An angiosperm-wide perspective on reproductive strategies and floral traits

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Keywords: flowering plants, floral morphology, reproduction, functional ecology, pollination, trait evolution, mating systems, sexual systems

Summary

Flowering plants have many different modes of sexual reproduction, notably varying from selfing to outcrossing and from bisexual flowers to individuals with separate sexes (dioecy). These reproductive modes are associated with a range of floral and other life-history traits. While several theories have sought to explain how these correlations arose, many questions remain open, particularly because these traits themselves have not evolved independently from one another. These observations stress the need for an integrative analysis of plant traits to determine whether the vast array of trait associations can be summarized as major reproductive strategies, which we perform here. We assembled a set of 361 species representative of flowering plant diversity and 21 traits including those related to flowers, pollination, mating and sexual systems as well as classical life history traits. As expected, outcrossing was mainly found among long-lived, large-stature plants, but hermaphroditic (monoclinous) outcrossers and dioecious species were remarkably distinct in the trait space. Level of floral investment seemed to be the main difference between these strategies, with dioecious species having smaller, less rewarding flowers in general, a pattern that was not only typical of abiotic pollination but present in biotically pollinated species as well. This work adds to growing evidence that floral and pollination traits can yield new insights into the evolution and ecology of flowering plants, and we argue that the important variation they underlie must be accounted for going forward. Based on our findings, we propose a conceptual framework that will help understand how different traits contribute to reproductive strategies.

Introduction

Angiosperms (flowering plants) are by far the most species-rich group of plants today. Its reproductive organ, the flower, presents an exceptional diversity, as illustrated by the fact it has traditionally been used as a key element to distinguish species, genera, and families. It is thought this diversity has evolved to deal with the challenge of fertilization, for which flowering plants have to rely on external vectors, either animals or abiotic factors (wind, water) to mate with other individuals. Sex is considered to have evolved to facilitate the recombination of genetic material, allowing species to adapt to their environment (Maynard Smith, 1978), and recombination is more effective when individuals mate with other individuals (outcrossing) than with themselves (selfing). Indeed, most species rely on outcrossing to produce offspring (Igic & Kohn, 2006), and it has been identified as a main driver of evolutionary success (Glémin, 2007). For instance, it has been shown that self-incompatible (SI) species, i.e. obligate outcrossers, have higher diversification rates than self-compatible (SC) species (Goldberg et al., 2010).

Most flowering plant species have bisexual flowers (here referred to using the botanical term 'monocliny'), which is probably the ancestral state of the clade (Sauquet et al., 2017). In these species, outcrossing is often facilitated by genetic SI, but many morphological features also exist that are thought to favour outcrossing (Barrett, 2002). Among others, they concern the disposition of pistils and stamens in the flower (herkogamy, distyly), and differential maturity of pistils and stamens (dichogamy). The strongest separation of sexual functions is found in dioecious plants, which have separate ovule- and pollen-producing individuals (females and males), rendering selfing impossible. The evolution of dioecy has intrigued naturalists for more than a century (Darwin, 1884). It has frequently arisen but is found in only a small minority of species (Renner, 2014). It has been argued that dioecy is a "second-rate" outcrossing mechanism compared to genetic SI, as individual plants can only reproduce through one sexual function in dioecy, which would lead to lower fitness, all else being equal (Barrett, 2010). Genetic SI is thought difficult to re-evolve once lost due to its complex underlying genetic architecture (Barrett, 2013), and thus might be replaced by dioecy to achieve outcrossing. For instance, if an SC species manages to colonize a remote island due to the reproductive assurance self-compatibility confers it will subsequently be confronted with strong inbreeding depression, which could lead to the selection of dioecy (Baker & Cox, 1984). The view of dioecy as inferior to SI has been promoted by studies suggesting dioecious species suffer from higher extinction rates (Heilbuth, 2000; Vamosi & Vamosi, 2005), but this result has proven incorrect more recently (Käfer et al., 2014; Sabath et al., 2016). Another sexual system, monoecy, in which individuals bear unisexual flowers of both kinds, has been much less studied although it is about as frequent as dioecy (Renner, 2014). Finally, some sexual systems are characterized by a combination of unisexual and bisexual flowers, such as gynodioecy and andromonoecy, but they are much rarer and seem to be more restricted to particular areas or plant families (Bawa & Beach, 1981; Torices et al., 2011; Dufay et al., 2014; Renner, 2014).

The diverse modes of reproduction in angiosperms are known to be linked to other traits, and several explanations have been proposed for these associations (Table 1). For example, variation in mating system (predominant outcrossing to predominant selfing) is associated with lifespan and plant size. Selfing is mainly found among smaller, annual species because they rely heavily on the reproductive assurance selfing provides while large, long-lived species with multiple opportunities for reproduction are thought to suffer more from inbreeding depression and thus typically reproduce through outcrossing (Scofield & Schultz, 2006; Petit & Hampe, 2006). Indeed, lifespan and outcrossing rate are thought to evolve jointly to give rise to long-lived outcrossing species and short-lived selfers (Lesaffre & Billiard, 2020). Dioecy on the other hand is often found in large plants (Renner & Ricklefs, 1995; Vamosi et al., 2003). Such species produce many flowers, increasing the risk that pollen is primarily transferred to flowers within the same individual, which can result in the clogging of stigmas and pollen discounting. In this case, dioecy could be more efficient than self-incompatibility, herkogamy or dichogamy to realize outcrossing (cf Thomson & Brunet, 1990).

Additional traits associated with reproductive mode could be indirectly linked to the degree of outcrossing. This might be the case with dispersal traits; however, the direction of the association and the underlying evolutionary forces are still debated. Initially, Baker (1955) proposed that selfing favored establishment after long-distance dispersal, which is supported by the higher proportion of self-compatible species on islands (Grossenbacher et al., 2017) or among alien and invasive species (Razanajatovo et al., 2016; Van Kleunen et al., 2010). However, this can be due to an ecological filter that does not necessarily imply coevolution of selfing and dispersal traits. More recent theory provides a contrasting prediction that under spatial heterogeneity in pollen limitation, outcrossing-dispersal vs selfing-nondispersal syndromes can evolve (Cheptou & Massol, 2009; Massol & Cheptou, 2011), although different ecological conditions can also select for the opposite association (Rodger et al., 2018). In dioecious species, long-range dispersal, in particular by animal dispersers, has been thought to be favorable to compensate for the effect of the absence of seed production by males (Heilbuth et al., 2001).

reproductive mode	trait	explanation	reference
selfing	low flower attractiveness	reduction in the investment in pollen export and attraction	Sicard and Lenhard (2011)
	low pollen-ovule ratio	less necessary investment in the male function	Charnov (1987)
	annuality	reproductive assurance is primordial in annual species, that often occur in disturbed habitats	Barrett et al. (1997)
	annuality	"time limitation" hypothesis: self-fertilized ovules are more likely to develop into mature seeds than cross-fertilized ovules	Aarssen (2000)
	short life span	effects of inbreeding depression less severe than in long-lived species	Morgan et al. (1997), Morgan (2001), Scofield and Schultz (2006), and Lesaffre and Billiard (2020)
	colonizing ability	uniparental reproduction facilitates establishment after dispersal when mate availability is limited in the new area	Baker (1955) and Rodger et al. (2018)
	non-dispersal	reproductive assurance removes the selective pressure for dispersal when mating is locally limiting	Cheptou and Massol (2009), Massol and Cheptou (2011), and Rodger et al. (2018)
dioecy	wind pollination	less investment shared by female and male function in flower; accelerating fitness gain curves more likely	Charnov et al. (1976) and de Jong and Klinkhamer (2005)
	wind pollination	less scope for sexual selection and associated differences in attraction between the sexes	Vamosi and Otto (2002)
	wind pollination	a way to ensure pollen transfer when pollinators are absent	Friedman and Barrett (2008)
	dull flowers	less scope for sexual selection and associated differences in attraction between the sexes	Vamosi and Otto (2002)
	open, non-specialized flowers	less pollen discounting by selfing and more efficient pollen transport between plants	Bawa (1980)
	specialized pollinating insects	dioecious species need reliable pollen transfer that cannot be achieved by generalists	Renner and Feil (1993)
	woody growth form	lesser importance of reproductive assurance when seeds can produced over longer times	Vamosi et al. (2003)
	woody growth form	with many flowers on an individual, self-pollen might saturate the stigmas and render self-incompatibility inefficient	Holsinger (1988) and Harder and Wilson (1998)
	fleshy fruits	uneven costs for reproduction	Bawa (1980) and Charnov (1982)
	fleshy fruits	more long-range dispersal by animals is needed because half of the population doesn't produce seeds	Heilbuth et al. (2001)
monoecy	wind pollination	separation of sexes in different flowers prevents self-pollination and clogging of stigmas	Faegri and Van Der Pijl (2013)
	wind pollination	facilitates selfing and reproductive assurance in plants with unisexual flowers	Friedman and Barrett (2008)

Table 1: Correlates of mating and sexual systems.

