation of geographical areas of the world. Although these studies differ in sampling effort and methodology, all studies provided information about plant-pollinator interactions (weighted and non-weighted) allowing us to build a database of plants that are likely to be animal pollinated. Some of these networks have been already used in past studies of plant-pollinator networks (Olesen et al. 2007, Fortuna et al. 2010, Carvalheiro et al. 2014) and are available on the online networks archives The Web of Life (Fortuna et al. 2014) and Mangal (Poisot et al. 2016). In total, our network dataset (Table S1) constituted 60 weighted (interaction frequency) and 4 binary networks, each sampled at a unique location and year, as well as 8 meta-webs where sampled interactions were pooled across several locations and multiple years.

Taxonomy of plants and pollinators

All plant species names, genera, families and orders were retrieved and standardized from the taxonomy data sources NCBI (https://www.ncbi.nlm.nih.gov/taxonomy) (plants) and ITIS (https://www.itis.gov/) (pollinators) using the R package taxize (version 0.9.99, 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.

Functional traits

We selected 20 different functional traits based on their relevance to plant reproduction and data availability (Table 1). The selected traits were quantitative (12) and categorical (8) and belonged to three different trait types: vegetative, floral and reproductive. For each 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 x 1,506 spp) we were able to fill 23,969 cells (79.6% of the dataset, see Figure S1 for missing values information per variable).

Phylogenetic Distance

We calculated the phylogenetic distance between different plant species using the function get_tree from the package rtrees (downloaded from github, https://github.com/daijiang/rtrees), which downloads phylogenetic distances from the extended R implementation of the Open Tree of Life (Smith and Brown 2018) developed by Jin and Qian (2019).

Table 1: List of the 20 traits compiled in this study divided in quantitative and categorical traits. The different types of trait (vegetative 'V', floral 'F' and reproductive 'R'), total records found for the 1,506 species and categories of the qualitative traits are also provided.

Quantitative traits			Categorical traits			
Type	Traits	Records	Type	Traits	Categories	Records
V	Plant height (m)	1470	V	Lifepan	Short-lived Perennial	1466
F	Flower width (mm)	1472	V	Life form	Herb Shrub Tree	1472
F	Flower length (mm)	1401	F	Flower shape	Brush Campanulate Capitulum Open Papilionaceous Tube	1458
F	Inflorescence width (mm)	1496	F	Flower symmetry	Actinomorphic Zygomorphic	1478
F	Style length (mm)	1497	F	Nectar	Presence Absence	1407
F	Ovules per flower	1457	R	Autonomous selfing	None Low Medium High	987
F	Flowers per plant	1468	R	Compatibility system	Self-incomp. Partially self-comp. Self-comp.	1253
F	Nectar (μl)	485	R	Breeding system	Hermaphrodite Monoecious Dioecious	1489
F	Nectar (mg)	415				
F	Nectar concentration (%)	508				
F	Pollen grains per flower	298				
R	Autonomous selfing (fruit set)	992				

Data Imputation

Missing values were imputed with the function missForest (Stekhoven and 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 (Santos et al. 2018) based on the conceptual framework of Diniz-Filho et al. (2012). 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%, 50.8% and 80% 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 impute nectar and pollen quantity due to the high percentage of missing values (Figure S1). The imputed dataset had 9.7% of missing values with a total of 8 categorical and 8 numerical variables. Finally, we conducted an additional imputation for the subset of species with quantitative information of nectar and pollen; all variables had lower than 30% of missing values (N = 636) and the total proportion of missing values in this dataset considering all variables was 13%.

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

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moderately correlated to flower width (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. In addition, we explored the location of different qualitative traits in the trait space. Prior to the analyses, we excluded outliers and standardized the data. Due to the high sensitivity of dimensionality reduction to outliers, we excluded values in the 2.5th-97.5th percentile range (Legendre and Legendre 2012). 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 (version number 0.7-70, 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 our variables are on the same scale after the log and z-transformation (Abdi and 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 (Figure S2). We found little difference between the variance explained with the imputed dataset (51.08%) and the dataset without missing values (56.26%). 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 explored with the imputed dataset with quantitative information of pollen and nectar the compromises in the trait space of these two floral rewards with the other quantitative traits. For this, we considered solely one variable of nectar quantity (microlites of nectar per flower) in order to avoid overemphasizing nectar on the spectrum of trait variation.

