

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

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<b>Full Title:</b>	Community context determines competition vs. facilitation trade-offs in pollination systems
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<b>Abstract:</b>	Plant-pollinator interactions are commonly viewed as mutualistic. However, plants that share pollinators also compete for effective pollination. The extent of this competition for pollination and its effects on pollination service are poorly understood at the community level; many species interact simultaneously and multiple intertwined factors might play a role (abundance, visitation, traits). By examining comprehensive empirical data, we confirm that competition for pollination is pervasive and is only partially influenced by the number of shared pollinators. Furthermore, the factors that most influence the pollination service (abundance and visit effectiveness) also introduce a trade-off between the absolute amount of conspecific pollen received and the amount relative to eterospecific pollen. Most importantly, the ways plants balance these trade-offs depend on the community context, as most species showed flexibility in the strategy they used to cope with competition for pollination. Plant-pollinator mutualisms could be better understood as comprising mutualistic and competitive interactions.
<b>Additional Information:</b>	
<b>Question</b>	<b>Response</b>

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Dr. Emma Ganley,  
Editorial Office,  
Plos Biology

Dear Doctor Ganley,

We are submitting the manuscript entitled “Community context determines competition vs. facilitation trade-offs in pollination systems” to be considered for publication in *Plos Biology*. The main goal of this study, to explore the balance between competition and facilitation in plants belonging to the same community.

Although the idea that plants can compete for pollinators or facilitate each other has been on the table for a long time, a definitive answer has not been reached yet. Many of the key theoretical papers on mutualistic communities<sup>1</sup> almost always focus on the inherently beneficial aspects of plant-pollinator interactions. Empirical work has often mirrored this focus, though a few community-level studies<sup>2</sup> have explored the extent to which plants who share pollinators compete or facilitate each other. Importantly, these studies only measured the deposition of pollen, whereas plants can modulate competition by partitioning their pollination niche in many ways, such as through

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<sup>1</sup>Jordi Bascompte, Pedro Jordano, and Jens M Olesen. “Asymmetric Coevolutionary Networks Facilitate Biodiversity Maintenance”. In: *Science* 312.5772 (Apr. 21, 2006), pp. 431–433; Ugo Bastolla et al. “The Architecture of Mutualistic Networks Minimizes Competition and Increases Biodiversity”. In: *Nature* 458.7241 (Apr. 2009), pp. 1018–1020; Rudolf P Rohr, Serguei Saavedra, and Jordi Bascompte. “On the Structural Stability of Mutualistic Systems”. In: *Science* 345.6195 (July 25, 2014), p. 1253497.

<sup>2</sup>C. Tur et al. “Evaluating the Effects of Pollinator-Mediated Interactions Using Pollen Transfer Networks: Evidence of Widespread Facilitation in South Andean Plant Communities”. In: *Ecology Letters* 19.5 (May 2016). Ed. by Jos Mara Gmez, pp. 576–586; Marcelo A. Aizen and Adriana E. Rovere. “Reproductive Interactions Mediated by Flowering Overlap in a Temperate Hummingbird-Plant Assemblage”. In: *Oikos* 119.4 (Jan. 15, 2010), pp. 696–706.

flowering time, attractiveness, or how they attach pollen to pollinators. We, therefore, quantified, for the first time, the true pollination niche of plants, by incorporating measures of visitation, pollen transfer, floral abundance, phenology, and traits.

In this manuscript, we show that the realised pollination niche (which can also be viewed as a plant species' strategy to minimise competition for pollination) is strongly determined by the community to which it belongs. Furthermore, we show that even in pollination there is no such thing as a free lunch, and plants need to balance multiple trade-offs when minimising competition for pollination. On the one hand, factors that increase the quantity of pollen deposited by animals may also decrease its purity (and vice-versa). On the other, factors that increase both the quantity and purity do so only mildly and potentially only in the short-term.

This work provides fundamental understanding of plant reproductive biology, while also *calling for a shift in the way we think about pollination in community ecology*, especially from a theoretical perspective. In contrast to the predominant literature, our study provides compelling evidence that animal-mediated pollination is really a fluid dance between competition and facilitation. Thus, we believe that this manuscript will be interesting to the broad readership of PLoS Biology.

Lastly, please note that the data used in this manuscript have been previously published<sup>3</sup> by one of the co-authors. However, the enclosed work represents a novel contribution from all involved.

Thank you for your consideration.