As one might expect given their role, floral traits have been found to be associated with the different modes of reproduction, although in most cases the underlying mechanism is not clear. An exception is the "selfing syndrome", in which species that mainly reproduce through self-pollination experience a reduction in flower size and attractiveness (showiness, scent, rewards) (Sicard & Lenhard, 2011), presumably because the selection pressure to maintain pollinator attraction has disappeared. Additional floral traits might be related to selfing, such as zygomorphy (bilateral symmetry): it is thought to lead to more effective pollen transfer between individuals, and make autogamous pollination more difficult (Joly & Schoen, 2021), so it seems likely that it occurs less often in selfing plants.

Like selfing species, many dioecious species have small flowers (Vamosi et al., 2003), but the reasons behind this association should be different because dioecious species cannot self-fertilize. Theory based on resource allocation predicts that small flowers resulting from less investment into pollinator attraction could favor the evolution of dioecy (Charnov et al., 1976). Indeed, non-attractive flowers pollinated by wind have been thought to be associated with dioecy for this reason. However this theory falls short in tropical rainforests, where many dioecious species are found but pollination by wind is rare (Bawa & Opler, 1975). It has also been proposed that the type of pollinator might influence the evolution of dioecy, but again the predictions are contrasting (see Table 1). Strikingly, monoecy and its associations have been much less studied. Monoecy is often not considered in its own right, but instead as a form of hermaphroditism alongside monocliny (e.g. Maynard Smith, 1978; Charlesworth & Charlesworth, 1978), or as a moderate form of unisexuality (but see for example Bawa & Beach, 1981).

The many mechanisms that have been proposed to influence the degree of outcrossing and how it is achieved (Table 1) indicate that there's no single optimal mode of reproduction (cf Anderson et al., 2023). Instead, it may be that the different trait combinations found in nature are the result of tradeoffs. This is probably the case for the correlation between outcrossing and lifespan, which involves a tradeoff between the benefits of outcrossing and the need for reproductive assurance. Likewise, efficient pollen transfer between individuals might not always be possible with monoclinous flowers and would thus result in dioecy, despite its disadvantages. Reproductive strategies (or mating strategies; Barrett, 2003), i.e. trait combinations that have repeatedly arisen across angiosperms, could result from the outcome of these tradeoffs. They are akin to the plant ecological strategies that have been amply described using vegetative traits (Grime, 1974; Westoby, 1998): there are tradeoffs between the speed of growth and resistance to stress, or between the quantity and the quality (mass) of seeds. These tradeoffs determine community composition with respect to the levels of stress, disturbance and competition the community experiences.

Inspired by this work, we ask whether the plant traits, and in particular floral traits, can be grouped to inform us about the possible reproductive strategies in plants. While size is often found as the main source of variation in plants (Díaz et al., 2016), several studies have highlighted that reproductive traits play an important role in explaining plant diversity (Salguero-Gómez et al., 2016; E-Vojtkó et al., 2022). Our hypothesis is that traits related to plant reproduction, notably including floral traits, account for considerable variation that is not distributed randomly at the angiosperm scale. However, due to the large number of observed patterns and sometimes contrasting mechanisms (Table 1), how floral traits vary with mating and sexual systems to form reproductive strategies is currently not clear. In particular, given the well-established association of outcrossing with lifespan and size, we are left wondering if additional correlations are simply a byproduct of this relationship. For instance, trees, due to their larger size, can invest more resources in seed dispersal, and more often use animals for dispersal than small species for which dispersal is mostly unassisted (Thomson et al., 2018). Similarly, flower characteristics might be different between trees and herbs, as suggested by the observation that zygomorphy is characteristic of several large, mainly herbaceous families such as the Orchidaceae, Gesneriaceae and Lamiaceae, although this has not explicitly been tested to our knowledge. Dioecy, which, as any outcrossing mechanism, is predominantly found among trees, could be statistically correlated to other features of trees by coincidence, and without any direct link with floral and dispersal traits.

To disentangle covariation in sexual, mating, floral, and other life-history traits, they must be studied together. This will help uncover what traits are most closely associated with outcrossing itself, as well as with the different ways to promote outcrossing. In this study we compile a dataset of 21 traits related to or associated with reproduction for 361 species sampled from across the angiosperm tree of life. We use these data to answer the question: what role do sexual system, flower morphology and pollination mode play in shaping angiosperm reproductive strategies? We build reproductive trait spaces to (1) determine the extent to which flower and pollination traits co-vary at the angiosperm level, (2) explore how mating and sexual systems are distributed across the main axes of variation and (3) establish whether major reproductive strategies can be characterized among flowering plants.

Materials and Methods

Data collection

We collated trait data for angiosperm species using the PROTEUS collaborative database (Sauquet, 2019). Our aim was to obtain a representative sample of the angiosperm diversity. We started with species from the angiosperm-wide dataset of López-Martínez et al. (2023) for which reproductive information (e.g., outcrossing rates, self-compatibility, dioecy) was available. Then, we expanded the species sampling by adding at least one species from each family with more than 100 species. We added more species for the most species-rich families (e.g., Asteraceae, Orchidaceae), choosing species that represented the main clades of these large families to best represent their diversity. This process led to an initial set of 363 species.

We selected a list of traits based on prior knowledge of how reproduction-related and associated traits influence evolutionary success (Helmstetter et al., 2023; Anderson et al., 2023). These traits were selected primarily to encompass the main aspects of angiosperm reproduction and included those related to mating system, sexual system, floral morphology (flower sex, ovary position, flower colour, flower size, flower symmetry), dispersal distance/mode and pollination mode. We also included several vegetative traits related to growth form and lifespan, which can also be related to reproduction. For each trait, detailed scoring instructions were followed; for traits already in PROTEUS, we used the instructions from Sauquet et al. (2017) and Schönenberger et al. (2020), whereas for newly added traits, we compiled instructions (Appendix S1) based on previously available guidelines (Perez-Harguindeguy et al., 2013; Cardoso et al., 2018). Seed mass was added outside PROTEUS as the species mean according to the Seed Information Database (SER et al., 2023).

To compare our results with those derived from classical functional traits, we also analysed a data set of six plant traits (leaf area, leaf mass per area, leaf nitrogen per mass, diaspore mass, stem specific density and plant height) for $> 45{,}000$ species (Díaz et al., 2016; Díaz et al., 2022).

