

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

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17 **Running title:** Floral traits in plant community assembly

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19 **Abstract**

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

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

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

35

36 **Keywords:** community assembly, competition, facilitation, functional diversity, plant-pollinator
37 interactions, reproductive success, trophic interactions

38

40 **1. Introduction**

41 Understanding the rules of community assembly and species coexistence is one of the oldest and
42 most fundamental aims of ecological research (Götzenberger et al., 2012). To date, numerous
43 potential ecological processes have been identified as drivers of species sorting into communities.
44 Among these, abiotic conditions and biotic interactions, as well as dispersal, are generally agreed
45 to have an important role, beside stochastic events (Cornwell, & Ackerly, 2009). Abiotic and biotic
46 processes act as a series of filters, selecting species from a regional species pool into local
47 communities (Zobel, 2016) based on their functional characteristics which make them suitable for
48 the particular habitat (Díaz, Cabido, & Casanoves, 1998). Such characteristics, i.e. “functional
49 traits”, are defined as “*any morphological, physiological or phenological feature measurable at*
50 *the individual level, which impacts fitness indirectly via its effects on growth, reproduction and*
51 *survival*” (Violle et al., 2007). Although, by definition, reproduction is one of the three main pillars
52 of fitness, some reproductive traits, and especially floral traits have only played a minor role in
53 functional trait ecology in general, and in trait based community assembly studies in particular.

54 Traits frequently used in functional ecology are principally those related to the leaf-height-
55 seed (LHS) strategy scheme (Westoby, 1998). These traits are connected to growth and survival,
56 i.e. canopy height determining competitive ability, seed mass affecting dispersal and establishment
57 ability, and specific leaf area defining resource investment. Although these traits are easy to
58 measure and are good proxies for crucial biological functions, they fail to provide information
59 about some of the most important organs and structures involved in sexual reproduction. Floral
60 traits, in this sense, provide a very useful and complementary tool for understanding various
61 reproductive processes (e.g. Karron et al., 2012). Unfortunately, they are generally neglected in

62 functional ecology research which is also reflected by their absence from the most recent handbook
63 of standardized protocols of plant traits (Pérez-Harguindeguy et al., 2013). However we can expect
64 that floral traits may vary in response to both biotic and abiotic drivers (as “response traits”), and
65 affect ecosystem functioning (as “effect traits”, Lavorel, & Garnier, 2002) through providing a
66 connection to other trophic levels (Lavorel et al., 2013).

67 We use the term “floral traits” to refer to characteristics of the flower having a biological
68 function, and an ecological importance by affecting the fitness of the individual. We do not use
69 the term “reproductive traits” to avoid confusion, since this generally includes seed and fruit
70 characteristics, which we do not consider here. As flowers provide the setting for seed and fruit
71 development that, when mature, replace the floral structures, there is also a temporal distinction
72 between the two groups of traits in their general effect on plant fitness. These criteria help to
73 distinguish floral traits (neglected in trait-based plant community studies) from traits that are
74 frequently employed and for which data are widely available, e.g. seed size. Floral traits, in this
75 sense, include traits involved in (i) sexual reproduction ability (as opposed to vegetative
76 reproduction), (ii) cross-pollination vs. self-fertilization potential, and (iii) the physiology,
77 morphology and phenology of flowers or inflorescences and the way they get pollinated (Klotz,
78 Kühn, & Durka, 2002). Although the connection between fitness and floral traits might seem weak
79 in the case of certain species or habitats, in general, during the sexual reproduction phase in the
80 plant’s life cycle, floral traits, such as flower morphology and flowering time, become crucial for
81 maximizing reproductive output (Larson and Funk 2016). In fact, flowering time can have a huge
82 impact on the fitness of several type of species irrespective of their pollination type, as it has been
83 shown that flowering during a time of high resource availability can have a critical benefit for
84 viable seed production (Craine et al 2012). It is important to mention that not all species rely,

85 always, on sexual reproduction and the importance of vegetative propagation could be
86 predominant for certain species and in certain habitat types (Klimešová, Danihelka, Chrtěk, de
87 Bello, & Herben, 2017). However, we hypothesize that a careful selection of floral traits will be
88 relevant for the assembly of plant communities within several vegetation types.