Fernando Cagua, Hugo Marrero, Jason Tylianakis & Daniel Stouffer

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<sup>3</sup>H.J. Marrero, J.P. Torretta, and D. Medan. "Effect of Land Use Intensification on Specialization in Plant-Floral Visitor Interaction Networks in the Pampas of Argentina". In: *Agriculture, Ecosystems & Environment* 188 (Apr. 2014), pp. 63–71; H.J. Marrero et al. "Agricultural Land Management Negatively Affects Pollination Service in Pampean Agro-Ecosystems". In: *Agriculture, Ecosystems & Environment* 218 (Feb. 2016), pp. 28–32; Hugo J. Marrero et al. "Exotic Plants Promote Pollination Niche Overlap in an Agroecosystem". In: *Agriculture, Ecosystems & Environment* 239 (Feb. 2017), pp. 304–309.

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

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bioRxiv

## 16 **Abstract**

17 Plant-pollinator interactions are commonly viewed as mutualistic. However,  
18 plants that share pollinators also compete for effective pollination. The  
19 extent of this competition for pollination and its effects on pollination  
20 service are poorly understood at the community level; many species interact  
21 simultaneously and multiple intertwined factors might play a role (abundance,  
22 visitation, traits). By examining comprehensive empirical data, we confirm  
23 that competition for pollination is pervasive and is only partially influenced  
24 by the number of shared pollinators. Furthermore, the factors that most  
25 influence the pollination service (abundance and visit effectiveness) also  
26 introduce a trade-off between the absolute amount of conspecific pollen  
27 received and the amount relative to heterospecific pollen. Most importantly,  
28 the ways plants balance these trade-offs depend on the community context,  
29 as most species showed flexibility in the strategy they used to cope with  
30 competition for pollination. Plant-pollinator mutualisms could be better  
31 understood as comprising mutualistic 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  
38 pollinators that share plants [4–7]. This inter-species facilitation is able to  
39 promote species coexistence by offsetting the effects of direct resource com-  
40 petition [8]. Indeed, studies at the core of our current theoretical knowledge  
41 of mutualisms predict that the maximum number of coexisting species is  
42 achieved when the number of shared mutualistic partners is maximised in a  
43 community [9].

44 However, in natural communities, plants rarely share all available pollinators.  
45 One explanation is that plants are effectively competing for mutualistic part-  
46 ners because there is a trade-off between the benefits gained from maximising  
47 the number of partners and the costs of sharing them with other plant species  
48 [10]. It has been clear for a long time that when competition for pollination  
49 is strong enough, these costs can make pollination detrimental to plants’  
50 fitness [11–13]. In fact, it can be sufficient to drive ecological differentiation  
51 [14,15]. However, it is less clear how exactly this ecological differentiation  
52 may, in turn, favour (or hinder) the pollination service.

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

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

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

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

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



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

## 127 **Methods**

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

### 133 **Competition vs. facilitation**

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

## 144 **Data collection**

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

## 156 **Data analysis**

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

## 167 **Factors affecting quantity and purity of pollination service**

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

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

## 179 **Data collection**

180 To obtain the number of shared pollinators for each species, we collected data  
181 to construct qualitative and quantitative pollination networks. Qualitative  
182 networks were constructed based on ten-hour observations of floral visits  
183 in each fragment. Quantitative networks were constructed using two 50 m  
184 randomly located transects in each fragment. We counted and collected all  
185 floral visitors found in a 2 m wide strip while walking at a pace of 10 m  
186 per minute [36,40]. We visited the transects each month between November  
187 2010 and March 2011. To obtain floral abundance, we counted all units of  
188 floral attraction found during an independent sampling of the same transects  
189 used to construct the quantitative visitation networks. To estimate visit  
190 potential, we need to construct pollen transfer networks in addition to the  
191 visitation networks. To do this, we examined the pollen loads present on  
192 the floral visitors collected [41]. When the pollen count on an individual  
193 animal was estimated to be less than 2,000 grains, we identified every grain  
194 to the species level when possible and to pollen complexes when it was not.  
195 When the pollen count was above 2,000 grains, we classified approximately  
196 50% of pollen and total pollen counts were extrapolated [42]. Finally, we  
197 also recorded morphological traits that relate to plant type (herb, shrub,

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

## 201 **Data analysis**

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

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

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

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

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

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

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

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

## 249 Flexibility of plant strategies

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

## 271 Results

### 272 Competition vs. facilitation

273 We first examined the degree of facilitation/competition in natural commu-  
274 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

