

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

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20 Abstract

21 Plant-pollinator interactions are commonly viewed as mutualistic. However,
22 plants that share pollinators also compete for effective pollination. The
23 extent of this competition for pollination and its effects on pollination
24 service are poorly understood at the community level; many species interact
25 simultaneously and multiple intertwined factors might play a role (abundance,
26 visitation, traits). By examining comprehensive empirical data, we confirm
27 that competition for pollination is pervasive and is only partially influenced
28 by the number of shared pollinators. Furthermore, the factors that most
29 influence the pollination service (abundance and visit effectiveness) also
30 introduce a trade-off between the absolute amount of conspecific pollen
31 received and the amount relative to heterospecific pollen. Most importantly,
32 the ways plants balance these trade-offs depend on the community context,
33 as most species showed flexibility in the strategy they used to cope with
34 competition for pollination. Plant-pollinator mutualisms could be better
35 understood as comprising mutualistic and competitive interactions.

36 Introduction

37 Animal pollination plays a disproportionately important role in food produc-
38 tion and maintenance of global biodiversity (Bascompte & Jordano 2007;
39 Klein *et al.* 2007; Ollerton *et al.* 2011). Alongside the direct benefits of mu-
40 tualisms between plants and their pollinators, biodiversity can be supported
41 as a result of inter-species “facilitation”—the indirect positive feedback loops
42 that exist between plant species that share pollinators or pollinators that
43 share plants (Moeller 2004; Ghazoul 2006; Molina-Montenegro *et al.* 2008;
44 Liao *et al.* 2011). This inter-species facilitation is able to promote species
45 coexistence by offsetting the effects of direct resource competition (Stachow-
46 icz 2001). Indeed, studies at the core of our current theoretical knowledge
47 of mutualisms predict that the maximum number of coexisting species is
48 achieved when the number of shared mutualistic partners is maximised in a
49 community (Bastolla *et al.* 2009).

50 However, in natural communities, plants rarely share all available pollinators.
51 One explanation is that plants are effectively competing for mutualistic part-
52 ners because there is a trade-off between the benefits gained from maximising
53 the number of partners and the costs of sharing them with other plant species
54 (Waser 1978). It has been clear for a long time that when competition for
55 pollination is strong enough, these costs can make pollination detrimental to
56 plants’ fitness (shown both experimentally and theoretically; Robertson 1895;
57 Lewis 1961; Levin & Anderson 1970). In fact, it can be sufficient to drive
58 ecological differentiation (Caruso 2000; for example by driving the evolution
59 of both traits and reproductive strategies; Mitchell *et al.* 2009). However, it
60 is less clear how exactly this ecological differentiation may, in turn, favour
61 (or hinder) the pollination service.

62 There are two main mechanisms through which competition for pollinators
63 can affect plant fertilization (Morales & Traveset 2008). The first is by

64 changes in intraspecific pollen transfer. This happens, for example, when
65 plants with more attractive flowers might reduce the number of visits to
66 those less of attractive neighbouring plants, and hence reduce the amount
67 of *conspecific pollen* deposited by animals (Yang *et al.* 2011). The second
68 is via interspecific pollen transfer and occurs when plants share pollination
69 partners. In that case, even receiving a visit might not necessarily translate
70 into fertilization (Campbell & Motten 1985) because a focal plant might
71 receive *heterospecific pollen* or because pollen from the focal plant might be
72 lost to different species. Generally speaking, provided pollen is viable and
73 compatible (de Jong *et al.* 1992; Dafni & Firmage 2000; Ramsey & Vaughton
74 2000), the higher the quantity of conspecific pollen and its purity (relative
75 to heterospecific pollen), the better the pollination service received by the
76 focal plant. By definition, these two mechanisms of competition occur at the
77 community scale. However, with few exceptions (Aizen & Rovere 2010; Tur
78 *et al.* 2016), most of what we know about them and their relationship with
79 key ecological factors is based on studies with two plant species.

