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Requests to co-authors

- Title suggestions/feedback?
- Feedback primarly on abstract, introduction and discussion prior to submission.

Changes since the last draft

- Adjusted langage away from competition for pollination towards pollination service and pollen deposition across the paper.
- Removed the section where we calculated competition/facilitation in ecological communities
- Other minor adjustments to address comments by reviews received when submitted to Proceedings B
- Rewrote abstract
- Updated title

To-do

• Update supplementary information

The trade-offs of pollinator sharing: pollination service is determined by the community context

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Abstract

A fundamental feature of pollination systems is the indirect facilitation and competition that arises when plants species share pollinators. When plants share pollinators, the pollination service can be influenced, not only how many partners plant species share, but also by multiple intertwined factors like abundance, visitation, or traits. These factors inherently operate at the community level. However, most of our understanding of how these factors may affect the pollination service is based on systems of up to a handful of species. By 21 examining comprehensive empirical data in eleven natural communities, here we show that 22 the pollination service is—surprisingly—only partially influenced by the number of shared 23 pollinators. The factors that most influence the pollination service (abundance and visit 24 effectiveness) also introduce a trade-off between the absolute amount of conspecific pollen 25 received and the amount relative to heterospecific pollen. Importantly, the ways plants appear 26 to balance these trade-offs depend strongly on the community context, as most species showed 27 flexibility in the strategy they used to cope with competition for pollination. 28

- 29 Keywords: interspecific pollen transfer, pollen deposition, pollination costs and benefits,
- pollination network, pollination niche, and pollinator sharing

1 Introduction

Animal pollination plays a disproportionally important role in food production and maintenance of global biodiversity (Klein et al. 2007, Bascompte and Jordano 2007, Ollerton et al. 2011). At a pairwise level, the mutually beneficial relationship between plants and pollinators underpins the pollination service. At a community level, sometimes involving hundreds of species, both plant and pollinator species are connected in a myriad of indirect connections when pollination partners are shared. These indirect connections can dramatically alter the 37 quality of the pollination service that plants receive because they determine how conspecific 38 and heterospecific pollen is transferred across the community (Morales and Traveset 2008). 39 Generally speaking, there is a trade-off between the benefits gained from maximising the it number of partners and the costs of sharing them with other plant species (Waser 1978). However, due to the large number of factors that operate at the community level, we do not understand how sharing pollinators affect the pollination service beyond systems with more than a handful of species. Here we investigate how pollinator sharing affects pollen transfer in natural communities and how it compares to other factors known to play a role in community dynamics like abundance, traits, and visitation patterns. There are two main mechanisms through which sharing pollinators can affect plant fertilisation (Morales and Traveset 2008). The first is by changes in intraspecific pollen transfer.

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Interspecific pollen transfer happens, for example, when plants with more attractive flowers
might reduce the number of visits to those less of attractive neighbouring plants, and hence
reduce the amount of conspecific pollen deposited by animals (Yang et al. 2011). The second
is via interspecific pollen transfer. In that case, even receiving a visit might not necessarily
translate into fertilisation (Campbell and Motten 1985) because a focal plant might receive
heterospecific pollen or because pollen from the focal plant might be lost to different species.
Naturally, the precise effects on female or male plant fitness of conspecific and heterospecific
pollen deposition depend on the species involved and are unknown for many plant species.

57 How, Even for species well adapted to pollinator sharing, receiving foreign pollen on 58 stigmas or losing pollen to foreign stigmas, is neutral (at best). Indeed, there is substantial 59 evidence supporting the idea that heterospecific pollen deposition can be detrimental to seed 60 production and plant fitness (Ashman and Arceo-Gómez 2013, Arceo-Gómez and Ashman 61 2016).

All together, provided pollen is viable and compatible (de Jong et al. 1992, Dafni and Firmage 2000, Ramsey and Vaughton 2000), the higher the quantity of conspecific pollen and its purity (relative to heterospecific pollen), the better the pollination service received by the focal plant. As such, measuring conspecific and heterospecific pollen deposition provides a good indication of the potential levels of facilitation and competition a plant population might experience.

By definition, intra- and interspecific pollen transfer, occur at the community scale. However, with few exceptions (Aizen and Rovere 2010, Tur et al. 2016), most of what we know about pollen transfer and its relationship with key ecological factors are based on studies with two plant species. That is partly because at the community scale the factors that determine the patterns of pollen deposition are tightly intertwined, operate simultaneously, and may lead to emergent phenomena not observed at smaller scales (Flanagan et al. 2011). For instance, recent empirical evidence suggests that plants with flowering traits that are "original" relative to others in the community generally have fewer interaction partners (Coux et al. 2016).