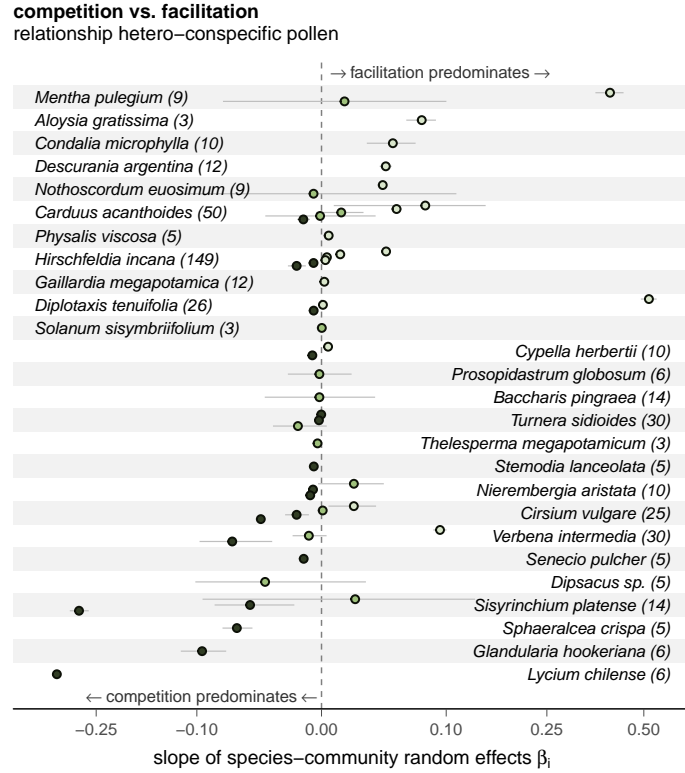


Figure 1: Competition vs. facilitation at the community level. Points indicate the estimated slopes for the relationship between the amount of heterospecific and conspecific pollen deposited per stigma across species in each of their communities. Statistically significant negative slopes (darkest shade)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



303 pollen (Table S4).

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

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

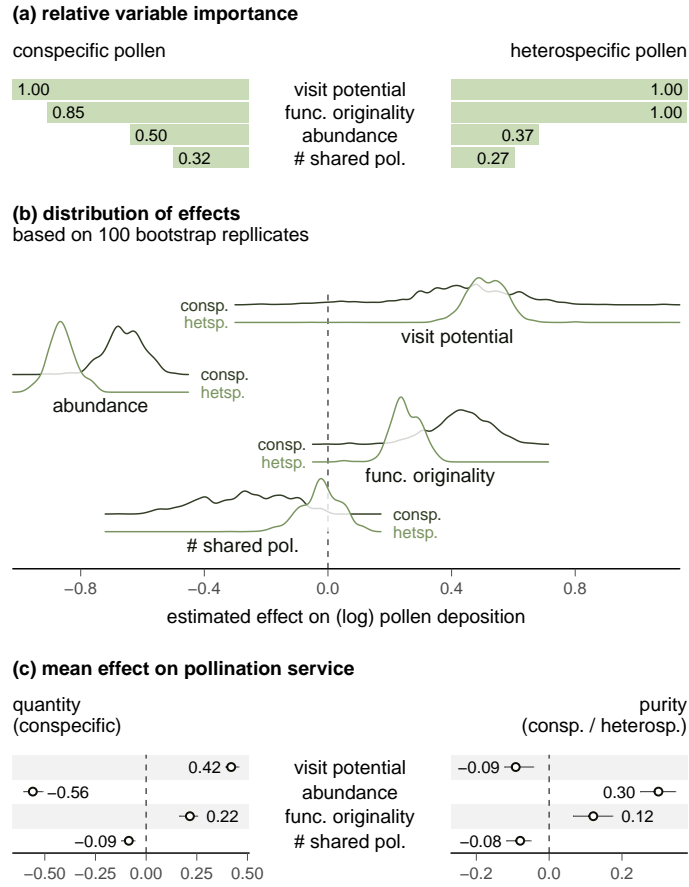


Figure 2: Effect of ecological factors on the pollination service. (a) The plant's visit potential and relative floral abundance are the most important factors determining the deposition of conspecific and heterospecific pollen. Meanwhile, the number of shared pollinators was generally less important.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

