

Community context determines competition vs. facilitation trade-offs in pollination systems

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9 Abstract

10 Plant-pollinator interactions are commonly viewed as mutualistic. However,
11 plants that share pollinators also compete for effective pollination. The
12 extent of this competition for pollination and its effects on pollination
13 service are poorly understood at the community level; many species interact
14 simultaneously and multiple intertwined factors might play a role (abundance,
15 visitation, traits). By examining comprehensive empirical data, here we
16 show that competition for pollination is pervasive in natural communities
17 and, surprisingly, is only partially influenced by the number of shared
18 pollinators. Furthermore, the factors that most influence the pollination
19 service (abundance and visit effectiveness) also introduce a trade-off between
20 the absolute amount of conspecific pollen received and the amount relative to
21 heterospecific pollen. Importantly, the ways plants balance these trade-offs
22 depend strongly on the community context, as most species showed flexibility
23 in the strategy they used to cope with competition for pollination. Plant-
24 pollinator mutualisms could be better understood as comprising mutualistic
25 and competitive interactions.

26 **Keywords:** interspecific pollen transfer, pollen deposition, pollination costs
27 and benefits, pollination network, pollination niche, and pollinator sharing

28 Introduction

29 Animal pollination plays a disproportionately important role in food pro-
30 duction and maintenance of global biodiversity [1–3]. Alongside the direct
31 benefits of mutualisms between plants and their pollinators, biodiversity can
32 be supported as a result of inter-species “facilitation”—the indirect positive
33 feedback loops that exist between plant species that share pollinators or
34 pollinators that share plants [4–7]. This inter-species facilitation is able to
35 promote species coexistence by offsetting the effects of direct resource com-
36 petition [8]. Indeed, studies at the core of our current theoretical knowledge
37 of mutualisms predict that the maximum number of coexisting species is
38 achieved when the number of shared mutualistic partners is maximised in a
39 community [9].

40 However, in natural communities, plants rarely share all available pollinators.
41 One explanation is that plants are effectively competing for mutualistic part-
42 ners because there is a trade-off between the benefits gained from maximising
43 the number of partners and the costs of sharing them with other plant species
44 [10]. It has been clear for a long time that when competition for pollination
45 is strong enough, these costs can make pollination detrimental to plants’
46 fitness [11–13]. In fact, it can be sufficient to drive ecological differentiation
47 [14,15]. However, it is less clear how exactly this ecological differentiation
48 may, in turn, favour (or hinder) the pollination service.

49 There are two main mechanisms through which competition for pollinators
50 can affect plant fertilization [16]. The first is by changes in intraspecific pollen
51 transfer. This happens, for example, when plants with more attractive flowers
52 might reduce the number of visits to those less of attractive neighbouring
53 plants, and hence reduce the amount of *conspecific pollen* deposited by
54 animals [17]. The second is via interspecific pollen transfer and occurs
55 when plants share pollination partners. In that case, even receiving a visit

56 might not necessarily translate into fertilization [18] because a focal plant
 57 might receive *heterospecific pollen* or because pollen from the focal plant
 58 might be lost to different species. Naturally, the precise effects on plant
 59 fitness of conspecific and heterospecific pollen deposition depend on the
 60 species involved (and are unknown for many plant species). However, there
 61 is substantial evidence supporting the link between pollen deposition and
 62 seed production; in particular for the detrimental effect of heterospecific
 63 pollen deposition on plant fitness [19,20]. All together, provided pollen is
 64 viable and compatible [21–23], the higher the quantity of conspecific pollen
 65 and its purity (relative to heterospecific pollen), the better the pollination
 66 service received by the focal plant. As such, measuring conspecific and
 67 heterospecific pollen deposition provides a good indication of the potential
 68 levels of facilitation and competition a plant population might experience.

