

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

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Short title: Competition for pollination vs. facilitation

Content type: Article.

Number of words: 158 in abstract; 4,597 in main text (including Methods
section).

Number of displays: 3 figures; 0 tables; 0 text boxes.

Author for correspondence: E. Fernando Cagua (+64 20 4026 8153).

Data accessibility: Data supporting the results will be accessible in an
appropriate data repository after publication.

Competing interests: The authors have declared that no competing
interests exist.

15 **Abstract**

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

32 Introduction

33 Animal pollination plays a disproportionately important role in food pro-
34 duction and maintenance of global biodiversity^{1–3}. Alongside the direct
35 benefits of mutualisms between plants and their pollinators, biodiversity can
36 be supported as a result of inter-species “facilitation”—the indirect positive
37 feedback loops that exist between plant species that share pollinators or pol-
38 linators that share plants^{4–7}. This inter-species facilitation is able to promote
39 species coexistence by offsetting the effects of direct resource competition⁸.
40 Indeed, studies at the core of our current theoretical knowledge of mutualisms
41 predict that the maximum number of coexisting species is achieved when
42 the number of shared mutualistic partners is maximised in a community⁹.
43 However, in natural communities, plants rarely share all available pollinators.
44 One explanation is that plants are effectively competing for mutualistic
45 partners because there is a trade-off between the benefits gained from max-
46 imising the number of partners and the costs of sharing them with other plant
47 species¹⁰. It has been clear for a long time that when competition for pollina-
48 tion is strong enough, these costs can make pollination detrimental to plants’
49 fitness^{11–13}. In fact, it can be sufficient to drive ecological differentiation^{14,15}.
50 However, it is less clear how exactly this ecological differentiation may, in
51 turn, favour (or hinder) the pollination service.

52 There are two main mechanisms through which competition for pollinators
53 can affect plant fertilization¹⁶. The first is by changes in intraspecific pollen
54 transfer. This happens, for example, when plants with more attractive flowers
55 might reduce the number of visits to those less of attractive neighbouring
56 plants, and hence reduce the amount of *conspecific pollen* deposited by
57 animals¹⁷. The second is via interspecific pollen transfer and occurs when
58 plants share pollination partners. In that case, even receiving a visit might
59 not necessarily translate into fertilization¹⁸ because a focal plant might

60 receive *heterospecific pollen* or because pollen from the focal plant might
61 be lost to different species. Naturally, the precise effects on plant fitness
62 of conspecific and heterospecific pollen deposition depend on the species
63 involved (and are unknown for many plant species). However, there is
64 substantial evidence supporting the link between pollen deposition and seed
65 production; in particular for the detrimental effect of heterospecific pollen
66 deposition on plant fitness^{19,20}. All together, provided pollen is viable and
67 compatible^{21–23}, the higher the quantity of conspecific pollen and its purity
68 (relative to heterospecific pollen), the better the pollination service received
69 by the focal plant. As such, measuring conspecific and heterospecific pollen
70 deposition provides a good indication of the potential levels of facilitation
71 and competition a plant population might experience.

72 By definition, these two mechanisms of competition, intra and interspe-
73 cific pollen transfer, occur at the community scale. However, with few
74 exceptions^{24,25}, most of what we know about them and their relationship
75 with key ecological factors is based on studies with two plant species. That
76 is partly so because, at the community scale, the factors that determine the
77 patterns of pollen deposition are tightly intertwined, operate simultaneously,
78 and may lead to emergent phenomena not observed at smaller scales²⁶. For
79 instance, recent empirical evidence suggests that plants with flowering traits
80 that are “original” relative to others in the community generally have fewer
81 interaction partners²⁷. This evidence is aligned with the notion that a species
82 that interacts with few species does so strongly with each of them whereas a
83 species that interacts with a large number of species does so comparatively
84 weakly^{28–30}. If evolutionary specialisation occurs by changing traits to focus
85 on fewer but better partners¹⁵, we should expect a reduction of competition
86 for pollinators in species with “original” traits and an increase of competition
87 in species with a large number of interaction partners^{31,32}. Alternatively, it
88 might also be the case that abundance (for example in terms of flower or

pollen counts) is the dominant force driving pollen transfer³³. Abundant plant species might experience a dilution of available pollinators^{34,35} but might also receive more effective visits by capitalising on a larger share of both visits and the pollen carried by pollinators. In this case, a potential reduction in the absolute amount of conspecific pollen received could be compensated by an increase in the amount of conspecific pollen relative to heterospecific pollen. Altogether, it is clear that these ecological factors can indeed shape pollen deposition at the community level. However, their relative importance and how exactly they can minimise competition for pollination—or equivalently, maximise facilitation—in plant populations (across species and communities) has not been determined.