## 329 Flexibility of plant strategies

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

## 342 Discussion

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

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

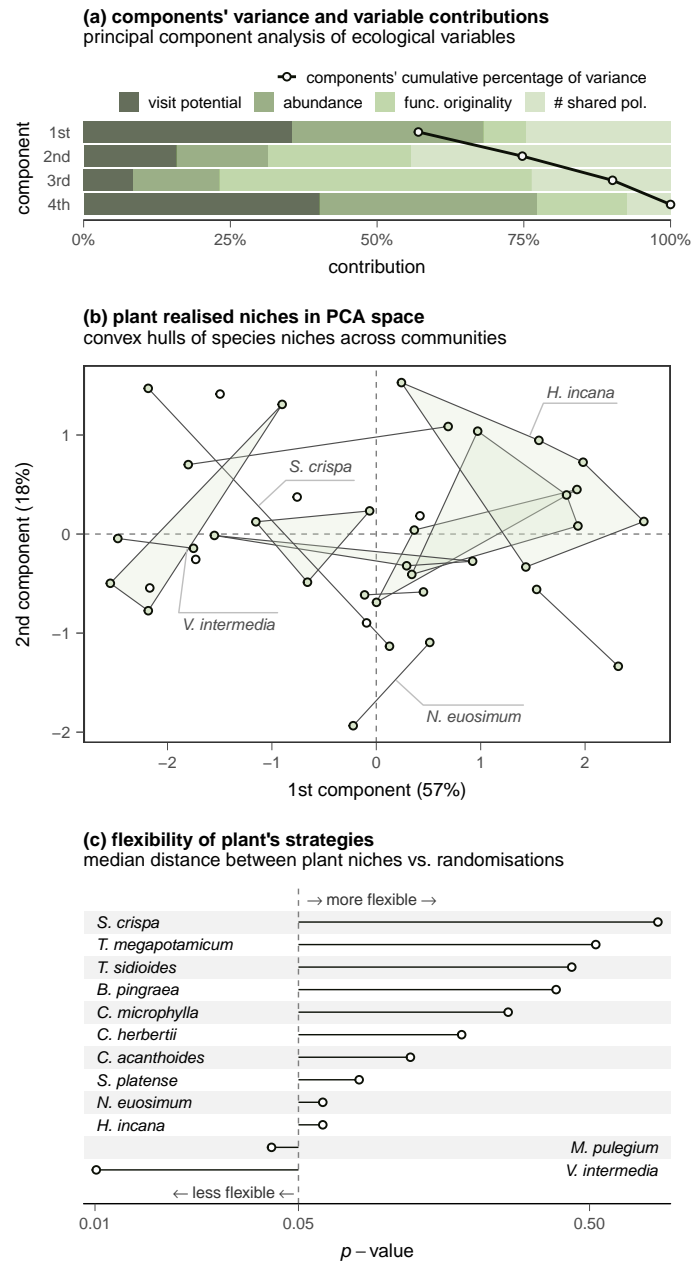


Figure 3: The flexibility of plant strategies. (a) The two first components explain a large proportion of the total variance. (b) When plants that were sampled in more than one community are plotted in terms of these two components, we observe that their points, which represent the strategy (the particular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

valuable reward to make visiting worthwhile to pollinators.

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

We observed, as expected, that the effects of pollen deposition can vary widely among species. For instance, while the fitness of some plant species can be hurt even by low amounts of heterospecific pollen, for others, fitness can instead be limited by the amount of conspecific pollen [18,57]. 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 [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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# Community context determines competition vs. facilitation trade-offs in pollination systems

Supplementary information

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Table S1: Summary of the model used to analyse the relationship between heterospecific and conspecific pollen

predictor	estimate	S.E.	z-value
<b>fixed component</b>			
(Intercept)	4.976	0.279	17.862
heterospecific	0.008	0.017	0.474
<b>random component (species:community)</b>			
S.D. random intercept	1.964	-	-
S.D. random slope	0.120	-	-