69 By definition, these two mechanisms of competition, intra and interspecific
 70 pollen transfer, occur at the community scale. However, with few exceptions
 71 [24,25], most of what we know about them and their relationship with key
 72 ecological factors is based on studies with two plant species. That is partly
 73 so because, at the community scale, the factors that determine the patterns
 74 of pollen deposition are tightly intertwined, operate simultaneously, and may
 75 lead to emergent phenomena not observed at smaller scales [26]. For instance,
 76 recent empirical evidence suggests that plants with flowering traits that are
 77 “original” relative to others in the community generally have fewer interaction
 78 partners [27]. This evidence is aligned with the notion that a species that
 79 interacts with few species does so strongly with each of them whereas a
 80 species that interacts with a large number of species does so comparatively
 81 weakly [28–30]. If evolutionary specialisation occurs by changing traits to
 82 focus on fewer but better partners [15], we should expect a reduction of
 83 competition for pollinators in species with “original” traits and an increase
 84 of competition in species with a large number of interaction partners [31,32].

85 Alternatively, it might also be the case that abundance (for example in terms
86 of flower or pollen counts) is the dominant force driving pollen transfer [33].
87 Abundant plant species might experience a dilution of available pollinators
88 [34,35] but might also receive more effective visits by capitalising on a larger
89 share of both visits and the pollen carried by pollinators. In this case, a
90 potential reduction in the absolute amount of conspecific pollen received
91 could be compensated by an increase in the amount of conspecific pollen
92 relative to heterospecific pollen. Altogether, it is clear that these ecological
93 factors can indeed shape pollen deposition at the community level. However,
94 their relative importance and how exactly they can minimise competition
95 for pollination—or equivalently, maximise facilitation—in plant populations
96 (across species and communities) has not been determined.

97 Here, we investigate the balance between competition for pollination and
98 facilitation at the community scale using empirical data from eleven plant-
99 pollinator communities in the Argentinian Pampas. First, we estimate the
100 extent to which the net outcome of plants sharing pollinators is facilitation
101 or competition. If facilitation is the primary outcome, we could expect
102 an overall positive relationship between the amount of conspecific pollen
103 deposited in stigmas and the amount of heterospecific pollen [24]. The higher
104 the deposition of conspecific pollen relative to heterospecific, the larger the
105 slope of this relationship. Second, we investigate the relative contribution
106 that four ecological factors have to the pollination service. Specifically, we
107 hypothesize that the quantity and purity of conspecific pollen deposition
108 should decrease for plants that share many pollination partners. However, we
109 also hypothesize that other factors like the plant’s functional originality, its
110 relative floral abundance, and the visit potential should have the potential to
111 compensate for this increase in competition. Third and finally, we examine
112 how much the community context influences the way plants use these factors
113 to minimise competition/maximise facilitation. We use these four ecological

114 factors as a proxy of the realised pollination niche of a plant species in
115 their community. Although some plant species might be widespread across
116 multiple locations, competition for pollinators occurs at the community level
117 and hence we predict that pollination niche will be influenced by the local
118 context. If plant strategy is not flexible across the communities in our study,
119 we could expect niches to be more similar within species than across species.
120 On the contrary, if a species' strategy is flexible, we should expect plants to
121 be able to occupy different niches in each community such that intraspecific
122 competition could ultimately be minimised regardless of the context.

123 **Methods**

124 We collected data from eleven co-flowering plant communities and their
125 pollinators in three locations in the Argentinian Pampas. In each location,
126 we sampled two restored and two agricultural fragments, except in one
127 located in the Flooding Pampas, where we were only able to sample one
128 restored fragment due to the lack of available sites.

129 **Competition vs. facilitation**

130 Our first objective was to identify whether the net outcome of plants sharing
131 pollinators at the community level is facilitation or competition. To do
132 that we examine the relationship between heterospecific and conspecific
133 pollen deposited in plant stigmas [24]. This is because heterospecific pollen
134 can be seen as an unavoidable cost that plants must pay for receiving
135 conspecific pollen from shared pollinators. A negative relationship (when
136 shared pollinators increase heterospecific pollen loads and decrease conspecific
137 loads) may indicate that competition for pollination is strong. In contrast,
138 a positive relationship is what would be observed when facilitation is the
139 dominant outcome.

140 **Data collection**

141 In each of the studied communities, we quantified pollen deposition in a subset
142 of plant species between December 2010 and February 2011. This subset
143 comprised between three and nine common insect-pollinated (entomophilous)
144 plant species that were flowering during the sampling period. Based on
145 data from previous years [36], we chose plant species such that they cover
146 a wide range on a specialization-generalization gradient as well as a wide
147 range of abundances. In each of the selected plants, we removed all flowers
148 leaving only buds that were expected to go into florescence on the next day.
149 Two days after flowering, we collected all remaining flowers and counted the
150 number of conspecific and heterospecific pollen grains in their pistils. More
151 details can be found in [37].