Trait encoding

To facilitate downstream analyses, we modified the initial trait encoding to create a tractable and interpretable set of traits (Table S1). For qualitative traits, we reduced the number of states to between two and four for comparisons to be informative. In some cases we split an initially complex trait into multiple different ones for easier interpretation of results. For example, habit

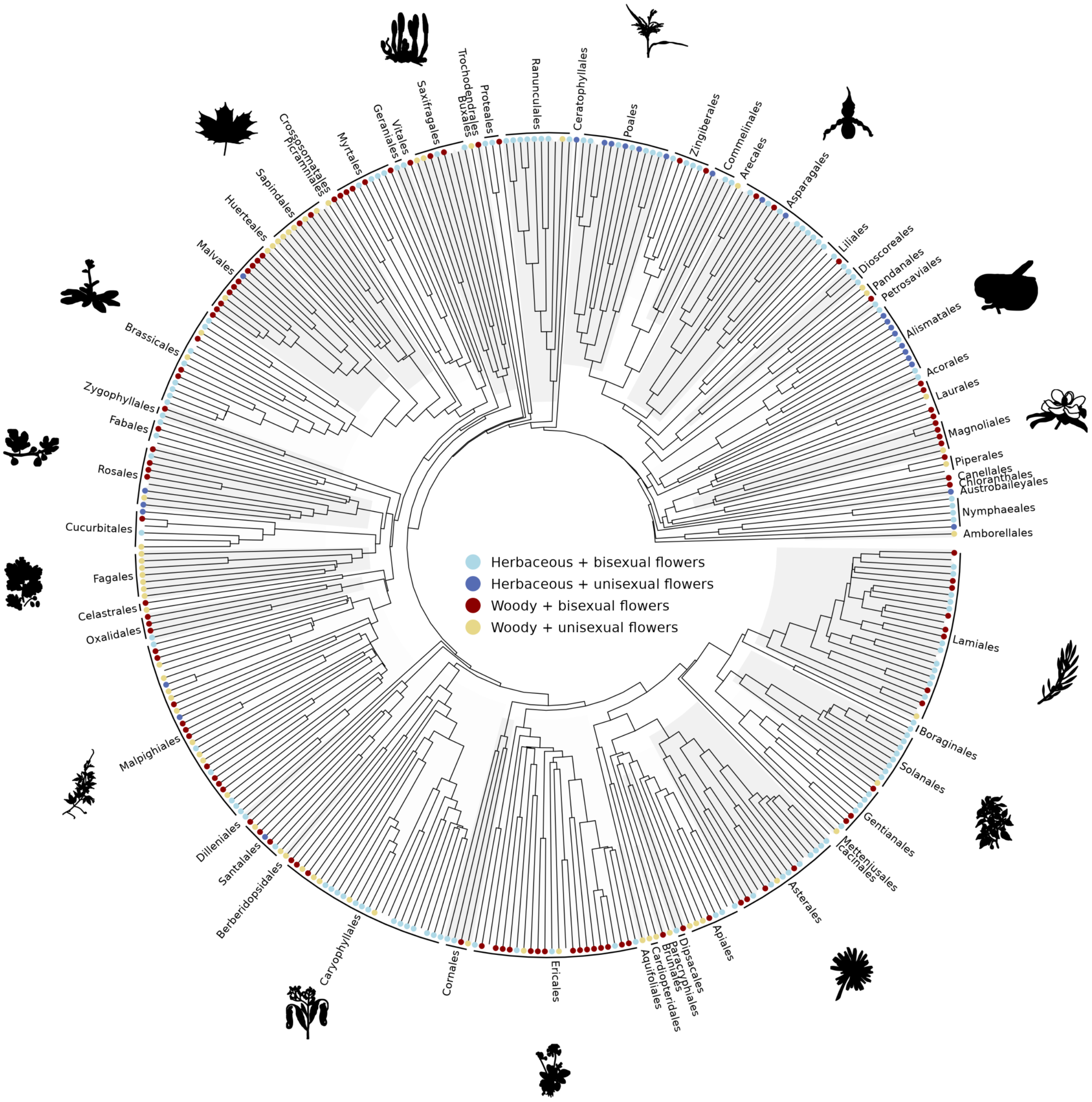

Figure 1: Phylogenetic tree representing the 361 species used in our analyses. Tips are labelled with coloured circles indicating the combination of woodiness and flower sex each species possesses. Species without data or those that are polymorphic for either trait are left blank. Orders that are represented in our set of species are highlighted around the outside of the tree alongside a selection of species' silhouettes from phylopic.org.

was recoded into three binary traits: woodiness, climbing and aquatic. Similarly, the original sexual system (including monocliny, dioecy, monoecy, gynodioecy, andromonoecy, etc.) was split into two binary traits: (1) flower sex coded as unisexual vs bisexual and (2) sexual system, coded as monomorphic (including monocliny, monoecy, andromonoecy and gynomonoecy) vs dimorphic (including dioecy, androdioecy and gynodioecy). For quantitative traits, if several values were available for a species/trait combination (either several measurements or indication of minimum and maximum values), we used their mean. The outcrossing rate was transformed into a qualitative trait “mating” using three bins: selfing (< 0.2), mixed mating ($0.2 - 0.8$) and outcrossing (> 0.8). This allowed us to combine species with a quantitative estimate of outcrossing rate with those for which only a qualitative classification was available (phenotypic mating system, self-incompatibility and dioecy, see Table S1).

We encoded the qualitative traits in two ways to facilitate different downstream analyses. The first had one variable per trait with as many values as there are states in the trait, plus separate values for cases in which the trait was polymorphic for a species (e.g. the trait woodiness has the states: woody, herbaceous, woody_herbaceous). We refer to this encoding as the “original” data set. In the second, qualitative traits were encoded using a one-hot approach, where each category of a trait is treated as a distinct binary variable (e.g. woodiness is split into two variables, each with two states: (1) woody vs. non-woody, (2) herbaceous vs. non-herbaceous). While one-hot encoding may introduce some redundancy (e.g., most species that are herbaceous are not woody and vice-versa), it is an alternative way of dealing with polymorphic states while keeping the relations between values. For example, in the original encoding, a species that can be both woody and herbaceous is assigned to a separate category with no explicit relation to other woody and herbaceous species, while in the one-hot encoding, such a species is similar to both herbaceous and woody species.

For visualization purposes, we chose to divide species in five categories. Among species with bisexual flowers (monocliny), species were assigned according to their predominant mating system (selfing, mixed mating, and outcrossing). The two other categories concern species with unisexual flowers, among which we distinguish dioecious and monoecious species. The few species with both bisexual and unisexual flowers were considered monoclinous for this purpose, as usually, unisexual flowers are not found in all populations (e.g. in gynodioecy) or only represent a small fraction of the flowers. Species having both monoecious and dioecious populations were labeled according to their major sexual system, if this information was available, or not labeled. Again, this labeling was only used to aid the interpretation of the figures and data, and not in the multivariate analyses.

Filtering, transformations and missing data imputation

To limit the impact of missing data on our analyses, traits were removed if more than 50% of values were missing in the original data set. Likewise, species were removed if more than 50% of their traits were unknown. We log-transformed quantitative traits to conform better to normality expectations, except for fusion of ovaries that is coded as a proportion. We also centered and scaled these variables to limit potential biases caused by using traits with different units of measurement.

After filtering, many of the traits still contained missing data. We conducted imputation with 'missForest' R package (Stekhoven & Bühlmann, 2012) to determine how this affected distances between species. We followed the approach outlined in Debastiani et al. (2021). Briefly, a pairwise phylogenetic distance matrix (see below for how the phylogenetic tree was generated) containing all species was decomposed to a set of eigenvectors using the function *PVRdecomp()* from the 'PVR' R package (Santos, 2018). The first 10 eigenvectors were added to the trait data as additional, complete traits to conduct imputation of missing data with the *missForest()* function.

We then examined pairwise correlations between traits in our original data set using different approaches depending on the type of traits being compared. For qualitative vs qualitative trait comparisons we calculated Cramer's V using the *cramerV()* function in the R package 'rcompanion' (Mangiafico, 2025). For other comparisons we performed ANOVA (qualitative vs quantitative) or Pearson's correlation coefficient (quantitative vs quantitative). We then used hierarchical clustering to group traits together with the *hclustvar()* function from the R package 'ClustOfVar' (Chavent et al., 2017).

