

Draft information

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Requests to coauthors

- Check text between page 4, line 59 and page 4, line 73 where there were changes.
- Check the cover letter. I made small changes based on assessment from EL editor and swapped the order of a couple paragraphs.
- **Jason:** Could you please double check your grant numbers? They look different to Daniel's.

Changes since the last draft

- Renamed visit effectiveness as visit potential throughout to reduce confusion with previous uses of the term.
- Corrected a mistake on the names used for the model terms in Table S5. It used to say “degree” where it should have been “# shared pollinators”.
- Corrected caption of Fig S3 which used “trait originality” instead of “functional originality” which is the term we use in the paper
- Paper has been formatted with minimum requirements for initial submission at Plos Biology.
- Added some sentences in the intro to strengthen the link between competition/facilitation and conspecific/heterospecific pollen.

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May 15, 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 *Plos Biology*. The main goal of this study¹ 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. 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.



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.

Within the literature, studies of pollination communities almost always focus on the inherently mutualistic aspects of plant-pollinator interactions. In contrast, ours provides compelling evidence that animal-mediated pollination is really a fluid dance 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 published¹ 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



¹H.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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appropriate data repository after publication.

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interests exist.

14 **Abstract**

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

30 Introduction

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

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

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

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

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

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

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

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

125 **Methods**

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

131 **Competition vs. facilitation**

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

142 **Data collection**

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

154 **Data analysis**

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

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

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

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

177 **Data collection**

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

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

199 Data analysis

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

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

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

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

221 , 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 potential 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 [27,39]. 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 [44]. Finally, we scaled all four factors to have a zero mean and unitary variance.

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

247 Flexibility of plant strategies

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

269 Results

270 Competition vs. facilitation

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

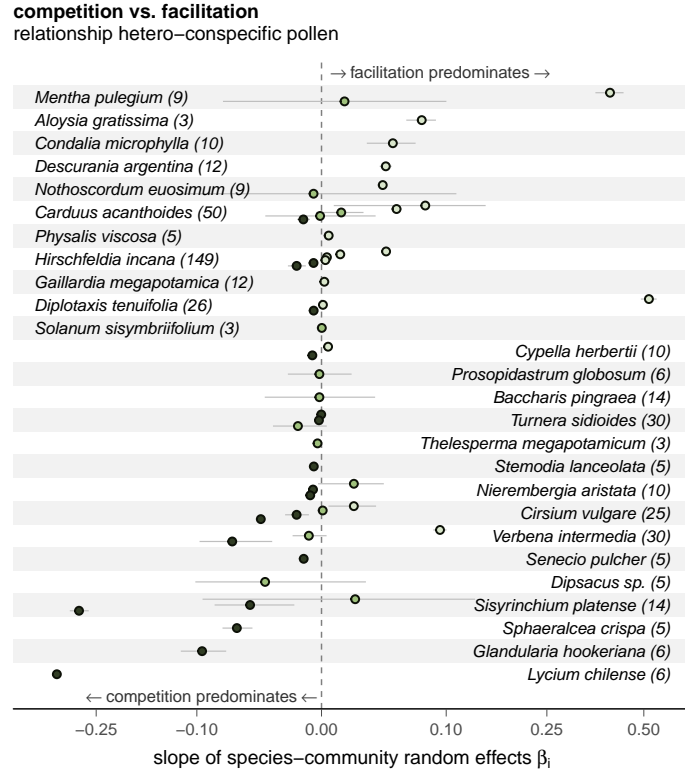


Figure 1: Competition vs. facilitation at the community level. Points indicate the estimated slopes for the relationship between the amount of heterospecific and conspecific pollen deposited per stigma across species in each of their communities. Statistically significant negative slopes (darkest shade)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

301 pollen (Table S4).