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

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

108 community assembly studies. Finally, we provide a concise list of future steps to overcome data
109 limitations and suggestions for research.

110

111 **2. Approaches used in community level pollination ecology**

112 The field of pollination ecology has a vast array of publications focusing on evolutionary
113 processes, population dynamics and pollination mechanisms of single species or genera. However,
114 few studies have dealt with pollination ecology on the community scale, where the main focus is
115 shifted towards species co-existence patterns and assembly rules of interacting communities of
116 plants and pollinators. It is important to note here that the field of pollination ecology has rarely
117 applied the concept of community ecology on which much of vegetation ecology relies on. In
118 pollination ecology a clade of co-occurring taxa are often considered a community. Though in
119 vegetation ecology, and particularly in community assembly studies, communities consist of all or
120 the majority of species co-occurring in a specific site, regardless of phylogenetic relationships or
121 other criteria. In some cases, pollination studies on a well-defined component of the whole plant
122 community (e.g. only animal pollinated species in network analysis) might also represent a
123 meaningful community-level analyses. In the following sections, we briefly introduce the most
124 common approaches of pollination ecology studies which consider communities (i.e. assemblages
125 of co-existing species in a specified location) as the ecological unit of their research (Figure 1.,
126 Table 1).

127 In recent years the number of pollination network studies increased dramatically (Figure
128 1., Table 1. “A”; e.g., Junker et al., 2013; Junker, Blüthgen, & Keller, 2015; Bennett et al., 2018a).
129 The interaction networks between communities of plants and pollinators (reviewed by Vázquez,

130 Blüthgen, Cagnolo, & Chacoff, 2009 and Knight et al., 2018) offer a perfect study system for
131 understanding mutualistic relationships between trophic levels (Blüthgen, Menzel, Hovestadt,
132 Fiala, & Blüthgen, 2007), and therefore, are strongly constrained by both animal and plant traits
133 (e.g. Junker et al., 2013; Chamberlain et al., 2014; Maglianesi, Blüthgen, Böhning-Gaese, &
134 Schleuning, 2014; Schleuning, Fründ, & García, 2015). Interaction networks combined with
135 functional traits (Figure 1., Table 1. “AB”) can provide a deeper understanding of plant-pollinator
136 trait matching (Sazatornil et al., 2016) and the validity of using pollination syndromes, i.e. whether
137 a certain set of plant traits predetermine the group of potential pollinators (Lázaro, Hegland, &
138 Totland, 2008; Ollerton et al., 2009; Rosas-Guerrero et al., 2014). Evolutionary relationships might
139 also have the potential to explain the structure of pollination networks. On the one hand, pollinators
140 are known to show “clade-specialization”, a preference on more closely related plant species
141 (Vamosi, Moray, Garcha, Chamberlain, & Mooers, 2014), which can be seen as sign of niche
142 conservatism, i.e. closely related species share similar (pollination) niches due to shared
143 evolutionary history (Losos, 2008). On the other hand, in certain plant-pollinator networks,
144 phylogeny might be a weak predictor (Chamberlain et al., 2014).

145 In this rapidly developing field, new analytical tools have been proposed for approaches
146 combining traits, phylogeny and networks (Ibanez, 2012; Ibanez, Lavorel, Puijalon, & Moretti,
147 2013; Rafferty & Ives, 2013; Bastazini et al., 2017; Laigle et al., 2018; Kantsa et al., 2018).
148 Furthermore, methods for comparing networks along environmental and resource gradients
149 (Tinoco, Graham, Aguilar, & Schleuning, 2017; Pellissier et al., 2018), as well as ones explaining
150 non-random community assembly patterns based on network structure (Kemp, Bergh, Soares, &
151 Ellis, 2019) are advancing fast and have a strong potential to contribute to fully addressing the role
152 of traits shaping species interactions and community structures (Figure 1., Table 1. “ABC”).

