

Community context determines competition/facilitation trade-offs in pollination systems

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20 Abstract

21 Plant-pollinator interactions are commonly viewed as mutualistic interac-
22 tions. When plants share pollinators, however, interspecific pollen transfer
23 occurs and plants can start competing. The extent of competition for polli-
24 nation and its effects in the pollination service are not well understood at
25 the community level where species interact simultaneously and intertwined
26 factors like abundance, visitation, and traits might play a role. By examining
27 comprehensive empirical data, we confirm that competition for pollination is
28 pervasive. Furthermore, the factors that influence the pollination service the
29 most (abundance and visit effectiveness) also introduce a trade-off between
30 the absolute amount of conspecific pollen and the amount relative to het-
31 erospecific pollen. Most importantly, the way plants balance these trade-offs
32 are dependent on the community context as most species showed flexibility
33 on their strategy used to cope with competition for pollination. Achieving
34 a better understanding of plant-pollination communities will require seeing
35 them as both mutualistic and competitive communities.

36 Introduction

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

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

63 There are two main mechanisms through which competition for pollinators

64 can affect plant fertilization (Morales & Traveset 2008). The first is in-
 65 traspecific pollen transfer. This happens, for example, when plants with
 66 distinctively attractive flowers might reduce the number of visits to those less
 67 attractive neighbouring plants, and hence reduce the amount of *conspecific*
 68 *pollen* deposited by animals (Yang *et al.* 2011). The second is intraspecific
 69 pollen transfer and occurs when plants share pollination partners. In that
 70 case, even receiving a visit might not necessarily translate into fertilization
 71 (Campbell & Motten 1985) because a focal plant might receive *heterospecific*
 72 *pollen* or because pollen from the focal plant might be lost to different species.
 73 Generally speaking, the higher the amount of conspecific pollen (both in
 74 absolute terms and relative to heterospecific pollen) the better the pollination
 75 service received by the focal plant. These two mechanisms of competition,
 76 by definition, occur at the community scale. However, with few exceptions
 77 (Rathcke 1988; Lopezaraiza-Mikel *et al.* 2007; Hegland *et al.* 2009; Aizen &
 78 Rovere 2010; Tur *et al.* 2016), most of what we know about the deposition
 79 of conspecific and heterospecific pollen—and its relationship to competition
 80 vs. facilitation in pollination systems—is based on studies with two plant
 81 species.

82 At the community scale, the factors that determine the patterns of conspecific
 83 and heterospecific pollen deposition are tightly intertwined, operate simulta-
 84 neously, 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). This
 88 evidence is aligned with the notion that a species which 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. If evolutionary
 91 specialisation occurs by changing traits to focus on fewer but better partners
 92 (Caruso 2000), we should expect a reduction of competition for pollinators in

93 species with “original” traits and an increase of competition in species with
94 a large number of interaction partners (Gibson *et al.* 2012; Carvalheiro *et al.*
95 2014). Alternatively, it might also be the case that density (for example in
96 terms of flower or pollen counts) is the dominant force driving pollen transfer
97 (Seifan *et al.* 2014). Abundant plant species might experience a dilution of
98 available pollinators (Feinsinger 1987) but might also receive more effective
99 visits by capitalising on a larger share of both visits and the pollen carried
100 by pollinators. In this case, a potential reduction in the absolute amount
101 of conspecific pollen received could be compensated by an increase in the
102 amount of conspecific pollen relative to heterospecific pollen. Altogether,
103 it is clear that some ecological factors can influence pollen deposition and
104 that these factors, in the specific context of pollination, could be used to
105 roughly define a species *realised niche* in their community. However, the
106 intertwined nature of these factors makes it hard to determine whether they
107 favour or hinder the pollination service at the community level. Moreover,
108 their relative importance has not yet been empirically evaluated in natural
109 plant communities.

110 Here, we investigate competition for pollination at the community scale using
111 empirical data from eleven plant-pollinator communities in the Argentinian
112 Pampas. First, we estimate the extent to which the net outcome of plants
113 sharing pollinators is facilitation or competition. If facilitation is the primary
114 outcome, we could expect two things. On the one hand, we could expect
115 an overall positive relationship between the amount of conspecific pollen
116 deposited in stigmas and the amount of heterospecific pollen (Tur *et al.* 2016).
117 The higher the deposition of conspecific pollen relative to heterospecific, the
118 larger the slope of that relationship. On the other, we could also expect a
119 larger amount of conspecific pollen deposited in stigmas when flowers are open
120 to animal pollinators than what is deposited due to self-pollination. Second,
121 we investigate the relative contribution that four ecological factors have

122 on the pollination service. Specifically, we hypothesize that competition,
123 measured as the quantity of conspecific pollen deposition and its purity
124 (relative to heterospecific pollen), should increase for plants that share
125 many pollination partners. However, we also hypothesize that other factors
126 like the plant's functional originality, its relative abundance, and the visit
127 effectiveness should have the potential to compensate for this increase in
128 competition. Third and finally, we examine how much does the community
129 context influences the way plants use these factors to minimise competition.
130 Although some plant species might be widespread across multiple locations,
131 competition for pollinators occurs at the community level and hence we
132 predict the competition for pollination niche to be influenced by the local
133 context. If plant strategy is not flexible across communities, we could expect
134 niches to be more similar within species than across species in the study. On
135 the contrary, if a species' strategy is flexible, we should expect plants to be
136 able to occupy different niches in each community such that competition
137 could be minimised regardless of the context.

138 **Methods**

139 We collected data from eleven co-flowering plant communities and their
140 pollinators in three locations in the Argentinian Pampas. These locations are
141 distributed across a precipitation gradient with a humid temperate climate
142 of the eastern Flooding Pampas becoming drier as one moves inland and
143 westward towards the Pampean Grasslands. This precipitation gradient
144 generated a natural gradient of network architecture which allowed us to
145 examine the generality of our findings. In each location, we sampled two
146 restored and two agricultural fragments, except in the Flooding Pampas,
147 where we were only able to sample one restored fragment due to the lack of
148 available sites.

