


# The neglected importance of floral traits in trait-based plant community assembly

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## Abstract

**Aims:** Floral traits are frequently studied in population biology and evolutionary ecology but are rarely considered in functional trait-based studies focusing on the assembly of communities. We address this gap in trait-based community assembly by synthesizing the existing literature on processes driving floral and pollination-related trait patterns at community scales. We highlight limitations of the field due to lack of data and suggest potential directions of future research.

**Methods:** We conducted a systematic literature search collating studies that investigated floral traits in the context of plant community assembly, which allowed us to synthesize the current state of the art and point out important gaps in our knowledge.

**Conclusions:** The literature review shows that including pollination-related traits in community assembly studies can shed new light on species coexistence patterns not accounted for by other types of traits. The synthesis presented here shows the diversity of approaches and existing techniques which can generate a step forward in this open field of research. What currently seems to hinder comprehensive analyses of floral traits at community levels is the lack of data, particularly in existing large repositories for traits worldwide, as well as a gap in linking modern coexistence theory with floral traits.

## KEYWORDS

community assembly, competition, facilitation, functional diversity, plant–pollinator interactions, reproductive success, trophic interactions

## 1 | INTRODUCTION

Understanding the rules of community assembly and species coexistence is one of the oldest and most fundamental aims of ecological research (Götzenberger et al., 2012). To date, numerous potential ecological processes have been identified as drivers of species sorting into communities. Among these, abiotic conditions and biotic interactions, as well as dispersal, are generally agreed to have an important role, beside stochastic events (Cornwell

and Ackerly, 2009). Abiotic and biotic processes act as a series of filters, selecting species from a regional species pool into local communities (Zobel, 2016) based on their functional characteristics which make them suitable for the particular habitat (Díaz et al., 1998). Such characteristics, i.e. “functional traits,” are defined as “any morphological, physiological or phenological feature measurable at the individual level, which impacts fitness indirectly via its effects on growth, reproduction and survival” (Violle et al., 2007). Although, by definition, reproduction is one of the three

main pillars of fitness, some reproductive traits, and especially floral traits have only played a minor role in functional trait ecology in general, and in trait-based community assembly studies in particular.

Traits frequently used in functional ecology are principally those related to the leaf-height-seed (LHS) strategy scheme (Westoby, 1998). These traits are connected to growth and survival, i.e. canopy height determining competitive ability, seed mass affecting dispersal and establishment ability, and specific leaf area defining resource investment. Although these traits are easy to measure and are good proxies for crucial biological functions, they fail to provide information about some of the most important organs and structures involved in sexual reproduction. Floral traits, in this sense, provide a very useful and complementary tool for understanding various reproductive processes (e.g. Karron et al., 2012). Unfortunately, they are generally neglected in functional ecology research, which is also reflected by their absence from the most recent handbook of standardized protocols of plant traits (Pérez-Harguindeguy et al., 2013). However, we can expect that floral traits may vary in response to both biotic and abiotic drivers (as “response traits”), and affect ecosystem functioning (as “effect traits;” Lavorel and Garnier, 2002) through providing a connection to other trophic levels (Lavorel et al., 2013).

We use the term “floral traits” to refer to characteristics of the flower having a biological function and an ecological importance by affecting the fitness of the individual. We do not use the term “reproductive traits” to avoid confusion, since this generally includes seed and fruit characteristics, which we do not consider here. As flowers provide the setting for seed and fruit development that, when mature, replace the floral structures, there is also a temporal distinction between the two groups of traits in their general effect on plant fitness. These criteria help to distinguish floral traits (neglected in trait-based plant community studies) from traits that are frequently employed and for which data are widely available, e.g. seed size. Floral traits, in this sense, include traits involved in: (a) sexual reproduction ability (as opposed to vegetative reproduction); (b) cross-pollination vs self-fertilization potential; and (c) the physiology, morphology and phenology of flowers or inflorescences and the way they get pollinated (Klotz et al., 2002). Although the connection between fitness and floral traits might seem weak in the case of certain species or habitats, in general, during the sexual reproduction phase in the plant's life cycle, floral traits, such as flower morphology and flowering time, become crucial for maximizing reproductive output (Larson and Funk, 2016). In fact, flowering time can have a huge impact on the fitness of several types of species irrespective of their pollination type, as flowering during a time of high resource availability has been shown to possibly have a critical benefit for viable seed production (Craine et al., 2012). It is important to mention that not all species always rely on sexual reproduction and that the importance of vegetative propagation could be predominant for certain species and in certain habitat types (Klimešová et al., 2017). However, we hypothesize that a careful selection of floral traits will be relevant for the assembly of plant communities within several vegetation types.

The main goal of this synthesis is to link evidence from studies on community-scale pollination to current species coexistence and community assembly theory to better understand mechanisms driving floral trait patterns in diverse communities. We aim to review and synthesize the general trends in floral trait patterns and related processes, in order to support and direct future developments in this field. We carried out a systematic literature search to assess existing evidence on community assembly patterns of floral traits. We specifically incorporate studies that are explicitly focusing on the community scale in a wide sense, thus including both biogeographical and local-scale findings, but that do not focus on only a limited component of the whole community (i.e. species of a particular family, tribe, or genus occurring within a community). We also aim at demonstrating that floral traits are important determinants of community assembly and that they are a vital component of the ecological strategy of plants that has so far been mostly neglected in studying the assembly of diverse plant communities.

In the review, we first summarize the different types of methodological approaches that are generally used to assess plant and pollinator communities and their interactions. In this synthesis, we then turn our attention to the particular approaches that use floral traits at the plant community level to describe assembly patterns. Based on a literature review, we synthesize reported patterns and related processes, and discuss the relevance of scale, as we incorporate studies on both biogeographical and local scales. In the succeeding section, we point out the lack of available floral trait data in most current databases as an important hindrance in advancing their involvement in community assembly studies. Finally, we provide a concise list of future steps to overcome data limitations and suggestions for research.

## 2 | APPROACHES USED IN COMMUNITY-LEVEL POLLINATION ECOLOGY

The field of pollination ecology has a vast array of publications focusing on evolutionary processes, population dynamics and pollination mechanisms of single species or genera. However, few studies have dealt with pollination ecology on the community scale, where the main focus is shifted towards species coexistence patterns and assembly rules of interacting communities of plants and pollinators. It is important to note here that the field of pollination ecology has rarely applied the concept of community ecology on which much of vegetation ecology relies. In pollination ecology a clade of co-occurring taxa is often considered a community. In vegetation ecology, and particularly in community assembly studies, though, communities consist of all or the majority of species co-occurring at a specific site, regardless of phylogenetic relationships or other criteria. In some cases, pollination studies on a well-defined component of the whole plant community (e.g. only animal-pollinated species in network analysis) might also represent a meaningful community-level analysis. In the following sections, we briefly introduce the most common approaches of pollination ecology studies which consider

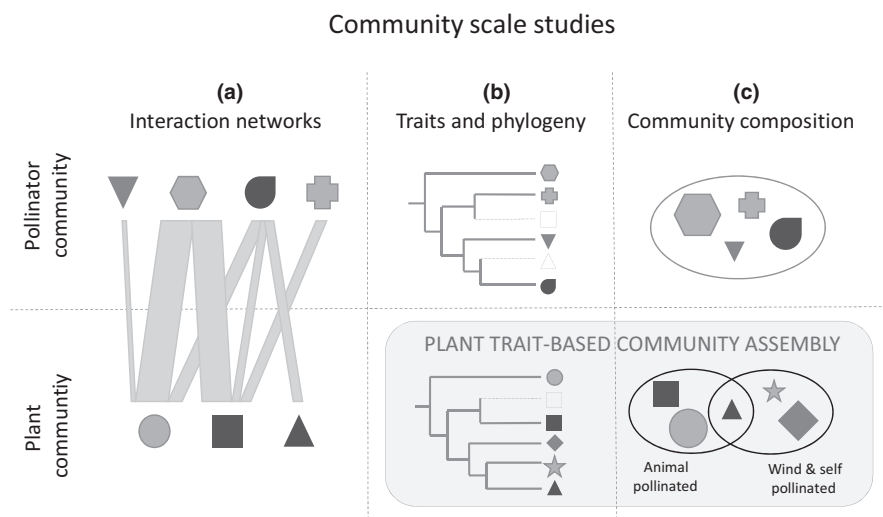
communities (i.e. assemblages of coexisting species in a specified location) as the ecological unit of their research (Figure 1, Table 1).