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

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

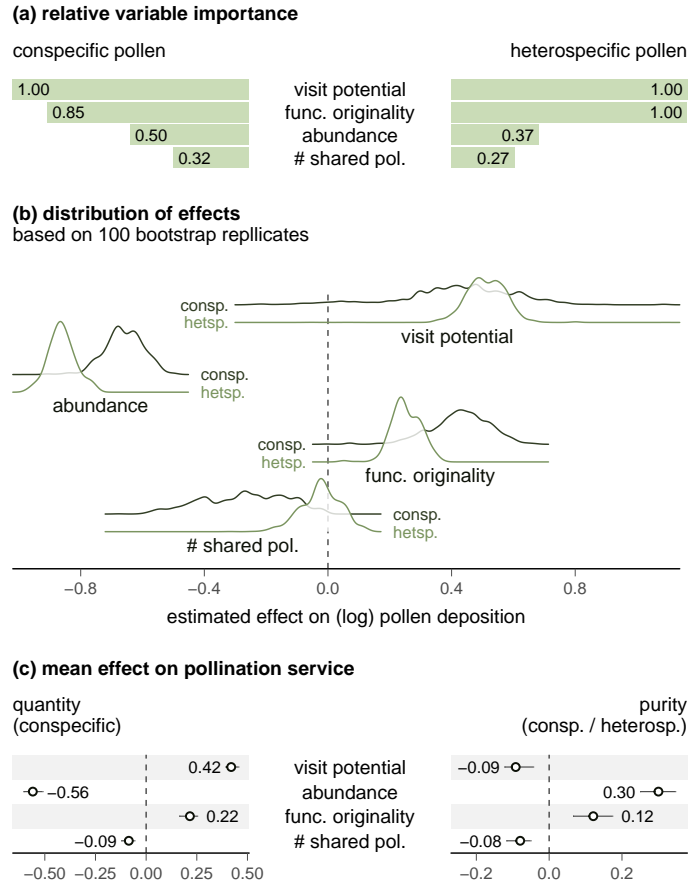


Figure 2: Effect of ecological factors on the pollination service. (a) The plant's visit potential and relative floral abundance are the most important factors determining the deposition of conspecific and heterospecific pollen. Meanwhile, the number of shared pollinators was generally less important.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