80 That is partly so because, at the community scale, the factors that determine
81 the patterns of pollen deposition are tightly intertwined, operate simultane-
82 ously, and may lead to emergent phenomena not observed at smaller scales
83 (Flanagan *et al.* 2011). For instance, recent empirical evidence suggests
84 that plants with flowering traits that are “original” relative to others in the
85 community generally have fewer interaction partners (Coux *et al.* 2016).
86 This evidence is aligned with the notion that a species that interacts with few
87 species does so strongly with each of them whereas a species that interacts
88 with a large number of species does so comparatively weakly (Bascompte *et*
89 *al.* 2006; Vázquez *et al.* 2007; Thébault & Fontaine 2008). If evolutionary
90 specialisation occurs by changing traits to focus on fewer but better partners
91 (Caruso 2000), we should expect a reduction of competition for pollinators in
92 species with “original” traits and an increase of competition in species with

93 a large number of interaction partners (Gibson *et al.* 2012; Carvalheiro *et al.*
94 2014). Alternatively, it might also be the case that abundance (for example in
95 terms of flower or pollen counts) is the dominant force driving pollen transfer
96 (Seifan *et al.* 2014). Abundant plant species might experience a dilution of
97 available pollinators (Feinsinger 1987; Feldman *et al.* 2004) but might also
98 receive more effective visits by capitalising on a larger share of both visits and
99 the pollen carried by pollinators. In this case, a potential reduction in the
100 absolute amount of conspecific pollen received could be compensated by an
101 increase in the amount of conspecific pollen relative to heterospecific pollen.
102 Altogether, it is clear that these ecological factors can indeed shape pollen
103 deposition at the community level. However, their relative importance and
104 how exactly they can minimise competition for pollination—or equivalently,
105 maximise facilitation—in plant populations (across species and communities)
106 has not been determined.

107 Here, we investigate the balance between competition for pollination and
108 facilitation at the community scale using empirical data from eleven plant-
109 pollinator communities in the Argentinian Pampas. First, we estimate the
110 extent to which the net outcome of plants sharing pollinators is facilitation or
111 competition. If facilitation is the primary outcome, we could expect an overall
112 positive relationship between the amount of conspecific pollen deposited in
113 stigmas and the amount of heterospecific pollen (Tur *et al.* 2016). The higher
114 the deposition of conspecific pollen relative to heterospecific, the larger the
115 slope of this relationship. Second, we investigate the relative contribution
116 that four ecological factors have to the pollination service. Specifically, we
117 hypothesize that the quantity and purity of conspecific pollen deposition
118 should decrease for plants that share many pollination partners. However, we
119 also hypothesize that other factors like the plant’s functional originality, its
120 relative floral abundance, and the visit effectiveness should have the potential
121 to compensate for this increase in competition. Third and finally, we examine

122 how much the community context influences the way plants use these factors
123 to minimise competition/maximise facilitation. We use these four ecological
124 factors as a proxy of the realised pollination niche of a plant species in
125 their community. Although some plant species might be widespread across
126 multiple locations, competition for pollinators occurs at the community level
127 and hence we predict that pollination niche will be influenced by the local
128 context. If plant strategy is not flexible across the communities in our study,
129 we could expect niches to be more similar within species than across species.
130 On the contrary, if a species' strategy is flexible, we should expect plants to
131 be able to occupy different niches in each community such that intraspecific
132 competition could ultimately be minimised regardless of the context.

133 **Methods**

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

139 **Competition vs. facilitation**

140 Our first objective was to identify whether the net outcome of plants sharing
141 pollinators at the community level is facilitation or competition. To do that
142 we examine the relationship between heterospecific and conspecific pollen
143 deposited in plant stigmas (Tur *et al.* 2016). This is because heterospecific
144 pollen can be seen as an unavoidable cost that plants must pay for receiving
145 conspecific pollen from shared pollinators. A negative relationship (when
146 shared pollinators increase heterospecific pollen loads and decrease conspecific
147 loads) may indicate that competition for pollination is strong. In contrast,

148 a positive relationship is what would be observed when facilitation is the
149 dominant outcome.

150 **Data collection**

151 In each of the studied communities, we quantified pollen deposition in a subset
152 of plant species between December 2010 and February 2011. This subset
153 comprised between three and nine common insect-pollinated (entomophilous)
154 plant species that were flowering during the sampling period (see Figure 1a).
155 Based on data from previous years (Marrero *et al.* 2014), we chose plant
156 species such that they cover a wide range on a specialization-generalization
157 gradient as well as a wide range of abundances. In each of the selected
158 plants, we removed all flowers leaving only buds that were expected to go
159 into florescence on the next day. Two days after flowering, we collected all
160 remaining flowers and counted the number of conspecific and heterospecific
161 pollen grains in their pistils. More details can be found in Marrero *et al.*
162 (2016).