In recent years the number of pollination network studies increased dramatically (Figure 1, Table 1: “A;” e.g. Junker et al., 2013; Junker et al., 2015; Bennett et al., 2018a). The interaction networks between communities of plants and pollinators (reviewed by Vázquez et al., 2009 and Knight et al., 2018) offer a perfect study system for understanding mutualistic relationships between trophic levels (Blüthgen et al., 2007) and therefore are strongly constrained by both animal and plant traits (e.g. Junker et al., 2013; Chamberlain et al., 2014; Maglianesi et al., 2014; Schleuning et al., 2015). Interaction networks combined with functional traits (Figure 1, Table 1: “AB”) can provide a deeper understanding of plant–pollinator trait matching (Sazatornil et al., 2016) and the validity of using pollination syndromes, i.e. whether a certain set of plant traits predetermine the group of potential pollinators (Lázaro et al., 2008; Ollerton et al., 2009; Rosas-Guerrero et al., 2014). Evolutionary relationships might also have the potential to explain the structure of pollination networks. On the one hand, pollinators are known to show “clade-specialization,” a preference for more closely related plant species (Vamosi et al., 2014), which can be seen as sign of niche conservatism, i.e. closely related species share similar (pollination) niches due to shared evolutionary history (Losos, 2008). On the other hand, in certain plant–pollinator networks, phylogeny might be a weak predictor (Chamberlain et al., 2014).

In this rapidly developing field, new analytical tools have been proposed for approaches combining traits, phylogeny and networks (Ibanez, 2012; Ibanez et al., 2013; Rafferty and Ives, 2013; Bastazini et al., 2017; Kantsa et al., 2018; Laigle et al., 2018). Furthermore,

methods for comparing networks along environmental and resource gradients (Tinoco et al., 2017; Pellissier et al., 2018), as well as ones explaining non-random community assembly patterns based on network structure (Kemp et al., 2019), are advancing fast and have a strong potential to contribute to fully addressing the role of traits shaping species interactions and community structures (Figure 1, Table 1: “ABC”).

Floral characteristics are one of the most important diagnostic features used in classical taxonomy; thus the assumption of a connection between certain morphological patterns (i.e. number of petals, stamens etc.) and phylogeny is implicit in this study subject. However, such expected niche conservatism of floral traits along phylogenetic trees has been met with very few attempts to explore whether floral traits indeed adhere to conservatism, e.g. through estimating the phylogenetic signal of these traits. Moreover, trait conservatism has been addressed at the community scale, where the phylogeny of the co-occurring species is considered. Although these approaches could help to reveal evolutionary processes driving functional trait-based community assembly (Figure 1, Table 1: “B”), results on this topic are scarce and have hitherto been contradictory. For instance, flower colour had a strong phylogenetic signal among species of a temperate grassland (Binkenstein et al., 2013), but only a weak signal was found among species growing along an altitudinal gradient in the Himalayas (Shrestha et al., 2014). Junker et al. (2015) reported a phylogenetic signal for three out of eight different quantitative floral traits, in the most comprehensive study on the phylogenetic and functional assembly based on floral traits at the community scale to date. There is some evidence for phylogenetic clustering of floral traits in both small sets of closely related



**FIGURE 1** The most common approaches to study plant and pollinator communities. A, Pollination networks; B, phylogenetic signal of floral traits; C, species co-occurrence studies (abundance or frequency-based); and the combination of these: AB, trait matching in plants and pollinators and the testing of pollination syndromes; AC, pollination networks in plant communities taking into account the abundance and co-occurrence of species; BC, species coexistence patterns driven by floral traits and/or phylogenetic relationships (i.e. highlighted area, indicating the main focus of this synthesis). ABC, functional trait-based community assembly driven by trophic interactions. The different shades and shapes represent different functional trait values. The sizes of shapes are proportional to species abundances. In section B empty symbols with dashed branches represent species present in the habitat species pool but missing from local communities. Thus, approaches of section B generally work on the habitat species pool rather than on the plot level

**TABLE 1** Types of methodological approaches used for answering research questions on the importance of floral traits in the structuring of plant (and pollinator) communities, metrics, methodological tools within the R statistical environment (R Core Team, 2019) and examples from the literature. The lettering of approaches (A, B, C...) follows Figure 1

	Type of approach	Metrics	R packages	Examples
A	Visitation networks	Network structure and motifs: nestedness, connectivity, modularity	bipartite, bmotif	Bennett et al., (2018a)
B	Phylogenetic signal, evolution of traits	Indices of phylogenetic signal: Pagel's $\lambda$ , Blomberg's K	ape, phytools, phangorn, picante	Chamberlain et al., (2014), Reverté et al., (2016)
C	Community composition and diversity	Classical diversity indices: Shannon, Simpson	vegan	Bosch et al., (1997), de Deus and Oliviera (2016)
AB	Trait matching, testing of pollination syndromes	Network structure functional and phylogenetic dissimilarities	bipartite, vegan, FD, picante	Chamberlain et al., (2014)
AC	Network stability, ecosystem services	Network properties related to diversity measures	bipartite	Souza et al., (2018)
BC	Species coexistence related to functional traits and phylogeny	Functional diversity indices, phylogenetic clustering/overdispersion	vegan, picante, FD, ape	Fornoff et al., (2017)
ABC	Visitor specialization and pollination niche breadth based on floral traits	Network properties related to trait diversity and phylogeny	<i>under development</i>	Junker et al., (2013), Kemp et al., (2019)

species (trait evolution within phylogenetic clades) and small local communities representing a phylogenetically “dispersed” set of species. However, explicit assessments of larger species pools covering a larger part of the phylogenetic tree and thus including “deeper” nodes (early diversification) are still scarce and conducted only for few vegetative traits (Pennell et al., 2015).

The above-mentioned approaches focus on plant–pollinator interactions by analysing patterns in functional traits and phylogenetic relationships between species. However, to date, very few published studies have reviewed this in a comprehensive way. The above questions and themes are worth exploring further in the future, to shed new light on the ecology of plant–pollinator interactions. Moreover, we must remark that these approaches completely ignore the abiotically pollinated plant species coexisting within the community (Figure 1). Species with different pollination modes might not be relevant in terms of pollination networks, but still have an effect on the abundance and/or fitness of neighbouring plants through competition for abiotic resources (Flacher et al., 2015) or through heterospecific pollen transfer (Ashman and Arceo-Gomez, 2013).

### 3 | FLORAL TRAITS IN COMMUNITY ECOLOGY

From the plants' perspective the available pool of pollinators can be considered a limiting “resource.” Similar to other abiotic resources, pollinator scarcity might have a negative impact on the fitness of the plant, and the pollinators' capacity can be depleted. However, unlike abiotic resources, an increase in plant population size can

increase pollinator availability by attracting more pollinators or providing better habitat and thus enhancing the amount and diversity of interactions. It might result, though, also in increased competition for pollinators. Due to the ambiguity of this feedback, in natural communities both competition and facilitation for pollinators can occur between coexisting plant species (Feldman et al., 2004; Pauw, 2013; Benadi and Pauw, 2018; Pauw, 2018). The presence or absence of given pollinators will thus potentially exert a biotic filtering effect favouring certain types of plants and limiting others within local communities (Wolowski et al., 2017). Although studying plant community assembly through floral traits without pollinator observations might not serve as an actual “shortcut” in understanding plant–pollinator patterns, as suggested by Pellissier et al. (2012), it could help us disentangle how plant communities are structured indirectly by this “biotic resource” (Fantinato et al., 2017). Despite this potential, analysing floral traits does not have a long history in the field of community ecology. There have been, however, a growing number of studies published in recent years focusing on floral trait distribution patterns (Kantsa et al., 2017) in response to different abiotic (e.g. altitude, Junker and Larue-Kontic, 2018) and biotic drivers (Warring et al., 2016) on different spatial scales (review on the scale dependency of facilitative processes: Braun and Lortie, 2019).