153 Floral characteristics are one of the most important diagnostic features used in classical
154 taxonomy; thus the assumption of a connection between certain morphological patterns (i.e.
155 number of petals, stamens etc.) and phylogeny is implicit in this study subject. However, such
156 expected niche conservatism of floral traits along phylogenetic trees has been met with very few
157 attempts to explore whether floral traits indeed adhere to conservatism, e.g. through estimating the
158 phylogenetic signal of these traits. Moreover, trait conservatism has been addressed at the
159 community scale, where the phylogeny of the co-occurring species is considered. Although these
160 approaches could help to reveal evolutionary processes driving functional trait-based community
161 assembly (Figure 1., Table 1. “B”), results on this topic are scarce and have hitherto been
162 contradictory. For instance, flower colour had a strong phylogenetic signal among species of a
163 temperate grassland (Binkenstein, Renoult, & Schaefer, 2013), but only a weak signal was found
164 among species growing along an altitudinal gradient in the Himalayas (Shrestha, Dyer, Bhattarai,
165 & Burd, 2014). Junker, et al. (2015) reported a phylogenetic signal for three out of eight different
166 quantitative floral traits, which is the most comprehensive study on the phylogenetic and functional
167 assembly based on floral traits at the community scale to this date. There is some evidence on
168 phylogenetic clustering of floral traits in both small sets of closely related species (trait evolution
169 within phylogenetic clades) and small local communities representing a phylogenetically
170 “dispersed” set of species. However, explicit assessments of larger species pools covering a larger
171 part of the phylogenetic tree and thus including “deeper” nodes (early diversification) are still
172 scarce and conducted only for few vegetative traits (Pennell et al., 2015).

173 The above-mentioned approaches focus on plant-pollinator interactions through analysing
174 patterns in functional traits and phylogenetic relationships between species. However, to date,
175 there are very few published studies to review in a comprehensive way. The above questions and

176 themes are worth exploring further in the future, to shed new light on the ecology of plant-
177 pollinator interactions. Moreover, we must remark that these approaches completely ignore the
178 abiotically pollinated plant species co-existing within the community (Figure 1). Species with
179 different pollination modes might not be relevant in terms of pollination networks, but still have
180 an effect on the abundance and/or fitness of neighbouring plants through competition for abiotic
181 resources (Flacher, Raynaud, Hansart, Motard, & Dajoz, 2015) or through heterospecific pollen
182 transfer (Ashman, & Arceo-Gomez, 2013).

183

184 **3. Floral traits in community ecology**

185 From the plants' perspective the available pool of pollinators can be considered a limiting
186 "resource". Similar to other abiotic resources, pollinator scarcity might have a negative impact on
187 the fitness of the plant, and the pollinators' capacity can be depleted. However, unlike abiotic
188 resources, an increase in plant population size can increase pollinator availability by attracting
189 more pollinators or providing better habitat and thus enhancing the amount and diversity of
190 interactions. It might result, though, also in an increased competition for pollinators. Due to the
191 ambiguity of this feedback, in natural communities both competition and facilitation for pollinators
192 can occur between coexisting plant species (Feldman, Morris, & Wilson, 2004; Pauw, 2013;
193 Benadi, & Pauw, 2018; Pauw, 2018). The presence or absence of given pollinators will thus
194 potentially exert a biotic filtering effect favouring certain types of plants and limiting others within
195 local communities (Wolowski, Carvalheiro, & Freitas 2017). Although studying plant community
196 assembly through floral traits without pollinator observations might not serve as an actual
197 "shortcut" in understanding plant-pollinator patterns, as suggested by Pellissier, Alvarez, & Guisan
198 (2012), it could help us disentangle how plant communities are structured indirectly by this "biotic

199 resource” (Fantinato, Del Vecchio, Giovanetti, Acosta, & Buffa, 2017). Despite this potential,
200 analysing floral traits does not have a long history in the field of community ecology. There have
201 been, however, a growing number of studies published in recent years focusing on floral trait
202 distribution patterns (Kantsa et al., 2017) in response to different abiotic (e.g. altitude, Junker, &
203 Larue-Kontic, 2018) and biotic drivers (Warring, Cardoso, Marques, & Varassin, 2016) on
204 different spatial scales (review on the scale dependency of facilitative processes: Braun, & Lortie,
205 2019).