163 **Data analysis**

164 To evaluate the relationship between heterospecific and conspecific pollen,
165 we used a generalised linear mixed model (GLMM) with a Poisson error
166 distribution (following Tur *et al.* 2016). In this model, the number of
167 conspecific pollen grains per flower was the response variable and the number
168 of heterospecific grains the predictor variable (the log number of stigmas
169 sampled was added as an offset term). The slope and intercept of this
170 relationship were allowed to differ between populations (plant species \times
171 community), which were modelled as a random effect. Models were fitted
172 using the function `glmer` from the R package `lme4` 1.1-19 (Bates *et al.*
173 2015). A positive slope for a plant population indicates facilitation while a

174 negative slope competition (Tur *et al.* 2016).

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

176 Our second objective was to investigate the relative contribution that different
177 ecological factors have on the mechanisms of pollinator-mediated competition.
178 Generally speaking, we expect that any factor that increases the amount
179 of conspecific pollen deposited in stigmas, both in quantity and purity
180 relative to heterospecific pollen, also has a positive effect on the pollination
181 service. Specifically, we investigated the effect of (*i*) a plant's number of
182 shared pollinator species, (*ii*) a plant's abundance relative to the rest of the
183 community, (*iii*) the mean visit effectiveness—a metric that combines the
184 amount and type of pollen carried by floral visitors and the number of visits
185 it receives from them, and (*iv*) the plant's functional originality (Laliberté &
186 Legendre 2010). See *Data Analysis* section below for more details on these
187 four factors.

188 **Data collection**

189 To obtain the number of shared pollinators for each species, we collected data
190 to construct qualitative and quantitative pollination networks. Qualitative
191 networks were constructed based on ten-hour observations of floral visits
192 in each fragment. Quantitative networks were constructed using two 50 m
193 randomly located transects in each fragment. We counted and collected all
194 floral visitors found in a 2 m wide strip while walking at a pace of 10 m per
195 minute (Memmott 1999; Marrero *et al.* 2014). We visited the transects each
196 month between November 2010 and March 2011. To obtain floral abundance,
197 we counted all units of floral attraction found during an independent sampling
198 of the same transects used to construct the quantitative visitation networks.
199 To estimate visit effectiveness, we need to construct pollen transfer networks

in addition to the visitation networks. To do this, we examined the pollen loads present on the floral visitors collected (Marrero *et al.* 2017). When the pollen count on an individual animal was estimated to be less than 2,000 grains, we identified every grain to the species level when possible and to pollen complexes when it was not. When the pollen count was above 2,000 grains, we classified approximately 50% of pollen and total pollen counts were extrapolated (Bosch *et al.* 2009). Finally, we also recorded morphological traits that relate to plant type (herb, shrub, climber), life cycle (annual, perennial), flower colouration, phenology, and whether the species is native in the study region. More details can be found in Marrero *et al.* (2014 and 2017).

Data analysis

To investigate the impact of ecological factors on pollination services, we used two sets of linear mixed models (LMM) with bootstrap resampling. The response variables for these model sets were the number of conspecific and heterospecific pollen grains deposited per stigma in flowers open to animal-mediated pollination. We used LMMs in which pollen loads were log-transformed because these models offered a better fit than equivalent GLMMs with Poisson (or quasi-Poisson) error structure. Models were fitted using the R package `nlme` 3.1-131 (Pinheiro *et al.* 2018).

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

As fixed predictors in the models, we included the four ecological factors

described above. Specifically, we calculated the number of shared pollinators for each plant species by pooling data from the qualitative and quantitative pollination networks. To calculate the plants' relative floral abundance in their community, we aggregated floral counts for each species. We then calculated the mean visit effectiveness of pollinator species i to plant species j as

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

, where v_{ij} is the observed number of visits by i to j , p_{ji} is the number of pollen grains from j attached to i , v_i is the total number of visits performed by i , and p_j is the total number of grains carried by j . We log-transformed the number of shared pollinators, floral abundance, and visit effectiveness before including them in the model.

Finally, functional originality is defined as the distance of a species from the community trait average—the centroid of functional space of the community (Laliberté & Legendre 2010; Coux *et al.* 2016). To include phenological variation, we treated floral abundance in each of the survey months (November to March) as a “trait” in our analysis. To account for the non-independence of floral counts and weight all traits equally, we assigned a weight of 1/5 to these abundances (one for each month). We scaled all traits prior to calculating the centroid of the functional space and calculated the species-specific functional coordinates using the R package FD 1.0-12 (Laliberté *et al.* 2014). Finally, we scaled all four factors to have a zero mean and unitary variance.