#### 3.1 | Literature search

We carried out a systematic literature search of studies on plant community assembly and floral traits in Web of Science. Our search terms were (plant\* AND (pollinat\* OR flower\* OR floral\*) AND trait\*



AND communit\*) yielding 982 results (last accessed: 22.02.2018). While we scanned visually all titles from this list, we focussed more closely on the first 300 papers (ordered by relevance according to Web of Science) which were scanned also by abstract. Among the selected studies we skimmed all references and the context in which they were cited resulting in other potentially relevant articles. We excluded studies on: (a) populations/“communities” consisting of a limited selection of species (e.g. genera or small clades); (b) evolutionary processes without describing spatial patterns; and (c) review, viewpoint/commentary or forum papers, book chapters and theoretical frameworks. The described criteria resulted in 21 studies which were clearly related to empirical studies on community assembly in the broad sense (for a brief summary on the aims of study, floral traits used and most important findings of each paper, see Appendix S1). In the next sections, we describe and discuss the papers found in the context of current community assembly theory, in terms of processes shaping species coexistence and functional trait patterns on different spatial scales.

### 3.2 | Local scale

The main processes driving non-random community assembly through plant–pollinator interactions are filtering, competition and facilitation (Sargent and Ackerly, 2008), which can create non-random patterns in floral traits among the co-occurring species of a community (Figure 1, Table 1: “BC”). In the traditional sense, filtering is mainly thought to be caused by environmental (i.e. abiotic) conditions directly. However, due to the connection that floral traits enable between trophic levels, abiotic conditions might also affect plants indirectly through the available pool of pollinators. Plant adaptations to maximize reproductive output by e.g. producing easily accessible flowers (Pellissier et al., 2010), increasing biomass allocation to floral structures (Fabbro and Körner, 2004) or promoting earlier and prolonged flowering (Makrodimos et al., 2008) were found to be correlated with environmental gradients. However, correlation does not necessarily mean causation, as environmental filtering is equally likely to act on potential pollinators or directly on the plants themselves.

Plant species can also experience reduced reproductive output (pollen limitation) due to pollinator scarcity or environmental perturbations directly (reviewed by Bennett et al., 2018a). Loss in reproductive success can occur in certain environmental conditions, when plants fail to attract their potential pollinators because of e.g. poor light availability or other unsuitable abiotic conditions (Sargent and Ackerly, 2008). Therefore, small-scale habitat filtering needs to be studied in the context of plant–pollinator interactions (e.g. Burkle and Irwin, 2010; Lázaro et al., 2015), thus combining the effects of abiotic and biotic conditions as well as temporal changes in plant communities (de Deus and Oliviera, 2016; Warring et al., 2016).

Similarly, disentangling the effect of biotic interactions – competition and facilitation – on the observed community patterns is not straightforward (e.g. Hegland and Totland, 2012). In theory,

pollinator sharing leads to competition that can be disadvantageous to at least one of the species involved (reviewed by Mitchell et al., 2009). On the one hand, competition for pollinators can cause reduced reproductive success when: (a) pollinators are scarce, due to decreased visitation rates (i.e., pollinators are a limiting resource); or (b) the shared pollinator is common, due to dilution by an increased amount of interspecific pollen transfer (Sargent and Ackerly, 2008). The effect on the reproductive success of competing partners is highly dependent on the density of conspecific and heterospecific individuals (Benadi and Pauw, 2018) and can be modified by other factors, such as the presence of invasive super-attractive flowers (Chittka and Schürkens, 2001). Moreover, competition between insect- and wind-pollinated species for abiotic resources can also have a negative impact on insect-pollinated species in terms of resource allocation to floral traits involved in pollinator attraction (Flacher et al., 2015). On the other hand, having attractive neighbours might be beneficial, as they can increase the frequency of visitations by shared pollinators (Pellissier et al., 2012), which is most effective when the co-flowering species have similar floral traits or when they are super-generalists (e.g. alien species; Vilà et al., 2009). Another type of trait similarity is quite frequent among food-deceptive orchids (e.g. *Traunsteinera globosa*), which take advantage of and mimic the floral traits of other nectar-producing neighbouring plants (in this example *Trifolium pratense*) – often referred to as “magnet” species – thus deceiving pollinators unable to distinguish them (Juillet et al., 2007). To disentangle the two contrasting mechanisms – competition and facilitation – Mesgaran et al. (2017) proposed a model for predicting the optimal density of co-flowering species that is beneficial for a given plant in terms of pollination rate, and found that it is largely dependent on the attractiveness of the neighbours. Besides this modelling approach, in recent years there has been an increase in empirical studies on the density dependence of pollinator-mediated plant–plant interactions in natural communities (e.g. Bergamo et al., 2020).

In community ecology, abiotic drivers and biotic interactions shaping species distributions are often inferred from observing functional trait patterns. Non-random trait distribution, convergent (more similar) or divergent (more dissimilar than expected by chance) trait values can indicate which mechanisms and interactions are dominant within the community. According to contemporary coexistence theory (Chesson, 2000), species coexistence depends on the stabilizing effect of niche differences when fitness differences between species are small. Although this theory has been exemplified with vegetative plant functional traits (e.g. HilleRisLambers et al., 2012), one can apply the same theory to pollinator-mediated plant–plant interactions as well. Coexisting plant species having similar fitness (e.g. similar display size) have a similarly high probability of getting pollinated (Hegland and Totland, 2012). However, a high degree of trait convergence and pollinator sharing increases the probability of receiving heterospecific pollen. Therefore, plant species need to separate their pollination niches in order to coexist in a community. We propose that niche partitioning between similar species can happen via three main mechanisms: (a) partitioning in

time by having asynchronous flowering phenology (Oleques et al., 2017); (b) partitioning in interaction partners by specialization on particular (groups of) pollinators (e.g. difference in spectral reflectance; McEwen and Vamosi, 2010; van der Kooi et al., 2016) or (c) partitioning in morphology by different pollen placement mechanisms to avoid heterospecific pollen transfer (e.g. anther position; Fantinato et al., 2017). While the above-described mechanisms were extensively studied in certain clades and specialized systems (e.g. Muchhala and Potts, 2007; de Jager et al., 2011; Muchhala et al., 2014), evidence on diverse multi-clade communities remains scarce. As such mechanisms can result in both convergent and divergent floral trait patterns, one should be cautious when inferring community assembly rules, and attempt to distinguish traits reflecting fitness differences vs niche differences.

Contrary to vegetative functional traits, floral trait patterns of coexisting species are mainly relevant when species overlap in their time of flowering to a certain extent. Although some evidence suggests that facilitation can also occur among non-co-flowering species via maintaining pollinator populations by providing high floral diversity (Braun and Lortie, 2019), these interactions are poorly studied. The interplay between co-flowering plants is widely known and well tested, but still, results remain contradictory (Jensen et al., 2019). Therefore, developing new tools for assessing the overlap in flowering period among co-occurring species within communities are highly encouraged (Fantinato et al., 2016).