Trait spaces

To build trait spaces, we first calculated pairwise distance matrices among species using Gower's distance (Gower, 1971) with the function *daisy()* from R package 'cluster' (Maechler et al., 2022). Gower's distance was used because it can deal with missing data and mixed data types (e.g. qualitative and quantitative). We then performed principal coordinates analysis (PCoA), a dimensionality reduction approach used to summarize similarities in the data, on the resultant distance matrix. We used the *pcoa()* function of the R package 'ape' (Paradis & Schliep, 2019) to generate a set of orthogonal eigenvectors and their associated eigenvalues. For the one-hot data, we used the *wcmdscale()* function in the R package 'vegan' for the PCoA, and fitted the individual traits on the resulting trait space with the function *envfit()*. We also built an additional trait space using the vegetative traits in the Díaz et al. (2022) data set. To do so we first removed those species that had information for fewer than four of the six traits. This ensured distances could be calculated between all species pairs while increasing computational feasibility and accuracy of distance calculations. To compare these trait spaces we extracted the 159 species common to both datasets and re-built the two corresponding trait spaces using only these species.

We quantified the "quality" of dimensionality reduction of the resultant trait spaces using the method outlined in Mouillot et al. (2021). Briefly, the difference between the initial distance matrix and the distance matrix after dimensionality reduction using PCoA was examined. High-quality trait spaces are those in which a reduced number of PCoA dimensions accurately represents initial distances among species, thus indicating high redundancy among traits. Quality was quantified using the area under curve (AUC) metric relating the increase in quality with increasing number of retained PCoA axes. This approach also provides an indication for how many axes are sufficient to summarize the variation in the initial dataset.

PCoA is a linear dimensionality reduction approach that does not account for more complex non-linear patterns. Therefore we also used an alternative dimensionality reduction approach, Uniform Manifold Approximation and Projection (UMAP, McInnes et al., 2020), to visualise non-linear patterns in our data. UMAP is based on manifold learning techniques and allows the user to assess patterns at local and global scales simultaneously, depending on the size of the neighbourhood ('n_neighbours') chosen. We applied UMAP to our Gower's distance matrices calculated using the original data set, and used the default configuration. We set the number of components (dimensions) targeted to two and varied 'n_neighbours' (10, 25, 50, 100) to test the effect of changing this parameter on the distribution of species in the space.

Clustering

To help define reproductive strategies we assigned species to different groups using the partitioning around medoids (PAM) (Kaufman & Rousseeuw, 1990) clustering approach, as implemented in the 'cluster' R package (Maechler et al., 2022). This method takes a distance matrix as an input and is based on determining a set of medoids (points) that represent the structure of the data. Each species is assigned to a medoid, with the goal of minimizing the sum of the dissimilarities of each species to their closest medoid. PAM clustering was done using Gower's distance matrices for both original and one-hot encoded data sets.

The number of clusters (i.e. values of k) was initially selected using silhouette width. This metric ranges from -1 to +1, where high values indicate that a point is similar to its cluster and different from neighbouring clusters. However it can be difficult to objectively determine the appropriate number of clusters that should be used to summarise the data set. To tackle this subjectivity issue, we examined how cluster membership changed as values of k were changed using Sankey plots, a type of flow diagram. We then identified groups of species that consistently grouped together as k was increased from $k = 2$ to $k = 7$. We took the largest groups until the total number of species reached 80% of the species in our data and considered these as 'robust groups'.

Phylogenetic tree and simulated data sets

We built a phylogenetic tree among our species using V.PhyloMaker2 (Jin & Qian, 2022). We used the default 'GBOTB.extended.TPL' tree that was derived from a large phylogenetic tree of all seed plants (Smith & Brown, 2018) and built the tree using the default approach described as 'scenario 3' (Jin & Qian, 2022). Prior to building the tree we standardized genus and species epithets using the R package 'TNRS' (Boyle et al., 2013) and retrieved higher level taxonomy using 'TNRS' and another R package, 'taxize' (Chamberlain & Szöcs, 2013).

To determine how phylogeny influences trait space for our set of species and traits we simulated trait data using the phylogenetic tree of our species. To do so we first fitted trait evolution models to each trait in the original data set with missing data imputed. For quantitative traits we fitted Ornstein-Uhlenbeck (OU) models using the *fitContinuous()* function in the R package 'geiger' (Pennell et al., 2014) to estimate OU model parameters and root state values. For qualitative traits we fitted fixed-rate, continuous-time Markov (Mk) models using the *asr_mk_model()* function in 'castor' (Louca & Doebeli, 2018) to generate transition rate matrices and ancestral likelihoods for the root state. We allowed all transition rates to be different by using all-rates-different (ARD) models. We then used the estimated parameters and the phylogenetic tree to simulate new datasets with *rTraitCont* from the 'ape' R package (Paradis et al., 2004) and *sim.history* from 'phytools' (Revell, 2012). Traits were simulated independently and then combined into a single simulated dataset, from which we calculated distance matrices and ran PCoAs, as above.

Results

After recoding and filtering, the final data set consisted of 21 traits (Table S1) for 361 species and 13% missing data (Fig. S1). With representatives from 260 of 416 families, and 61 of 64 orders

(Fig. 1, Table S2; APGIV, 2016), our dataset included a broad range of angiosperm diversity. Imputing missing data only slightly changed Gower's distances between species (Fig. S2, Mantel statistic r = 0.87), and so would likely have little impact on the following results. Using one-hot encoding also had a minor effect on distances, which remained highly correlated (Mantel statistic r = 0.95). In the following we used the "original" and the "one-hot encoded" data; the imputed data were only used for comparisons among data sets and in the simulations to test for phylogenetic effects.

Reproductive trait space: quality and dimensions

The first two PCoA axes of our trait space explained 30 to 34% of the variation (Figs. 2a and 3a), depending on the data encoding used. To characterize this trait space, we first compared it to the one built with data for six traits classically used in plant functional ecology (Díaz et al., 2022) from 7968 species. The species in our dataset were scattered throughout the mainly vegetative trait space (Fig. S3a). Using a set of 159 species shared between the two datasets, we found that the species' distances based on the six (vegetative) traits from Díaz et al. (2022) were only weakly correlated with those based on the 21 traits in our study (Mantel statistic r = 0.285; Fig. S4).

Then, using the approach of Mouillot et al. (2021), we calculated statistics allowing comparison of our trait space to others. The AUC criterion, which indicates how well the first n axes summarize the total variation in the data set, indicated that to get a good representation of our trait space, we must keep more dimensions than for the data set derived from Díaz et al. (2022) (Fig. S3b). This was equally the case when comparing our results to those of the other trait spaces analyzed by Mouillot et al. (2021). This means that, in our data set, traits were weakly redundant and most of them contribute small but significant amounts of variation that cannot be reduced to variation in other, more structurally important traits. We did not see notable differences in the trait space quality analyses between our different data sets (original, imputed, one-hot; Fig. S5).