To estimate the coefficients, perform model selection, and quantify the associated uncertainty, we used a combination of multi-model inference and bootstrap resampling with 99 replicates. First, we performed model selection using the AICc and determined the likelihood of each candidate model (a particular combination of predictors) by calculating the median ΔAICc (relative to the most likely model) for each bootstrap sample. As we wanted model coefficients from more likely candidate models to carry more weight

255 in our results, we sampled the coefficients for our factors proportionally to
256 the likelihood of their candidate model. Finally, we used these distributions
257 of the model coefficients to estimate their mean impact on the pollination
258 service (in terms of quantity and purity of conspecific pollen deposition).

259 **Flexibility of plant strategies**

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

281 Results

282 Competition vs. facilitation

283 We first examined the degree of facilitation/competition in natural commu-
284 nities. Specifically, we examined the slope of the relationship between the
285 quantities of heterospecific and conspecific pollen deposited on stigmas of
286 each species in a community. Overall, we found that neither net facilitation
287 nor net competition dominates (Table S1). Indeed, we found that the
288 proportions of species that experienced a statistically significant positive
289 or negative relationship between heterospecific and conspecific pollen were
290 very similar (35% and 37%, respectively; Figure 1; Table S2). Most of the
291 variation between plants in a facilitation-competition gradient was driven
292 by differences *between* species; however, we also observed some important
293 differences *within* species. For instance, six of the species sampled across
294 multiple communities (*Carduus acanthoides*, *Cirsium vulgare*, *Cypella her-*
295 *bertii*, *Diplotaxis tenuifolia*, *Hirschfeldia incana*, and *Verbena intermedia*)
296 showed evidence that the same species, can experience facilitation (positive
297 relationships) in some communities and competition (negative relationships)
298 in others. Interestingly, although there was wide variation in the slope of the
299 relationship between heterospecific and conspecific pollen, almost all plants
300 had more conspecific than heterospecific pollen deposited on their stigmas
301 (Figure S1).

302 Factors affecting quantity and purity of pollination service

303 We then examined the potential roles played in pollen deposition by four
304 ecological factors (number of shared pollinators, abundance, mean visit
305 effectiveness, and functional originality). We found that our models of pollen
306 deposition had high explanatory power (the coefficient of determination R^2
307 ranged between 0.76 and 0.93) although a large portion of the explanatory

competition vs. facilitation
relationship hetero–conspecific pollen

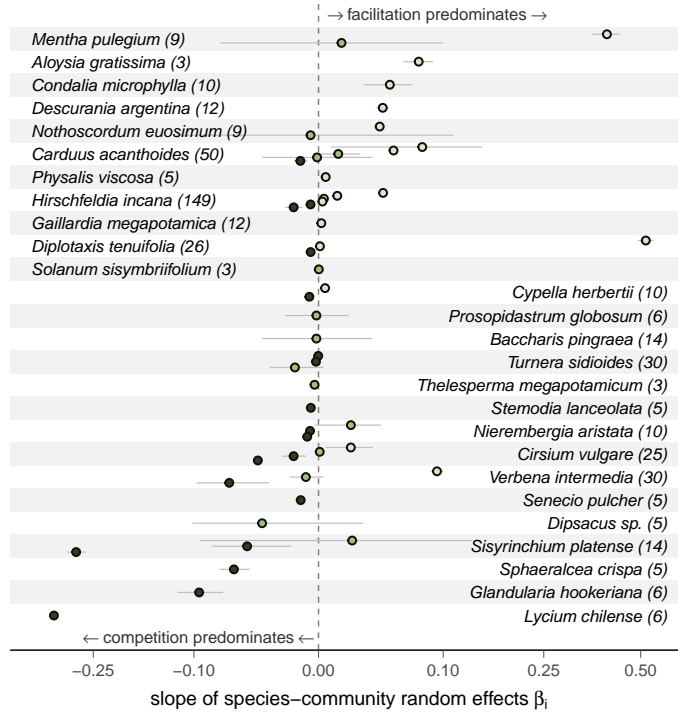


Figure 1: Competition vs. facilitation at the community level. Points indicate the estimated slopes for the relationship between the amount of heterospecific and conspecific pollen deposited per stigma across species in each of their communities. Statistically significant negative slopes (darkest shade) 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).