327 **Flexibility of plant strategies**

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

340 **Discussion**

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

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

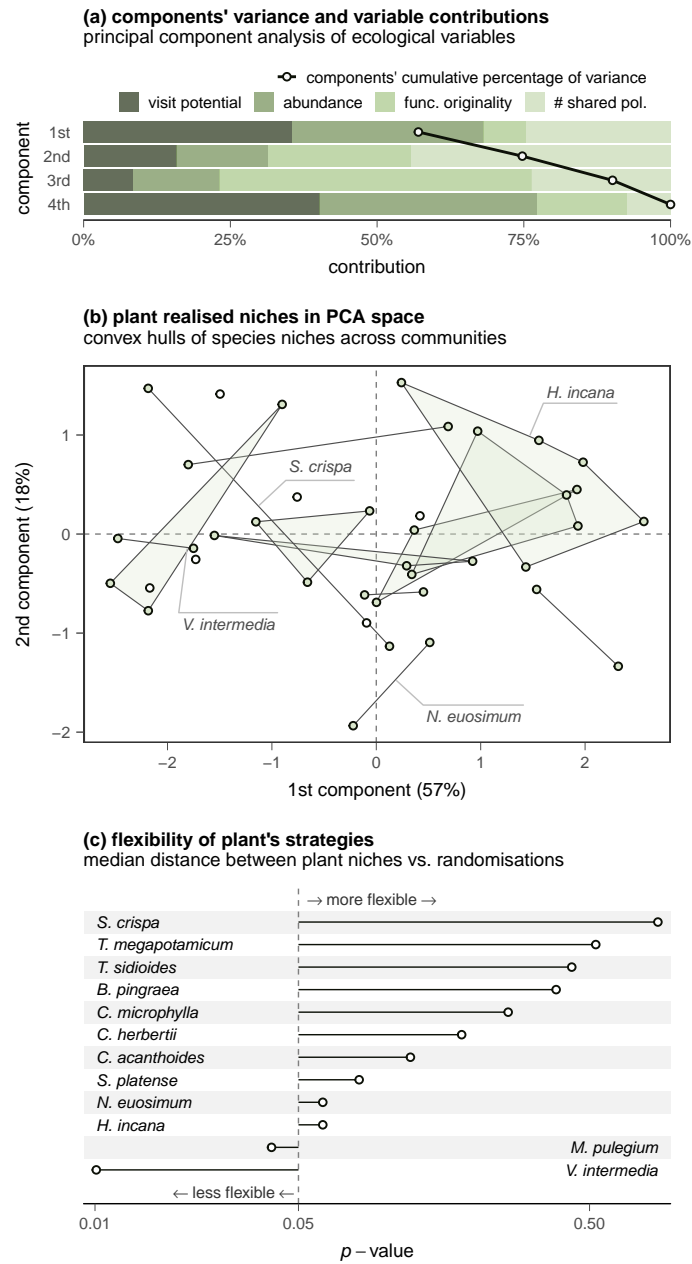


Figure 3: The flexibility of plant strategies. (a) The two first components explain a large proportion of the total variance. (b) When plants that were sampled in more than one community are plotted in terms of these two components, we observe that their points, which represent the strategy (the particular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

354 nation communities. A previous study showed that, in diverse pollination
355 communities, sharing pollinators does not necessarily translate to net com-
356 petition [24]. The overall extent of facilitation/competition of pollination
357 communities can depend on factors like the adversity of the environment
358 [24,46] or how disturbances affect pollinator populations [47]. However, why
359 some species experience more competition than others was not understood.
360 Although we were unable to measure the fitness outcomes, here we show that
361 the coexistence of facilitative and competitive effects of animal-mediated
362 pollination can be at least partially explained by trade-offs in the pollination
363 service—both the short and the long term. These trade-offs arise when plants
364 simultaneously maximise the deposition of conspecific pollen and minimise
365 that of heterospecific pollen.

366 In the short term, being a specialist and sharing no pollinators might reduce
367 competition [48] and hence be preferable, not only due to costs to male fitness
368 [16,49], but also because, as we show here, sharing pollinators reduces both
369 the quantity and purity of the conspecific pollen deposited. However, over
370 long periods of time, there could be a risk associated with a specialist plant
371 having few pollinators [50]. To ensure long-term survival, it is thus likely
372 that plants also need to balance this risk with the costs of sharing pollinators
373 [51]. One possible solution is to share pollinators *and* have original traits—as
374 we show that trait originality is generally beneficial to pollen deposition and
375 it is commonly thought that species that are further from others in trait
376 space benefit from reduced competition. Yet, there are two possible caveats
377 to this strategy that highlight the interrelatedness of the ecological factors.
378 First, in a mutualism context, it is also possible that trait originality could
379 come at the cost of being less ‘apparent’ to pollinators [52]. Second, the
380 negative relationship between originality and generalism [32] has been shown
381 to depend on plant abundance [27], with generalist species being able to
382 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
fixed component			
(Intercept)	4.976	0.279	17.862
heterospecific	0.008	0.017	0.474
random component (species:community)			
S.D. random intercept	1.964	-	-
S.D. random slope	0.120	-	-

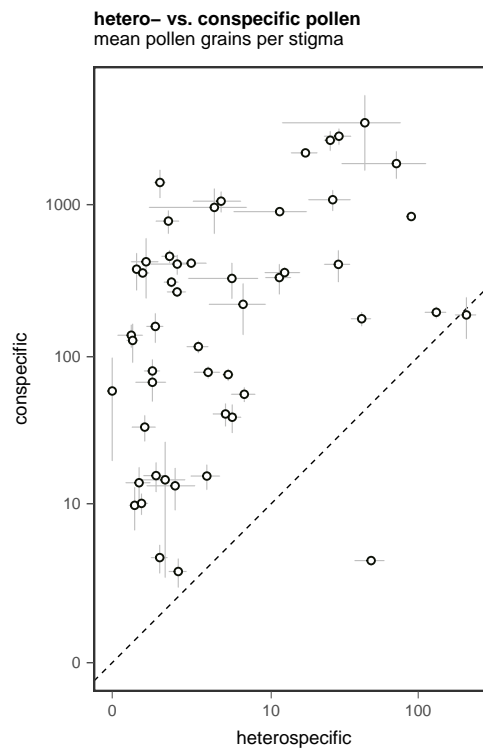


Figure S1: Despite the variation in these slopes, plants overall had more conspecific than heterospecific pollen deposited in their stigmas.