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 = 1506) with the package phytools version 0.7-70 (Revell 2012) and we used Pagel's lambda (λ) as a measurement of the phylogenetic signal. For pollen and nectar traits, phylogenetic signal was calculated on the imputed dataset that included these traits (N = 636).

Networks analysis

Our analyses were conducted on the subset of 60 weighted networks with interaction frequency sampled in a unique flowering season and site. Although floral visitors are not always pollinators and the frequency of visits does not consider each pollinator species efficiency (Ballantyne et al. 2015), interaction frequency provides valuable information of the impact of pollinators (Vázquez et al., 2005; Vázquez et al., 2012). Although not all networks were sampled using the same method, our aim was not to compare patterns across networks but within each network in order to obtain a general picture of associations between traits and the main axes of trait variation and plant species functional roles.

Functional groups visitation patterns

We explored the relevance of pollinator functional groups and the main axes of trait variation (pPCA with imputed dataset) on pollinator visitation per plant species. For this, we divided floral visitors into six main groups that differ in life form and behaviour: (i) Hymenoptera-Anthophila (bees), (ii) Hymenoptera-non-Anthophila (other non-bee Hymenoptera), (iii) Diptera-Syrphids, (iv) Diptera-Non-Syrphids, (v) Lepidoptera and (vi) Coleoptera. In addition, because Hymenoptera was the most represented group with 2,256

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records counted and had the highest frequency of visits of all groups, we also explored

visitation patterns of the most represented families of Hymenoptera on the trait space

(Andrenidae, Apidae, Colletidae, Halictidae and Megachilidae). Apis mellifera was the species

with the largest proportion of records (7.55% from the total) which is is consistent with the

results of Hung et al. (2018) that showed that A. mellifera was the most frequent visiting

species on a similar dataset of 80 interaction plant-pollinator networks on natural systems.

Hence, to control for the relevance of Apis mellifera on the observed visitation patterns of bees,

we conducted an analogous analysis excluding A. mellifera. We found that A. mellifera, was

driving, in part, some of the observed trends on PC1 (Figure S3). However, we did not find

major changes on PC2 and PC3.

Plant species functional roles

We investigated if the main axes of trait variation and traits explained plant species functional

roles. We considered all uncorrelated traits apart from the principal components because this

allowed us to consider quantitative and categorical traits. For this, we also used a modelling

approach and conducted decision trees which help to interpret visually how the different traits

determine species functional roles. We selected simple and complementary plant species level

metrics with a relatively straightforward ecological interpretation relevant to our research

goals: (i) sum of visits per plant species; (ii) normalized degree calculated as the number of

links per plant species divided by the possible number of partners which helps comparison

across networks; 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

(version 2.15, Dormann et al. 2008).

Analyses

First, we implemented Bayesian generalized linear mixed models using the R package brms (version 2.14.6, Bürkner 2017). We modelled the frequency of visits as a function of the main axes of trait variation and floral visitors functional groups (Visits~PC1xFG+PC2xFG+PC3xFG). Because we were interested in possible differences among main visitor guilds to plants with different strategies, we included the interaction between the main axes of trait variation and the distinct floral visitor functional groups. We added a nested random effect with networks nested on the study system to capture the network variability per study and within networks. We specified this model with a zero inflated negative binomial distribution and weakly informative priors from the brms function. Moreover, we included the phylogenetic covariance matrix as a random factor due to the possible shared evolutionary history of the species and therefore lack of independence across them.

Second, 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 in three different models for each metric (plant species level metric~PC1+PC2+PC3). In addition we also explored how all uncorrelated traits (13) explained these metrics in three other models (plant species level metric ~ plant height + lifespan + life form + flower shape + flower symmetry + flower width + style length + ovule number + flowers per plant + nectar provision + autonomous selfing + compatibility system + breeding system). For each response variable (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. Moreover, we included a nested random effect with networks nested on the study system and a phylogenetic random effect for species (as detailed above) in each model.

All analyses were conducted in R Version 4.0.3. In addition, all models were run for 3,000

259 iterations with 1000 warm up iterations. We set delta () to 0.99 to avoid divergent transitions

260 and visualized the posterior predictive checks with the function pp_check using the bayesplot

261 package (version 1.7.2, Gabry et al., 2019).