In order to test for phylogenetic inertia, we performed ancestral state reconstruction with the original dataset to produce rate matrices that were used to simulate new data sets where all traits evolved independently. As expected, distance matrices from these simulated data sets were not correlated to the real data sets (Mantel statistic r = -0.01) and maximum distances were greater when using real data (Fig. S2). When we ran PCoA on simulated data sets we found that the first three to four axes explained substantially less variation than in the real data sets (Fig. S6). Thus, at least the first three, perhaps four, PCoA axes from the analysis of our original data set are due

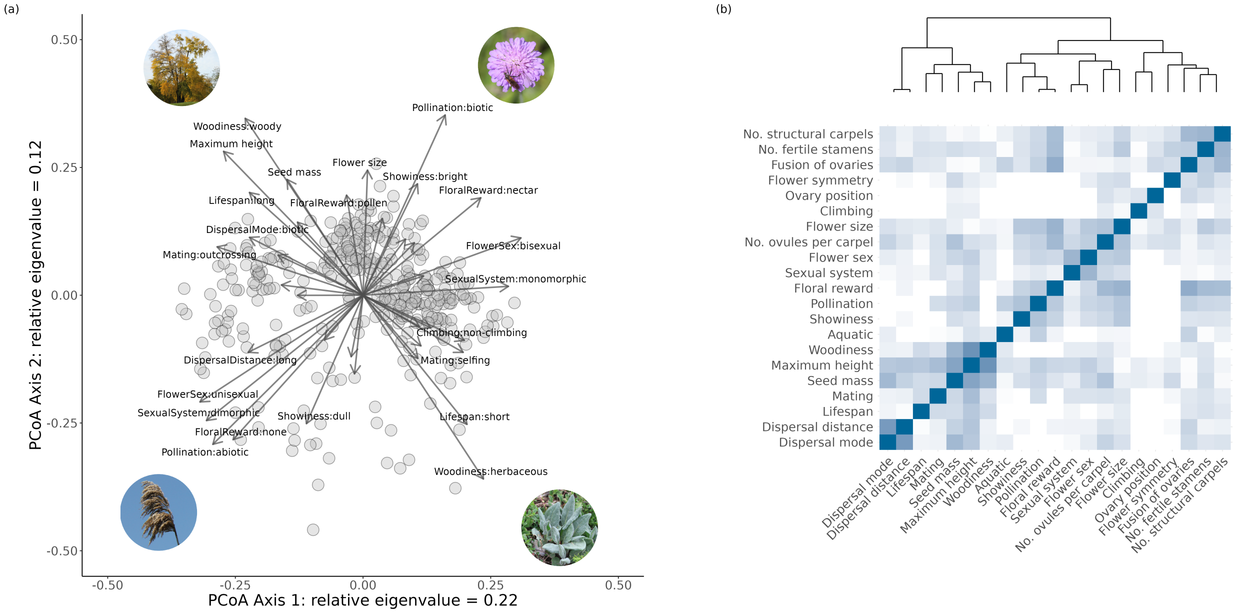

Figure 2: Multivariate analysis of plant traits. (a) The trait space obtained with a principal coordinates analysis (PCoA) performed on the one-hot encoded data set. The (linear) vectors of each trait in the first two dimensions are indicated as arrows and the species are indicated as circles. Images representing aspects of the trait space are shown in the four corners of the plot; photographs by A. J. Helmstetter. (b) A heat map showing the strength of the correlations between pairs of traits, where darker blues indicate higher correlation. The correlation coefficients were calculated using the original encoding of the data, so correlation coefficients are presented as absolute values as the direction of correlation is not meaningful for categorical data (see methods). The dendrogram is derived from hierarchical clustering of all traits.

to co-evolution of traits rather than neutral phylogenetic co-occurrence.

Trait covariance

The first four axes of the trait space were correlated with a combination of general life-history and floral traits (Table S3). Among the most important traits we found woodiness, lifespan, seed mass and plant height, and they were co-distributed along a diagonal in the 2D trait space defined by the first two PCoA axes (Fig. 2). This same diagonal also corresponded to mating system variation, from selfing associated with small size and short life span to outcrossing associated with woodiness, large size and long life span. Many flower and pollination-related traits contributed to variation that was orthogonal to this diagonal, including flower sex, floral reward, biotic vs. abiotic pollination, showiness and plant sexual system. The third PCoA axis, representing 9% of the variation, was mainly associated with dispersal (mode and distance), and the fourth axis, representing 7% of the variation, with ovary position and flower symmetry (Fig. S7).

We examined correlations among traits (Fig. 2b) and found two main groups reflecting patterns in the trait space; one containing vegetative traits, mating and dispersal, and another containing flower morphology, pollination and sexual system. Among the first group of traits, lifespan, height, seed mass, woodiness and mating were most strongly clustered, while dispersal traits were more weakly associated with the others. Among the floral traits, two groups could be identified, one mainly related to pollination and attraction (flower size, showiness, reward), and another more morphological group (carpel and stamen number, position and fusion of ovaries, flower symmetry). Flower sex and sexual system, although clearly morphological in nature, clustered with the pollination and attraction traits, not the other morphological traits.

Major reproductive strategies

Partitioning Around Medoids (PAM) clustering (Figs. 3 & S8) of the species based on their trait-based distances pointed to the existence of two major groups (light green and dark green points in Fig. 3a). These were well separated in the first two dimensions of the trait space, and can be predominantly characterized by species with bisexual flowers vs species with unisexual flowers. When the number of clusters was increased to three, the cluster of unisexual species remained (Squares in Fig. 3) while the cluster of species bisexual flowers was split into a herbaceous (circles) and a woody (diamonds) group (Figs. 3 & S9). Such a structure in three major groups was also revealed using UMAP (Fig. 3b; Fig. S10), which is based on an alternative decomposition approach

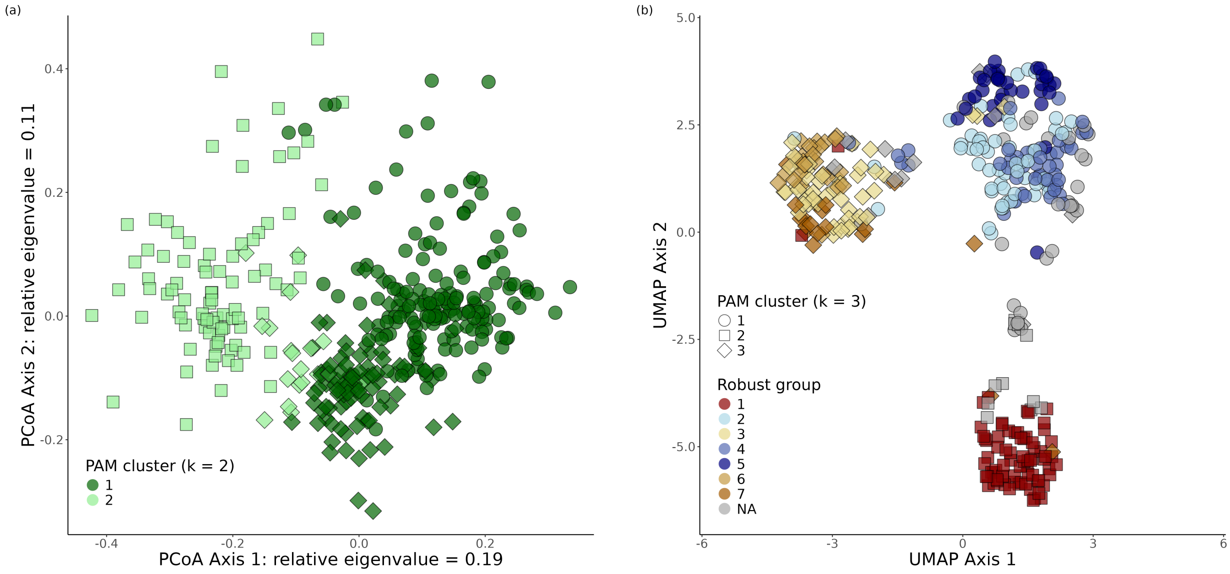

Figure 3: Trait spaces and clustering of species. (a) the position of species on the first two axes of a principal coordinates analysis (PCoA) on the original data set. Points are coloured by cluster membership derived from clustering using the partitioning around medoids (PAM) method when $k = 2$ (number of clusters). (b) the distribution of species along the first two axes of a UMAP (uniform manifold approximation) analysis with a neighbourhood size of 10, showing final-scale structure in the data. Points are coloured by robust group (see Figure S12 for further details). Point shape in both panels indicates their PAM cluster assignment when $k = 3$. Circles are mostly herbaceous species with bisexual flowers, squares are species with unisexual flowers and diamonds are woody species with bisexual flowers.

that allows the visualisation of non-linear and local patterns.