149 **Competition vs. facilitation**

150 Our first objective was to identify whether the outcome of plants sharing
151 pollinators at the community level is facilitation or competition. We use two
152 complementary lines of evidence.

153 The first line can be found via the relationship between heterospecific and
154 conspecific pollen deposited in plant stigmas (Tur *et al.* 2016). This is
155 because heterospecific pollen can be seen as an unavoidable cost that plants
156 must pay for receiving conspecific pollen from shared pollinators. A negative
157 relationship (when shared pollinators increase heterospecific pollen loads and
158 decrease conspecific loads) may indicate that competition for pollination is
159 strong. In contrast, a positive relationship is what would be observed when
160 facilitation is the dominant outcome.

161 The second line of evidence can be obtained by examining the difference
162 between the amount of conspecific pollen deposited in flower stigmas *with*
163 and *without* animal-mediated pollination. Self-pollination can be favourable
164 to plant reproduction when competition for pollination is strong because it
165 provides insurance against poor pollination service (Kalisz & Vogler 2003).
166 If competition is sufficiently strong, then the amount of conspecific pollen
167 deposited in flower stigmas when animal pollination is prevented should be
168 higher than when animal pollination is allowed. In contrast, the opposite
169 pattern may indicate that plants benefit from having pollen delivered directly
170 to the stigma by animals.

171 **Data collection**

172 In each of the studied communities, we quantified pollen deposition in a subset
173 of plant species between December 2010 and February 2011. This subset
174 comprised between three and nine common insect-pollinated (entomophilous)
175 plant species that were flowering during the sampling period (see Figure 1a).

176 We chose plant species such that they cover a wide range on a specialization-
177 generalization gradient as well as a wide range of abundances. In each of the
178 selected plants, we removed all flowers leaving only buds that were expected
179 to go into florescence on the next day. Approximately a quarter of these buds
180 were bagged to prevent animal pollination. Two days after inflorescence, we
181 collected all remaining flowers' and counted the number of conspecific and
182 heterospecific pollen grains in their pistils. More details can be found in
183 Marrero *et al.* (2016).



184 **Data analysis**

185 To evaluate the relationship between heterospecific and conspecific pollen,
186 we used a generalised linear mixed model (GLMM) with a Poisson error
187 distribution (Tur *et al.* 2016). In this model, the number of conspecific pollen
188 grains per flower was the response variable and the number of heterospecific
189 grains the predictor (the number of stigmas sampled was added as an offset
190 term). The slope and intercept of this relationship were allowed to differ
191 between plant species within each community, which were modelled as a
192 random effect. Models were fitted using the function `glmer` from the R
193 package `lme4` 1.1-19 (Bates *et al.* 2015). A positive slope for a plant-
194 community combination might indicate facilitation while a negative slope
195 might indicate competition (Tur *et al.* 2016).

196 To compare the conspecific pollen deposited with and without animal-
197 mediated pollination, we followed the same approach as above. In this
198 case, however, the predictor was the treatment (whether the flower was
199 bagged or unbagged) instead of the number of heterospecific grains.

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

201 Our second objective was to investigate the relative contribution of different
202 factors—that describe the plant competition for pollination niche—to the
203 pollination service. Generally speaking, in the context of competition for
204 pollination, we expect that a factor that increases the amount of conspecific
205 pollen deposited in stigmas, both in quantity and purity relative to heterospe-
206 cific pollen, also has a positive effect on the pollination service. Specifically,
207 we investigated the effect of (i) a plant’s number of shared pollinator species,
208 (ii) a plants abundance relative to the rest of the community, (iii) the mean
209 visit effectiveness—a metric that combines the share of pollen that a plant
210 species is able to place on each of their floral visitors and the number of visits
211 it receives from them, and (iv) the plants functional originality (Laliberté &
212 Legendre 2010). See *Data Analysis* section below for more details on these
213 four variables.

214 **Data collection**

215 To obtain the number of shared pollinators for each species, we collected data
216 to construct qualitative and quantitative pollination networks. Qualitative
217 networks were constructed based on two-hour observations of floral visits
218 in each fragment. Quantitative networks were constructed using two 50 m
219 randomly located transects in each fragment. We counted and collected all
220 floral visitors found in a 2 m wide strip while walking at a pace of 10 m per
221 minute (Memmott 1999; Marrero *et al.* 2014). We visited the transects each
222 month between November 2010 and March 2011. To obtain plant abundance,
223 we counted all units of floral attraction found during an independent sampling
224 of the transects used to construct the quantitative visitation networks. To
225 estimate visit effectiveness we need to construct pollen transfer networks
226 in addition to the visitation networks. To do this, we examined the pollen



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

Data analysis

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

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

As predictors in the models, we included the four ecological variables described above. Specifically, we calculated the number of shared pollinators

254 for each plant species by pooling data from the qualitative and quantitative
255 pollination networks. To calculate the plants' relative abundance in their
256 community, we simply aggregated floral counts for each species. We then
257 calculated the mean visit effectiveness. We define the effectiveness of a visit
258 by pollinator species i to plant species j as

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

259 where v_{ij} is the observed number of visits by i to j , p_{ji} is the number of
260 pollen grains from j attached to i , v_i is the total number of visits performed
261 by i , and p_j is the total number of grains carried by j . Because the number
262 of shared pollinators, floral abundance, visitation, and pollen production
263 roughly followed a power-law distribution, we log-transformed these three
264 predictors before including them in the model.

265 Finally, functional originality is defined as the distance of a species from the
266 community trait average—the centroid of functional space of the community
267 (Laliberté & Legendre 2010; Coux *et al.* 2016). To include phenology, we
268 treated plant abundance in each of the survey months (November to March)
269 as a “trait” in our analysis. To account for the non-independence of floral
270 counts and weight all traits equally, we assigned the abundances a weight of
271 $1/5$ (one for each month) compared to other functional traits. We scaled all
272 traits prior to calculating the centroid of the functional space and calculated
273 the species-specific functional coordinates using the R package FD 1.0-12
274 (Laliberté *et al.* 2014). Finally, to facilitate comparison across the four
275 continuous explanatory variables in our models, we rescaled them all to have
276 a zero mean and unitary variance.