262 [ADD REGRESSION TREE TO METHODS] We conducted regression trees in order to explore

263 the relevance of traits on the species plant functional role. We repeated the procedure as the

264 modelling analysis and we ran a decision tree for each plant level species metric (interaction

265 frequency, normalized degree and specialization). We used the full datase

266 rpart 4.1-15 (Therneau et al., 2019) rpart.plot 3.0.9 (Milborrow 2018)

267 # RESULTS

268 ## Plant strategies

269 The phylogenetically informed principal component analysis (pPCA) captured with the first

270 two and three axes 51.8% and 70.97% of the trait variation respectively (Figure 1 and Figure S4)

271 and had a phylogenetic correlation (λ) of 0.76. The first principal component (PC1) represented

272 26.72% of the trait variation and showed the flower number versus flower size compromise.

273 Thus, as flower number and plant height increase, flower size, style length and ovule number

274 decrease; and, as flower size, style length and ovule number increase, flower number and plant

275 height decrease. The main contributing traits to PC1 were plant height, flower number, ovule

276 number and flower size (loadings > |0.5|; Table S2) but style length also contributed

277 moderately on PC1 (loading = -0.33). The second principal component (PC2) represented

278 25.05% of the trait variation and showed the trade-off between low and high pollinator

279 dependence and we refer to this axis as the pollinator dependence trade-off. The main driver of

280 trait variation of PC2 was autonomous selfing (loading = 0.85) but the other traits (except ovule

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number) also made a moderate contribution to PC2 (loadings from 0.27 to 0.4; Table S2). We

found that high pollinator dependence was associated with larger and higher number of

flowers, greater plant height and longer styles. In contrast, species with high levels of

autonomous selfing had a general lower investment in flower number and size, plant height

and style length. Further, PC3 also explained a considerable amount of 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 S2). In addition,

the pPCA with the species subset that had nectar and pollen quantity showed that nectar

quantity (microlitres of nectar per flower) was positively associated with flower size, style

length and ovule number (PC1, 24.70%); and pollen quantity was positively correlated with

flower number and plant height and negatively associated with autonomous selfing (PC2,

20.59%; Figure S5). This pPCA also showed similar explained variance with two components

(50.06%) and similar associations of traits despite some variability in the loadings (Table S3).

Evaluation of qualitative variable positions in the trait space revealed statistical association on

both axes of trait variation for compatibility, breeding system, life form, lifespan and flower

shape (Figure 2 and Table S4). In addition, flower symmetry was associated with PC2 (Sum of

squares = 8.51, F-value = 14.72 , p < 0.01). Nectar provision was independent of both axes (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). Concerning self compatibility, we found larger differences in pollinator dependence the

trade off (i.e., species with unisexual flowers and self incompatibility were statistically

differentiated from species with partially and fullyself compatibility in trait space; Figure S3 A