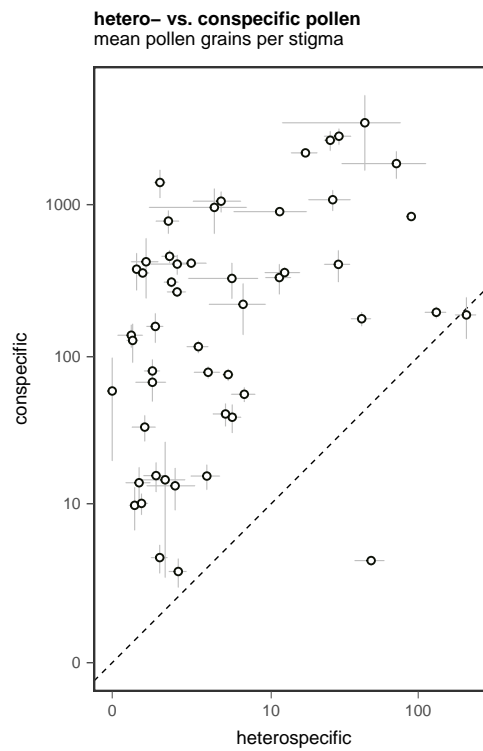


Figure S1: Despite the variation in these slopes, plants overall had more conspecific than heterospecific pollen deposited in their stigmas.

Table S2: The slope of the relationship between heterospecific and conspecific pollen for each species in their community (fixed effect + conditional effect). Community names are constructed by location - agricultural/restored - fragment number.

species name	community	slope	S.E.
<i>Aloysia gratissima</i>	Anquilóo - reserve - 2	0.0746	0.0144
<i>Baccharis pingraea</i>	San Claudio - reserve - 1	-0.0012	0.0359
<i>Carduus acanthoides</i>	Anquilóo - agricultural - 2	0.0116	0.0147
<i>Carduus acanthoides</i>	San Claudio - agricultural - 1	-0.0106	0.0040
<i>Carduus acanthoides</i>	San Claudio - agricultural - 2	0.0518	0.0044
<i>Carduus acanthoides</i>	San Claudio - reserve - 1	0.0781	0.0710
<i>Carduus acanthoides</i>	San Claudio - reserve - 2	-0.0008	0.0359
<i>Cirsium vulgare</i>	Anquilóo - agricultural - 2	-0.0401	0.0025
<i>Cirsium vulgare</i>	Las Chilcas - reserve - 1	0.0007	0.0012
<i>Cirsium vulgare</i>	San Claudio - agricultural - 2	0.0197	0.0158
<i>Cirsium vulgare</i>	San Claudio - reserve - 1	-0.0149	0.0076
<i>Condalia microphylla</i>	Anquilóo - reserve - 1	0.0487	0.0200
<i>Cypella herbertii</i>	Las Chilcas - agricultural - 2	0.0037	0.0002
<i>Cypella herbertii</i>	Las Chilcas - reserve - 1	-0.0052	0.0001
<i>Descurania argentina</i>	Anquilóo - agricultural - 2	0.0429	0.0048
<i>Diploaxis tenuifolia</i>	Anquilóo - reserve - 1	0.0008	0.0004
<i>Diploaxis tenuifolia</i>	Anquilóo - reserve - 2	0.5173	0.0270
<i>Diploaxis tenuifolia</i>	San Claudio - reserve - 2	-0.0045	0.0001
<i>Dipsacus sp.</i>	San Claudio - reserve - 2	-0.0368	0.0648
<i>Gaillardia megapotamica</i>	Anquilóo - reserve - 2	0.0016	0.0004
<i>Glandularia hookeriana</i>	Anquilóo - reserve - 2	-0.0942	0.0244
<i>Hirschfeldia incana</i>	Anquilóo - agricultural - 1	-0.0045	0.0013
<i>Hirschfeldia incana</i>	Anquilóo - agricultural - 2	-0.0148	0.0057
<i>Hirschfeldia incana</i>	San Claudio - agricultural - 1	0.0110	0.0020
<i>Hirschfeldia incana</i>	San Claudio - agricultural - 2	0.0031	0.0023
<i>Hirschfeldia incana</i>	San Claudio - reserve - 1	0.0022	0.0002
<i>Hirschfeldia incana</i>	San Claudio - reserve - 2	0.0432	0.0020
<i>Lycium chilense</i>	Anquilóo - reserve - 2	-0.3355	0.0087
<i>Mentha pulegium</i>	Las Chilcas - agricultural - 2	0.0136	0.0866
<i>Mentha pulegium</i>	Las Chilcas - reserve - 1	0.3973	0.0388
<i>Nierembergia aristata</i>	Anquilóo - agricultural - 1	0.0197	0.0217
<i>Nierembergia aristata</i>	Anquilóo - reserve - 1	-0.0065	0.0016
<i>Nierembergia aristata</i>	Anquilóo - reserve - 2	-0.0048	0.0011
<i>Nothoscordum euosimum</i>	Las Chilcas - agricultural - 1	0.0405	0.0034
<i>Nothoscordum euosimum</i>	Las Chilcas - agricultural - 2	-0.0045	0.1162
<i>Physalis viscosa</i>	Anquilóo - agricultural - 1	0.0041	0.0005
<i>Prosopidastrum globosum</i>	Anquilóo - reserve - 2	-0.0012	0.0194
<i>Senecio pulcher</i>	Las Chilcas - agricultural - 1	-0.0104	0.0007
<i>Sisyrinchium platense</i>	Las Chilcas - agricultural - 1	-0.2850	0.0203
<i>Sisyrinchium platense</i>	Las Chilcas - agricultural - 2	-0.0487	0.0324
<i>Sisyrinchium platense</i>	Las Chilcas - reserve - 1	0.0206	0.1143
<i>Solanum sisymbriifolium</i>	San Claudio - agricultural - 1	0.0002	0.0004
<i>Sphaeralcea crispa</i>	Anquilóo - reserve - 1	-0.0601	0.0133
<i>Stemodia lanceolata</i>	Las Chilcas - agricultural - 1	-0.0044	0.0001
<i>Thelesperma megapotamicum</i>	Anquilóo - agricultural - 1	-0.0022	0.0025
<i>Turnera sidioides</i>	Anquilóo - agricultural - 1	-0.0002	0.0001
<i>Turnera sidioides</i>	Anquilóo - agricultural - 2	-0.0140	0.0170
<i>Turnera sidioides</i>	Anquilóo - reserve - 2	-0.0014	0.0002
<i>Verbena intermedia</i>	Anquilóo - reserve - 2	-0.0643	0.0327
<i>Verbena intermedia</i>	San Claudio - agricultural - 2	0.0932	0.0071
<i>Verbena intermedia</i>	San Claudio - reserve - 2	-0.0073	0.0101