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 pollen (Table S4).

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

We found that the relationship between each of the ecological factors and pollen deposition was similar for both conspecific and heterospecific pollen. That is, strategies that were associated with an increase in conspecific pollen were also associated with an increase in heterospecific pollen deposition. Specifically, the plants' mean visit effectiveness had a positive effect on pollen deposition (Figure 2b). However, the effect size was slightly larger for heterospecific than for conspecific pollen. This indicates that, although there is a positive association between visit effectiveness and the quantity of pollen deposition, there is a negative relationship with its purity (Figure 2c). In contrast, a plants' relative floral abundance negatively affected its deposition quantity, but the mean difference between the coefficients in the models indicates a positive association with purity (Figure 2c). The third most important factor, functional originality, had a positive, although comparatively smaller, association with both the quantity and purity. Finally, the number of shared pollinators had negative and neutral associations with conspecific and heterospecific pollen, respectively, but these impacts were small when compared to the other factors. Although the ecological factors

337 were positively correlated (Figure S2), the collinearity between predictors
338 did not qualitatively affect our findings (Figure S3).

339 **Flexibility of plant strategies**

340 We used a PCA of the analysed species to investigate whether plants' realised
341 pollination niche is similar across communities or whether they are flexible
342 and therefore a reflection of the community context. The first two PCA
343 components explained 75% of the total variance (Figure 3a). The first
344 component was dominated by visit effectiveness and relative abundance while
345 the second component was dominated by the number of shared pollinators
346 and the plant's functional originality. When we locate the species that were
347 sampled in more than one community in the first two PCA components
348 (Figure 3b), we observe that the niches of any given species do not tend to be
349 close to each other. Indeed, when we measured the median distance between
350 the plants' coordinates, we found that it was only significantly smaller than
351 that of randomisations for only two of the twelve species analysed (Figure
352 3c).

353 **Discussion**

354 Our results suggest that community context plays a central role in deter-
355 mining the net cost or benefit of sharing pollinators. First, we found that
356 pollinator sharing can lead to both net facilitative and net competitive effects
357 to plant species in a community. Second, we found that multiple ecological
358 factors can modulate the intensity of competition; however, conspecific and
359 heterospecific pollen deposition are tightly coupled and this creates a clear
360 trade-off between the quantity and purity of pollination (Thomson *et al.*
361 2019). Third, we found that the way these factors influence competition
362 is strongly shaped by the community context. That is, if these factors

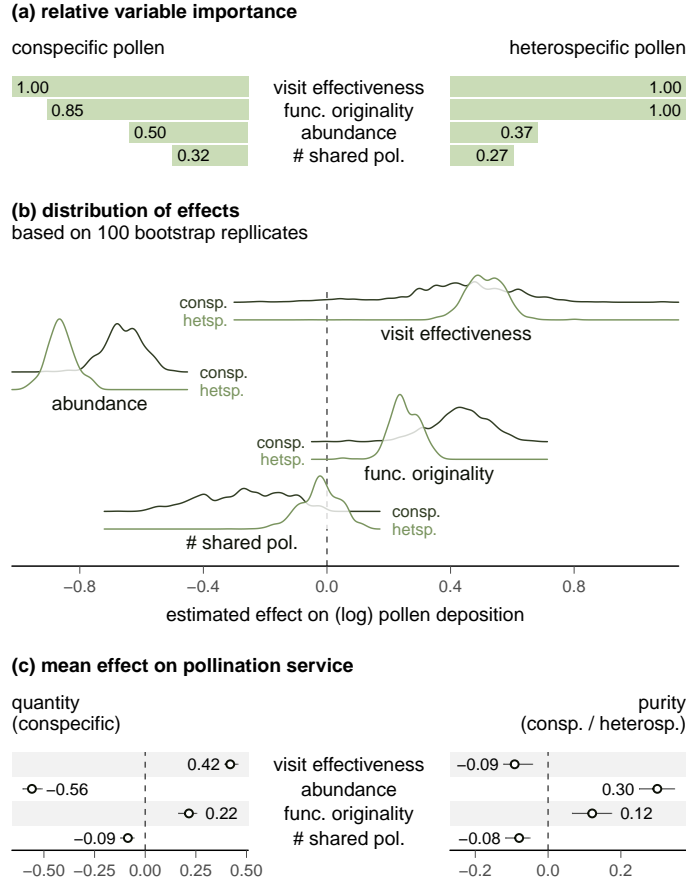


Figure 2: Effect of strategies to minimise competition in the pollination service. (a) The plant's visit effectiveness and relative floral abundance are the most important factors determining the deposition of conspecific and heterospecific pollen. Meanwhile, the number of shared pollinators was generally 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 effectiveness 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).