206 ***3.1. Literature search***

207 We carried out a systematic literature search of studies on plant community assembly and floral
208 traits in Web of Science. Our search terms were (plant* AND (pollinat* OR flower* OR floral*)
209 AND trait* AND communit*) yielding 982 results (last accessed: 22. 02. 2018). While we scanned
210 visually all titles from this list, we focussed more closely on the first 300 papers (ordered by
211 relevance according to Web of Science) which were scanned also by abstract. Among the selected
212 studies we skimmed all references and the context in which they were cited resulting in other
213 potentially relevant articles. We excluded studies on i) populations/“communities” consisting of a
214 limited selection of species (e.g. genera or small clades), ii) evolutionary processes without
215 describing spatial patterns and iii) review, viewpoint/commentary or forum papers, book chapters
216 and theoretical frameworks. The described criteria resulted in 21 studies which were clearly related
217 to empirical studies on community assembly in the broad sense (for a brief summary on the aims
218 of study, floral traits used and most important findings of each paper, see Appendix S1). In the
219 next sections we describe and discuss the papers found in the context of current community
220 assembly theory, in terms of processes shaping species co-existence and functional trait patterns
221 on different spatial scales.

222 *3.2. Local scale*

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

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

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

245 pollinator-sharing leads to competition that can be disadvantageous to at least one of the species
246 involved (reviewed by Mitchell, Flanagan, Brown, Waser, & Karron, 2009). On the one hand,
247 competition for pollinators can cause reduced reproductive success when (i) pollinators are scarce,
248 due to decreased visitation rates (i.e., pollinators are a limiting resource), or (ii) the shared
249 pollinator is common, due to dilution by an increased amount of interspecific pollen transfer
250 (Sargent, & Ackerly, 2008). The effect on the reproductive success of competing partners is highly
251 dependent on the density of conspecific and heterospecific individuals (Benadi and Pauw 2018)
252 and can be modified by other factors, such as the presence of invasive super-attractive flowers
253 (Chittka, & Schürkens, 2001). Moreover, competition between insect and wind pollinated species
254 for abiotic resources can also have a negative impact on insect pollinated species in terms of
255 resource allocation to floral traits involved in pollinator attraction (Flacher et al., 2015). On the
256 other hand, having attractive neighbours might be beneficial, as they can increase the frequency of
257 visitations by shared pollinators (Pellissier et al., 2012), which is most effective when the co-
258 flowering species have similar floral traits or when they are super-generalists (e.g. alien species,
259 Vilà et al., 2009). Another type of trait similarity is quite frequent among food-deceptive orchids
260 (e.g. *Traunsteinera globosa*), which take advantage of and mimic the floral traits of other nectar
261 producing neighbouring plants (in this example *Trifolium pratense*) – often referred to as “magnet”
262 species – thus deceiving pollinators unable to distinguish them (Juillet, Gonzalez, Page, & Gigord,
263 2007). To disentangle the two contrasting mechanisms – competition and facilitation – Mesgaran,
264 Bouhours, Lewis, & Cousens (2017) proposed a model for predicting the optimal density of co-
265 flowering species that is beneficial for a given plant in terms of pollination rate, and found that it
266 is largely dependent on the attractiveness of the neighbours. Besides this modelling approach, in
267 recent years there has been an increase in empirical studies on the density dependence of

268 pollinator-mediated plant-plant interactions in natural communities (e.g. Bergamo, Streher,
269 Traveset, Wolowski & Sazima, 2020).

270 In community ecology, abiotic drivers and biotic interactions shaping species distributions
271 are often inferred from observing functional trait patterns. Non-random trait distribution,
272 convergent (more similar) or divergent (more dissimilar than expected by chance) trait values can
273 indicate which mechanisms and interactions are dominant within the community. According to
274 contemporary coexistence theory (Chesson 2000), species coexistence depends on the stabilizing
275 effect of niche differences when fitness differences between species are small. Although this
276 theory has been exemplified with vegetative plant functional traits (e.g. HilleRisLambers et al.,
277 2012), one can apply the same theory to pollinator mediated plant-plant interactions as well.
278 Coexisting plant species having similar fitness (e.g. similar display size) have similarly high
279 probability of getting pollinated (Hegland, & Totland, 2012). However, a high degree of trait
280 convergence and pollinator sharing increases the probability of receiving heterospecific pollen.
281 Therefore, plant species need to separate their pollination niches in order to coexist in a
282 community. We propose that niche partitioning between similar species can happen via three main
283 mechanisms: (i) partitioning in time by having asynchronous flowering phenology (Oleques,
284 Overbeck, & de Avia, 2017); (ii) partitioning in interaction partners by specialization on particular
285 (groups of) pollinators (e.g. difference in spectral reflectance; McEwen, & Vamosi, 2010; van der
286 Kooi, Pen, Staal, Stavenga, & Elzenga, 2016) or (iii) partitioning in morphology by different pollen
287 placement mechanisms to avoid heterospecific pollen transfer (e.g. anther position, Fantinato et
288 al., 2017). While the above described mechanisms were extensively studied in certain clades and
289 specialized systems (e.g. Muchhala, & Potts, 2007; de Jager, Dreyer, & Ellis, 2011; Muchhala,
290 Johnsen, & Smith, 2014), evidence on diverse multi-clade communities remains scarce. As such