277 To estimate the coefficients, perform model selection, and quantify the
278 associated uncertainty, we used a combination of multi-model inference and
279 bootstrap resampling with 99 replicates. First, we performed model selection



280 using the AICc and determined the likelihood of each candidate model (a
281 particular combination of predicting variables) by calculating the median
282 ΔAICc (relative to the most likely model) for each bootstrap sample. As
283 we wanted model coefficients from more likely candidate models to carry
284 more weight in our results, we sampled the coefficients for our variables
285 proportional to the likelihood of its candidate model. Finally, we used these
286 distributions of the model coefficients to estimate their mean impact on the
287 pollination service (in terms of quantity and purity of conspecific pollen
288 deposition).

289 **Flexibility of plant strategies**

290 Our last objective was to tease apart the plant strategies that might reduce
291 competition and, importantly, how the community context influences these
292 strategies. If community context plays a relatively small role or the species
293 strategy is inflexible we would expect plants of the same species to fill similar
294 competition for pollination niches across different communities. Alternatively,
295 if the community plays a large role and plants strategies are flexible, we
296 should be able to observe differences in the realised niche a plant species
297 occupies across communities. First, we used a principal component analysis
298 (PCA) of the four ecological variables. We scaled variables across the whole
299 study to ensure that the PCA space does not change according to the species
300 present in each community. We define a species' niche in a community as
301 its coordinates in PCA space. For each species that was present in two or
302 more communities, we then calculated (*i*) the median distance between the
303 strategies that the species uses in different communities and (*ii*) the area of
304 the convex hull defined by these points in the first two principal components
305 (only for species present in three or more communities). We then compared
306 the magnitude of these two metrics to those obtained with 99 Monte Carlo
307 randomizations in which we replaced the strategy of the focal plant species

308 by that of another randomly selected species in the dataset.

309 Results

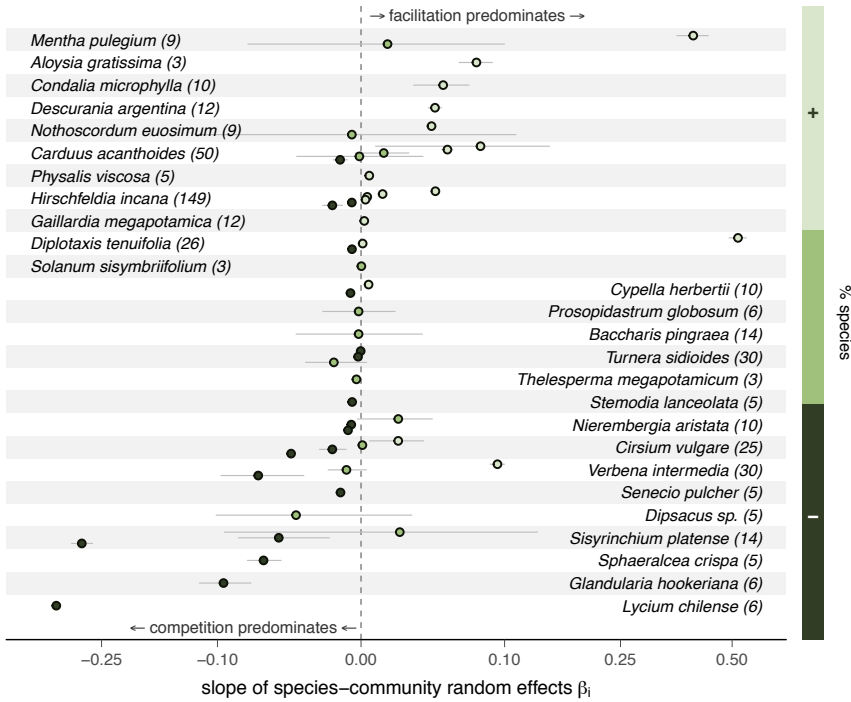
310 Competition vs. facilitation

311 We first examined the degree of facilitation/competition in natural commu-
312 nities. Specifically, we examined the slope of the relationship between the
313 heterospecific and conspecific pollen deposited on stigmas of each species
314 in a community. We found that overall neither facilitation nor competition
315 dominates (Table S1). Indeed, we found that the proportion of species
316 that experienced a statistically significant positive or negative relationship
317 between heterospecific and conspecific pollen than negative was very similar
318 (35% and 37%, respectively; Figure 1a; Table S2). Most of the variation be-
319 tween plants in a facilitation-competition gradient was driven by differences
320 *between* species; however, we also observed some important differences *within*
321 species. For instance, six of the species sampled across multiple communities
322 (*Carduus acanthoides*, *Cirsium vulgare*, *Cypella herbertii*, *Diploaxis tenuifo-*
323 *lia*, *Hirschfeldia incana*, and *Verbena intermedia*) showed evidence that the
324 same species, can experience facilitation (positive relationships) in some com-
325 munities and competition (negative relationships) in others. Interestingly,
326 although there was a wide variation in the slope of the relationship between
327 heterospecific and conspecific pollen almost all plants had more conspecific
328 than heterospecific pollen deposited on their stigmas (Figure 1b).

