

# Draft information

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## Requests to coauthors

- Specify grant numbers in the Acknowledgements and make sure the ones stated there now are correct.
- Suggestions to bring the abstract down to 150 words.
- Approve (or not) for submission.

## Changes since the last draft

- Removed the criterion to distinguish between competition and facilitation that was based on the difference between conspecific pollen in open and bagged flowers as it didn't add much to the story (said the same as the previously published criterion based on the relationship between conspecific and heterospecific pollen) and was based on some assumptions that are easy to question.
- This simplified Figure 1
- Added .git and .drake to .dockerignore to speed up build
- I refer to the variables on the main model's factors and use that term consistently throughout the paper. Previously I was using factor, variable, and sometimes mechanism interchangeably
- Many minor changes to the text
- Replaced instances of "plant abundance" to the more specific term "floral abundance" (Jamie suggested some people working in the field might be finicky with terminology).
- Some extra refs added
- Moved the sentences about variable collinearity to the supp. info. to save a bit of space in the main text

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May 7, 2019

Prof. Tim Coulson,  
Editorial Office,  
Ecology Letters

Dear Professor Coulson,

We are submitting the manuscript entitled “Community context determines competition vs. facilitation trade-offs in pollination systems” to be considered for publication in *Ecology Letters*.

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.

Very few studies have previously investigated how competition for pollination affects the pollination service using *empirical data at the community level*. When **they have** they have focused on pollen deposition alone and failed to incorporate other metrics that might influence the pollination service in natural communities. Here, we take a step beyond by not only collecting pollen-deposition data but also visitation, pollen transfer, plant abundance, phenology, and traits. These extra pieces of information allowed us to investigate the relationship between pollination service and multiple ecological factors, and, for the first time, quantify the pollination niche of plant populations.

Within the literature, studies of pollination almost always focus on the inherently mutualistic aspects of plant-pollinator communities. In contrast, ours provides compelling evidence that animal-mediated pollination is really a fluid **balance** between competition and facilitation. This calls for a shift in the way we think about pollination in community ecology, especially from a theoretical perspective.

Lastly, please note that the data used in this manuscript have been previously published<sup>1</sup> by one of the co-authors. However, the enclosed work represents a novel contribution for all involved, and no related work published, in press, or submitted during this or last year has been cited.

Thank you for your consideration.

Fernando Cagua

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<sup>1</sup>Hugo 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; Hugo 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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appropriate data repository after publication. The DOI will be included  
here.

**Author contributions:** EFC wrote the manuscript and performed all  
analyses with input from all authors; HJM collected the data; all authors  
contributed to the study design.

## 20 Abstract

21 Plant-pollinator interactions are commonly viewed as mutualistic. When  
22 plant species share pollinators, however, interspecific pollen transfer occurs  
23 and plants can compete for pollination. The extent of competition for  
24 pollination and its effects on pollination service are not well understood  
25 at the community level; many species interact simultaneously and multiple  
26 factors that might play a role (abundance, visitation, traits) are often  
27 intertwined.  By examining comprehensive empirical data, we confirm that  
28 competition for pollination is pervasive and is only partially influenced  
29 by the number of shared pollinators. Furthermore, the factors that most  
30 influence the pollination service (abundance and visit effectiveness) also  
31 introduce a trade-off between the absolute amount of conspecific pollen  
32 received and the amount relative to heterospecific pollen. Most importantly,  
33 the ways plants balance these trade-offs depend on the community context,  
34 as most species showed flexibility in the strategy they used to cope with  
35 competition for pollination. Achieving a better understanding of plant-  
36 pollinator communities will require seeing them as comprising mutualistic  
37 and competitive interactions.

## 38 Introduction

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


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

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

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

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

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

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

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

## 135 **Methods**

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

### 141 **Competition vs. facilitation**

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



150 a positive relationship is what would be observed when facilitation is the  
151 dominant outcome.

## 152 **Data collection**

153 In each of the studied communities, we quantified pollen deposition in a subset  
154 of plant species between December 2010 and February 2011. This subset  
155 comprised between three and nine common insect-pollinated (entomophilous)  
156 plant species that were flowering during the sampling period (see Figure 1a).  
157 Based on data from previous years (Marrero *et al.* 2014), we chose plant  
158 species such that they cover a wide range on a specialization-generalization  
159 gradient as well as a wide range of abundances. In each of the selected  
160 plants, we removed all flowers leaving only buds that were expected to go  
161 into florescence on the next day. Two days after inflorescence, we collected all  
162 remaining flowers and counted the number of conspecific and heterospecific  
163 pollen grains in their pistils. More details can be found in Marrero *et al.*  
164 (2016).