152 **Data analysis**

153 To evaluate the relationship between heterospecific and conspecific pollen,
154 we used a generalised linear mixed model (GLMM) with a Poisson error
155 distribution [24]. In this model, the number of conspecific pollen grains per
156 flower was the response variable and the number of heterospecific grains the
157 predictor variable (the log number of stigmas sampled was added as an offset
158 term). The slope and intercept of this relationship were allowed to differ
159 between populations (plant species \times community), which were modelled as
160 a random effect. Models were fitted using the function `glmer` from the R
161 package `lme4` 1.1-19 [38]. A positive slope for a plant population indicates
162 facilitation while a negative slope competition [24].

163 **Factors affecting quantity and purity of pollination service**

164 Our second objective was to investigate the relative contribution that different
165 ecological factors have on the mechanisms of pollinator-mediated competition.

166 Generally speaking, we expect that any factor that increases the amount
167 of conspecific pollen deposited in stigmas, both in quantity and purity
168 relative to heterospecific pollen, also has a positive effect on the pollination
169 service. Specifically, we investigated the effect of (i) a plant's number of
170 shared pollinator species, (ii) a plant's abundance relative to the rest of
171 the community, (iii) the mean visit potential—a metric that combines the
172 amount and type of pollen carried by floral visitors and the number of visits
173 it receives from them, and (iv) the plant's functional originality [39]. See
174 *Data Analysis* section below for more details on these four factors.

175 **Data collection**

176 To obtain the number of shared pollinators for each species, we collected data
177 to construct qualitative and quantitative pollination networks. Qualitative
178 networks were constructed based on ten-hour observations of floral visits
179 in each fragment. Quantitative networks were constructed using two 50 m
180 randomly located transects in each fragment. We counted and collected all
181 floral visitors found in a 2 m wide strip while walking at a pace of 10 m
182 per minute [36,40]. We visited the transects each month between November
183 2010 and March 2011. To obtain floral abundance, we counted all units of
184 floral attraction found during an independent sampling of the same transects
185 used to construct the quantitative visitation networks. To estimate visit
186 potential, we need to construct pollen transfer networks in addition to the
187 visitation networks. To do this, we examined the pollen loads present on
188 the floral visitors collected [41]. When the pollen count on an individual
189 animal was estimated to be less than 2,000 grains, we identified every grain
190 to the species level when possible and to pollen complexes when it was not.
191 When the pollen count was above 2,000 grains, we classified approximately
192 50% of pollen and total pollen counts were extrapolated [42]. Finally, we
193 also recorded morphological traits that relate to plant type (herb, shrub,

194 climber), life cycle (annual, perennial), flower colouration, phenology, and
195 whether the species is native in the study region. More details can be found
196 in Marrero *et al.* (2014 and 2017).

197 **Data analysis**

198 To investigate the impact of ecological factors on pollination services, we
199 used two sets of linear mixed models (LMM) with bootstrap resampling.
200 The response variables for these model sets were the number of conspecific
201 and heterospecific pollen grains deposited per stigma in flowers open to
202 animal-mediated pollination. We used LMMs in which pollen loads were
203 log-transformed because these models offered a better fit than equivalent
204 GLMMs with Poisson (or quasi-Poisson) error structure. Models were fitted
205 using the R package `nlme` 3.1-131 [43].

206 Because the amount of deposited pollen can vary widely across species, and
207 potentially also across communities, we evaluated two possible structures for
208 the random effects: one that includes a random intercept for plant species,
209 and one that treats measures from species across different communities
210 independently. We selected the best random structure by comparing the
211 median Akaike Information Criterion for small samples (AICc).

212 As fixed predictors in the models, we included the four ecological factors
213 described above. Specifically, we calculated the number of shared pollinators
214 for each plant species by pooling data from the qualitative and quantitative
215 pollination networks. To calculate the plants' relative floral abundance in
216 their community, we aggregated floral counts for each species. We then
217 calculated the mean visit potential of pollinator species i to plant species j
218 as

$$o_{ij} = \frac{v_{ij} p_{ji}}{v_i p_j}$$

219 , where v_{ij} is the observed number of visits by i to j , p_{ji} is the number of

220 pollen grains from j attached to i , v_i is the total number of visits performed
221 by i , and p_j is the total number of grains carried by j . We log-transformed
222 the number of shared pollinators, floral abundance, and visit potential before
223 including them in the model.