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
conspecific pollen					
0.91	0.87	0.93	0.09	0.06	0.14
heterospecific pollen					
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 Δ 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	Δ AIC	
	median	C.I.
conspecific pollen		
1 plant sp. * community	0.0	[0, 0]
1 plant sp.	30.7	[8.2, 58.1]
heterospecific pollen		
1 plant sp. * community	0.0	[0, 0]
1 plant sp.	44.6	[19.3, 88.4]

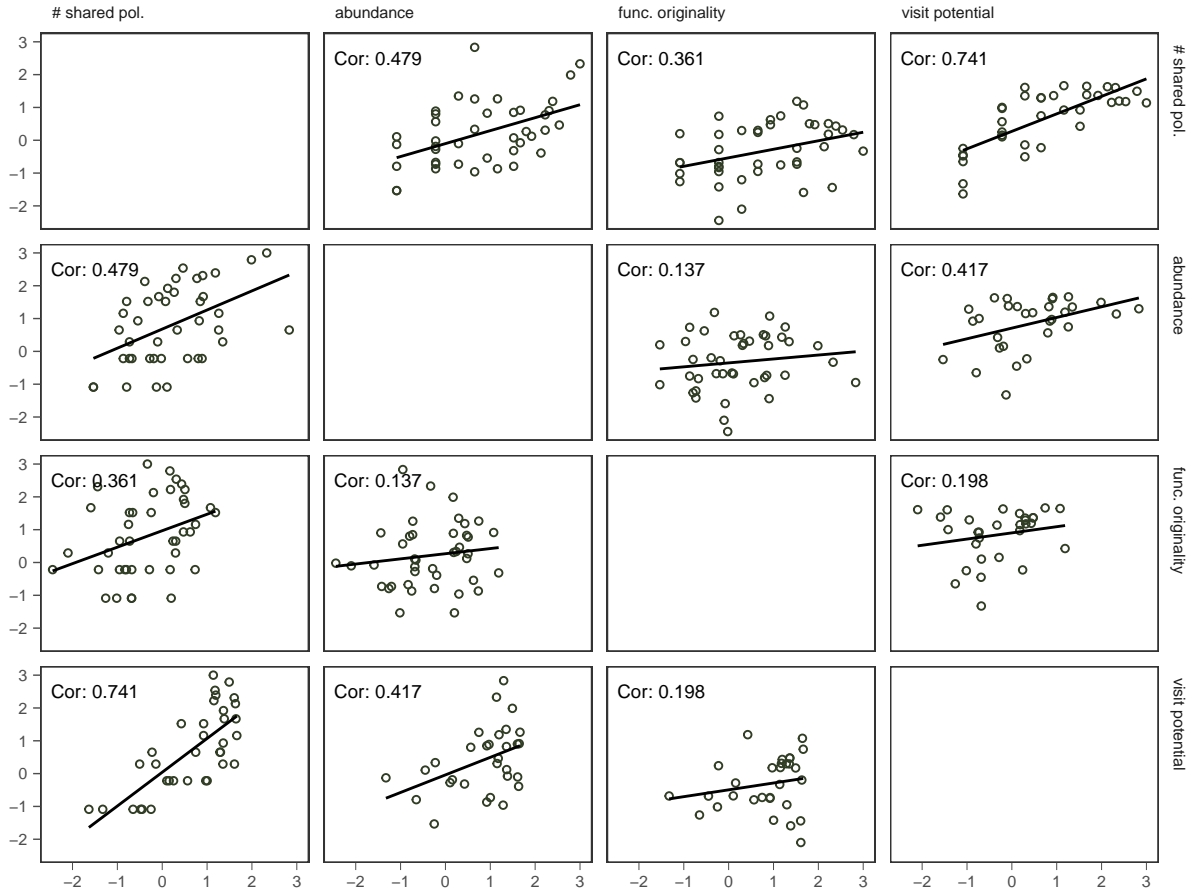


Figure S2: Correlation between the explanatory variables included in the statistical models.