and B). 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 (Figure S3 C and D). Consequently, lifespan also
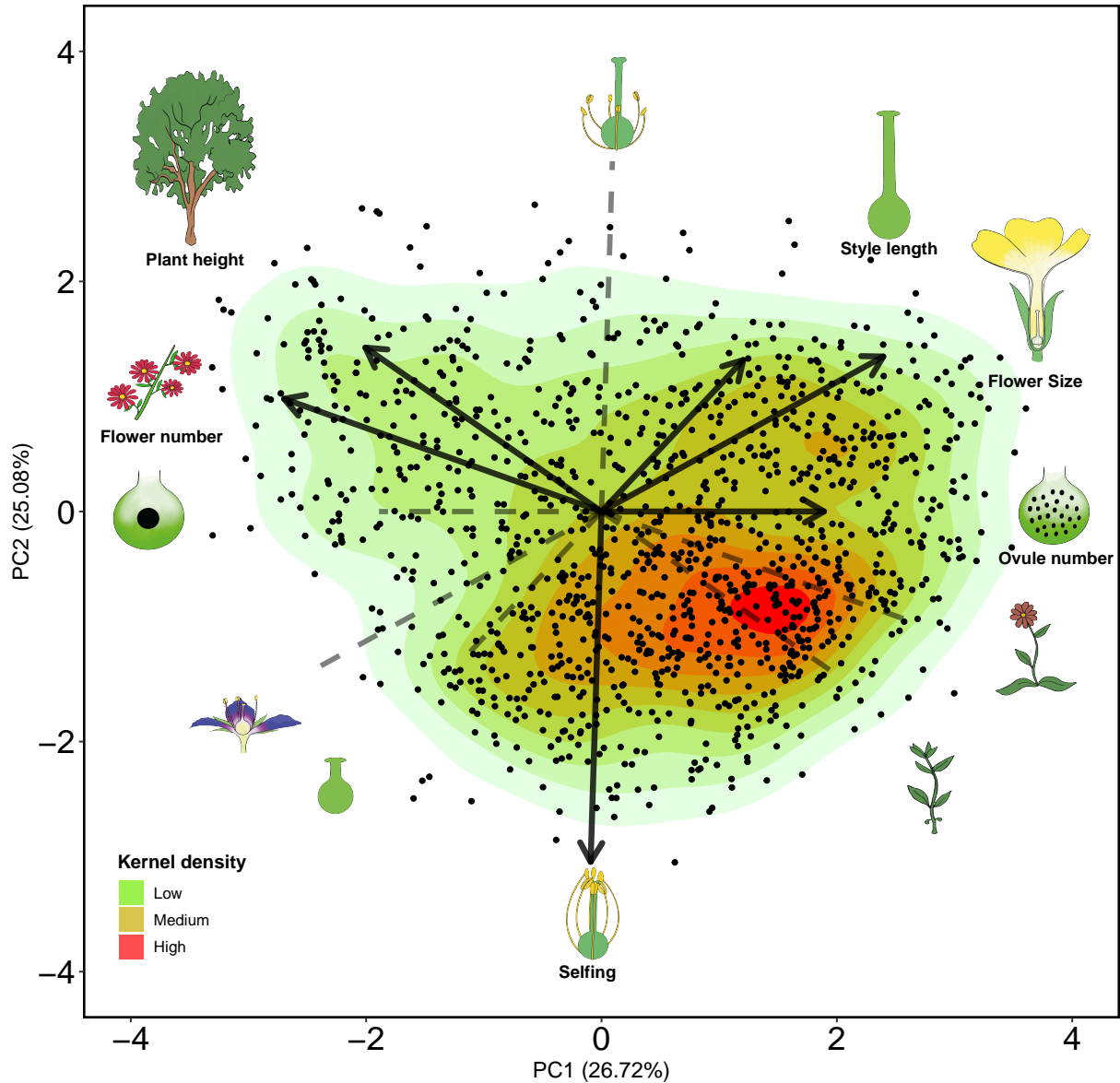
Figure 1: Life history strategies for 1,236 plant species from 29 plant-pollinator networks studies across the first two axes of variation from a phylogenetically informed principal component analysis (pPCA). The solid arrows indicate the direction and weights of the six quantitative traits (flower number, plant height, style length, flower size, ovule number and autonomous selfing level) and the labelled icons at their end represent the extreme form of the trait continuum. The dashed lines indicate the opposed direction of trait variation and the non-labelled icons at their end illustrate the other extreme of the continuum.