## 165 **Data analysis**

166 To evaluate the relationship between heterospecific and conspecific pollen,  
167 we used a generalised linear mixed model (GLMM) with a Poisson error  
168 distribution (following Tur *et al.* 2016). In this model, the number of  
169 conspecific pollen grains per flower was the response variable and the number  
170 of heterospecific grains the predictor variable (the log number of stigmas  
171 sampled was added as an offset term). The slope and intercept of this  
172 relationship were allowed to differ between populations (plant species  $\times$   
173 community), which were modelled as a random effect. Models were fitted  
174 using the function `glmer` from the R package `lme4` 1.1-19 (Bates *et al.*  
175 2015). A positive slope for a plant population indicates facilitation while a

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

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

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

## 190 **Data collection**

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

202 in addition to the visitation networks. To do this, we examined the pollen  
203 loads present on the floral visitors collected (Marrero *et al.* 2017). When the  
204 pollen count on an individual animal was estimated to be less than 2,000  
205 grains, we identified every grain to the species level when possible and to  
206 pollen complexes when it was not. When the pollen count was above 2,000  
207 grains, we classified approximately 50% of pollen and total pollen counts were  
208 extrapolated (Bosch *et al.* 2009). Finally, we also recorded morphological  
209 traits that relate to plant type (herb, shrub, climber), life cycle (annual,  
210 perennial), flower colouration, phenology, and whether the species is native  
211 in the study region. More details can be found in Marrero *et al.* (2014 and  
212 2017).

## 213 **Data analysis**

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

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

228 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  $\Delta\text{AICc}$  (relative to the most likely model) for each bootstrap sample. As we wanted model coefficients from more likely candidate models to carry more weight

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

## 261 **Flexibility of plant strategies**

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

## 283 Results

### 284 Competition vs. facilitation

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

### 304 Factors affecting quantity and purity of pollination service

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

**competition vs. facilitation**  
relationship hetero–conspecific pollen

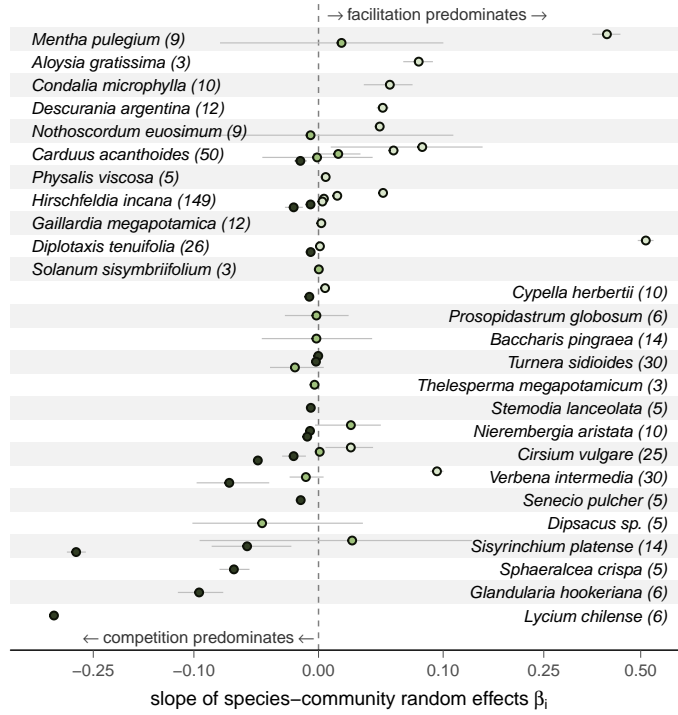


Figure 1: Competition vs. facilitation at the community level. Points indicate the estimated slopes for the relationship between the amount of heterospecific and conspecific pollen deposited per stigma across species in each of their communities. Statistically significant negative slopes (darkest shade)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

310 power came from the random effects (Table S3). As determined by AICc, the  
311 random structure best supported by the data was the one that fit an intercept  
312 for each species in each community (as opposed to a common intercept for  
313 each species irrespective of the community to which they belong). This  
314 structure was best for both the models of conspecific and heterospecific  
315 pollen (Table S4).