Table S3: The coefficient of determination  $R^2$  of the most parsimonious pollen deposition models (those with the lowest AICc). The marginal coefficient of determination describes the proportion of variance explained by just the fixed effects.

conditional $R^2_{(c)}$			marginal $R^2_{(m)}$		
mean	min	max	mean	min	max
<b>conspecific pollen</b>					
0.91	0.87	0.93	0.09	0.06	0.14
<b>heterospecific pollen</b>					
0.80	0.76	0.87	0.27	0.21	0.35

Table S4: Comparison of the two random structures we considered for the models of conspecific and heterospecific pollen deposition. The table shows median  $\Delta$ AIC values of 99 bootstrap resamples of the data. The 5th and 95th percentile are shown inside square brackets. Communities are defined by individual fragments but ignore the hierarchical arrangement of sampling sites.

random structure	$\Delta$ AIC	
	median	C.I.
<b>conspecific pollen</b>		
1   plant sp. * community	0.0	[0, 0]
1   plant sp.	30.7	[8.2, 58.1]
<b>heterospecific pollen</b>		
1   plant sp. * community	0.0	[0, 0]
1   plant sp.	44.6	[19.3, 88.4]

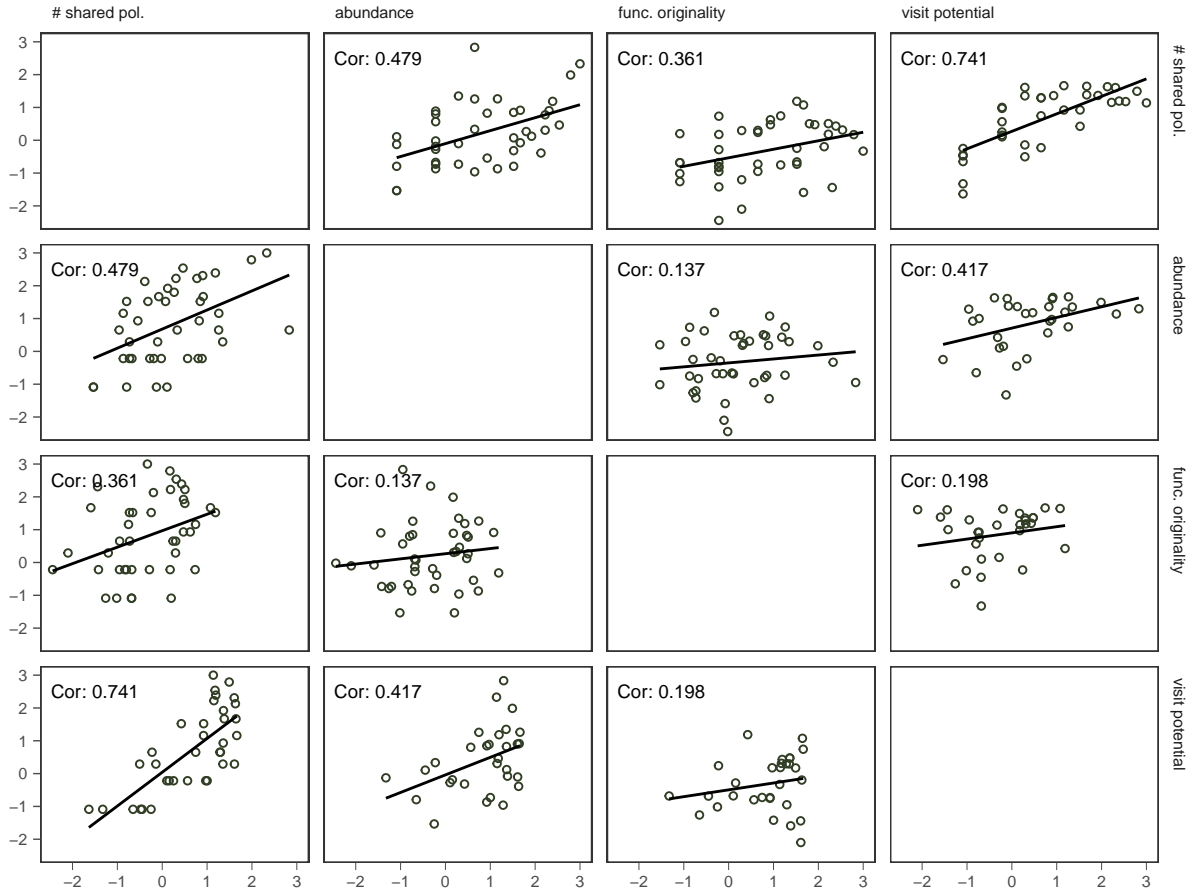


Figure S2: Correlation between the explanatory variables included in the statistical models.

Table S5: Comparison of the different fixed structures we considered for the models of conspecific and heterospecific pollen deposition. The table shows median  $\Delta\text{AIC}$  values of 99 bootstrap resamples of the data. The 5th and 95th percentile are shown inside square brackets.

fixed structure	$\Delta\text{AIC}$	
	median	C.I.
<b>conspecific pollen</b>		
~ abundance + visit potential	0.0	[0, 0]