followed this gradient but perennial and short lived species just differed statistically on PC2
(Figure S3 E and F). Species with unisexual flowers (monoecious and dioecious) were clustered
on both extremes of trait variation with the highest pollinator dependence and flower number
investment (Figure S3 G and H). 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 tended to occupy positions with larger flowers and greater
pollination dependence, while the latter positions had higher number of flowers and
autonomous selfing (Figure S3 I and J). Regarding flower symmetry, zygomorphic flowers were
associated with lower levels of pollinator dependence, whereas actinomorphic flowers had
higher pollinator dependence (Figure S3 K and L).
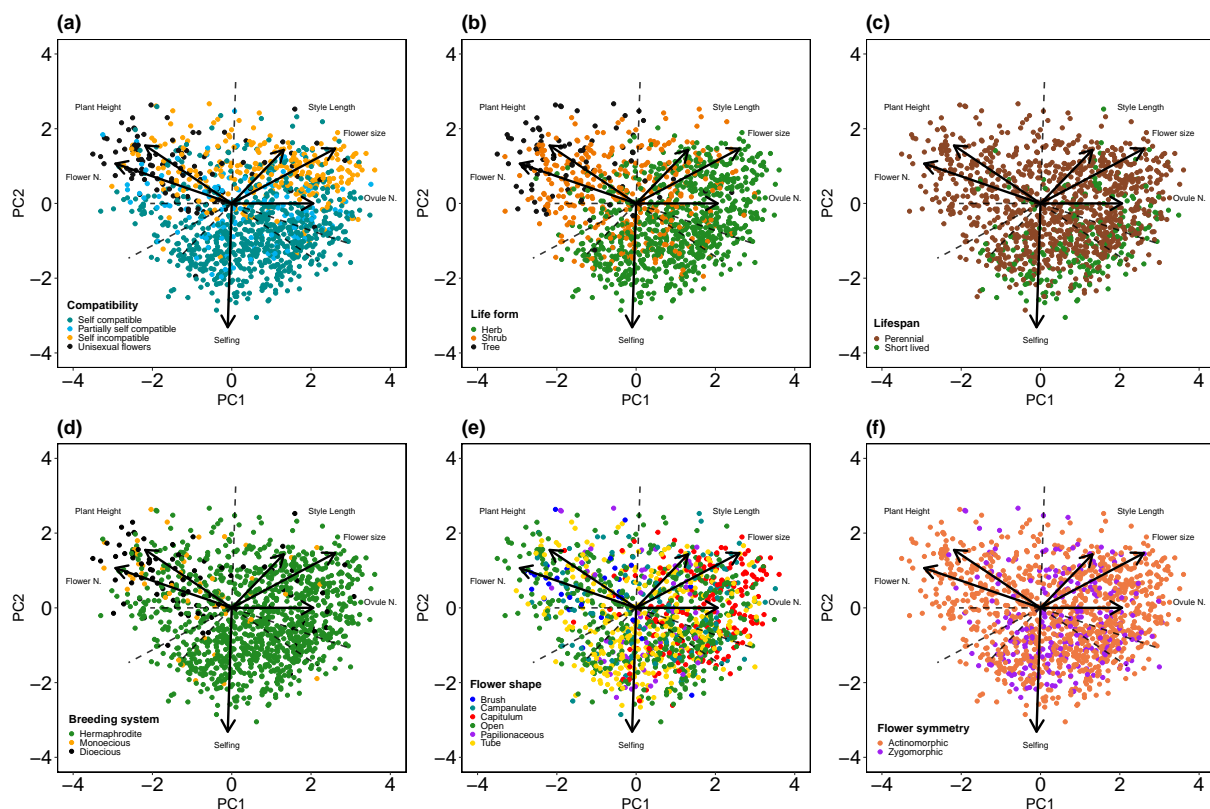
Figure 2: Location of the qualitative traits in the trait space for traits that showed a statistical
association with the main axis of trait variation. These different traits included: compatibility
system (a), life form (b), lifespan (c), breeding system (d), flower shape (e) and flower symmetry
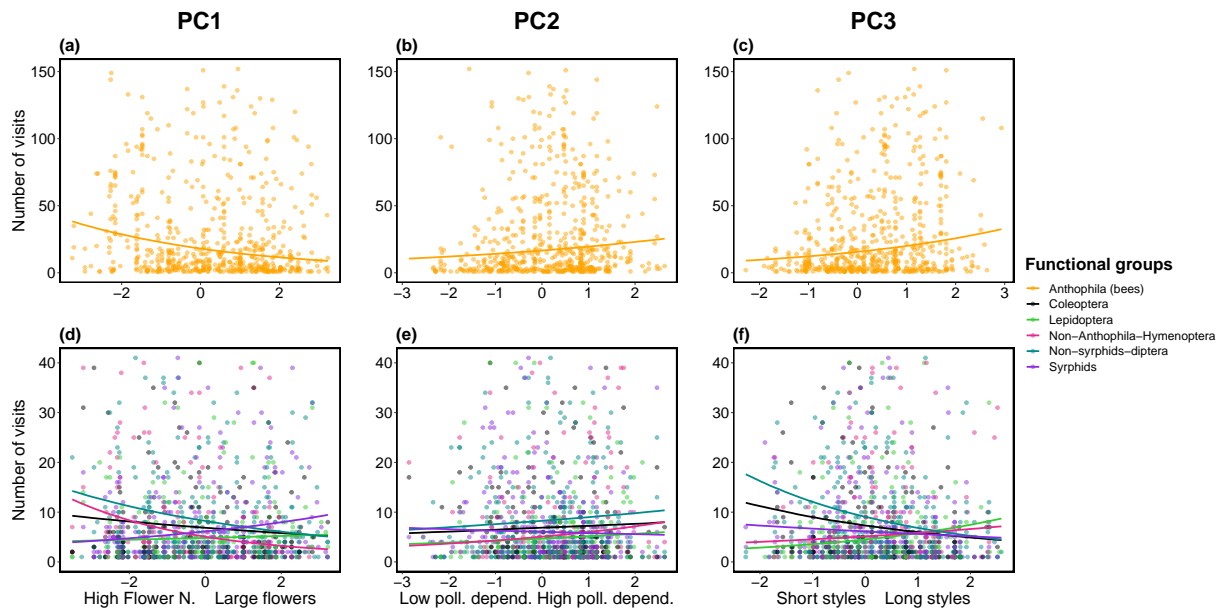(f).