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

322 We found that the relationship between each of the ecological factors and  
323 pollen deposition was similar for both conspecific and heterospecific pollen.  
324 That is, strategies that were associated with an increase in conspecific pollen  
325 were also associated with an increase in heterospecific pollen deposition.  
326 Specifically, the plants' mean visit effectiveness had a positive effect on  
327 pollen deposition (Figure 2b). However, the effect size was slightly larger  
328 for heterospecific than for conspecific pollen. This indicates that, although  
329 there is a positive association between visit effectiveness and the quantity  
330 of pollen deposition, there is a negative relationship with its purity (Figure  
331 2c). In contrast, a plants' relative floral abundance negatively affected its  
332 deposition quantity, but the mean difference between the coefficients in  
333 the models indicates a positive association with purity (Figure 2c). The  
334 third most important factor, functional originality, had a positive, although  
335 comparatively smaller, association with both the quantity and purity. Finally,  
336 the number of shared pollinators had negative and neutral associations with  
337 conspecific and heterospecific pollen, respectively, but these impacts were  
338 small when compared to the other factors. Although the ecological factors



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

## 341 Flexibility of plant strategies

342 We used a PCA of the analysed species to investigate whether plants' realised  
343 pollination niche is similar across communities or whether they are flexible  
344 and therefore a reflection of the community context. The first two PCA  
345 components explained 75% of the total variance (Figure 3a). The first  
346 component was dominated by visit effectiveness and relative abundance while  
347 the second component was dominated by the number of shared pollinators  
348 and the plant's functional originality. When we locate the species that were  
349 sampled in more than one community in the first two PCA components  
350 (Figure 3b), we observe that the niches of any given species do not tend to be  
351 close to each other. Indeed, when we measured the median distance between  
352 the plants' coordinates, we found that it was only significantly smaller than  
353 that of randomisations for only two of the twelve species analysed (Figure  
354 3c).

## 355 Discussion

356 Our results suggest that community context plays a central role in deter-  
357 mining the net cost or benefit of sharing pollinators. First, we found that  
358 pollinator sharing can lead to both net facilitative and net competitive effects  
359 to plant species in a community. Second, we found that multiple ecological  
360 factors can modulate the intensity of competition; however, conspecific and  
361 heterospecific pollen deposition are tightly coupled and this creates a clear  
362 trade-off between the quantity and purity of pollination (Thomson *et al.*  
363 2019). Third, we found that the way these factors influence competition  
364 is strongly shaped by the community context. That is, if these factors

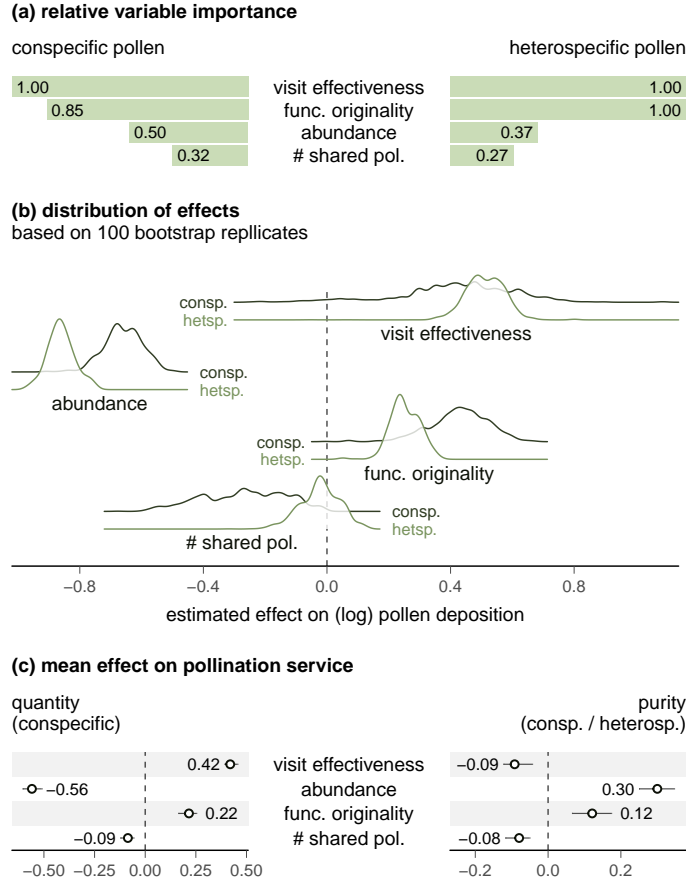


Figure 2: Effect of strategies to minimise competition in the pollination service. (a) The plant's visit effectiveness and relative floral abundance are the most important factors determining the deposition of conspecific and heterospecific pollen. Meanwhile, the number of shared pollinators was generally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