~ abundance + visit potential + func. originality	0.9	[0.4, 1.3]
~ abundance + visit potential + # shared pol.	1.9	[1.6, 2.1]
~ abundance + visit potential + # shared pol. + func. originality	2.2	[1.6, 2.8]
~ visit potential + func. originality	2.8	[2.1, 3.8]
~ visit potential + # shared pol. + func. originality	3.6	[2.3, 4.6]
~ visit potential	118.3	[75.3, 178.7]
~ visit potential + # shared pol.	119.0	[76, 179.9]
~ abundance	189.7	[150.1, 239.7]
~ abundance + func. originality	191.6	[151.7, 241.6]
~ abundance + # shared pol.	191.7	[151.9, 241.7]
~ func. originality	192.5	[152.9, 242.2]
~ abundance + # shared pol. + func. originality	193.7	[153.6, 243.6]
~ # shared pol. + func. originality	193.7	[154.6, 243.7]
~ # shared pol.	351.8	[293.5, 419.9]
<b>heterospecific pollen</b>		
~ abundance + visit potential	0.0	[0, 0]
~ abundance + visit potential + func. originality	1.1	[0.5, 1.5]
~ abundance + visit potential + # shared pol.	2.1	[1.9, 2.1]
~ abundance + visit potential + # shared pol. + func. originality	3.1	[2.6, 3.5]
~ visit potential + func. originality	11.9	[10, 13.9]
~ visit potential + # shared pol. + func. originality	13.2	[11.2, 15.2]
~ visit potential	67.5	[53.4, 87.5]
~ visit potential + # shared pol.	68.4	[54.2, 88.7]
~ abundance + # shared pol.	206.9	[160.6, 251.5]
~ abundance	207.6	[162.8, 251.7]
~ abundance + func. originality	208.6	[163.2, 252.6]
~ abundance + # shared pol. + func. originality	208.6	[162.2, 253.2]
~ func. originality	214.3	[168.3, 258.7]
~ # shared pol. + func. originality	216.3	[170.3, 260.6]
~ # shared pol.	336.0	[282.6, 391.5]