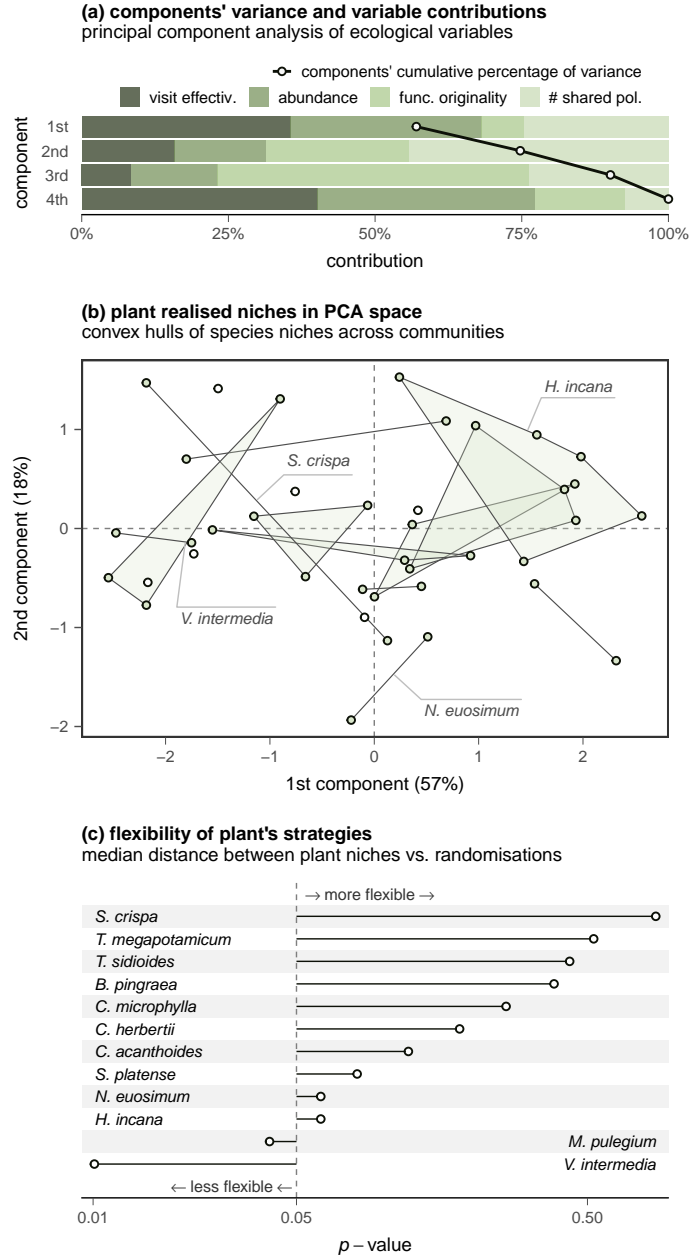


Figure 3: The flexibility of plant strategies. (a) The two first components explain a large proportion of the total variance. (b) When plants that were sampled in more than one community are plotted in terms of these two components, we observe that their points—which represent the strategy (the particular 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.

363 collectively define a species' pollination niche, the same plant species can
364 occupy dramatically different niches depending on the community to which
365 it belongs.

366 The criterion we used to identify the effect of animal-mediated pollination
367 suggested that neither facilitation nor competition are dominant in polli-
368 nation communities. A previous study showed that, in diverse pollination
369 communities, sharing pollinators does not necessarily translate to net com-
370 petition (Tur *et al.* 2016). The overall extent of facilitation/competition
371 of pollination communities can depend on factors like the adversity of the
372 environment (Callaway *et al.* 2002; Tur *et al.* 2016) or how disturbances
373 affect pollinator populations (Stavert *et al.* 2017). However, why some
374 species experience more competition than others was not understood. Al-
375 though we were unable to measure the fitness outcomes, here we show that
376 the coexistence of facilitative and competitive effects of animal-mediated
377 pollination can be at least partially explained by trade-offs in the pollination
378 service—both the short and the long term. These trade-offs arise when plants
379 simultaneously maximise the deposition of conspecific pollen and minimise
380 that of heterospecific pollen.