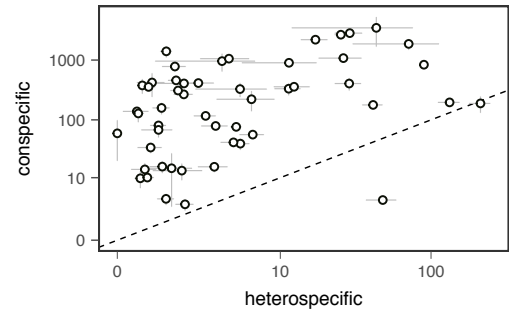
329 Second, we compared the amount of conspecific pollen deposited on flowers
330 that were open to animal-mediated pollinators with that of those that were
331 closed. Here, we again found large differences between plants but with a clear
332 tendency to find more pollen in open flowers (Table S3). Specifically, 66%
333 of plants had more pollen when open and 15% had less pollen when open
334 (the difference was statistically non-significant for the remaining 19%; Figure



(a) competition vs. facilitation – criterion #1
relationship hetero–conspecific pollen



(b) hetero– vs. conspecific pollen
mean pollen grains per stigma



(c) competition vs. facilitation – criterion #2
self– vs. animal–mediated pollination

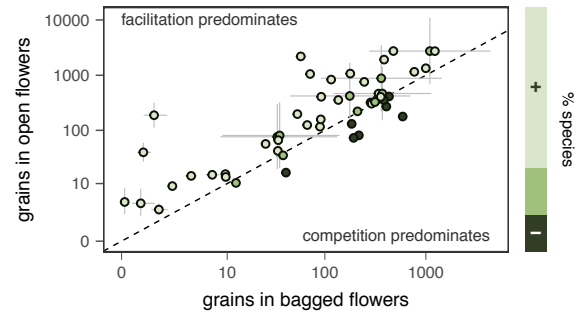


Figure 1: Competition vs. facilitation at the community level. (a) According to the first criterion we used, some species experience more competition for pollination than others. Points indicate the estimated slopes for the relationship between the amount of heterospecific and conspecific pollen deposited per stigma across species in their communities. Statistically significant negative slopes (darkest shade) indicate that plants experience competition for animal-mediated pollination, while significantly positive slopes (lightest shade) indicate that facilitation is the predominant outcome. The number of plants analysed for each species is shown within brackets next to the species name. (b) Despite the variety of slopes, overall plants had more conspecific than heterospecific pollen deposited in their stigmas. (c) The second criterion we used to distinguish between facilitation and competition shows similar patterns as the first one. Here we compare the amount of conspecific pollen deposited in plants' stigmas when they were open to animal-mediated pollination and when they were closed. Statistically significant negative differences (darkest shade) indicates competition while positive differences (lightest shade) indicates facilitation. In all plots, error bars correspond to \pm the standard error (SE).

1c; Table S4). Variation within species was slightly smaller and only four species (*C. acanthoides*, *C. vulgare*, *H. incana*, and *Sisyrinchium platense*) had both positive and negative differences.

Factors affecting quantity and purity of pollination service

We then examined the potential roles played by four ecological variables (number of shared pollinators, plant abundance, mean visit effectiveness, and functional originality) play in pollen deposition. 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 S5). 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 they belong to). This structure was best for both the models of conspecific and heterospecific pollen (Table S6).

Of the four variables, we considered, we found that a plant's mean visit effectiveness and abundance were the most important ecological variables predicting pollen deposition in plant stigmas (Figure 2a). Surprisingly, the number of shared pollinators was comparatively unimportant, particularly for models of heterospecific pollen deposition, as it was only ever included in models with relatively large AICc values (Table S7).

We found that the relationship between each of the ecological factors and pollen deposition was similar for both conspecific and heterospecific pollen. That is, strategies that were associated with an increase in conspecific pollen were also associated with an increase in heterospecific pollen deposition. Specifically, the plants' mean visit effectiveness had a positive effect on pollen deposition (Figure 2b). However, the effect size was slightly larger

for heterospecific than for conspecific pollen. This indicates that, although there is a positive association between visit effectiveness and the quantity pollen deposition, there is a negative relationship with its purity (Figure 2c). In contrast, a plants' relative abundance had a negative effect on the pollen deposition quantity, but the mean difference between the coefficients in the models indicates a positive association with the purity (Figure 2c). The third most important variable, functional originality, had a positive, although comparatively smaller, association with both the quantity and purity. Finally, the number of shared pollinators had a negative and neutral association with conspecific and heterospecific pollen, but these impacts were small when compared to the other variables.

Overall, collinearity did not affect our findings qualitatively. Although relative abundance, the number of shared pollinators, and the visit effectiveness were all positively correlated (Figure S1), the effect each had on conspecific pollen was similar among models that included all or just some of these three explanatory variables (Figure S2). 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.

Flexibility of plant strategies

We used a PCA of the analysed species to investigate whether plants' realised niche of competition for pollination is similar across communities or whether they are flexible, and therefore a reflection of the community context. The first two PCA components explained 75% of the total variance (Figure 3a). The first component was dominated by changes in visit effectiveness and relative abundance while the second component was dominated by the number of shared pollinators and the plant's functional originality. When we locate the species that were sampled in more than one community in

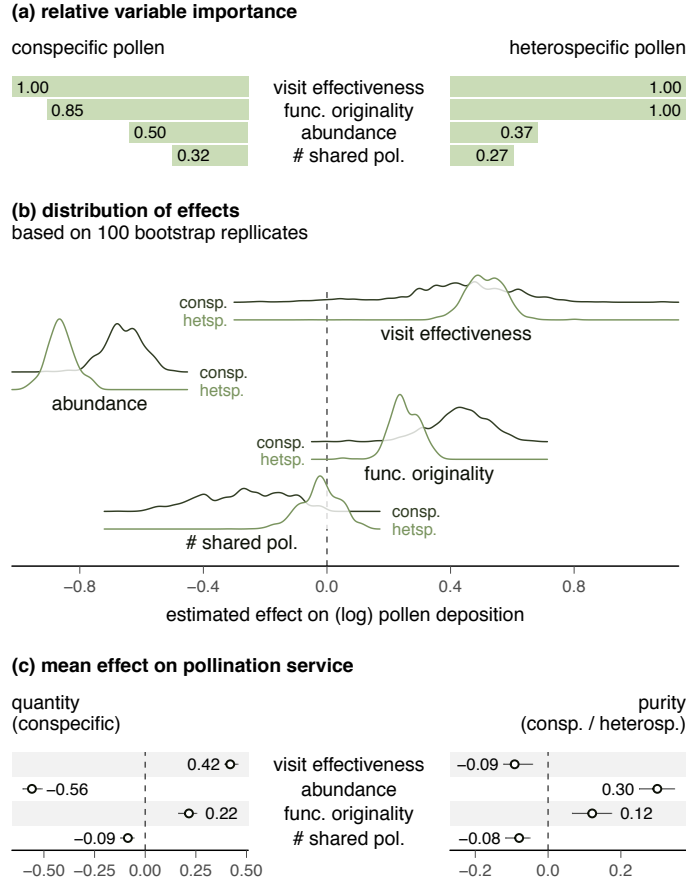


Figure 2: Effect of strategies to minimise competition in the pollination service. (a) The plant's visit effectiveness and relative abundance are the most important variables determining the deposition of conspecific and heterospecific pollen. Meanwhile, the number of shared pollinators was relatively unimportant. The graph shows the relative variable importance calculated as the sum of the Akaike weights of the candidate models that included the variable. (b) The association between ecological variables 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 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 variables 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).