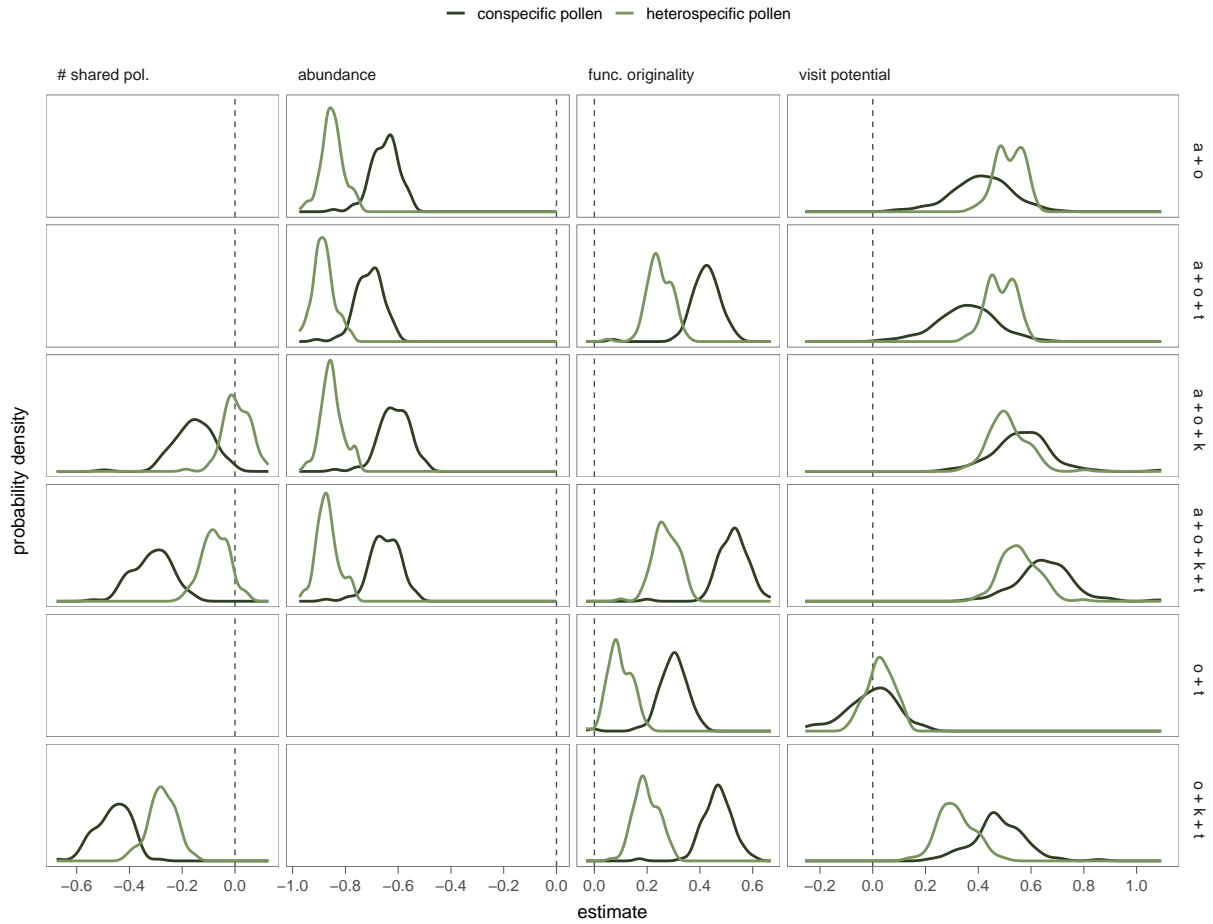


Figure S3: Distribution of effect estimates for models of conspecific and heterospecific pollen density gain. Model formulas have been abbreviated:  $a$  for abundance,  $k$  for the number of shared pollinators,  $o$  for the visit potential, and  $t$  for functional originality. Only candidate formulas with a  $\Delta AICc < 4$  for either conspecific or heterospecific pollen are shown. Models candidates are arranged in decreasing order of support. Although relative abundance, the number of shared pollinators, and the visit potential were all positively correlated, the effect each had on conspecific pollen was similar among models that included all or just some of these three explanatory variables. One exception was visit potential, which exhibits a positive association with the relative amount of conspecific pollen under some variable combinations. Nevertheless, these differences were observed only in model specifications with relatively low AICc support.