291 mechanisms can result in both convergent and divergent floral trait patterns, one should be cautious
292 when inferring community assembly rules, and attempt to distinguish traits reflecting fitness
293 differences vs. niche differences.

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

302 ***3.3. Biogeographical scale***

303 Local communities are assembled from a larger, regional pool of species via abiotic and biotic
304 filters. Therefore, exploring functional trait patterns on larger biogeographical scales is crucial for
305 understanding these filtering processes and thus local community assembly mechanisms. In the
306 case of floral traits, large-scale patterns were found to be driven by climatic gradients (e.g. Rech
307 et al., 2016), which might cause turnover in pollinator communities (e.g. Devoto, Medan, Roig-
308 Alsina, & Montaldo, 2009), biodiversity patterns (e.g. Ollerton, Winfree, & Tarrant, 2011), as well
309 as geology and/or land-use types (e.g. Kühn, Bierman, Durka, & Klotz, 2006; Binkenstein et al.,
310 2013). On the global scale, the majority of plant species are pollinated by insects and other animals
311 (78% and 94% in temperate and tropical communities, respectively) compared to the number of
312 wind or water-pollinated ones (Ollerton et al., 2011), and only a small proportion are capable of
313 obligate or facultative self-pollination. Another global trend is the increasing specialization of

314 pollination syndromes towards the tropics (Ollerton, Johnson, & Hingston, 2006). However, the
315 driver behind these two trends is still unclear (Schemske, Mittelbach, Cornell, Sobel, & Roy,
316 2009), and the existence of a latitudinal gradient in specialization has recently been questioned
317 (Moles, & Ollerton, 2016).

318 It is generally accepted that pollination other than via animals is selected for when
319 pollinators become scarce or unpredictable (e.g. on islands, Barrett, Emerson, & Mallet, 1996).
320 Therefore, under unsuitable conditions for pollinators, species with alternative reproductive
321 strategies become more abundant. Based on a global community dataset, Rech et al. (2016) showed
322 that the distribution of animal- and wind-pollinated species is non-random, but related to current
323 climatic conditions. Animal-pollination was more dominant in the tropics (warm habitats, closed
324 vegetation with high precipitation), whereas a higher proportion of wind-pollinated species could
325 be found on islands compared to continents (Rech et al., 2016). On the national scale of Germany,
326 Kühn et al. (2006) found that the proportion of wind-pollinated species was most strongly
327 correlated with wind speed and altitude (where, under both conditions, pollinator availability is
328 generally lower) as well as open-vegetation and moist habitats (such as bogs and fens). Dominance
329 of self-pollination was spatially more scattered, especially in areas that included habitats with high
330 disturbance, areas with a high proportion of alien species (e.g. riverbanks) and a high proportion
331 of annual species. It has also been shown that oceanic islands host a surprisingly high proportion
332 of self-compatible species (Lord, 2015; Grossenbacher et al., 2017) which therefore suggests that
333 securing sexual reproduction when the number of potential outcrossing partners is limited is crucial
334 for colonization success in remote locations (Baker 1955).

335 Considering biomes on the global scale, the ratio of outcrossing compared to selfing
336 declines with increasing latitude and is – in some cases – significantly different among major

337 biomes (Moeller et al., 2017). However, these patterns are most likely due to the distribution of
338 life forms rather than a consequence of actual plant-pollinator interactions, as there is a strong
339 correlation between the rate of outcrossing and life form, as expected in general (Michalski, &
340 Durka, 2009).