We sequentially increased the number of PAM clusters up to seven (Fig. S8) and tracked whether groups of species stayed together in the clusters ("robust groups") or not (Fig. S11). The species with unisexual flowers remained a markedly stable group (Fig. S12d), especially the woody dioecious species; the unisexual species that did not remain in this group were mostly monoecious and herbaceous. The species in the bisexual clusters were further split into three robust groups each: among the woody species, one group with smaller, rather dull flowers stands out (Fig. S12c,j), while among the herbaceous species, a distinct robust group with zygomorphic flowers appears (Fig. S12h). Thus, traits such as zygomorphy, flower size and dispersal mode, are characters that play different roles depending on the context of other traits (mainly woodiness). Remarkably, mating system was not clearly associated with one of the clusters, even among herbaceous species where most variation in this trait is found. A total of 55 species did not group with other species throughout the process and thus were not assigned to robust groups. Many of these were found in distinct, sparsely populated areas of the trait spaces - in the top centre of the PCoA plot (Fig. 3a) and in the middle of the UMAP plot (Fig. 3b). In general, these were long-lived, herbaceous species with small, dull, abiotically-pollinated flowers, many of which were aquatic.

Mating and sexual systems

In all analyses, variation in reproductive modes was encoded by three separate traits (mating, flower sex, sexual system; Table S1). Thus, for interpretation we plotted the original sexual systems (dioecy, monoecy, monocliny) and the mating systems of monoclinous spaces back on the trait space. This allowed us to visually assess that dioecious species occupied an area in the trait space that was largely distinct from the area occupied by the monoclinous species (Fig. 4a). Monoecious species were found between these two sets and overlapped substantially with both monoclinous and dioecious species, occupying a large area. Among the monoclinous species, the variation in mating system was associated with a gradual shift in the associated traits. We found that predominantly outcrossing and selfing species shared a large overlapping area in the trait space, despite being at opposite ends of a major axis of variation.

There was a gradual increase in average size from selfing to outcrossing monoclinous species, whereas dioecy and monoecy seemed more restricted to large-stature plants (Fig. 4b). Similarly, while monoclinous selfing species had on average smaller flowers than outcrossers, average flower size was even smaller among dioecious and monoecious species (Fig. 4c; see Fig. S13 for all quantitative traits). The associated categorical traits (Fig. 4d-h) confirmed the trait associations visible in Fig. 2. Unisexual flowers were almost always actinomorphic, while there was no notable difference in flower symmetry among the monoclinous species with different mating systems. Abiotic pollination was found more frequently among species with unisexual flowers, as was the absence of a floral reward. However, purely abiotic pollination was not the major mode of pollination among dioecious species, and its frequency was higher (about 45%) among monoecious species.

Discussion

We here present an angiosperm-scale synthetic analysis of the plant traits associated with mating and sexual system variation. We compiled information on 21 traits, combining classical life-history traits, with those relating to flowers, pollination and reproductive modes. Our study is based on 361 species, a small but representative sample of the angiosperm diversity, with species from more than 50% of the families and nearly all orders. Our multivariate analyses indicate that the different traits of these species are only moderately correlated and encapsulate substantially more diversity than vegetative traits alone.

Structure of the reproductive trait space

Sexual and mating systems had markedly different distributions in the trait space. Mating system variation was mainly correlated with variation in lifespan and size, as has been documented previously (e.g. Petit & Hampe, 2006; Salguero-Gómez et al., 2016). Sexual system variation, on the contrary, was linked to variation in floral and pollination traits. This pattern seems to be mainly driven by the contrast between dioecious and monoclinous species: among the species that are mainly outcrossing the dioecious species are those that have smaller, less rewarding flowers. Here we confirm the patterns that have been described before by naturalists (e.g. Bawa, 1980; Renner & Ricklefs, 1995) using a multi-trait analysis encompassing both sexual systems and mating systems. While it is important to note that we only describe correlations, not causal relationships (Table 1), between the modes of reproduction and their associated traits, a multi-trait analysis can nevertheless indicate more (or less) plausible causes by identifying which traits co-occur most often.

Along the lifespan-size axis, mating systems largely overlapped. Thus, outcrossing and selfing species cannot easily be distinguished, and floral traits were only weakly discriminative at this scale. Selfing species tend to have smaller flowers than mixed-mating or outcrossing species, consistent with the observation that the 'selfing syndrome' often involves a reduction in corolla size (Sicard & Lenhard, 2011). However, the fraction of species with zygomorphic flowers, often interpreted as being the sign of high-precision pollination favoring outcrossing, was similar among selfing, outcrossing and mixed-mating species (Fig 4). Indeed, a transition to predominant selfing can arise in very different pollination contexts, e.g., wind-pollinated grasses (Burgarella et al., 2023), small-flowered herbs with generalist pollinators (Sicard et al., 2011), or in groups where specialist pollination syndromes have evolved (Rose & Sytsma, 2021). Furthermore, selfing is associated with higher extinction rates (cf Goldberg et al., 2010), although this might depend on associated traits (Zenil-Ferguson et al., 2019; Helmstetter et al., 2023; Anderson et al., 2023). This would limit the scope for co-evolution of multiple traits, which could explain why floral traits associated to selfing are specific to each clade.

Traits associated with sexual systems have been described at the level of angiosperms (Renner & Ricklefs, 1995; Vamosi et al., 2003) or regional floras, including species from many families (Bawa, 1980). However, most studies contrasted dioecy with hermaphroditism, often either excluding monoecy or considering it as a particular case of hermaphroditism as, indeed, a monoecious individual can self-pollinate in the absence of an incompatibility mechanism (Bertin, 1993). Here we found that the traits of monoecious species were intermediate between those of monoclinous and dioecious species (Fig. 4), consistent with the idea that monoecy presents a lesser degree of sexual specialization than dioecy, and might serve as an evolutionary intermediate between dioecy and monocliny (Renner & Ricklefs, 1995). However, there was extensive variation in the traits associated with monoecious species (even though we sampled more dioecious than monoecious species), which could be related to the variation in the spatial organisation of unisexual flowers. For example, some species have inflorescences with both female and male flowers (e.g. *Hevea brasiliensis*, *Arum maculatum*) forming functionally bisexual floral units, while in others the female and male flowers are clearly separated (e.g. *Zea mays*). Monoecy has not been as intensively studied as dioecy (cf Cronk, 2022) but clearly warrants further consideration in its own right. Investigations into the drivers behind its evolution (e.g. resource allocation, sexual selection and interference (Willson, 1979; Bawa & Beach, 1981)) and the spatial (and even temporal) organisation of flowers more generally are ripe avenues for future research.