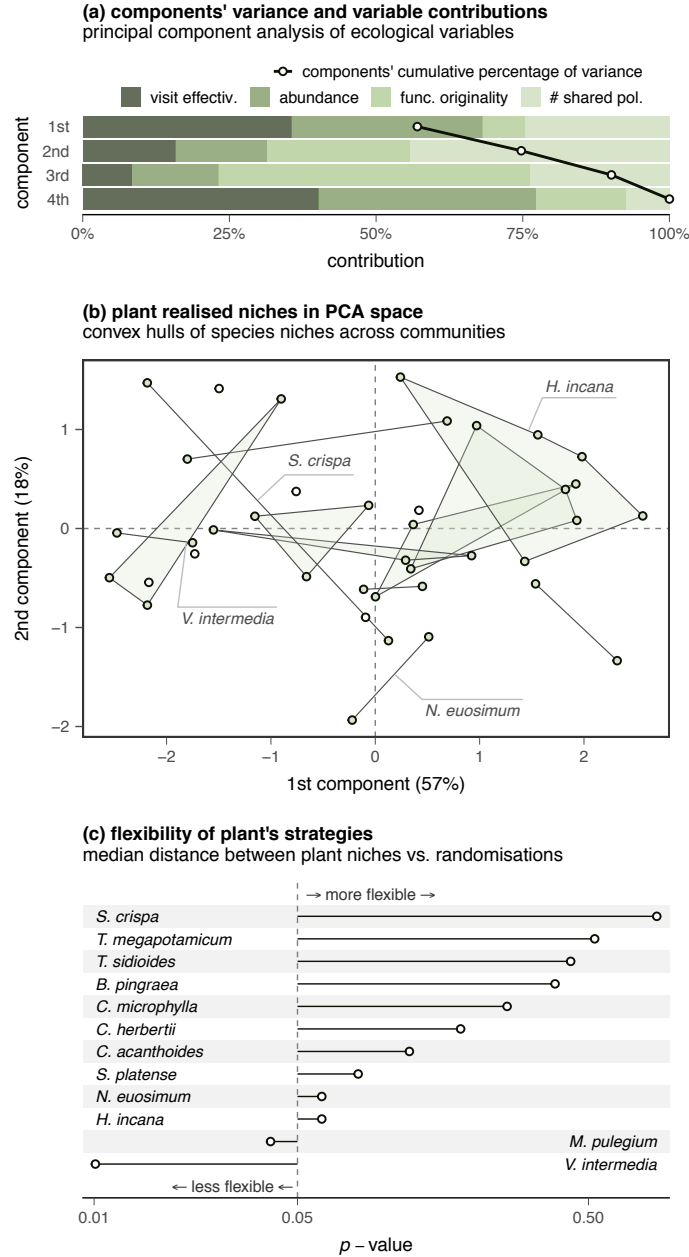


Figure 3: The flexibility of plant strategies. (a) The two first components explain a large proportion of the total variance. (b) When plants that were sampled in more than one community are plotted with these two components, we observe that points, which represent the strategy (the particular combination of ecological variables) of a species in a 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 one of the examined species had strategies that were more tightly connected than what would be expected at random.

the first two PCA components (Figure 3b), we observe that the niches of any given species do not tend to be close to each other. Indeed, when we measured the median distance between the plants coordinates, we found that it was only significantly smaller than that of randomisations for only two of the twelve analysed species (Figure 3c).

Discussion

Our results suggest that community context plays a central role in determining net cost or benefit of sharing pollinators. First, we found that pollinator sharing can lead to both overall facilitative and competitive effects to plant species in a community. Second, we found that multiple ecological factors can modulate the intensity of competition; however, conspecific and heterospecific pollen deposition are tightly coupled and therefore there is a clear trade-off between the quantity and purity of pollination (Thomson *et al.* 2019). Third, we found that the way these factors influence competition is strongly shaped by the community context, this is, if collectively these factors are used to define a niche of competition for pollination, the same plant species can occupy dramatically different niches depending on the community it belongs to.

Both of the criteria we used to identify the effect of animal-mediated pollination suggested the same outcome: that neither facilitation nor competition are dominant in pollination communities. A previous study showed that in diverse pollination communities, sharing pollinators does not necessarily translate to net competition (Tur *et al.* 2016). The overall extent of facilitation/competition of pollination communities can depend on factors like the adversity of the environment (Callaway *et al.* 2002; Tur *et al.* 2016) or how disturbances affect pollinator populations (Stavert *et al.* 2017) However, why some species experience more competition than others was not understood.

417 Here we show that the coexistence of facilitative and competitive effects of
418 animal-mediated pollination can be at least partially explained by the trade-
419 offs plants have to undergo when maximising the deposition of conspecific
420 pollen and simultaneously minimising that of heterospecific pollen both in
421 the short and the long term.