### 3.3 | Biogeographical scale

Local communities are assembled from a larger, regional pool of species via abiotic and biotic filters. Therefore, exploring functional trait patterns on larger biogeographical scales is crucial for understanding these filtering processes and thus local community assembly mechanisms. In the case of floral traits, large-scale patterns were found to be driven by climatic gradients (e.g. Rech et al., 2016), which might cause turnover in pollinator communities (e.g. Devoto et al., 2009) and in biodiversity patterns (e.g. Ollerton et al., 2011), as well as by geology and/or land-use types (e.g. Kühn et al., 2006; Binkenstein et al., 2013). On the global scale, the majority of plant species are pollinated by insects and other animals (78% and 94% in temperate and tropical communities, respectively) compared to the number of wind- or water-pollinated ones (Ollerton et al., 2011), and only a small proportion are capable of obligate or facultative self-pollination. Another global trend is the increasing specialization of pollination syndromes towards the tropics (Ollerton et al., 2006). However, the driver behind these two trends is still unclear (Schemske et al., 2009), and the existence of a latitudinal gradient in specialization has recently been questioned (Moles and Ollerton, 2016).

It is generally accepted that pollination other than via animals is selected for when pollinators become scarce or unpredictable (e.g. on islands, Barrett, 1996). Therefore, under unsuitable conditions for pollinators, species with alternative reproductive strategies become more abundant. Based on a global community dataset, Rech et al.

(2016) showed that the distribution of animal- and wind-pollinated species is non-random, but related to current climatic conditions. Animal pollination was more dominant in the tropics (warm habitats, closed vegetation with high precipitation), whereas a higher proportion of wind-pollinated species could be found on islands compared to continents (Rech et al., 2016). On the national scale of Germany, Kühn et al. (2006) found that the proportion of wind-pollinated species was most strongly correlated with wind speed and altitude (where, under both conditions, pollinator availability is generally lower) as well as open vegetation and moist habitats (such as bogs and fens). Dominance of self-pollination was spatially more scattered, especially in areas that included habitats with high disturbance, areas with a high proportion of alien species (e.g. riverbanks) and a high proportion of annual species. It has also been shown that oceanic islands host a surprisingly high proportion of self-compatible species (Lord, 2015; Grossenbacher et al., 2017) which therefore suggests that securing sexual reproduction when the number of potential outcrossing partners is limited is crucial for colonization success in remote locations (Baker, 1955).

Considering biomes on the global scale, the ratio of outcrossing compared to selfing declines with increasing latitude and is – in some cases – significantly different among major biomes (Moeller et al., 2017). However, these patterns are most likely due to the distribution of life forms rather than a consequence of actual plant-pollinator interactions, as there is a strong correlation between the rate of outcrossing and life form, as expected in general (Michalski and Durka, 2009).

Although certain life forms have a higher proportion of certain pollination types (Michalski and Durka, 2009; but see Ollerton et al., 2011) and mating systems (Moeller et al., 2017), it is less known how floral traits relate to other functional traits. Within communities, the proportion of pollination types was found to be correlated to certain optical spectral signals detected by remote sensing (Feilhauer et al., 2016). Based on models predicting leaf traits from spectral data, a number of strong correlations were detected between the community-weighted mean (CWM) values of leaf traits and pollination types. The CWM of specific leaf area (SLA) and leaf dry mass were positively related to the proportion of insect pollination and negatively to wind pollination, whereas for leaf dry matter content (LDMC) the relationship was reversed, and none of the traits were related to selfing. However, as CWM values were used throughout this study, the correlation between vegetative and reproductive traits at the species level remains unexplored. Assessments whether pollination-related traits form an independent axis of plant strategy are still lacking (but see Salguero-Gómez et al., 2016 for an assessment using reproduction-related parameters calculated from population matrices).

During our literature survey, we have found studies predominantly covering small scales with both small extents (i.e. samples cover small geographical areas) and grain sizes (each sample or plot is small, e.g. several square meters; for more on 'extent' and 'grain size' see Wiens, 1989). In contrast to this, among studies on the biogeographical scale (large extent in general), the majority was



sampled at a very coarse grain, while studies with high resolution (i.e. fine-grained) samples are limited in number, and often not evenly distributed along the studied gradient(s). Studies that investigate patterns at grid cell level (i.e. evenly distributed) or have small grain size but high extent are virtually missing (but see Kühn et al., 2006).

#### 4 | AVAILABILITY OF FLORAL TRAITS

Although there are a growing number of studies using pollination-related traits in community ecology, the amount of publicly available floral trait data is not increasing nearly as rapidly. As a part of TRY (Kattge et al., 2020), the largest collection of trait databases to date, predominantly categorical traits related to floral and reproductive ecology can be found sourced from BioFlor (Kühn et al., 2004), Ecoflora (Fitter and Peat, 1994) or PLANTSdata (Green, 2009). Although there is a general gap for continuous traits (but see FReD; Arnold et al., 2010), these are often more variable within than among species.

Floral traits are known to have considerable intraspecific variability (e.g. floral tube length: Anderson et al., 2014; floral scent: Delle-Vedove et al., 2017). This variability should be kept in mind when using database data especially on a small spatial scale. For leaf traits, there is evidence that database data can be a sufficient proxy for on-site measurements of moderately plastic traits such as LDMC, but not always for highly plastic ones, such as canopy height or SLA (Cordlandwehr et al., 2013). Although this has not been studied for the majority of floral traits, flowering phenology (measured as onset of flowering in Julian days) was shown to generally have higher interspecific than intraspecific variability (Kazakou et al., 2014), and therefore can be considered a “stable” trait, even when used as a continuous variable. However, besides trait plasticity, the suitability of database data might also depend on the strength of the environmental gradient (Cordlandwehr et al., 2013) and the spatial scale of the study, therefore calling for even more precautions.

Large amounts of floral trait data do exist, but these are mostly scattered or difficult to access. Old monographs (e.g. Müller, 1881; Knuth, 1898; Kugler, 1970; Faegri and van der Pijl, 1979), regional and national floras and other sources of “grey” literature can provide an extensive base for further syntheses of the current knowledge. However, empirical results for quantitative traits, e.g. nectar properties (Baude et al., 2016), will likely need to be collected to achieve consistent data. Despite the potential of these resources, there has been no initiative so far to pull these data together in a standardised way on a common platform, like has been achieved for other trait groups, such as clonal traits (CLO-PLA; Klimešová and de Bello, 2009), fine root traits (FRED; Iversen et al., 2017) or seed traits (SID; Royal Botanic Gardens Kew, 2018). Therefore, establishing standards in the measurement of floral traits as well as compiling existing and comparable data for a larger species pool and biogeographical extent (e.g. GloPL; Bennett et al., 2018b) is one of the upcoming challenges of this field.

## 5 | CONCLUSIONS AND FUTURE RESEARCH DIRECTIONS

In this synthesis, we reviewed predominantly recent studies using floral and pollination-related functional traits at the community scale. We summarised the most common themes and methodological approaches, and pointed to knowledge gaps that could be explored in the future. In general, we find evidence on community-level floral trait patterns to be inconsistent, mainly due to the scarcity and heterogeneity (context specificity) of empirical studies, which do not allow general conclusions, neither on the directionality of trait patterns nor on their relative importance compared to other functional traits. We therefore provide here a concise “catalogue” of future directions in exploring floral trait-based community ecology to improve our understanding of these patterns and processes.