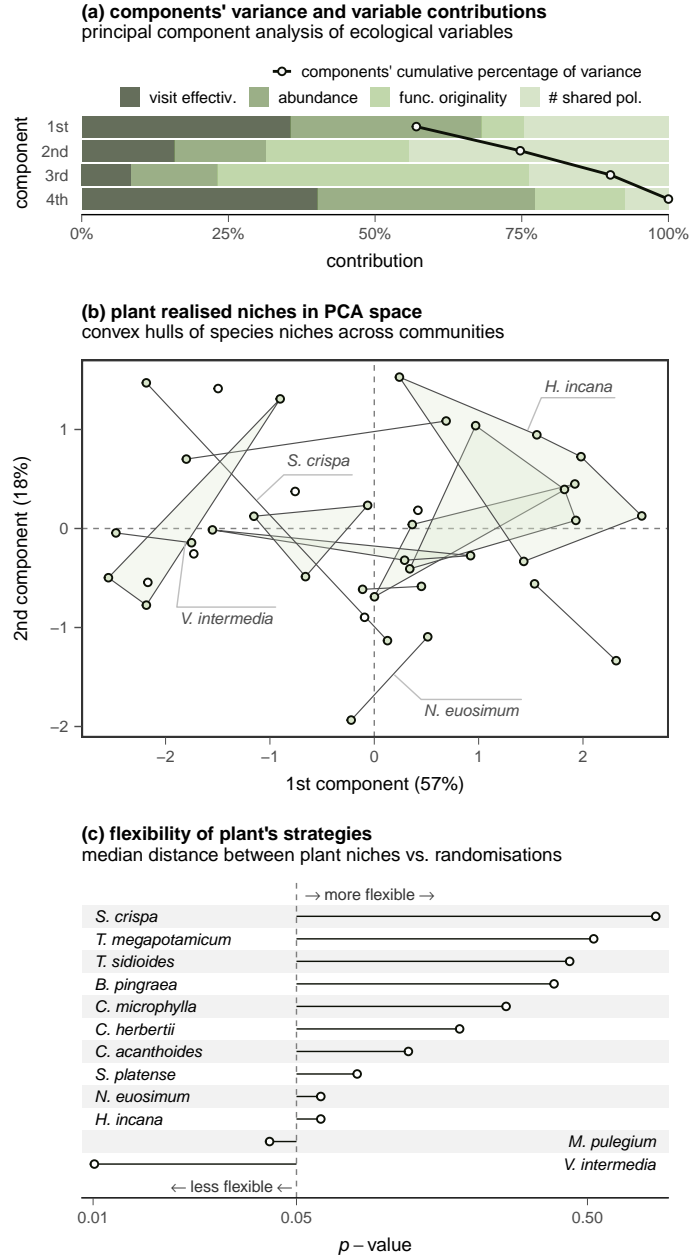


Figure 3: The flexibility of plant strategies. (a) The two first components explain a large proportion of the total variance. (b) When plants that were sampled in more than one community are plotted in terms of these two components, we observe that their points—which represent the strategy (the particular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

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



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

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

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

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

419 We observed, as expected, that the effects of pollen deposition can vary widely  
420 among species. For instance, while the fitness of some plant species can be  
421 hurt even by low amounts of heterospecific pollen, for others, fitness can  
422 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 **Great assertion!**  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