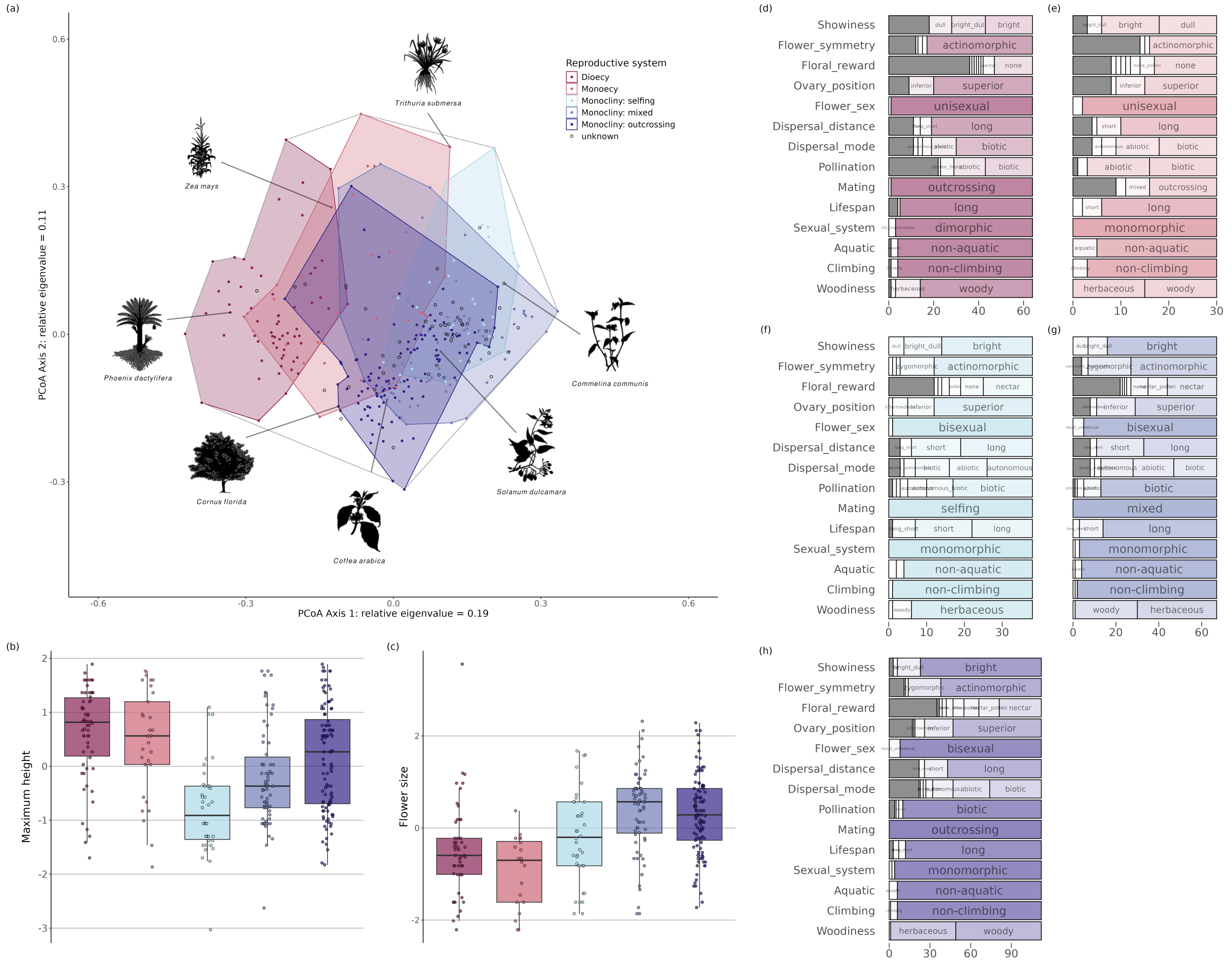

Figure 4: Sexual and mating systems in the angiosperm reproductive trait space. Panel (a) shows the position of 361 angiosperm species on the first two axes of a principal coordinates analysis (PCoA) on the original data set. Colours indicate the reproductive mode reduced to five categories for visualization. Species silhouettes, used to illustrate the diversity of species, are taken from phylopic.org. Boxplots show the distribution (after log transformation and scaling) of values for two traits per cluster: (b) maximum vertical height and (c) flower size. Points represent the values of species within each cluster. The stacked barplots (panels (d-h)) show the frequency of states for 14 categorical traits for each of the five reproductive modes: (d) dioecy, (e) monoecy, (f) monoclinous selfers, (g) monoclinous mixed mating species and (h) monoclinous outcrossers. Sections representing states with high frequencies are labelled and the dark grey sections correspond to missing data.

Traits differ between modes of outcrossing

In this study, monocliny and dioecy appear as two contrasting approaches to realize outcrossing. Although both occurred mainly among long-lived, large-stature plants, the floral traits associated with each of them show these approaches are clearly different. Is this difference driven by the way the species are pollinated? Fewer than half of the dioecious species for which pollination mode could be assessed were wind-pollinated, and most experienced at least some biotic pollination. It should furthermore be taken into account that pollination modes are often inferred from floral traits instead of pollination assays, and thus might not be correct. For example, although palms (a family with a high incidence of dioecy; Nadot et al., 2016) had long been thought to be mainly wind-pollinated based on their often rudimentary flowers, current knowledge indicates that a large majority are pollinated by insects (Barfod et al., 2011; Henderson, 2024). So, the correlation of dioecy with small, unrewarding and rather inconspicuous flowers does not seem to be a side-effect of wind pollination, as it affects biotically-pollinated species alike. Rather, our results indicate that dioecy is more likely to evolve in small-flowered species, possibly because there are fewer resources to be shared between the female and male functions of those flowers (cf Charnov et al., 1976). Monoecious species seem to resemble the dioecious species in these aspects, which suggests that it is flower sex (uni- vs. bisexual) rather than sexual system (mono- vs. dimorphic) that drives these correlations.

We found that dispersal traits were somewhat correlated with height, lifespan and thus mating, but not particularly with sexual system. This is in agreement with previously identified patterns of dispersal mode and plant size (Thomson et al., 2018), but does not lend support to hypotheses that link dispersal to sexual system (Table 1). The observation that dioecious species more often have fleshy, animal-dispersed fruits could thus be related to the correlation between plant size and biotic dispersal. So while allocation to floral structures might influence the evolution of sexual systems, allocation to seed dispersal may not. Indeed, as the primary male (pollen) and female (seed and fruit) contributions to reproduction do not occur simultaneously in plants, resource overlap is limited, which is thought not to favor the evolution of dioecy (Charnov et al., 1976).

This multi-trait view of the distribution of sexual and mating systems among angiosperms stresses that the evolution of dioecy results from two mechanisms, i.e. it promotes outcrossing, while small floral investment allows to optimize female and male fitness separately (cf Thomson & Brunet, 1990; Bawa, 1980; Charlesworth & Charlesworth, 1987; Käfer et al., 2017). Early modelling work has already shown that selfing avoidance is not enough to explain why dioecy evolves, as unisexuality comes with a fitness cost that can be overcome by resource reallocation (Charlesworth & Charlesworth, 1978). A recently-developed model includes both resource allocation and the quality of outbred offspring in the female and male fitness gain curves, demonstrating how allocation and outcrossing can jointly drive the transition towards separate sexes (Lesaffre et al., 2024).

Of course, much diversity remains unaccounted for, as is reflected by the fact that the first two axes of the trait space had relatively low eigenvalues compared to other datasets (Mouillot et al., 2021). This is partly due to traits that vary mostly in a subset of species, but not consistently among the whole set of species (e.g. zygomorphy, dispersal mode; Fig. S12). Furthermore, there are many exceptions to general patterns. Among the most striking ones is *Rafflesia*, the genus with the largest known flowers, which is dioecious. This species obviously also has some other traits making it difficult to compare to other plants - classifying it as herbaceous or woody would not reflect its unique, almost completely endoparasitic habit.

Reproductive strategies of flowering plants

Just as plants have “ecological strategies” resulting from tradeoffs involved in competition, stress-tolerance and dispersal (Grime, 1974; Westoby, 1998), they have “reproductive strategies” that determine how much they rely on outcrossing and how this is achieved. This term has been previously used to encompass life-history strategies that include diverse aspects of seed production and its contribution to population growth and persistence (Salguero-Gómez et al., 2016; Salguero-Gómez, 2017). We argue that these strategies should include floral and pollination traits: we have shown they account for substantial additional variation, and this variation could influence reproductive success and thus the composition of plant communities. On short timescales, pollination directly influences an individual’s fitness through the number of seeds produced (e.g., depending on pollen limitation; Ashman et al., 2004). Also, pollination can influence seed quality (if affected by inbreeding depression; Crnokrak and Roff, 1999), and could thus affect plants’ abilities to compete and cope with stress (Craig & Mertz, 1994; Cheptou et al., 2000; Petrone Mendoza et al., 2018). On longer timescales, pollination and reproduction affect genetic diversity and adaptive capacity, and thus most likely play an important role in long-term population and species survival (Burgarella & Glémin, 2017; Anderson et al., 2023). Hence, pollination could influence species’ ecological success, or maybe even its ecological strategy, although this remains to be investigated. Our framework could be used, for instance, to assess how floral and pollination traits vary in the context of plant communities.