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Phylogenetic signal of traits

We found a strong phylogenetic signal with statistical association ($P < 0.01$) for all quantitative traits (Table S4). The traits with the highest phylogenetic signal were ovule number ($\lambda = 1$) and plant height ($\lambda = 0.96$), followed by flower length ($\lambda = 0.75$), flower width ($\lambda = 0.73$) and flower number per plant ($\lambda = 0.69$). Finally the traits that showed lower phylogenetic signal were inflorescence width ($\lambda = 0.57$), style length ($\lambda = 0.49$) and autonomous selfing ($\lambda = 0.34$).

Add *pollen and nectar traits

Visitation patterns

The overall visitation records of functional groups differed considerably. There were 2,256 for bees, 1,768 for non-syrphid-Diptera, 845 for syrphids, 437 for Lepidoptera, 432 for Coleoptera and 362 for non-bee-Hymenoptera. The main axes of trait variation explained little of the visitation patterns (conditional $R2 = 0.31$; marginal $R2 = 0.06$) but showed interesting trends for the different functional groups (Figure 3). Furthermore, the additional model with interaction between the most represented families of Hymenoptera and the main axis of trait variation (marginal $R2 = 0.30$; conditional $R2 = 0.03$) showed that the family Apidae was the main driver of the observed patterns (Figure S2). Although Apis mellifera contributed substantially to floral visitation, the general pattern of bee visitation did not change when A. mellifera were removed (FSX).

PC1　　　**PC2**　　　**PC3**

(a) ... (b) ... (c)

(d) High Flower N. Large flowers (e) Low poll. depend. High poll. depend. (f) Short styles Long styles

Number of visits

Functional groups
Anthophila (bees)
Coleoptera
Lepidoptera
Non–Anthophila–Hymenoptera
Non–syrphids–diptera
Syrphids

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Plant species metrics

The three main axes of trait variation did not explain the position or role of the plant species in

the network (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 ,

marginal R^2 = 0.03). However, the functional groups showed different visitation patterns across

the three main axes of trait variation (Figure 3). On the flower number versus size compromise,

all functional groups showed higher visitation rates on plant species with greater vegetative

investment and more flowers except syrphids which showed the opposite trend (higher

visitation on species with larger flowers and associated traits). Remarkably, on the pollinator

dependence trade-off, all pollinator functional groups showed an increasing visitation pattern

for species with higher pollinator dependence. Lastly, we found that bees, Lepidoptera and

non-bee Hymenoptera visited more species with larger style length and Coleoptera,

Non-Syrphids Diptera and Syrphids had greater visitation patterns on species with shorter

styles. Furthermore, with the full model that included all traits, we found that a considerable

amount of variance for plant species network metrics was explained by the different qualitative

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and quantitative traits (Visits ~ Traits: conditional R2 =0.32 , marginal R2 = 0.07; Normalize

degree ~ Traits: conditional R2 =0.46 , marginal R2 = 0.16; Specialization ~ Traits: conditional

R2 =0.49, marginal R2 = 0.14).

DISCUSSION

Our work highlights that in plant-pollinator networks, plant species have displayed clear

trade-offs in life strategies. These trade-offs can be differentiated on two main axes of trait

variation: the flower number-size trade-off and the pollinator dependence trade-off. In

addition, we found that relevant qualitative traits were aggregated within trait space, showing

clear delimited strategies of different plant species within plant-pollinated systems. Moreover,

the distinct pollinator functional groups showed changes in their interaction strength along

these axes of trait variation. Although the main axes of trait variation explained little the

variation of plant species network metrics, the full model of uncorrelated traits explained

partially the plan level metrics.

CONCLUSIONS

Wrap up

ACKNOWLEDGEMENTS

On the shoulders of giants.

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