224 Finally, functional originality is defined as the distance of a species from the
225 community trait average—the centroid of functional space of the community
226 [27,39]. To include phenological variation, we treated floral abundance in
227 each of the survey months (November to March) as a “trait” in our analysis.
228 To account for the non-independence of floral counts and weight all traits
229 equally, we assigned a weight of 1/5 to these abundances (one for each month).
230 We scaled all traits prior to calculating the centroid of the functional space
231 and calculated the species-specific functional coordinates using the R package
232 FD 1.0–12 [44]. Finally, we scaled all four factors to have a zero mean and
233 unitary variance.

234 To estimate the coefficients, perform model selection, and quantify the
235 associated uncertainty, we used a combination of multi-model inference and
236 bootstrap resampling with 99 replicates. First, we performed model selection
237 using the AICc and determined the likelihood of each candidate model (a
238 particular combination of predictors) by calculating the median ΔAICc
239 (relative to the most likely model) for each bootstrap sample. As we wanted
240 model coefficients from more likely candidate models to carry more weight
241 in our results, we sampled the coefficients for our factors proportionally to
242 the likelihood of their candidate model. Finally, we used these distributions
243 of the model coefficients to estimate their mean impact on the pollination
244 service (in terms of quantity and purity of conspecific pollen deposition).

245 Flexibility of plant strategies

246 Our last objective was to tease apart the plant strategies that might reduce
247 competition and, importantly, how the community context influences these
248 strategies. If community context plays a relatively small role or the species
249 strategy is inflexible, we would expect plants of the same species to fill
250 similar pollination niches across different communities. Alternatively, if the
251 community plays a large role and/or plant strategies are flexible, we should
252 be able to observe differences in the realised niche a plant species occupies
253 across communities. To test this, we first used a principal component analysis
254 (PCA) of the four ecological factors (number of shared pollinators, floral
255 abundance, visit potential, and trait originality). We scaled factors across
256 the whole study to ensure that the PCA space does not change according
257 to the species present in each community. We define a species' niche in
258 a community as its coordinates in PCA space. For each species that was
259 present in two or more communities, we then calculated (*i*) the median
260 distance between the strategies that the species uses in different communities
261 and (*ii*) the area of the convex hull defined by these points in the first two
262 principal components (only for species present in three or more communities).
263 We then compared the magnitude of these two metrics to those obtained
264 with 99 Monte Carlo randomizations in which we replaced the strategy of
265 the focal plant species by that of another randomly selected species in the
266 dataset.

267 Results

268 Competition vs. facilitation

269 We first examined the degree of facilitation/competition in natural commu-
270 nities. Specifically, we examined the slope of the relationship between the

quantities of heterospecific and conspecific pollen deposited on stigmas of each species in a community. Overall, we found that neither net facilitation nor net competition dominates (Table S1). Indeed, we found that the proportions of species that experienced a statistically significant positive or negative relationship between heterospecific and conspecific pollen were very similar (35% and 37%, respectively; Fig. 1; Table S2). Most of the variation between plants in a facilitation-competition gradient was driven by differences *between* species; however, we also observed some important differences *within* species. For instance, six of the species sampled across multiple communities (*Carduus acanthoides*, *Cirsium vulgare*, *Cypella herbortii*, *Diplotaxis tenuifolia*, *Hirschfeldia incana*, and *Verbena intermedia*) showed evidence that the same species, can experience facilitation (positive relationships) in some communities and competition (negative relationships) in others. Interestingly, although there was wide variation in the slope of the relationship between heterospecific and conspecific pollen, almost all plants had more conspecific than heterospecific pollen deposited on their stigmas (Fig. S1).