Here, we investigate the balance between competition for pollination and facilitation at the community scale using empirical data from eleven plant-pollinator communities in the Argentinian Pampas. First, we estimate the extent to which the net outcome of plants sharing pollinators is facilitation or competition. If facilitation is the primary outcome, we could expect an overall positive relationship between the amount of conspecific pollen deposited in stigmas and the amount of heterospecific pollen²⁴. The higher the deposition of conspecific pollen relative to heterospecific, the larger the slope of this relationship. Second, we investigate the relative contribution that four ecological factors have to the pollination service. Specifically, we hypothesize that the quantity and purity of conspecific pollen deposition should decrease for plants that share many pollination partners. However, we also hypothesize that other factors like the plant's functional originality, its relative floral abundance, and the visit potential should have the potential to compensate for this increase in competition. Third and finally, we examine how much the community context influences the way plants use these factors to minimise competition/maximise facilitation. We use these four ecological factors as a proxy of the realised pollination niche of a plant species in

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

126 **Methods**

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

132 **Competition vs. facilitation**

133 Our first objective was to identify whether the net outcome of plants sharing
134 pollinators at the community level is facilitation or competition. To do that
135 we examine the relationship between heterospecific and conspecific pollen
136 deposited in plant stigmas²⁴. This is because heterospecific pollen can be seen
137 as an unavoidable cost that plants must pay for receiving conspecific pollen
138 from shared pollinators. A negative relationship (when shared pollinators
139 increase heterospecific pollen loads and decrease conspecific loads) may
140 indicate that competition for pollination is strong. In contrast, a positive
141 relationship is what would be observed when facilitation is the dominant
142 outcome.

143 **Data collection**

144 In each of the studied communities, we quantified pollen deposition in a subset
145 of plant species between December 2010 and February 2011. This subset
146 comprised between three and nine common insect-pollinated (entomophilous)
147 plant species that were flowering during the sampling period. Based on
148 data from previous years³⁶, we chose plant species such that they cover
149 a wide range on a specialization-generalization gradient as well as a wide
150 range of abundances. In each of the selected plants, we removed all flowers
151 leaving only buds that were expected to go into florescence on the next day.
152 Two days after flowering, we collected all remaining flowers and counted the
153 number of conspecific and heterospecific pollen grains in their pistils. More
154 details can be found in 37.

155 **Data analysis**

156 To evaluate the relationship between heterospecific and conspecific pollen,
157 we used a generalised linear mixed model (GLMM) with a Poisson error
158 distribution²⁴. In this model, the number of conspecific pollen grains per
159 flower was the response variable and the number of heterospecific grains the
160 predictor variable (the log number of stigmas sampled was added as an offset
161 term). The slope and intercept of this relationship were allowed to differ
162 between populations (plant species \times community), which were modelled as
163 a random effect. Models were fitted using the function `glmer` from the R
164 package `lme4` 1.1-19³⁸. A positive slope for a plant population indicates
165 facilitation while a negative slope competition²⁴.

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

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

169 Generally speaking, we expect that any factor that increases the amount
170 of conspecific pollen deposited in stigmas, both in quantity and purity
171 relative to heterospecific pollen, also has a positive effect on the pollination
172 service. Specifically, we investigated the effect of (i) a plant's number of
173 shared pollinator species, (ii) a plant's abundance relative to the rest of
174 the community, (iii) the mean visit potential—a metric that combines the
175 amount and type of pollen carried by floral visitors and the number of visits
176 it receives from them, and (iv) the plant's functional originality³⁹. See *Data*
177 *Analysis* section below for more details on these four factors.