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

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# The pollination trade-off

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	-	-

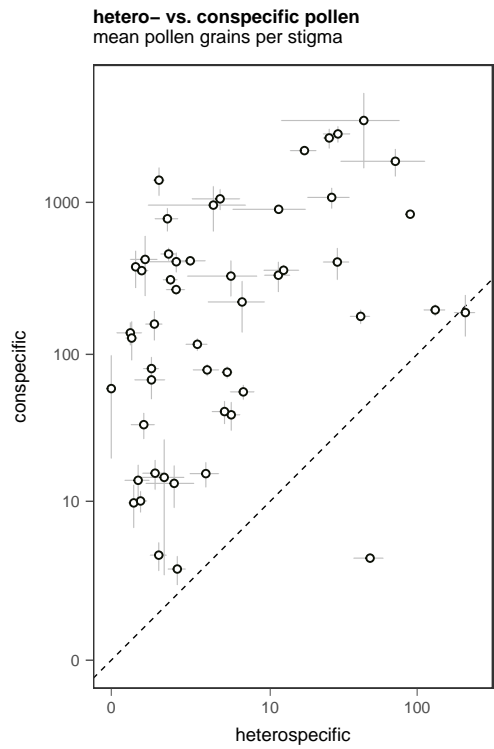


Figure S1: Despite the variation in these slopes, plants overall had more conspecific than heterospecific pollen deposited in their stigmas.



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</i> sp.	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]

Table S5: Comparison of the different fixed 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.

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

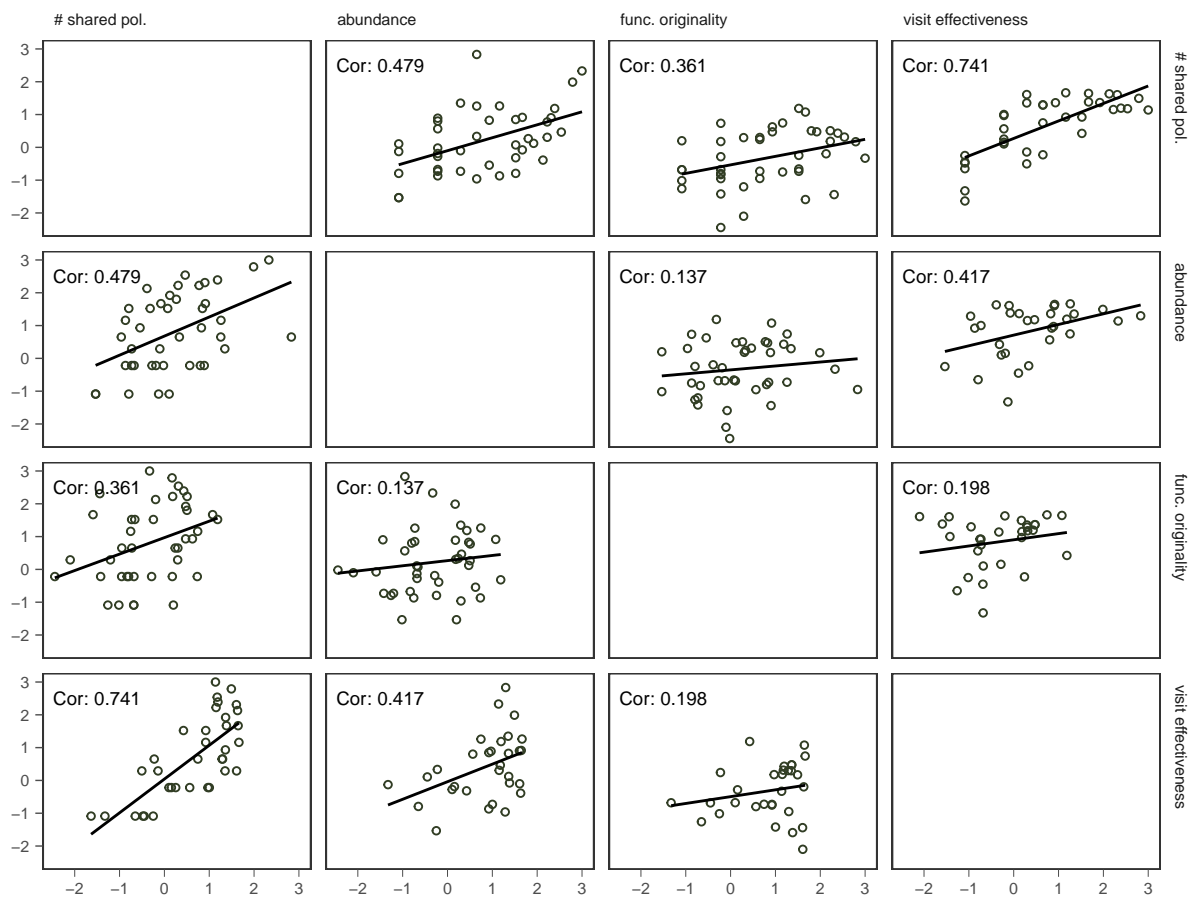


Figure S2: Correlation between the explanatory variables included in the statistical models.