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

355 During our literature survey, we have found studies predominantly covering small scales
356 with both small extents (i.e. samples cover small geographical areas) and grain sizes (each sample
357 or plot is small, e.g. several square meters; for more on ‘extent’ and ‘grain size’ see Wiens, 1989).
358 In contrast to this, among studies on the biogeographical scale (large extent in general), the
359 majority was sampled having very coarse grain, while studies with high resolution (i.e. fine grain)

360 samples are limited in number, and often not evenly distributed along the studied gradient(s).
361 Studies that investigate patterns at grid cell level (i.e. evenly distributed) or have small grain size
362 but high extent are virtually missing (but see Kühn et al., 2006).

363

364 **4. Availability of floral traits**

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

372 Floral traits are known to have considerable intraspecific variability (e.g. floral tube length,
373 Anderson, Ros, Wiese, & Ellis, 2014, floral scent, Delle-Vedove, Schatz, & Dufay, 2017). This
374 variability should be kept in mind when using database data especially on a small spatial scale.
375 For leaf traits, there is evidence that database data can be a sufficient proxy for on-site
376 measurements of moderately plastic traits such as LDMC, but not always for highly plastic ones,
377 such as canopy height or SLA (Cordlandwehr et al., 2013). Although this has not been studied for
378 the majority of floral traits, flowering phenology (measured as onset of flowering in Julian days)
379 was shown to generally have higher inter-specific than intra-specific variability (Kazakou et al.,
380 2014), therefore can be considered a “stable” trait, even when used as a continuous variable.
381 However, besides trait plasticity, the suitability of database data might also depend on the strength

382 of the environmental gradient (Cordlandwehr et al., 2013) and the spatial scale of the study,
383 therefore calling for even more precautions.

384 Large amounts of floral trait data do exist, but these are mostly scattered or difficult to
385 access. Old monographs (e.g. Müller, 1881, Knuth, 1898, Kugler, 1970, Faegri, & van der Pijl,
386 1979), regional and national floras and other sources of “grey” literature can provide an extensive
387 base for further syntheses of the current knowledge. However, empirical results for quantitative
388 traits, e.g. nectar properties (Baude et al. 2016), will likely need to be collected to achieve
389 consistent data. Despite the potential of these resources, there has been no initiative so far to pull
390 these data together in a standardised way on a common platform, like it has been achieved for
391 other trait groups, such as clonal traits (CLO-PLA, Klimešová, & de Bello, 2009), fine root traits
392 (FRED, Iversen et al., 2017) or seed traits (SID, Royal Botanic Gardens Kew, 2018). Therefore,
393 establishing standards in the measurement of floral traits as well as compiling existing and
394 comparable data for a larger species pool and biogeographical extent (e.g. GloPL, Bennett et al.
395 2018b) is one of the upcoming challenges of this field.

396

397 **5. Conclusions and future research directions**

398 In this synthesis we reviewed predominantly recent studies using floral and pollination-related
399 functional traits on the community scale. We summarised the most common themes and
400 methodological approaches, and pointed to knowledge gaps that could be explored in the future.
401 In general, we find evidence on community level floral trait patterns to be inconsistent, mainly due
402 to the scarcity and heterogeneity (context specificity) of empirical studies, which do not allow
403 general conclusions, neither on the directionality of trait patterns nor on their relative importance

404 compared to other functional traits. We therefore provide here a concise “catalogue” of future
405 directions in exploring floral-trait-based community ecology to improve our understanding of
406 these patterns and processes.

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

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

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

- 419 1. Flower colour, including reflectance and UV patterns (expanding already existing database:
420 FReD, Arnold, Faruq, Savolainen, McOwan, & Chittka, 2010)
- 421 2. Display size, including flower/inflorescence size, number of flowers in inflorescence, number
422 of flowers/inflorescences per square meter
- 423 3. Floral morphology, including nectar tube length and floral symmetry
- 424 4. Positioning of reproductive organs inside the flower in relevance to pollen placement on the
425 pollinator’s body

- 426 5. Floral reward production, sugar content and chemical profile
- 427 6. Floral scent chemical profile
- 428 7. Flowering phenology
- 429 8. Pollination syndrome based on or supplemented by observed pollinator species