Factors affecting quantity and purity of pollination service

We then examined the potential roles played in pollen deposition by four ecological factors (number of shared pollinators, abundance, mean visit potential, and functional originality). We found that our models of pollen deposition had high explanatory power (the coefficient of determination R^2 ranged between 0.76 and 0.93) although a large portion of the explanatory power came from the random effects (Table S3). As determined by AICc, the random structure best supported by the data was the one that fit an intercept for each species in each community (as opposed to a common intercept for each species irrespective of the community to which they belong). This structure was best for both the models of conspecific and heterospecific

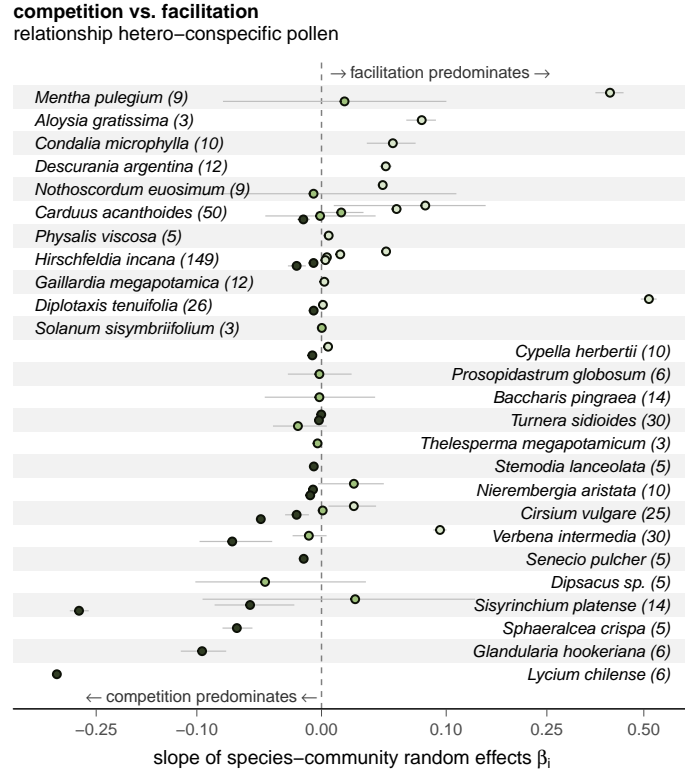


Figure 1: Competition vs. facilitation at the community level. Points indicate the estimated slopes for the relationship between the amount of heterospecific and conspecific pollen deposited per stigma across species in each of their communities. Statistically significant negative slopes (darkest shade) indicate that plants experience net competition for animal-mediated pollination, while significantly positive slopes (lightest shade) indicate that net facilitation is the predominant outcome. The number of plants analysed for each species is shown within brackets next to the species name. Error bars correspond to \pm the standard error (SE).

299 pollen (Table S4).

300 Of the four factors we considered, we found that a plant's mean visit po-
301 tential and relative floral abundance were the most important at predicting
302 pollen deposition in plant stigmas (Fig. 2a). Surprisingly, the number of
303 shared pollinators was comparatively unimportant, particularly for models
304 of heterospecific pollen deposition, as it was only ever included in models
305 with relatively large AICc values (Table S5).

306 We found that the relationship between each of the ecological factors and
307 pollen deposition was similar for both conspecific and heterospecific pollen.
308 That is, strategies that were associated with an increase in conspecific pollen
309 were also associated with an increase in heterospecific pollen deposition.
310 Specifically, the plants' mean visit potential had a positive effect on pollen
311 deposition (Fig. 2b). However, the effect size was slightly larger for het-
312 erospecific than for conspecific pollen. This indicates that, although there
313 is a positive association between visit potential and the quantity of pollen
314 deposition, there is a negative relationship with its purity (Fig. 2c). In
315 contrast, a plants' relative floral abundance negatively affected its deposition
316 quantity, but the mean difference between the coefficients in the models
317 indicates a positive association with purity (Fig. 2c). The third most impor-
318 tant factor, functional originality, had a positive, although comparatively
319 smaller, association with both the quantity and purity. Finally, the number
320 of shared pollinators had negative and neutral associations with conspecific
321 and heterospecific pollen, respectively, but these impacts were small when
322 compared to the other factors. Although the ecological factors were positively
323 correlated (Fig. S2), the collinearity between predictors did not qualitatively
324 affect our findings (Fig. S3).