Of course, other traits could contribute to the reproductive strategies of plants (Barrett, 2002; Barrett, 2003). For example, dichogamy, a difference in the timing of fertility of the pistils and stamens, could also lead to more effective pollen transfer between individuals. It has several variants (Bertin & Newman, 1993), including heterodichogamy, in which some individuals of a population are protogynous and others protandrous (Renner, 2001). Bertin and Newman (1993) rejected the hypothesis that dichogamy primarily evolved to avoid self-fertilization, and found intriguing differences in the traits associated with the several types of dichogamy. Similar patterns might exist for herkogamy and distyly. We suggest that these morphologies reflect a certain separation of the sexual functions, similar to the sexual systems.

In order to be able to integrate additional traits into the reproductive strategies we have identified, we propose a conceptual reproductive trait space with three dimensions: lifespan, floral investment and sexual separation (Fig. 5). While lifespan is not strictly a reproductive trait we use it here because it is an easily measurable trait that summarizes how much a species relies on outcrossing: short-lived species can be either selfing or outcrossing, while long-lived species are almost always outcrossing. Floral investment is the allocation of resources into the production of a flower, with small, non-attractive and non-rewarding flowers on one end and large, attractive, nectar-producing flowers on the other. Sexual separation encompasses the sexual systems, from monocliny through monoecy to dioecy. The main strategies we characterized in this study form a 2D triangle in this 3D space, with (1) monoclinous, small-flowered annuals, (2) monoclinous, large-flowered trees and (3) dioecious small-flowered trees at the vertices. As these are the most common strategies, most species will fall close to this triangle. Yet, this framework also incorporates less frequent strategies that occur at greater distances from this plane, such as wind pollinated herbs or showy annuals.

In defining dimensions this way, we allow the framework to be expanded to traits we have not studied. For example, dichogamy and herkogamy could be situated somewhere on the sexual separation axis; would their associated traits differ markedly from, say, those of monoecious species? Other traits could include floral longevity (Stephens et al., 2024) and 3D structure (Van der Niet et al., 2010), as further measures of floral investment. Finally, this framework could be compared to previously proposed spectra of angiosperm trait variation, such as the fast-slow continuum (Salguero-Gómez et al., 2016) and the flower economics spectrum (Roddy et al., 2021), that rely on measurements of reproductive output and floral investment. This would help uncover the extent

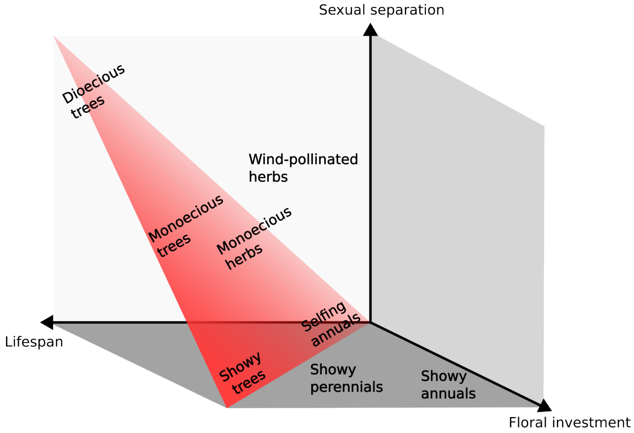

Figure 5: Conceptual representation of angiosperm reproductive strategies, defined by a 3D space with the most common strategies depicted on a 2D triangle. One main axis is lifespan, mainly related to outcrossing in the reproductive trait space: the longer the lifespan, the more a species will be outcrossing. The sexual separation axis includes the sexual systems included in our analysis (from monocliny to dioecy) but potentially also other ways of separating sexual functions, like dichogamy. The floral investment axis includes flower size and floral reward, and possibly flower longevity.

to which morphological variation correlates with quantitative variables such as net reproductive success and flower mass.

Integrating floral and mating traits in the study of functional diversity

It is increasingly recognized that floral traits should be considered when characterizing functional diversity in angiosperms (E-Vojtkó et al., 2020). Here we aimed to represent angiosperm diversity by working with an original dataset chosen to represent all major angiosperm clades. This is complementary to the approach taken in other studies dealing with specific floras or datasets. E-Vojtkó et al. (2022) studied two datasets of European species (central Europe and Alps), and found that floral traits vary largely independently of vegetative traits. Despite their exclusion of trees and grasses, and their focus on a different set of traits (notably not including sexual system), the trait spaces they obtain are rather similar to our own. Lanuza et al. (2023) analyzed plant reproductive strategies in light of interactions with pollinators. Wind-pollinated species were therefore excluded, and tree species were generally underrepresented. Despite this, they also found that variation in selfing and outcrossing was only weakly correlated with variation in flower traits. The relative importance of floral traits in their trait space was higher than in our study, which could be due to the larger number of floral traits they studied (including style length, flower number per plant, quantity of nectar and pollen).

A challenge for the inclusion of floral traits in large-scale evolutionary and ecological studies seems to be their lack of availability in databases. The largest plant database today, TRY, contains limited data about flowers as compared to vegetative and seed traits (Kattge et al., 2020). Many studies and floras contain such data, but collecting them requires botanical knowledge to correctly interpret the complex terminology. Although floras are increasingly available online, they still represent a small fraction of known plant species, with tropical floras typically being underrepresented (cf Römer et al., 2023). We argue that publicly available data with well-described trait standards are the most convenient way to ensure that datasets can be combined and extended.

The inclusion of floral and pollination-related traits in the description of the plant functional diversity is necessary to improve our understanding of ecosystem functioning. Indeed, vegetative functional diversity has proven instrumental in testing theories of diversity (e.g. Lamanna et al., 2014; Schuldt et al., 2019). However, interactions with pollinators have also been identified as playing a role in the maintenance of diversity in plant communities (Wei et al., 2021) and the decrease of pollinator abundance can destabilize the mechanisms promoting species coexistence (Johnson et al., 2022). As we are only starting to standardize floral trait data and make them available, we still have a very incomplete picture about how they influence pollinator diversity and abundance, and the subsequent effects on plant community composition. However, such understanding is urgently needed as pollinators are declining rapidly in many agricultural and semi-natural landscapes, and this angiosperm-wide study provides a framework for future research (Artamendi et al., 2025).

Acknowledgments: This research is supported by the Fondation pour la Recherche sur la Biodiversité (FRB) through the CESAB project 'DiveRS'; the FRB, Office Français de la Biodiversité and Ministère de Transition Ecologique project 'IndicatoRS'; and by the ANR project 'FloweRS' (ANR-23-CE02-0003). We thank the DiveRS members Sally Otto and Denis Roze for constructive discussions and feedback on the manuscript. We thank Nicolas Casajus, Nicolas Loiseau and Marion Chartier for advice on data analyses, Solenn Sarton for contributing data, and Maud Calmet for the organisation of the workshops of the DiveRS group. We thank the University of Vienna for hosting the PROTEUS database and eFLOWER server.

Competing interests: The authors declare no competing interests.

Authorship contributions: SG and JK initiated the project; BA, SB, CB, HdB, MD, SG, JK, MM, SPO, JP, DR, HS, DS, JS, MVM, RZF and AH conceived the project; MvB, HS and JS provided data management; MvB, CB, JC, PAD, SG, JK, MM, DSB, HS and JS entered data; AH, SG, JK and HS performed analyses; AH visualized results; AH, JK and SG drafted the first version of the manuscript; all authors contributed to and approved of the final version.

Data availability: The data set we compiled is available on the PROTEUS/eFLOWER website: https://eflower.myspecies.info/publications. Data and all scripts are available at the following github repository: https://github.com/divers-it/rs-traitspace.

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