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

- 431 1. Phylogenetic signal for floral traits within and across communities (encompassing large
432 species pools) thus enabling the assessment of floral trait clustering/overdispersion in
433 communities and their relation to phylogenetic relationships.
- 434 2. Assessment of whether floral and sexual reproduction traits form an independent axis of plant
435 strategy.
- 436 3. More comprehensive large scale studies both encompassing larger biogeographical extent and
437 higher resolution data.
- 438 4. Pollinator mediated plant-plant interactions – such as competition and facilitation – and how
439 these are governed by abiotic conditions in natural communities.
- 440 5. Experiments on the role of floral traits in trait-based plant community assembly testing
441 hypotheses generated in observational studies. This may necessitate experiments distributed in
442 areas with different pollinator communities in which plant communities with various flower
443 trait combinations are experimentally established and monitored.

444

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450

451 **Author contributions**

452 The study was conceived by L.G. and A.E-V. A.E-V with major contributions from L.G., took
453 leadership in writing the manuscript and the remaining authors contributed substantially to the
454 different versions. All co-authors have read and approved the final version of the manuscript.

455

456 **Data accessibility**

457 This synthesis article does not contain original data.

458

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807 **Supplementary Information**

808 Appendix S1. Short summary of studies resulted from the systematic literature search in Web of
809 Science.

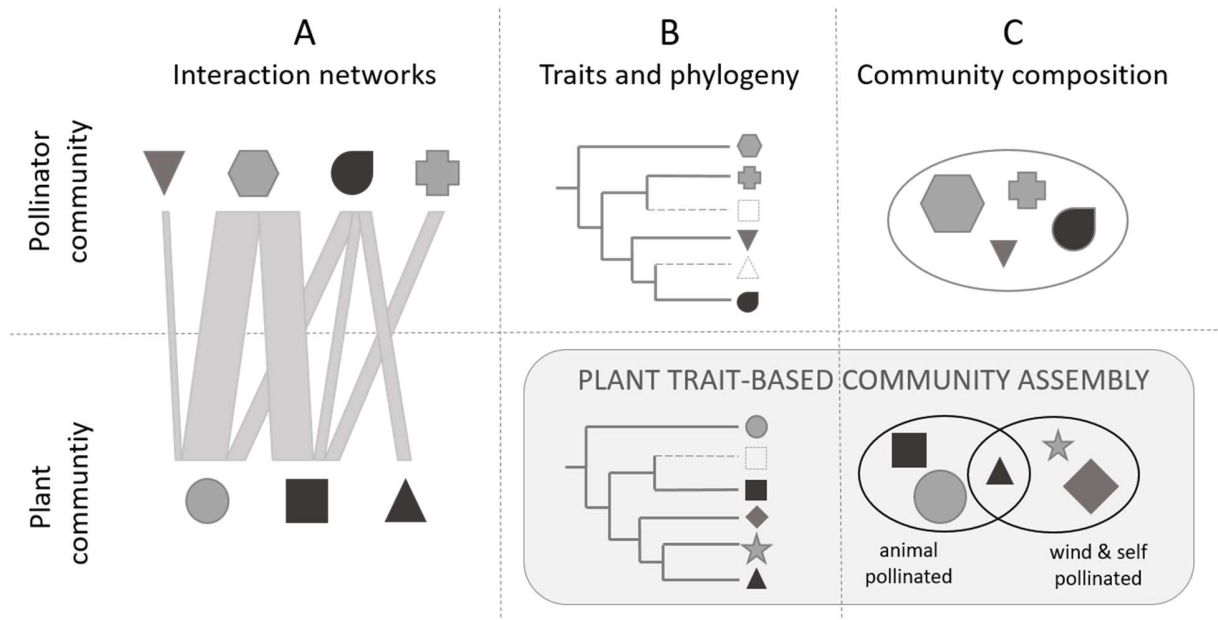
810

811 **Table 1.** Types of methodological approaches used for answering research questions on the
812 importance of floral traits in the structuring of plant (and pollinator) communities, metrics,
813 methodological tools within the R statistical environment (R Development Core Team 2019) and
814 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 λ , 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

815

COMMUNITY SCALE STUDIES



816

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