First, the necessary steps to overcome current limitations due to lack of data are:

1. Establishment of floral and pollination trait standards
2. Compilation and organization of floral and pollination trait data into a dedicated database specifically recognizing, among others, grey literature, non-English literature and recent empirical studies
3. Making available more trait data for larger pools of species from larger biographical extents, to enable studies beyond local scales
4. More observational vegetation data including phenological status, focusing especially on co-flowering and not only co-occurrence of species

Secondly, based on our current knowledge of ecological function and importance for plant community assembly we propose the following groups of floral traits to be considered for future compilation and sampling efforts:

1. Flower colour, including reflectance and UV patterns (expanding already existing database: FReD; Arnold et al., 2010)
2. Display size, including flower/inflorescence size, number of flowers in inflorescence, number of flowers/inflorescences per square meter
3. Floral morphology, including nectar tube length and floral symmetry
4. Positioning of reproductive organs inside the flower in relation to pollen placement on the pollinator's body
5. Floral reward production, sugar content and chemical profile
6. Floral scent chemical profile
7. Flowering phenology
8. Pollination syndrome based on or supplemented by observed pollinator species

Finally, we think that the following research directions and prospects are of particular interest:

1. Phylogenetic signal for floral traits within and across communities (encompassing large species pools) thus enabling the assessment

of floral trait clustering/overdispersion in communities and their relation to phylogenetic relationships

2. Assessment of whether floral and sexual reproduction traits form an independent axis of plant strategy
3. More comprehensive large-scale studies encompassing both larger biogeographical extent and higher resolution data
4. Pollinator-mediated plant-plant interactions — such as competition and facilitation — and how these are governed by abiotic conditions in natural communities
5. Experiments on the role of floral traits in trait-based plant community assembly testing hypotheses generated in observational studies. This may necessitate experiments distributed in areas with different pollinator communities in which plant communities with various flower trait combinations are experimentally established and monitored

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## AUTHOR CONTRIBUTIONS

The study was conceived by LG and AE-V. AE-V with major contributions from LG took leadership in writing the manuscript and the remaining authors contributed substantially to the different versions. All co-authors have read and approved the final version of the manuscript.

## DATA AVAILABILITY STATEMENT

This synthesis article does not contain original data.

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## REFERENCES

- Anderson, B., Ros, P., Wiese, T.J. and Ellis, A.G. (2014) Intraspecific divergence and convergence of floral tube length in specialized pollination interactions. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20141420. <https://doi.org/10.1098/rspb.2014.1420>.
- Arnold, S.E., Faruq, S., Savolainen, V., McOwan, P.W. and Chittka, L. (2010) FReD: the floral reflectance database—a web portal for analyses of flower colour. *PLoS ONE*, 5, e14287. <https://doi.org/10.1371/journal.pone.0014287>.
- Ashman, T.L. and Arceo-Gómez, G. (2013) Toward a predictive understanding of the fitness costs of heterospecific pollen receipt and its importance in co-flowering communities. *American Journal of Botany*, 100, 1061–1070. <https://doi.org/10.3732/ajb.1200496>.
- Baker, H.G. (1955) Self-compatibility and establishment after long distance dispersal. *Evolution*, 9, 347–349. <https://doi.org/10.1111/j.1558-5646.1955.tb01544.x>.
- Barrett, S.C. H. (1996) The reproductive biology and genetics of island plants. *Philosophical Transactions: Biological Sciences*, 351, 725–733. <https://doi.org/10.1098/rstb.1996.0067>.
- Bastazini, V.A., Ferreira, P.M., Azambuja, B.O., Casas, G., Debastiani, V.J., Guimarães, P.R. et al. (2017) Untangling the tangled bank: a novel method for partitioning the effects of phylogenies and traits on ecological networks. *Evolutionary Biology*, 44, 312–324. <https://doi.org/10.1007/s11692-017-9409-8>.
- Baude, M., Kunin, W.E., Boatman, N.D., Conyers, S., Davies, N., Gillespie, M.A.K. et al. (2016) Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature*, 530, 85–88. <https://doi.org/10.1038/nature16532>.
- Benadi, G. and Pauw, A. (2018) Frequency dependence of pollinator visitation rates suggests that pollination niches can allow plant species coexistence. *Journal of Ecology*, 106, 1892–1901. <https://doi.org/10.1111/1365-2745.13025>.
- Bennett, J.M., Thompson, A., Goia, I., Feldmann, R., Ștefan, V., Bogdan, A. et al. (2018a) A review of European studies on pollination networks and pollen limitation, and a case study designed to fill in a gap. *AoB Plants*, 10, ply068. <https://doi.org/10.1093/aobpla/ply068>.
- Bennett, J.M., Steets, J.A., Burns, J.H., Durka, W., Vamosi, J.C., Arceo-Gómez, G. et al. (2018b) GloPL, a global data base on pollen limitation of plant reproduction. *Scientific Data*, 5, 180249. <https://doi.org/10.1038/sdata.2018.249>.
- Bergamo, P.J., Streher, N.S., Traveset, A., Wolowski, M. and Sazima, M. (2020) Pollination outcomes reveal negative density-dependence coupled with interspecific facilitation among plants. *Ecology Letters*, 23, 129–139. <https://doi.org/10.1111/ele.13415>.
- Binkenstein, J., Renoult, J.P. and Schaefer, H.M. (2013) Increasing land-use intensity decreases floral colour diversity of plant communities in temperate grasslands. *Oecologia*, 173, 461–471. <https://doi.org/10.1007/s00442-013-2627-6>.
- Blüthgen, N., Menzel, F., Hovestadt, T., Fiala, B. and Blüthgen, N. (2007) Specialization, constraints, and conflicting interests in mutualistic networks. *Current Biology*, 17, 341–346. <https://doi.org/10.1016/j.cub.2006.12.039>.
- Bosch, J., Retana, J. and Cerda, X. (1997) Flowering phenology, floral traits and pollinator composition in a herbaceous Mediterranean plant community. *Oecologia*, 109, 583–591. <https://doi.org/10.1007/s004420050120>.
- Braun, J. and Lortie, C. (2019) Finding the bees knees: a conceptual framework and systematic review of the mechanisms of pollinator-mediated facilitation. *Perspectives in Plant Ecology, Evolution and Systematics*, 36, 33–40. <https://doi.org/10.1016/j.ppees.2018.12.003>.
- Burkle, L.A. and Irwin, R.E. (2010) Beyond biomass: Measuring the effects of community-level nitrogen enrichment on floral traits, pollinator visitation and plant reproduction. *Journal of Ecology*, 98, 705–717. <https://doi.org/10.1111/j.1365-2745.2010.01648.x>.
- Chamberlain, S.A., Cartar, R.V., Worley, A.C., Semmler, S.J., Gielens, G., Elwell, S. et al. (2014) Traits and phylogenetic history contribute to network structure across Canadian plant-pollinator communities. *Oecologia*, 176, 545–556. <https://doi.org/10.1007/s00442-014-3035-2>.
- Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31, 343–366. <https://doi.org/10.1146/annurev.ecolsys.31.1.343>.
- Chittka, L. and Schürkens, S. (2001) Successful invasion of a floral market - An exotic Asian plant has moved in on Europe's river-banks by bribing pollinators. *Nature*, 411, 653–653. <https://doi.org/10.1038/35079676>.
- Cordlandwehr, V., Meredith, R.L., Ozinga, W.A., Bekker, R.M., Groenendael, J.M. and Bakker, J.P. (2013) Do plant traits retrieved from a database accurately predict on-site measurements? *Journal of Ecology*, 101, 662–670. <https://doi.org/10.1111/1365-2745.12091>.
- Cornwell, W.K. and Ackerly, D.D. (2009) Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, 79, 109–126. <https://doi.org/10.1890/07-1134.1>.