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

fixed structure	ΔAIC	
	median	C.I.
conspecific pollen		
~ 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]
heterospecific pollen		
~ 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]

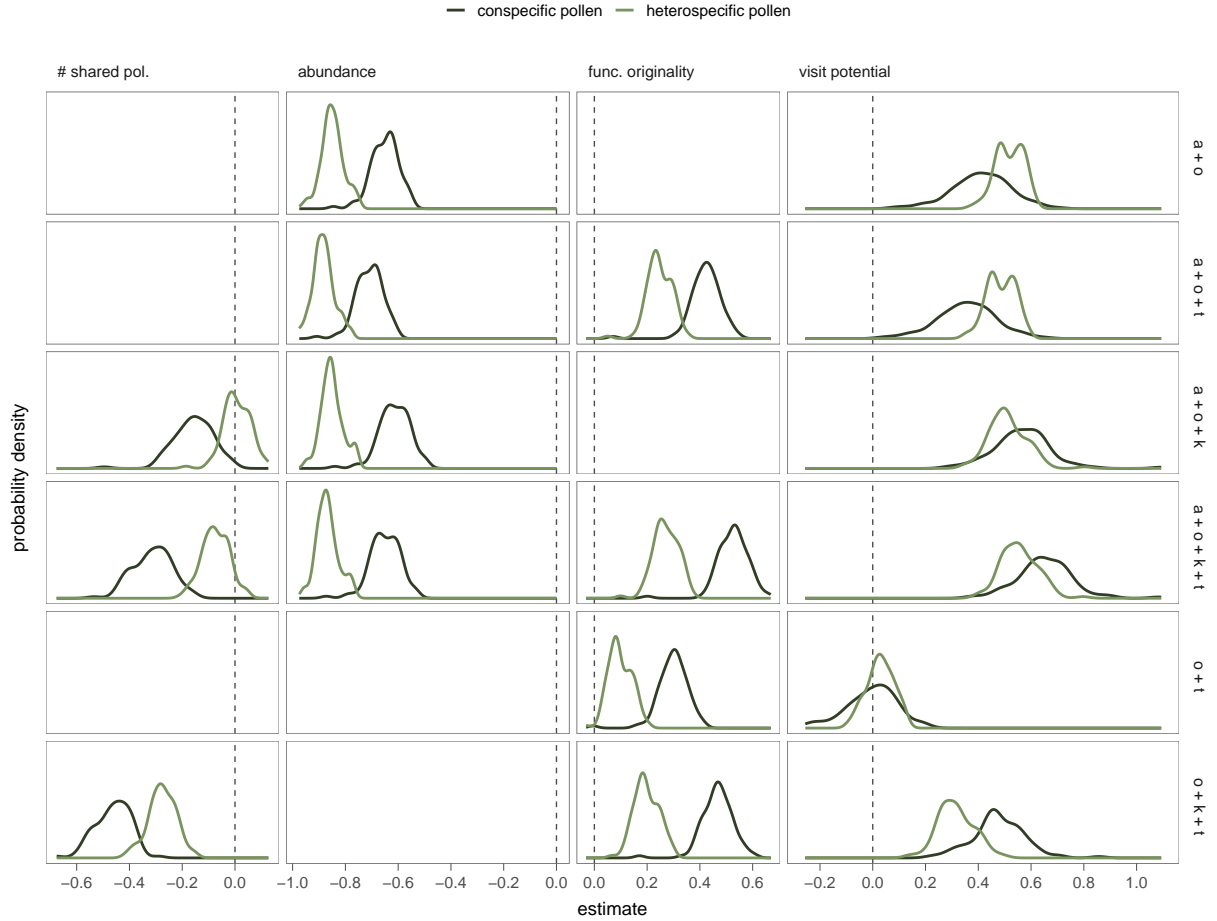


Figure S3: Distribution of effect estimates for models of conspecific and heterospecific pollen density gain. Model formulas have been abbreviated: a for abundance, k for the number of shared pollinators, o for the visit potential, and t for functional originality. Only candidate formulas with a $\Delta AICc < 4$ 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.