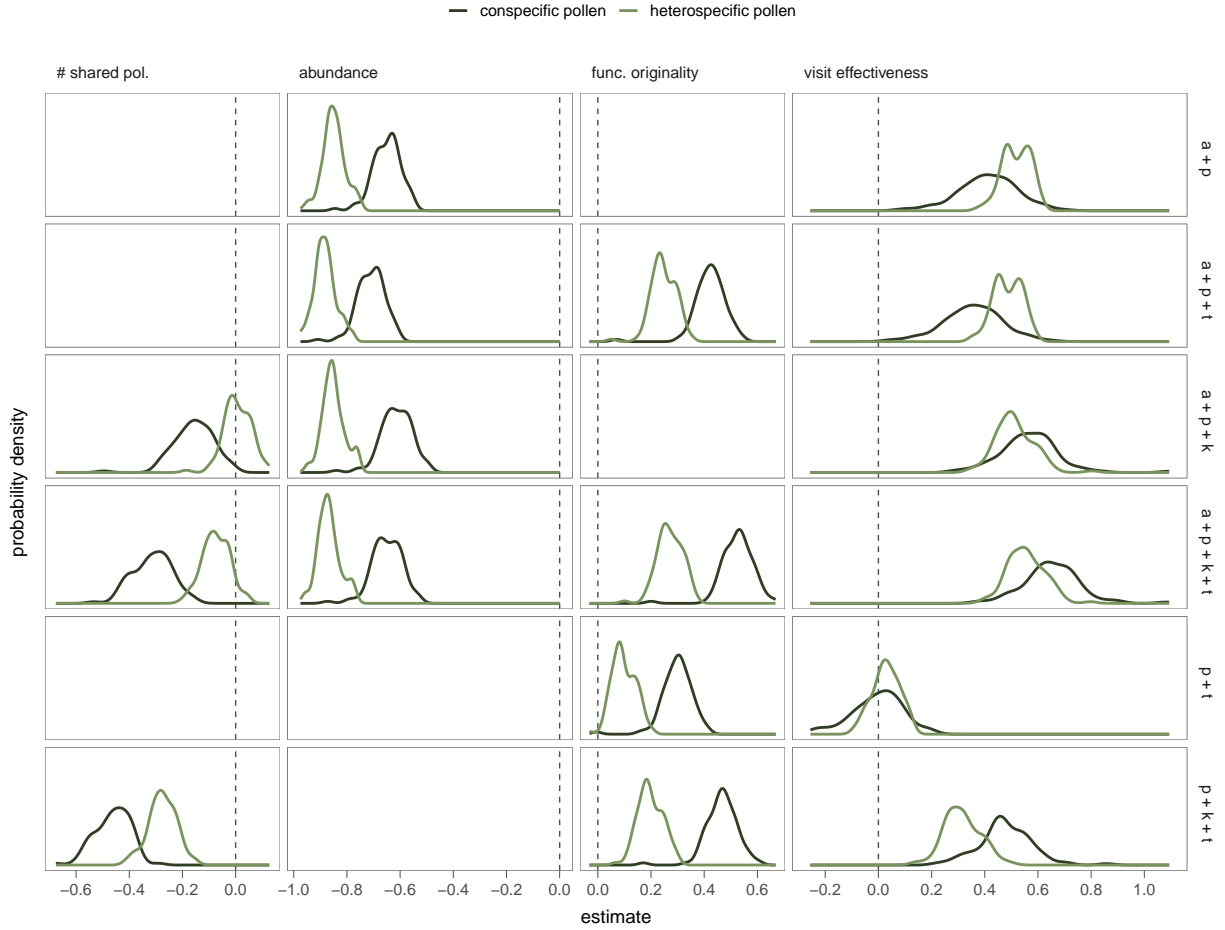


Figure S3: Distribution of effect estimates for models of conspecific and heterospecific pollen density gain. Model formulas have been abbreviated:  $a$  for abundance,  $k$  for the number of shared pollinators,  $p$  for the visit effectiveness, and  $t$  for trait originality. Only candidate formulas 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 effectiveness 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-effectiveness, 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.