- Craine, J.M., Wolkovich, E.M., Towne, E.G. and Kembel, S.W. (2012) Flowering phenology as a functional trait in a tall-grass prairie. *New Phytologist*, 193, 673–682. <https://doi.org/10.1111/j.1469-8137.2011.03953.x>.
- Delle-Vedove, R., Schatz, B. and Dufay, M. (2017) Understanding intraspecific variation of floral scent in light of evolutionary ecology. *Annals of Botany*, 120, 1–20. <https://doi.org/10.1093/aob/mcx055>.
- de Deus, F.F. and Oliveira, P.E. (2016) Changes in floristic composition and pollination systems in a “Cerrado” community after 20 years of fire suppression. *Revista Brasileira de Botânica*, 39, 1051–1063. <https://doi.org/10.1007/s040415-016-0304-9>.
- de Jager, M.L., Dreyer, L.L. and Ellis, A.G. (2011) Do pollinators influence the assembly of flower colours within plant communities? *Oecologia*, 166, 543–553. <https://doi.org/10.1007/s00442-010-1879-7>.
- Devoto, M., Medan, D. Roig-alsina, A. and Montaldo, N. (2009) Patterns of species turnover in plant-pollinator communities along a precipitation gradient in Patagonia (Argentina). *Austral Ecology*, 34, 848–857. <https://doi.org/10.1111/j.1442-9993.2009.01987.x>.
- Díaz, S., Cabido, M. and Casanoves, F. (1998) Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science*, 9, 113–122. <https://doi.org/10.2307/3237229>.
- Fabbro, T. and Körner, C. (2004) Altitudinal differences in flower traits and reproductive allocation. *Flora - Morphology, Distribution, Functional Ecology of Plants*, 199, 70–81. <https://doi.org/10.1078/0367-2530-00128>.
- Faegri, K. and van der Pijl, L. (1979) *Principles of Pollination Ecology*. Oxford, UK: Pergamon Press.
- Fantinato, E., Del Vecchio, S., Slaviero, A., Conti, L., Acosta, A.T.R. and Buffa, G. (2016) Does flowering synchrony contribute to the sustainment of dry grassland biodiversity? *Flora - Morphology, Distribution, Functional Ecology of Plants*, 222, 96–103. <https://doi.org/10.1016/j.flora.2016.04.003>.
- Fantinato, E., Del Vecchio, S., Giovanetti, M., Acosta, A.T.R. and Buffa, G. (2017) New insights into plants coexistence in species-rich communities: the pollination interaction perspective. *Journal of Vegetation Science*, 29, 6–14. <https://doi.org/10.1111/jvs.12592>.
- Feilhauer, H., Doktor, D., Schmidlein, S. and Skidmore, A.K. (2016) Mapping pollination types with remote sensing. *Journal of Vegetation Science*, 27, 999–1011. <https://doi.org/10.1111/jvs.12421>.
- Feldman, T.S., Morris, W.F. and Wilson, W.G. (2004) When can two plant species facilitate each other's pollination? *Oikos*, 105, 197–207. <https://doi.org/10.1111/j.0030-1299.2004.12845.x>.
- Fitter, A.H. and Peat, H.J. (1994) The ecological flora database. *Journal of Ecology*, 82, 415–425. <https://doi.org/10.2307/2261309>.
- Flacher, F., Raynaud, X., Hansart, A., Motard, E. and Dajoz, I. (2015) Competition with wind-pollinated plant species alters floral traits of insect-pollinated plant species. *Scientific Reports*, 5, 13345. <https://doi.org/10.1038/srep13345>.
- Fornoff, F., Klein, A.M., Hartig, F., Benadi, G., Venjakob, C., Schaefer, H.M. et al. (2017) Functional flower traits and their diversity drive pollinator visitation. *Oikos*, 126, 1020–1030. <https://doi.org/10.1111/oik.03869>.
- Götzenberger, L., de Bello, F., Bräthen, K.A., Davison, J., Dubuis, A., Guisan, A. et al. (2012) Ecological assembly rules in plant communities—approaches, patterns and prospects. *Biological Reviews*, 87, 111–127. <https://doi.org/10.1111/j.1469-185X.2011.00187.x>.
- Green, W. (2009). *USDA PLANTS Compilation, version 1, 09-02-02*. (<https://plants.sc.egov.usda.gov/java/>, 14 March 2018).
- Grossenbacher, D.L., Brandvain, Y., Auld, J.R., Burd, M., Cheptou, P.-O., Conner, J.K. et al. (2017) Self-compatibility is over-represented on islands. *New Phytologist*, 215, 469–478. <https://doi.org/10.1111/nph.14534>.
- Hegland, S.J. and Totland, Ø. (2012) Interactions for pollinator visitation and their consequences for reproduction in a plant community. *Acta Oecologica*, 43, 95–103. <https://doi.org/10.1016/j.actao.2012.06.002>.
- HilleRisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M. and Mayfield, M.M. (2012) Rethinking community assembly through the lens of co-existence theory. *Annual Review of Ecology, Evolution, and Systematics*, 43, 227–248. <https://doi.org/10.1146/annurev-ecolsys-110411-160411>.
- Ibanez, S. (2012) Optimizing size thresholds in a plant-pollinator interaction web: towards a mechanistic understanding of ecological networks. *Oecologia*, 170, 233–242. <https://doi.org/10.1007/s00442-012-2290-3>.
- Ibanez, S., Lavorel, S., Puijalon, S. and Moretti, M. (2013) Herbivory mediated by coupling between biomechanical traits of plants and grasshoppers. *Functional Ecology*, 27, 479–489. <https://doi.org/10.1111/1365-2435.12058>.
- Iversen, C.M., McCormack, M.L., Powell, A.S., Blackwood, C.B., Freschet, G.T., Kattge, J. et al. (2017) A global Fine-Root Ecology Database to address below-ground challenges in plant ecology. *New Phytologist*, 215, 15–26. <https://doi.org/10.1111/nph.14486>.
- Jensen, A.M., Schamp, B.S. and Belleau, A. (2019) Evidence of temporal niche separation over low flowering time overlap in an old-field plant community. *Oecologia*, 1–12. <https://doi.org/10.1007/s00442-019-04386-0>.
- Juillet, N., Gonzalez, M.A., Page, P.A. and Gigord, L.D.B. (2007) Pollination of the European food-deceptive *Traunsteinera globosa* (Orchidaceae): The importance of nectar-producing neighbouring plants. *Plant Systematics and Evolution*, 265, 123–129. <https://doi.org/10.1007/s00606-006-0507-9>.
- Junker, R.R. and Larue-Kontic, A.A.C. (2018) Elevation predicts the functional composition of alpine plant communities based on vegetative traits, but not based on floral traits. *Alpine Botany*, 128, 13–22. <https://doi.org/10.1007/s00035-017-0198-6>.
- Junker, R.R., Blüthgen, N., Brehm, T., Binkenstein, J., Paulus, J., Martin Schaefer, H. et al. (2013) Specialization on traits as basis for the niche-breadth of flower visitors and as structuring mechanism of ecological networks. *Functional Ecology*, 27, 329–341. <https://doi.org/10.1111/1365-2435.12005>.
- Junker, R.R., Blüthgen, N. and Keller, A. (2015) Functional and phylogenetic diversity of plant communities differently affect the structure of flower-visitor interactions and reveal convergences in floral traits. *Evolutionary Ecology*, 29, 437–450. <https://doi.org/10.1007/s10682-014-9747-2>.
- Kantsa, A., Raguso, R.A., Dyer, A.G., Sgardelis, S.P., Olesen, J.M. and Petanidou, T. (2017) Community-wide integration of floral colour and scent in a Mediterranean scrubland. *Nature Ecology & Evolution*, 1, 1502–1510. <https://doi.org/10.1038/s41559-017-0298-0>.
- Kantsa, A., Raguso, R.A., Dyer, A.G., Olesen, J.M., Tscheulin, T. and Petanidou, T. (2018) Disentangling the role of floral sensory stimuli in pollination networks. *Nature Communications*, 9, 1041. <https://doi.org/10.1038/s41467-018-03448-w>.
- Karron, J.D., Ivey, C.T., Mitchell, R.J., Whitehead, M.R., Peakall, R. and Case, A.L. (2012) New perspectives on the evolution of plant mating systems. *Annals of Botany*, 109, 493–503. <https://doi.org/10.1093/aob/mcr319>.
- Kattge, J., Bönsch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P. et al. (2020) TRY plant trait database - enhanced coverage and open access. *Global Change Biology*, 26, 119–188. <https://doi.org/10.1111/gcb.14904>.
- Kazakou, E., Violle, C., Roumet, C., Navas, M.L., Vile, D., Kattge, J. et al. (2014) Are trait-based species rankings consistent across data sets and spatial scales? *Journal of Vegetation Science*, 25, 235–247. <https://doi.org/10.1111/jvs.12066>.
- Kemp, J.E., Bergh, N.G., Soares, M. and Ellis, A.G. (2019) Dominant pollinators drive non-random community assembly and shared flower