178 **Data collection**

179 To obtain the number of shared pollinators for each species, we collected data
180 to construct qualitative and quantitative pollination networks. Qualitative
181 networks were constructed based on ten-hour observations of floral visits
182 in each fragment. Quantitative networks were constructed using two 50 m
183 randomly located transects in each fragment. We counted and collected all
184 floral visitors found in a 2 m wide strip while walking at a pace of 10 m
185 per minute^{36,40}. We visited the transects each month between November
186 2010 and March 2011. To obtain floral abundance, we counted all units of
187 floral attraction found during an independent sampling of the same transects
188 used to construct the quantitative visitation networks. To estimate visit
189 potential, we need to construct pollen transfer networks in addition to the
190 visitation networks. To do this, we examined the pollen loads present on the
191 floral visitors collected⁴¹. When the pollen count on an individual animal
192 was estimated to be less than 2,000 grains, we identified every grain to the
193 species level when possible and to pollen complexes when it was not. When
194 the pollen count was above 2,000 grains, we classified approximately 50% of
195 pollen and total pollen counts were extrapolated⁴². Finally, we also recorded
196 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` 3.1-131⁴³.

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 potential of pollinator species i to plant species j as

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

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

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

227 Finally, functional originality is defined as the distance of a species
228 from the community trait average—the centroid of functional space of
229 the community^{27,39}. To include phenological variation, we treated floral
230 abundance in each of the survey months (November to March) as a “trait”
231 in our analysis. To account for the non-independence of floral counts and
232 weight all traits equally, we assigned a weight of 1/5 to these abundances
233 (one for each month). We scaled all traits prior to calculating the centroid
234 of the functional space and calculated the species-specific functional
235 coordinates using the R package FD 1.0-12⁴⁴. Finally, we scaled all four
236 factors to have a zero mean and unitary variance.

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

248 Flexibility of plant strategies

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

270 Results

271 Competition vs. facilitation

272 We first examined the degree of facilitation/competition in natural commu-
273 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

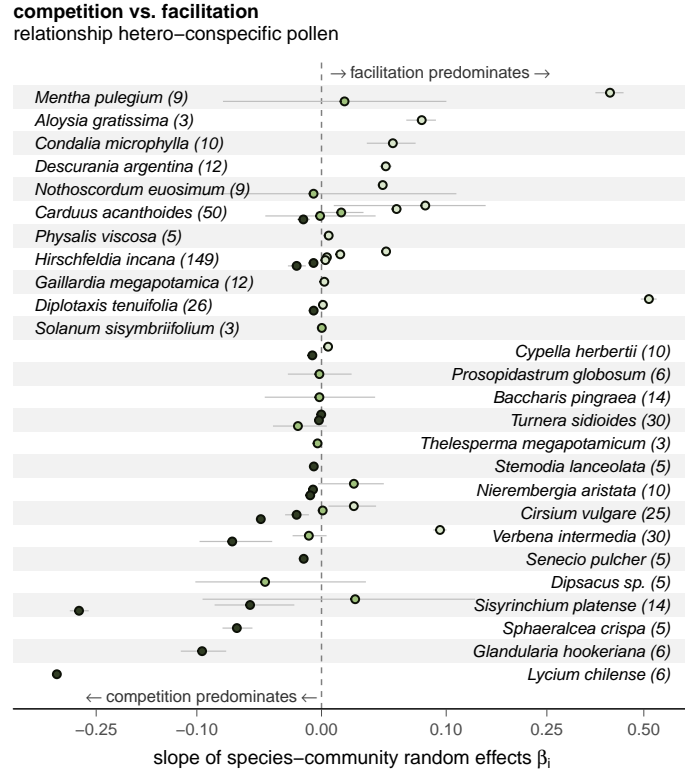


Figure 1: Competition vs. facilitation at the community level. Points indicate the estimated slopes for the relationship between the amount of heterospecific and conspecific pollen deposited per stigma across species in each of their communities. Statistically significant negative slopes (darkest shade)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

302 pollen (Table S4).