422 In the short term, being a specialist and sharing no pollinators might reduce
423 competition (Muchhala *et al.* 2010) and hence be preferable, as we show that
424 sharing pollinators reduces both the quantity and purity of the conspecific
425 pollen deposited. However, over long periods of time, there could be a risk
426 associated with a specialist plant having no pollinators. Hence, is likely that
427 to ensure long term survival, plants also need to balance this risk with the
428 costs of sharing pollinators. One possible solution is to share pollinators *and*
429 have original traits—as we show that trait originality is generally beneficial
430 to pollen deposition and it’s commonly thought that species that are further
431 from others in trait space benefit from reduced competition. Yet, there are
432 two possible caveats to this strategy that highlight the interrelatedness of
433 the ecological factors. First, in a mutualism context, it is also possible that
434 trait originality could come at the cost of being less ‘apparent’ to pollinators
435 (Reverté *et al.* 2016). Second, the negative, relationship between originality
436 and generalism (Carvalheiro *et al.* 2014) has been shown depend on the
437 plant’s abundance (Coux *et al.* 2016), with generalist species being able to
438 also have original traits only when they are abundant enough to provide a
439 valuable reward to make it worth to pollinators. Visit effectiveness (high
440 pollen and visits) and abundance, which were the most important predictors
441 of pollen deposition, involved an even more explicit trade-off between gaining
442 conspecific pollen and avoiding heterospecific pollen. On the one hand,
443 receiving high visitation increases conspecific pollen deposition but increases
444 heterospecific pollen to a greater extent—even when the visitors are likely to
445 carry a high proportion of conspecific pollen (Fang & Huang 2016). On the

446 other, being abundant reduces the amount of heterospecific pollen deposited
447 but this comes at the expense of a noticeable reduction in the amount of
448 conspecific pollen. Our results corroborate the importance that two-species
449 studies have ascribed to visitation and abundance (Feldman *et al.* 2004;
450 Morales & Traveset 2008; Muñoz & Cavieres 2008). But importantly, they
451 also suggest that (because visitation, pollen production and abundance are
452 usually correlated; Sargent & Otto 2006) balancing the pros and cons of
453 sharing pollinators at the community level is not trivial and might even
454 be partially responsible for the diversity of plant-pollinator communities
455 (Benadi & Pauw 2018).

456 We observed, as expected, that the effects of pollen deposition can vary
457 widely among species. For instance, while the fitness of some plant species
458 can be hurt even by low amounts of heterospecific pollen, for others species,
459 fitness can instead be limited by the amount of conspecific pollen (Campbell
460 & Motten 1985; Arceo-Gómez *et al.* 2019). Alternatively, plant species
461 can also differ substantially on the extent to which self- vs. outcross-pollen
462 differ in their value for fertilization. The difference can be particularly
463 relevant for species that are not self-fertile or those in which self-fertilization
464 is rarely effective due to a temporary separation in the maturation of the
465 sexes (dichogamy).

466 Importantly, here we show that the balances between cost and benefits are
467 determined not only by species identity but also on the community plants
468 belong to. Specifically, most plant species appear to be flexible enough
469 to adopt markedly different niches in different communities. Although
470 there are many exceptions, some plant families (Asteraceae for example)
471 are often generalists in their communities while others (Orchidaceae) are
472 known to be more commonly specialised (Johnson & Steiner 2000). From
473 an evolutionary perspective, our results suggest that that selection for a
474 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 plant might use to minimise competition for pollination must be relative to other species in the community, rather than an absolute property of the species.

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 on 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 (but see Rohr *et al.* 2014 and similar). However, achieving a better understanding of species coexistence and how plant biodiversity is supported by pollination communities will require seeing them as both

504 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
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	-	-

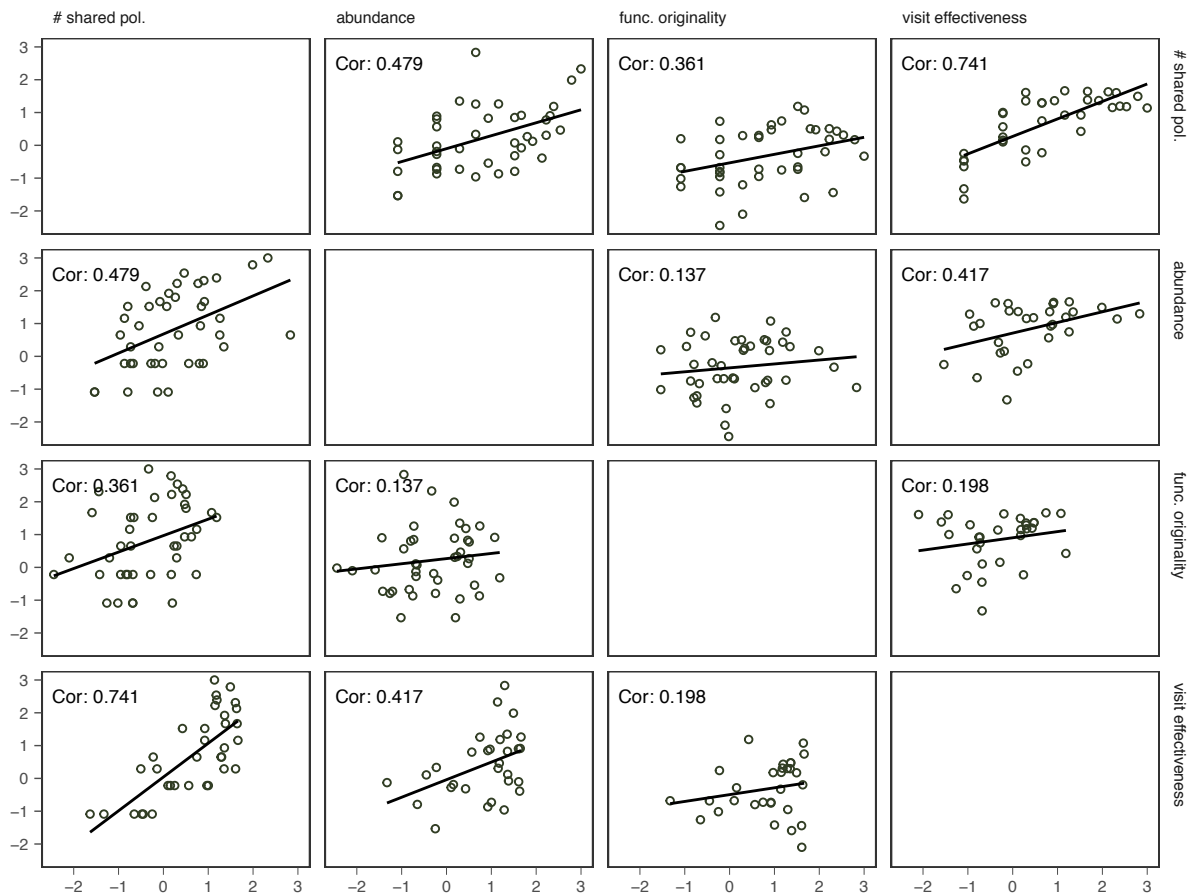


Figure S1: Correlation between the explanatory variables included in the statistical models.