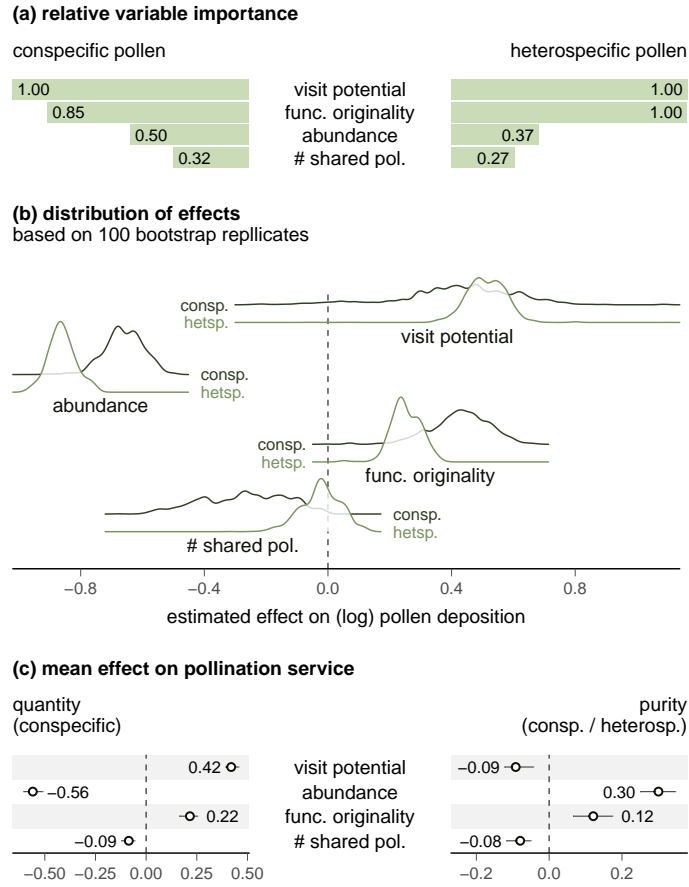


Figure 2: Effect of ecological factors on the pollination service. (a) The plant's visit potential and relative floral abundance are the most important factors determining the deposition of conspecific and heterospecific pollen. Meanwhile, the number of shared pollinators was generally less important. The graph shows the relative importance calculated as the sum of the Akaike weights of the candidate models that included the selected factor. (b) The association between ecological factors and heterospecific pollen tended to align with their association with conspecific pollen. Visit potential and functional originality had a positive association with pollen deposition, while floral abundance and the number of shared pollinators had a negative association. The plot shows the distribution of the effects (across 99 bootstrap replicates) of the four ecological factors for conspecific and heterospecific pollen. (c) The end result of these associations is that only the plants' functional originality has a positive impact on both the quantity and purity of conspecific pollen deposition (relative to heterospecific pollen). The plot shows the model averaged mean effect (\pm SE of 99 bootstrap replicates).

325 **Flexibility of plant strategies**

326 We used a PCA of the analysed species to investigate whether plants' re-
327 alised pollination niche is similar across communities or whether they are
328 flexible and therefore a reflection of the community context. The first two
329 PCA components explained 75% of the total variance (Fig. 3a). The first
330 component was dominated by visit potential and relative abundance while
331 the second component was dominated by the number of shared pollinators
332 and the plant's functional originality. When we locate the species that were
333 sampled in more than one community in the first two PCA components (Fig.
334 3b), we observe that the niches of any given species do not tend to be close
335 to each other. Indeed, when we measured the median distance between the
336 plants' coordinates, we found that it was only significantly smaller than that
337 of randomisations for only two of the twelve species analysed (Fig. 3c).

338 **Discussion**

339 Our results suggest that community context plays a central role in deter-
340 mining the net cost or benefit of sharing pollinators. First, we found that
341 pollinator sharing can lead to both net facilitative and net competitive effects
342 to plant species in a community. Second, we found that multiple ecological
343 factors can modulate the intensity of competition; however, conspecific and
344 heterospecific pollen deposition are tightly coupled and this creates a clear
345 trade-off between the quantity and purity of pollination [45]. Third, we
346 found that the way these factors influence competition is strongly shaped by
347 the community context. That is, if these factors collectively define a species'
348 pollination niche, the same plant species can occupy dramatically different
349 niches depending on the community to which it belongs.