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

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

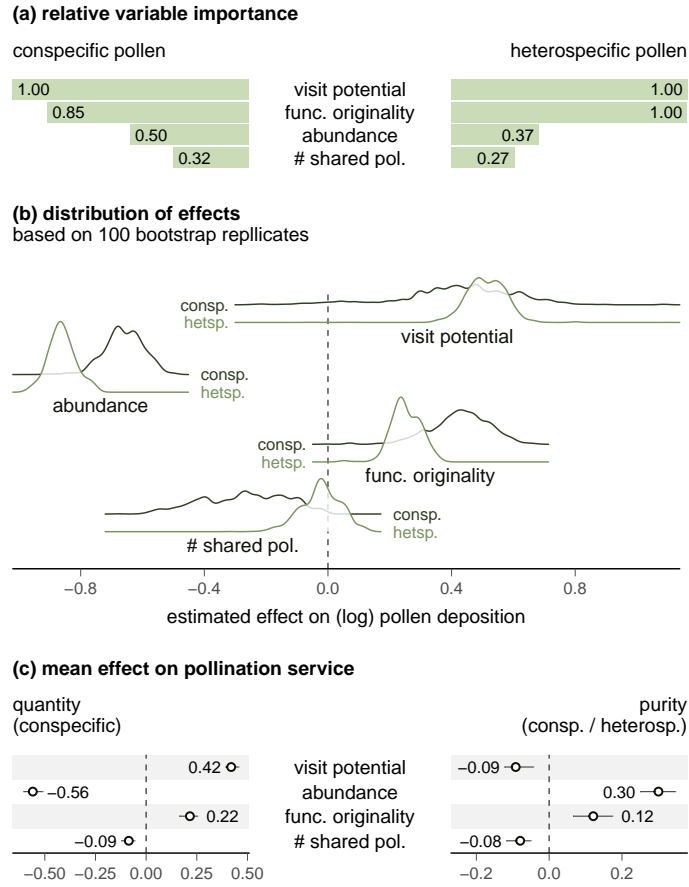


Figure 2: Effect of ecological factors on the pollination service. (a) The plant's visit potential and relative floral abundance are the most important factors determining the deposition of conspecific and heterospecific pollen. Meanwhile, the number of shared pollinators was generally less important. 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).

328 Flexibility of plant strategies

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

341 Discussion

342 Our results suggest that community context plays a central role in deter-
343 mining the net cost or benefit of sharing pollinators. First, we found that
344 pollinator sharing can lead to both net facilitative and net competitive effects
345 to plant species in a community. Second, we found that multiple ecological
346 factors can modulate the intensity of competition; however, conspecific and
347 heterospecific pollen deposition are tightly coupled and this creates a clear
348 trade-off between the quantity and purity of pollination⁴⁵. Third, we found
349 that the way these factors influence competition is strongly shaped by the
350 community context. That is, if these factors collectively define a species'
351 pollination niche, the same plant species can occupy dramatically different
352 niches depending on the community to which it belongs.

353 The criterion we used to identify the effect of animal-mediated pollina-
354 tion suggested that neither facilitation nor competition are dominant in