- colour patterns in daisy communities. *Annals of Botany*, 123, 277–288. <https://doi.org/10.1093/aob/mcy126>.
- Royal Botanic Gardens Kew (2018). *Seed Information Database (SID). Version 7.1*. Available from: <http://data.kew.org/sid/>. [Accessed 14 March 2018].
- Klimešová, J. and de Bello, F. (2009) CLO-PLA: the database of clonal 817 and bud bank traits of Central European flora. *Journal of Vegetation Science*, 20, 511–516. <https://doi.org/10.1111/j.1654-1103.2009.01050.x>.
- Klimešová, J., Danihelka, J., Chrtěk, J., de Bello, F. and Herben, T. (2017) CLO-PLA: A database of clonal and bud-bank traits of the Central European flora. *Ecology*, 98, 1179–1179. <https://doi.org/10.1002/ecy.1745>.
- Klotz, S., Kühn, I. and Durka, W. (2002) *BIOLFLOR – Eine Datenbank zu biologisch-ökologischen Merkmalen der Flora von Deutschland*. Bonn: Bundesamt für Naturschutz.
- Knight, T.M., Ashman, T.L., Bennett, J.M., Burns, J.H., Passonneau, S. and Steets, J.A. (2018) Reflections on, and visions for, the changing field of pollination ecology. *Ecology letters*, 21, 1282–1295. <https://doi.org/10.1111/ele.13094>.
- Knuth, P. (1898) *Handbuch der Blütenbiologie*. Leipzig: W. Engelmann.
- van der Kooij, C.J., Pen, I., Staal, M., Stavenga, D.G. and Elzenga, J.T.M. (2016) Competition for pollinators and intra-communal spectral dissimilarity of flowers. *Plant Biology*, 18, 56–62. <https://doi.org/10.1111/plb.12328>.
- Kugler, H. (1970) *Blütenökologie*, 2nd edition. Stuttgart: G. Fischer.
- Kühn, I., Durka, W. and Klotz, S. (2004) BiolFlor: a new plant-trait database as a tool for plant invasion ecology. *Diversity and Distributions*, 10, 363–365.
- Kühn, I., Bierman, S.M., Durka, W. and Klotz, S. (2006) Relating geographical variation in pollination types to environmental and spatial factors using novel statistical methods. *New Phytologist*, 172, 127–139. <https://doi.org/10.1111/j.1469-8137.2006.01811.x>.
- Laigle, I., Aubin, I., Digel, C., Brose, U., Boulangeat, I. and Gravel, D. (2018) Species traits as drivers of food web structure. *Oikos*, 127, 316–326. <https://doi.org/10.1111/oik.04712>.
- Larson, J.E. and Funk, J.L. (2016) Regeneration: an overlooked aspect of trait-based plant community assembly models. *Journal of Ecology*, 104, 1284–1298. <https://doi.org/10.1111/1365-2745.12613>.
- Lavorel, S. and Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, 16, 545–556. <https://doi.org/10.1046/j.1365-2435.2002.00664.x>.
- Lavorel, S., Storkey, J., Bardgett, R.D., de Bello, F., Berg, M.P., Le Roux, X. et al. (2013) A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *Journal of Vegetation Science*, 24, 942–948. <https://doi.org/10.1111/jvs.12083>.
- Lázaro, A., Hegland, S.J. and Totland, Ø. (2008) The relationships between floral traits and specificity of pollination systems in three Scandinavian plant communities. *Oecologia*, 157, 249–257. <https://doi.org/10.1007/s00442-008-1066-2>.
- Lázaro, A., Lundgren, R. and Totland, Ø. (2015) Pollen limitation, species' floral traits and pollinator visitation: Different relationships in contrasting communities. *Oikos*, 124, 174–186. <https://doi.org/10.1111/oik.01525>.
- Lord, J.M. (2015) Patterns in floral traits and plant breeding systems on Southern Ocean Islands. *AoB Plants*, 7, plv095. <https://doi.org/10.1093/aobpla/plv095>.
- Losos, J.B. (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology letters*, 11, 995–1003. <https://doi.org/10.1111/j.1461-0248.2008.01229.x>.
- Maglianesi, M.A., Blüthgen, N., Böhning-Gaese, K. and Schleuning, M. (2014) Morphological traits determine specialization and resource use in plant-hummingbird networks in the neotropics. *Ecology*, 95, 3325–3334. <https://doi.org/10.1890/13-2261.1>.
- Makrodimos, N., Bliionis, G.J., Krigas, N. and Vokou, D. (2008) Flower morphology, phenology and visitor patterns in an alpine community on Mt Olympos, Greece. *Flora - Morphology, Distribution, Functional Ecology of Plants*, 203, 449–468. <https://doi.org/10.1016/j.flora.2007.07.003>.
- McEwen, J.R. and Vamosi, J.C. (2010) Floral colour versus phylogeny in structuring subalpine flowering communities. *Proceedings of the Royal Society B: Biological Sciences*, 277, 2957–2965. <https://doi.org/10.1098/rspb.2010.0501>.
- Mesgaran, M.B., Bouhours, J., Lewis, M.A. and Cousens, R.D. (2017) How to be a good neighbour: facilitation and competition between two co-flowering species. *Journal of Theoretical Biology*, 422, 72–83. <https://doi.org/10.1016/j.jtbi.2017.04.011>.
- Michalski, S.G. and Durka, W. (2009) Pollination mode and life form strongly affect the relation between mating system and pollen to ovule ratios. *New Phytologist*, 183, 470–479. <https://doi.org/10.1111/j.1469-8137.2009.02861.x>.
- Mitchell, R.J., Flanagan, R.J., Brown, B.J., Waser, N.M. and Karron, J.D. (2009) New frontiers in competition for pollination. *Annals of Botany*, 103, 1403–1413. <https://doi.org/10.1093/aob/mcp062>.
- Moeller, D.A., Runquist, R.D.B., Moe, A.M., Geber, M.A., Goodwillie, C., Cheptou, P.-O. et al. (2017) Global biogeography of mating system variation in seed plants. *Ecology Letters*, 20, 375–384. <https://doi.org/10.1111/ele.12738>.
- Moles, A.T. and Ollerton, J. (2016) Is the notion that species interactions are stronger and more specialized in the tropics a zombie idea? *Biotropica*, 48, 141–145. <https://doi.org/10.1111/btp.12281>.
- Muchhala, N. and Potts, M.D. (2007) Character displacement among bat-pollinated flowers of the genus *Burmeistera*: analysis of mechanism, process and pattern. *Proceedings of the Royal Society B: Biological Sciences*, 274, 2731–2737. <https://doi.org/10.1098/rspb.2007.0670>.
- Muchhala, N., Johnsen, S. and Smith, S.D. (2014) Competition for hummingbird pollination shapes flower color variation in Andean Solanaceae. *Evolution*, 68, 2275–2286. <https://doi.org/10.1111/evo.12441>.
- Müller, H. (1881) *Alpenblumen, ihre Befruchtung durch Insekten und ihre Anpassungen an dieselben*. Leipzig: W. Engelmann.
- Oleques, S.S., Overbeck, G.E. and de Avia, R.S. (2017) Flowering phenology and plant-pollinator interactions in a grassland community of Southern Brazil. *Flora: Morphology, Distribution, Functional Ecology of Plants*, 229, 141–146. <https://doi.org/10.1016/j.flora.2017.02.024>.
- Ollerton, J., Johnson, S.D. and Hingston, A.B. (2006) Geographical Variation in Diversity and Specificity of Pollination Systems. In: Waser, N.M. and Ollerton, J. (Eds.) *Plant-pollinator interactions: from specialization to generalization*. Chicago, US: The University of Chicago Press, pp. 283–308.
- Ollerton, J., Alarcón, R., Waser, N.M., Price, M.V., Watts, S., Cranmer, L. et al. (2009) A global test of the pollination syndrome hypothesis. *Annals of Botany*, 103, 1471–1480. <https://doi.org/10.1093/aob/mcp031>.
- Ollerton, J., Winfree, R. and Tarrant, S. (2011) How many flowering plants are pollinated by animals? *Oikos*, 120, 321–326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>.
- Pauw, A. (2013) Can pollination niches facilitate plant coexistence? *Trends in Ecology & Evolution*, 28, 30–37. <https://doi.org/10.1016/j.tree.2012.07.019>.
- Pauw, A. (2018) Flower wars. *Journal of Vegetation Science*, 29, 4–5. <https://doi.org/10.1111/jvs.12603>.
- Pellissier, L., Pottier, J., Vittoz, P., Dubuis, A. and Guisan, A. (2010) Spatial pattern of floral morphology: Possible insight into the effects of pollinators on plant distributions. *Oikos*, 119, 1805–1813. <https://doi.org/10.1111/j.1600-0706.2010.18560.x>.