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: Summary of the model used to analyse the relationship between conspecific pollen deposited in bagged and unbagged flowers (open to animal pollination).

predictor	estimate	S.E.	z-value
fixed component			
(Intercept)	4.215	0.318	13.235
treatment (unbagged flower)	0.845	0.205	4.128
random component (species:community)			
S.D. random intercept	2.240	-	-
S.D. random slope	1.377	-	-

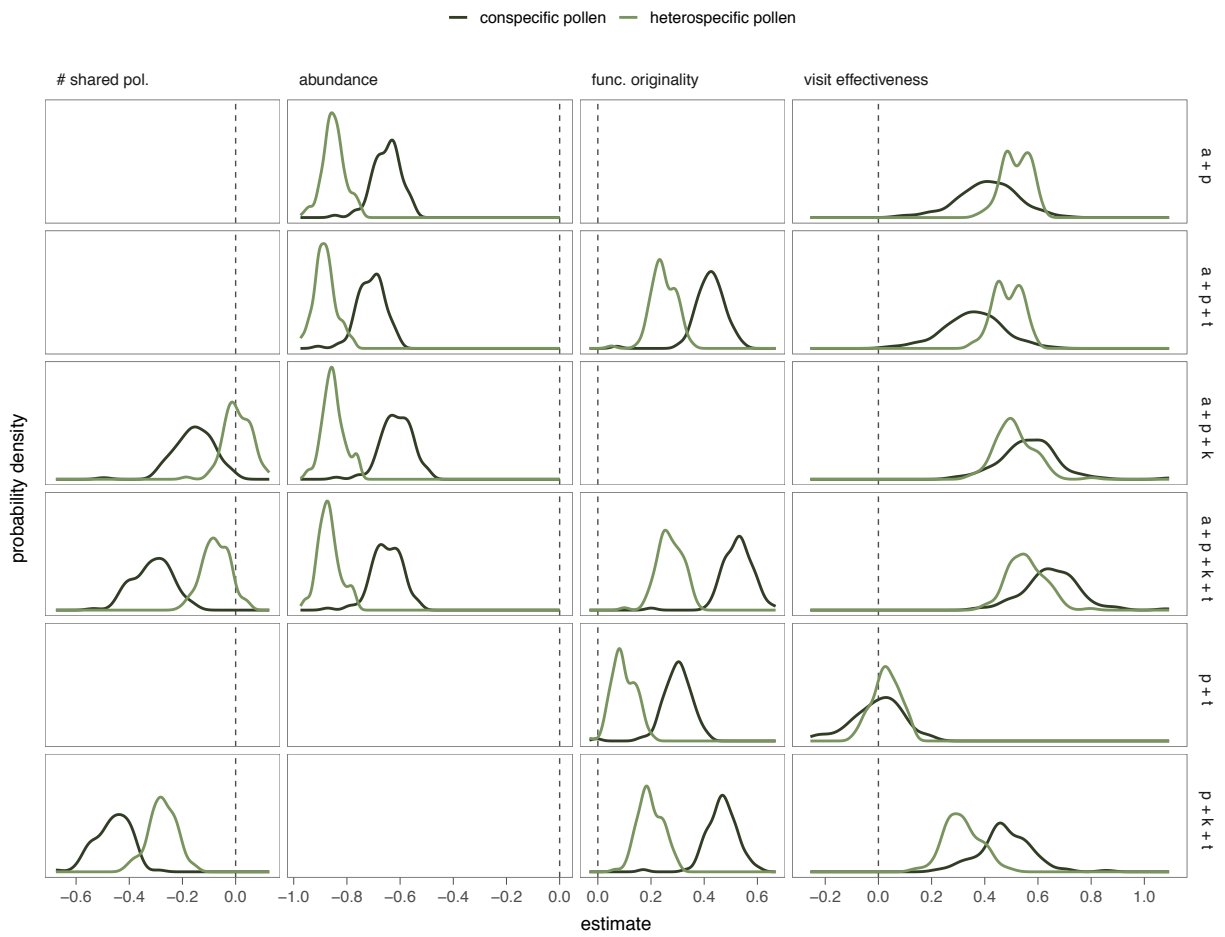


Figure S2: Distribution of effect estimates for models of conspecific and heterospecific pollen density gain. Model formulas have been abbreviated: *a* for abundance, *k* for the number of shared pollinators, *p* for the visit effectiveness, and *t* for trait originality. Only candidate formulas with a $\Delta AICc < 4$ for either conspecific or heterospecific pollen are shown. Models candidates are arranged in decreasing order of support.