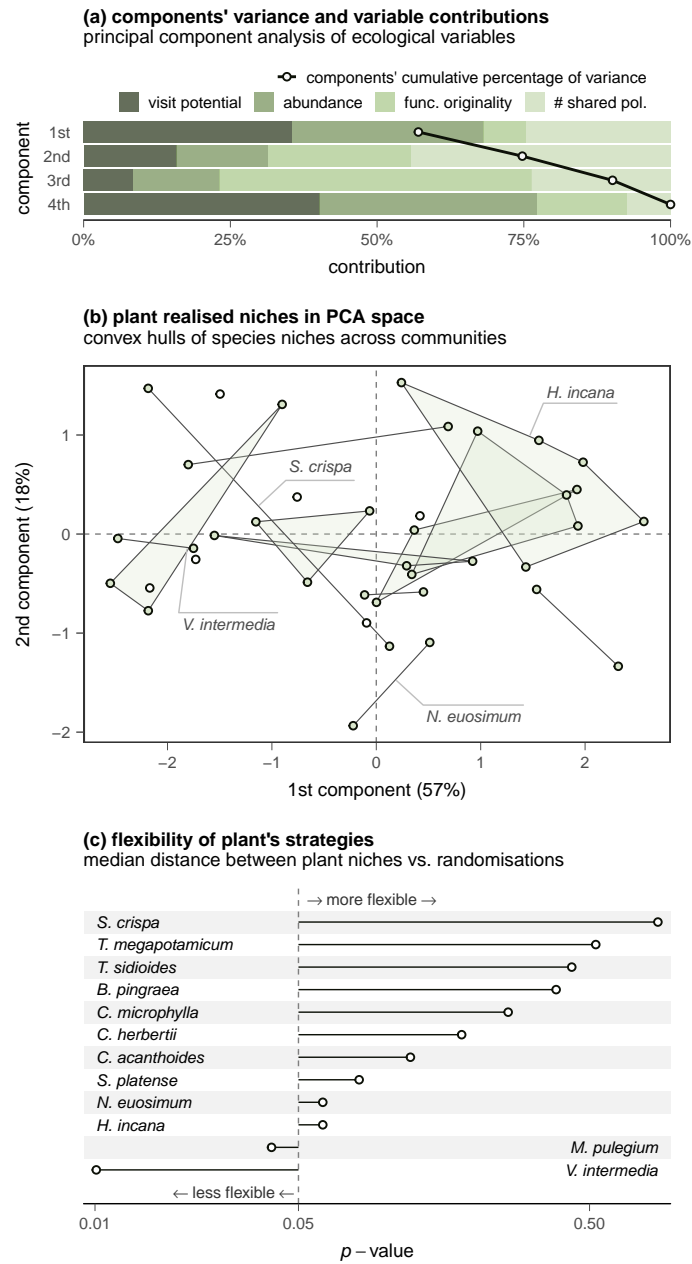


Figure 3: The flexibility of plant strategies. (a) The two first components explain a large proportion of the total variance. (b) When plants that were sampled in more than one community are plotted in terms of these two components, we observe that their points, which represent the strategy (the particular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

pollination communities. A previous study showed that, in diverse pollination communities, sharing pollinators does not necessarily translate to net competition²⁴. 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 populations⁴⁷. 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 competition⁴⁸ 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 pollinators⁵⁰. To ensure long-term survival, it is thus likely that plants also need to balance this risk with the costs of sharing pollinators⁵¹. 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 pollinators⁵². Second, the negative relationship between originality and generalism³² has been shown to depend on plant abundance²⁷, with generalist species being able to also have original traits only when they are abundant enough to

384 provide a valuable reward to make visiting worthwhile to pollinators.

385 Visit potential (high pollen and visits) and floral abundance, which were
386 the most important predictors of pollen deposition here, introduced an
387 even more explicit trade-off between gaining conspecific pollen and avoiding
388 heterospecific pollen. Receiving high visitation increases conspecific pollen
389 deposition but increases heterospecific pollen deposition to a greater extent—
390 even when the visitors are likely to carry a high proportion of conspecific
391 pollen⁵³. Contrastingly, being abundant reduces the amount of conspecific
392 pollen deposited and simultaneously reduces heterospecific pollen at a faster
393 rate. Our results corroborate the importance that two-species studies have
394 ascribed to visitation and abundance^{16,35,54}, but they also suggest that⁵⁵
395 balancing the pros and cons of sharing pollinators at the community level
396 is not trivial and might even be partially responsible for the diversity of
397 plant-pollinator communities⁵⁶.

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

407 Importantly, we show here that the balances between costs and benefits
408 are determined not only by species identity but also by the community to
409 which plants belong. Specifically, most plant species appear to be flexible
410 enough to adopt markedly different niches in different communities. From an
411 evolutionary perspective, our results suggest that selection for a particular
412 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 effects³¹. 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 neighbours⁵⁸. 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 pollinators⁶¹. 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 communities⁶².

442 Acknowledgements

443 We thank Jamie Stavert, Bernat Bramon Mora, Laís Maia, and Michelle
444 Marraffini for feedback and valuable discussions. We also thank Cátedra de
445 Botánica General, Facultad de Agronomía, Universidad de Buenos Aires,
446 the Agrasar and Bordeu families, and the University of Buenos Aires, for
447 logistical support and permission to conduct this study at estancias Anquilóo,
448 Las Chilcas and San Claudio, respectively. Fieldwork was supported by
449 grants PICT 08–12504 and 0851. EFC acknowledges the support from
450 the University of Canterbury Doctoral Scholarship and a New Zealand
451 International Doctoral Research Scholarship administered by New Zealand
452 Education. DBS and JMT acknowledge the support of Rutherford Discovery
453 Fellowships (RDF-13-UOC-003 and RDF-UOC-1002) and the Marsden Fund
454 Council (UOC-1705), administered by the Royal Society of New Zealand Te
455 Apārangi.

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