- Pellissier, L., Alvarez, N. and Guisan, A. (2012) Pollinators as drivers of plant distribution and assemblage into communities. In: Patiny, S. (Ed.) *Evolution of Plant-Pollinator Relationships*. Cambridge, UK: Cambridge University Press, pp. 392–413.
- Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M. et al. (2018) Comparing species interaction networks along environmental gradients. *Biological Reviews*, 93, 785–800. <https://doi.org/10.1111/brv.12366>.
- Pennell, M.W., FitzJohn, R.G., Cornwell, W.K. and Harmon, L.J. (2015) Model adequacy and the macroevolution of angiosperm functional traits. *The American Naturalist*, 186, E33–E50. <https://doi.org/10.1086/682022>.
- Pérez-Harguindeguy, N., Díaz, S., Gamier, E., Lavorel, S., Poorter, H., Jaureguiberry, P. et al. (2013) New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61, 167–234. [https://doi.org/10.1071/BT12225\\_CO](https://doi.org/10.1071/BT12225_CO).
- R Core Team (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rafferty, N.E. and Ives, A.R. (2013) Phylogenetic trait-based analyses of ecological networks. *Ecology*, 94, 2321–2333. <https://doi.org/10.1890/12-1948.1>.
- Rech, A.R., Dalsgaard, B., Sandel, B., Sonne, J., Svenning, J.-C., Holmes, N. et al. (2016) The macroecology of animal versus wind pollination: ecological factors are more important than historical climate stability. *Plant Ecology and Diversity*, 9, 253–262. <https://doi.org/10.1080/17550874.2016.1207722>.
- Reverté, S., Retana, J., Gómez, J.M. and Bosch, J. (2016) Pollinators show flower colour preferences but flowers with similar colours do not attract similar pollinators. *Annals of Botany*, 118, 249–257. <https://doi.org/10.1093/aob/mcw103>.
- Rosas-Guerrero, V., Aguilar, R., Martín-Rodríguez, S., Ashworth, L., Lopezaraiza-Mikel, M., Bastida, J.M. et al. (2014) A quantitative review of pollination syndromes: do floral traits predict effective pollinators? *Ecology Letters*, 17, 388–400. <https://doi.org/10.1111/ele.12224>.
- Salguero-Gómez, R., Jones, O.R., Jongejans, E., Blomberg, S.P., Hodgson, D.J., Mbeau-Ache, C. et al. (2016) Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proceedings of the National Academy of Sciences*, 113, 230–235. <https://doi.org/10.1073/pnas.1506215112>.
- Sargent, R.D. and Ackerly, D.D. (2008) Plant-pollinator interactions and the assembly of plant communities. *Trends in Ecology and Evolution*, 23, 123–130. <https://doi.org/10.1016/j.tree.2007.11.003>.
- Sazatornil, F.D., Moré, M., Benitez-Vieyra, S., Cocucci, A.A., Kitching, I.J., Schlumpberger, B.O. et al. (2016) Beyond neutral and forbidden links: morphological matches and the assembly of mutualistic hawkmoth-plant networks. *Journal of Animal Ecology*, 85, 1586–1594. <https://doi.org/10.1111/1365-2656.12509>.
- Schemske, D.W., Mittelbach, G.G., Cornell, H.V., Sobel, J.M. and Roy, K. (2009) Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology, Evolution, and Systematics*, 40, 245–269. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173430>.
- Schleuning, M., Fründ, J. and Garcia, D. (2015) Predicting ecosystem functions from biodiversity and mutualistic networks: an extension of trait-based concepts to plant–animal interactions. *Ecography*, 38, 380–392. <https://doi.org/10.1111/ecog.00983>.
- Shrestha, M., Dyer, A.G., Bhattarai, P. and Burd, M. (2014) Flower colour and phylogeny along an altitudinal gradient in the Himalayas of Nepal. *Journal of Ecology*, 102, 126–135. <https://doi.org/10.1111/1365-2745.12185>.
- Souza, C.S., Maruyama, P.K., Aoki, C., Sigrist, M.R., Raizer, J., Gross, C.L. et al. (2018) Temporal variation in plant–pollinator networks from seasonal tropical environments: Higher specialization when resources are scarce. *Journal of Ecology*, 106, 2409–2420. <https://doi.org/10.1111/1365-2745.12978>.
- Tinoco, B.A., Graham, C.H., Aguilar, J.M. and Schleuning, M. (2017) Effects of hummingbird morphology on specialization in pollination networks vary with resource availability. *Oikos*, 126, 52–60. <https://doi.org/10.1111/oik.02998>.
- Vamosi, J.C., Moray, C.M., Garcha, N.K., Chamberlain, S.A. and Mooers, A. (2014) Pollinators visit related plant species across 29 plant-pollinator networks. *Ecology and Evolution*, 4, 2303–2315. <https://doi.org/10.1002/ece3.1051>.
- Vázquez, D.P., Blüthgen, N., Cagnolo, L. and Chacoff, N.P. (2009) Uniting pattern and process in plant–animal mutualistic networks: a review. *Annals of Botany*, 103, 1445–1457. <https://doi.org/10.1093/aob/mcp057>.
- Vilà, M., Bartomeus, I., Dietzsch, A.C., Petanidou, T., Steffan-Dewenter, I., Stout, J.C. and Tscheulin, T. (2009). Invasive plant integration into native plant-pollinator networks across Europe. *Proceedings of the Royal Society B: Biological Sciences*, 276(1674), 3887–3893. <https://doi.org/10.1098/rspb.2009.1076>.
- Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. et al. (2007) Let the concept of trait be functional!. *Oikos*, 116, 882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>.
- Warring, B., Cardoso, F.C.G., Marques, M.C.M. and Varassin, I.G. (2016) Functional diversity of reproductive traits increases across succession in the Atlantic forest. *Rodriguesia*, 67, 321–333. <https://doi.org/10.1590/2175-7860201667204>.
- Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, 199, 213–227. <https://doi.org/10.1023/A:1004327224729>.
- Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, 3, 385–397. <https://doi.org/10.2307/2389612>.
- Wolowski, M., Carvalheiro, L.G. and Freitas, L. (2017) Influence of plant–pollinator interactions on the assembly of plant and hummingbird communities. *Journal of Ecology*, 105, 332–344. <https://doi.org/10.1111/1365-2745.12684>.
- Zobel, M. (2016) The species pool concept as a framework for studying patterns of plant diversity. *Journal of Vegetation Science*, 27, 8–18. <https://doi.org/10.1111/jvs.12333>.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**Appendix S1.** Research articles on floral trait patterns driven by biotic or abiotic factors in plant communities

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