381 In the short term, being a specialist and sharing no pollinators might reduce
382 competition (Muchhala *et al.* 2010) and hence be preferable, not only due to
383 costs to male fitness (Morales & Traveset 2008; Muchhala & Thomson 2012),
384 but also because, as we show here, sharing pollinators reduces both the
385 quantity and purity of the conspecific pollen deposited. However, over long
386 periods of time, there could be a risk associated with a specialist plant having
387 few pollinators (Ricketts 2004). To ensure long-term survival, it is thus likely
388 that plants also need to balance this risk with the costs of sharing pollinators
389 (Aizen *et al.* 2012). One possible solution is to share pollinators *and* have
390 original traits—as we show that trait originality is generally beneficial to
391 pollen deposition and it is commonly thought that species that are further

392 from others in trait space benefit from reduced competition. Yet, there are
393 two possible caveats to this strategy that highlight the interrelatedness of
394 the ecological factors. First, in a mutualism context, it is also possible that
395 trait originality could come at the cost of being less ‘apparent’ to pollinators
396 (Reverté *et al.* 2016). Second, the negative relationship between originality
397 and generalism (Carvalheiro *et al.* 2014) has been shown to depend on plant
398 abundance (Coux *et al.* 2016), with generalist species being able to also have
399 original traits only when they are abundant enough to provide a valuable
400 reward to make visiting worthwhile to pollinators.

401 Visit effectiveness (high pollen and visits) and floral abundance, which were
402 the most important predictors of pollen deposition here, introduced an
403 even more explicit trade-off between gaining conspecific pollen and avoiding
404 heterospecific pollen. Receiving high visitation increases conspecific pollen
405 deposition but increases heterospecific pollen deposition to a greater extent—
406 even when the visitors are likely to carry a high proportion of conspecific
407 pollen (Fang & Huang 2016). Contrastingly, being abundant reduces the
408 amount of conspecific pollen deposited and simultaneously reduces heterospe-
409 cific pollen at a faster rate. Our results corroborate the importance that
410 two-species studies have ascribed to visitation and abundance (Feldman
411 *et al.* 2004; Morales & Traveset 2008; Muñoz & Cavieres 2008), but they
412 also suggest that (because visitation, pollen production and abundance are
413 usually correlated; Sargent & Otto 2006) balancing the pros and cons of
414 sharing pollinators at the community level is not trivial and might even
415 be partially responsible for the diversity of plant-pollinator communities
416 (Benadi & Pauw 2018).

417 We observed, as expected, that the effects of pollen deposition can vary widely
418 among species. For instance, while the fitness of some plant species can be
419 hurt even by low amounts of heterospecific pollen, for others, fitness can
420 instead be limited by the amount of conspecific pollen (Campbell & Motten

1985; Arceo-Gómez *et al.* 2019). Alternatively, plant species can also differ substantially in the extent to which self- vs. outcross-pollen differ in their value for fertilization. The difference can be particularly relevant for species that are not self-fertile or those in which self-fertilization is rarely effective due to a temporary separation in the maturation of the sexes (dichogamy). Importantly, we show here that the balances between costs and benefits are determined not only by species identity but also by the community to which plants belong. Specifically, most plant species appear to be flexible enough to adopt markedly different niches in different communities. From an evolutionary perspective, our results suggest that selection for a particular 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 (Gibson *et al.* 2012). 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 (Bartomeus *et al.* 2008). 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 (Cariveau & Norton 2009; Flanagan *et al.* 2011; Ye *et al.* 2014; Thomson *et al.* 2019). 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

450 competition is pervasive in pollination communities. The potential strategies
451 to minimise competition are likely to involve strong trade-offs in the pollina-
452 tion service both in the short and long-term. Most remarkably, despite large
453 differences in the quantity and purity of conspecific pollen deposition among
454 species, our results provide solid evidence that competition for pollination is
455 inherently a community process and the same species can occupy different
456 niches in different communities. Many of the widely used theoretical models
457 of plant-pollinator communities do not account for the negative effects of
458 sharing pollinators (but see Rohr *et al.* 2014 and similar). However, achiev-
459 ing a better understanding of species coexistence and how plant biodiversity
460 is supported by pollination communities will require seeing them as both
461 mutualistic and competitive communities (Johnson & Bronstein 2019).

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