Table S4: Amount of conspecific pollen deposited in bagged and unbagged flowers (open to animal pollination) for each species in their community. Community names are constructed by location - agricultural/restored - fragment number.

species name	community	bagged		unbagged	
		mean	C.I.	mean	C.I.
<i>Aloysia gratissima</i>	Anquilóo - reserve - 2	1	[0, 1]	39	[26, 59]
<i>Baccharis pingraea</i>	San Claudio - reserve - 1	0	[0, 0]	4	[2, 8]
<i>Carduus acanthoides</i>	Anquilóo - agricultural - 2	25	[23, 27]	56	[52, 61]
<i>Carduus acanthoides</i>	San Claudio - agricultural - 1	34	[32, 35]	42	[40, 44]
<i>Carduus acanthoides</i>	San Claudio - agricultural - 2	41	[39, 43]	16	[16, 17]
<i>Carduus acanthoides</i>	San Claudio - reserve - 1	12	[11, 14]	10	[9, 11]
<i>Carduus acanthoides</i>	San Claudio - reserve - 2	10	[9, 11]	15	[14, 17]
<i>Cirsium vulgare</i>	Anquilóo - agricultural - 2	211	[205, 217]	222	[215, 228]
<i>Cirsium vulgare</i>	Las Chilcas - reserve - 1	284	[277, 291]	320	[313, 328]
<i>Cirsium vulgare</i>	San Claudio - agricultural - 2	33	[8, 132]	76	[19, 302]
<i>Cirsium vulgare</i>	San Claudio - reserve - 1	218	[210, 226]	81	[78, 84]
<i>Condalia microphylla</i>	Anquilóo - reserve - 1	38	[36, 41]	35	[33, 37]
<i>Cypella herbertii</i>	Las Chilcas - agricultural - 2	1095	[276, 4336]	2738	[691, 10844]
<i>Cypella herbertii</i>	Las Chilcas - reserve - 1	478	[462, 494]	2743	[2652, 2836]
<i>Descurania argentina</i>	Anquilóo - agricultural - 2	90	[86, 93]	117	[113, 121]
<i>Diplotaxis tenuifolia</i>	Anquilóo - reserve - 1	362	[92, 1435]	881	[222, 3489]
<i>Diplotaxis tenuifolia</i>	Anquilóo - reserve - 2	177	[45, 700]	422	[107, 1671]
<i>Diplotaxis tenuifolia</i>	San Claudio - reserve - 2	769	[762, 776]	1153	[1143, 1163]
<i>Dipsacus sp.</i>	San Claudio - reserve - 2	4	[3, 5]	14	[12, 17]
<i>Gaillardia megapota mica</i>	Anquilóo - reserve - 2	590	[580, 601]	179	[175, 182]
<i>Glandularia hookeriana</i>	Anquilóo - reserve - 2	185	[178, 192]	131	[127, 136]
<i>Hirschfeldia incana</i>	Anquilóo - agricultural - 1	432	[427, 437]	412	[408, 417]
<i>Hirschfeldia incana</i>	Anquilóo - agricultural - 2	246	[240, 252]	758	[740, 778]
<i>Hirschfeldia incana</i>	San Claudio - agricultural - 1	407	[403, 412]	271	[268, 274]
<i>Hirschfeldia incana</i>	San Claudio - agricultural - 2	291	[288, 294]	305	[302, 308]
<i>Hirschfeldia incana</i>	San Claudio - reserve - 1	384	[380, 389]	355	[351, 359]
<i>Hirschfeldia incana</i>	San Claudio - reserve - 2	340	[337, 344]	465	[460, 470]
<i>Lycium chilense</i>	Anquilóo - reserve - 2	998	[987, 1009]	1339	[1325, 1354]
<i>Mentha pulegium</i>	Las Chilcas - agricultural - 2	1	[1, 2]	3	[2, 4]
<i>Mentha pulegium</i>	Las Chilcas - reserve - 1	7	[6, 8]	15	[12, 18]
<i>Nierembergia aristata</i>	Anquilóo - agricultural - 1	116	[105, 128]	835	[756, 922]
<i>Nierembergia aristata</i>	Anquilóo - reserve - 1	179	[171, 187]	1072	[1024, 1121]
<i>Nierembergia aristata</i>	Anquilóo - reserve - 2	71	[67, 76]	1054	[984, 1129]
<i>Nothoscordum euosimum</i>	Las Chilcas - agricultural - 1	92	[88, 97]	408	[388, 428]
<i>Nothoscordum euosimum</i>	Las Chilcas - agricultural - 2	324	[315, 334]	352	[343, 362]
<i>Oxalis violeata</i>	San Claudio - reserve - 2	371	[122, 1131]	467	[153, 1423]
<i>Physalis viscosa</i>	Anquilóo - agricultural - 1	1227	[1211, 1244]	2732	[2696, 2769]
<i>Prosopidastrum globosum</i>	Anquilóo - reserve - 2	10	[8, 11]	13	[12, 15]
<i>Senecio pulcher</i>	Las Chilcas - agricultural - 1	358	[348, 367]	406	[395, 417]
<i>Sisyrinchium platense</i>	Las Chilcas - agricultural - 1	91	[88, 95]	159	[152, 165]
<i>Sisyrinchium platense</i>	Las Chilcas - agricultural - 2	35	[9, 139]	81	[20, 319]
<i>Sisyrinchium platense</i>	Las Chilcas - reserve - 1	193	[179, 208]	73	[67, 79]
<i>Solanum sisymbriifolium</i>	San Claudio - agricultural - 1	57	[50, 66]	2194	[1923, 2502]
<i>Sphaeralcea crispa</i>	Anquilóo - reserve - 1	2	[2, 2]	9	[8, 10]
<i>Stemodia lanceolata</i>	Las Chilcas - agricultural - 1	387	[380, 394]	1919	[1884, 1955]
<i>Thelesperma megapota mica</i>	Anquilóo - agricultural - 1	314	[306, 322]	327	[319, 336]
<i>Turnera sidoides</i>	Anquilóo - agricultural - 1	53	[51, 55]	198	[189, 206]
<i>Turnera sidoides</i>	Anquilóo - agricultural - 2	1	[0, 1]	4	[2, 8]
<i>Turnera sidoides</i>	Anquilóo - reserve - 2	1	[1, 2]	189	[113, 315]
<i>Verbena intermedia</i>	Anquilóo - reserve - 2	67	[64, 70]	125	[119, 131]
<i>Verbena intermedia</i>	San Claudio - agricultural - 2	34	[32, 36]	66	[63, 70]
<i>Verbena intermedia</i>	San Claudio - reserve - 2	136	[133, 139]	356	[348, 365]

Table S5: 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 S6: Comparison of the two random 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. Communities are defined by individual fragments but ignore the hierarchical arrangement of sampling sites.

random structure	ΔAIC	
	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]

Table S7: 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 + 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]
heterospecific pollen		
~ 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]