350 The criterion we used to identify the effect of animal-mediated pollination
351 suggested that neither facilitation nor competition are dominant in polli-

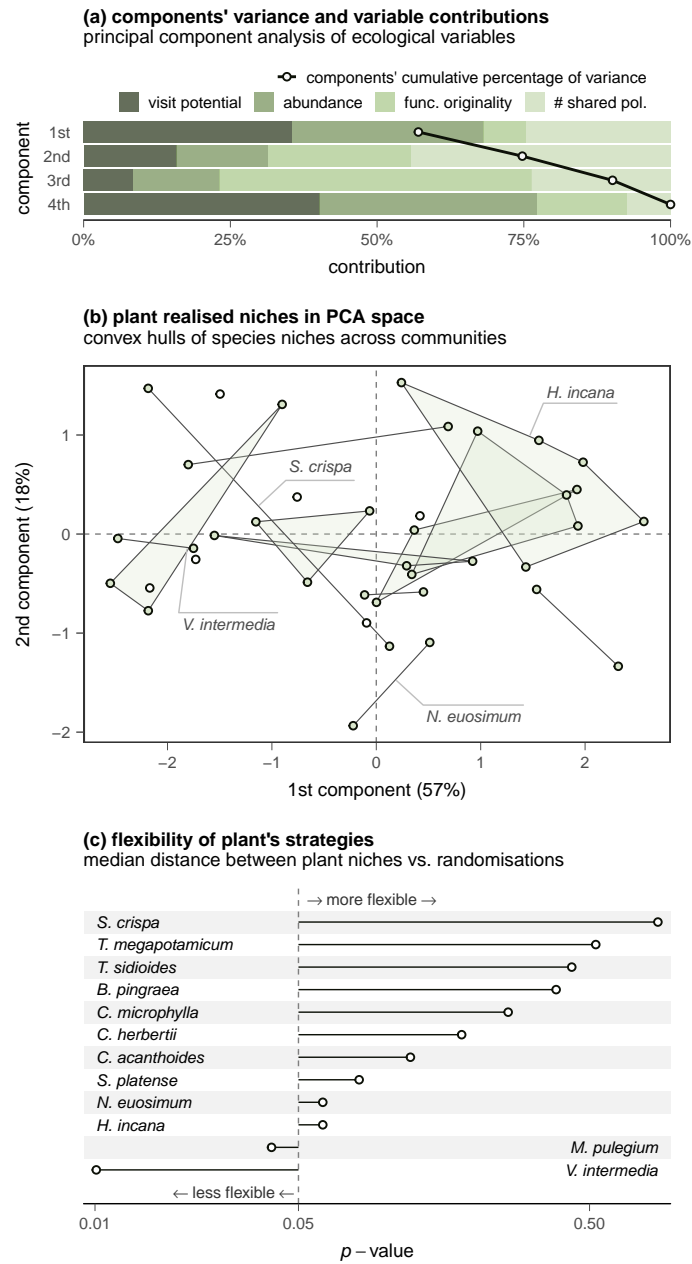


Figure 3: The flexibility of plant strategies. (a) The two first components explain a large proportion of the total variance. (b) When plants that were sampled in more than one community are plotted in terms of these two components, we observe that their points, which represent the strategy (the particular combination of ecological factors) of that species in its community, do not seem to be grouped by plant species. (c) This was confirmed using Monte Carlo randomizations of the median distance between strategies of a plant species. Only two of the examined species had strategies that were less flexible than would be expected at random.

nation communities. A previous study showed that, in diverse pollination
 communities, sharing pollinators does not necessarily translate to net com-
 petition [24]. The overall extent of facilitation/competition of pollination
 communities can depend on factors like the adversity of the environment
 [24,46] or how disturbances affect pollinator populations [47]. However, why
 some species experience more competition than others was not understood.
 Although we were unable to measure the fitness outcomes, here we show that
 the coexistence of facilitative and competitive effects of animal-mediated
 pollination can be at least partially explained by trade-offs in the pollination
 service—both the short and the long term. These trade-offs arise when plants
 simultaneously maximise the deposition of conspecific pollen and minimise
 that of heterospecific pollen.

In the short term, being a specialist and sharing no pollinators might reduce
 competition [48] and hence be preferable, not only due to costs to male fitness
 [16,49], but also because, as we show here, sharing pollinators reduces both
 the quantity and purity of the conspecific pollen deposited. However, over
 long periods of time, there could be a risk associated with a specialist plant
 having few pollinators [50]. To ensure long-term survival, it is thus likely
 that plants also need to balance this risk with the costs of sharing pollinators
 [51]. One possible solution is to share pollinators *and* have original traits—as
 we show that trait originality is generally beneficial to pollen deposition and
 it is commonly thought that species that are further from others in trait
 space benefit from reduced competition. Yet, there are two possible caveats
 to this strategy that highlight the interrelatedness of the ecological factors.
 First, in a mutualism context, it is also possible that trait originality could
 come at the cost of being less ‘apparent’ to pollinators [52]. Second, the
 negative relationship between originality and generalism [32] has been shown
 to depend on plant abundance [27], with generalist species being able to
 also have original traits only when they are abundant enough to provide a

381 valuable reward to make visiting worthwhile to pollinators.

382 Visit potential (high pollen and visits) and floral abundance, which were
383 the most important predictors of pollen deposition here, introduced an
384 even more explicit trade-off between gaining conspecific pollen and avoiding
385 heterospecific pollen. Receiving high visitation increases conspecific pollen
386 deposition but increases heterospecific pollen deposition to a greater extent—
387 even when the visitors are likely to carry a high proportion of conspecific
388 pollen [53]. Contrastingly, being abundant reduces the amount of conspecific
389 pollen deposited and simultaneously reduces heterospecific pollen at a faster
390 rate. Our results corroborate the importance that two-species studies have
391 ascribed to visitation and abundance [16,35,54], but they also suggest that
392 [55] balancing the pros and cons of sharing pollinators at the community
393 level is not trivial and might even be partially responsible for the diversity
394 of plant-pollinator communities [56].

395 We observed, as expected, that the effects of pollen deposition can vary
396 widely among species. For instance, while the fitness of some plant species
397 can be hurt even by low amounts of heterospecific pollen, for others, fitness
398 can instead be limited by the amount of conspecific pollen [18,57]. Alter-
399 natively, plant species can also differ substantially in the extent to which
400 self- vs. outcross-pollen differ in their value for fertilization. The difference
401 can be particularly relevant for species that are not self-fertile or those in
402 which self-fertilization is rarely effective due to a temporary separation in
403 the maturation of the sexes (dichogamy).

404 Importantly, we show here that the balances between costs and benefits
405 are determined not only by species identity but also by the community to
406 which plants belong. Specifically, most plant species appear to be flexible
407 enough to adopt markedly different niches in different communities. From an
408 evolutionary perspective, our results suggest that selection for a particular
409 strategy might say something about the community in which a species has

typically inhabited during its evolutionary history. Furthermore, from a more applied perspective, flowering plants are sometimes introduced to attract pollinators on other nearby plants. On the one hand, our results suggest that introduced plants that increase the relative originality of natives (e.g. through distinct phenology) might have positive effects [31]. On the other, because different niches can lead to different outcomes across communities, our results also highlight the difficulties involved in predicting whether the introduced plant species will facilitate or compete with neighbours [58]. Other factors that we were unable to measure (e.g. pollinator behaviour and densities or the spatial context) have also been shown to play a role in the outcome of animal-mediated pollination [26,45,59,60]. Nevertheless, our results indicate that the strategies a plant might use to successfully minimise competition for pollination (or maximise facilitation) must be determined relative to other species in the community, rather than an absolute property of the species itself.

Overall, pollination communities might not necessarily be the paradigmatic mutualistic communities we often believe. Instead, we confirm that plant competition is pervasive in pollination communities. The potential strategies to minimise competition are likely to involve strong trade-offs in the pollination service both in the short and long-term. Most remarkably, despite large differences in the quantity and purity of conspecific pollen deposition among species, our results provide solid evidence that competition for pollination is inherently a community process and the same species can occupy different niches in different communities. Many of the widely used theoretical models of plant-pollinator communities do not account for the negative effects of sharing pollinators [61]. However, achieving a better understanding of species coexistence and how plant biodiversity is supported by pollination communities will require seeing them as both mutualistic and competitive communities [62].

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