This evidence aligns with the notion that a species that interacts with few species does so strongly with each of them whereas a species that interacts with a large number of species does so comparatively weakly (Bascompte et al. 2006, Vázquez et al. 2007, Thébault and Fontaine 2008). If evolutionary specialisation occurs by changing traits to focus on fewer but better partners (Caruso 2000), we should expect a reduction of competition for pollinators in species with "original" traits and an increase of competition in species with a large number

of interaction partners (Gibson et al. 2012, Carvalheiro et al. 2014). Alternatively, it might also be the case that abundance (for example, in terms of flower or pollen counts) is the dominant force driving pollen transfer (Seifan et al. 2014). Abundant plant species might experience a dilution of available pollinators (Feinsinger 1987, Feldman et al. 2004) but might 86 also receive more effective visits by capitalising on a larger share of both visits and the pollen 87 carried by pollinators (???). In this case, a potential reduction in the absolute amount of conspecific pollen received could be compensated by an increase in the amount of conspecific 89 pollen relative to heterospecific pollen. Altogether, it is clear that these ecological factors can 90 indeed shape pollen deposition at the community level. However, we still do not understand 91 their relative importance and the trade-offs that might exist between them. 92

Here, we investigate pollen deposition dynamics at the community scale using empirical data 93 from eleven plant-pollinator communities in the Argentinian Pampas. First, we investigate the 94 relative contribution that four ecological factors have to the pollination service. Specifically, 95 we hypothesise that there are trade-offs on how these factors affect the quantity and purity of 96 conspecific pollen deposition. While quantity and purity should decrease for plants that share 97 many pollination partners, other factors like the plant's functional originality, its relative floral abundance, and its visitation patterns should have the potential to compensate for this decrease Second, we examine how these four factors that might affect pollen deposition 100 can change across communities where species are present. Because these factors may affect the pollination service in contrasting ways, and a species role is relative to other species in 102 the community, we predict that species present in multiple communities should be flexible enough to compete for pollinators under different community contexts.

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$_{\scriptscriptstyle{105}}$ Methods

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

Factors affecting quantity and purity of pollination service

Our first objective was to investigate the relative contribution that different ecological factors 111 have on pollen deposition. Generally speaking, we expect that any factor that increases the 112 amount of conspecific pollen deposited in stigmas, both in quantity and purity relative to 113 heterospecific pollen, also has a positive effect on the pollination service. Specifically, we 114 investigated the effects of (i) a plant's number of shared pollinator species, (ii) a plant's 115 abundance relative to the rest of the community, (iii) the mean visit potential—a metric that 116 combines the amount and type of pollen carried by floral visitors and the number of visits it 117 receives from them, and (iv) the plant's functional originality (Laliberté and Legendre 2010). See Data Analysis section below for more details on these four factors. 119

120 Data collection

In each of the studied communities, we quantified pollen deposition in a subset of plant species between December 2010 and February 2011. This subset comprised between three and nine common insect-pollinated (entomophilous) plant species that were flowering during the sampling period. Based on data from previous years (Marrero et al. 2014), we chose plant species such that they cover a wide range on a specialization-generalization gradient as well as a wide range of abundances. In each of the selected plants, we removed all flowers leaving only buds that were expected to go into florescence on the next day. Two days after flowering,

we collected all remaining flowers and counted the number of conspecific and heterospecific pollen grains in their pistils. More details can be found in Marrero et al. (2016).

To obtain the number of shared pollinators for each species, we collected data to construct 130 qualitative and quantitative pollination networks. Qualitative networks were constructed 131 based on ten-hour observations of floral visits in each fragment. Quantitative networks were 132 constructed using two 50 m randomly located transects in each fragment. We counted and 133 collected all floral visitors found in a 2 m wide strip while walking at a pace of 10 m per 134 minute (Memmott 1999, Marrero et al. 2014). We visited the transects each month between 135 November 2010 and March 2011. To obtain floral abundance, we counted all units of floral 136 attraction found during an independent sampling of the same transects used to construct the quantitative visitation networks. To estimate visit potential, we need to construct pollen 138 transfer networks in addition to the visitation networks. To do this, we examined the pollen 139 loads present on the floral visitors collected (Marrero et al. 2017). When the pollen count on 140 an individual animal was estimated to be less than 2,000 grains, we identified every grain 141 to the species level when possible and to pollen complexes when it was not. When the 142 pollen count was above 2,000 grains, we classified approximately 50% of pollen and total 143 pollen counts were extrapolated (Bosch et al. 2009). Finally, we also recorded morphological 144 traits that relate to plant type (herb, shrub, climber), life cycle (annual, perennial), flower 145 colouration, phenology, and whether the species is native in the study region. More details 146 can be found in Marrero et al. (2014 and 2017).

148 Data analysis

To investigate the impact of ecological factors on pollination services, we used two sets of linear mixed models (LMM) with bootstrap resampling. The response variables for these model sets were the number of conspecific and heterospecific pollen grains deposited per stigma in flowers open to animal-mediated pollination. We used LMMs in which pollen loads

were log-transformed because these models offered a better fit than equivalent GLMMs with Poisson (or quasi-Poisson) error structure. Models were fitted using the R package nlme 3.1-131 (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).

the median Akaike Information Criterion for small samples (AICc).

As fixed predictors in the models, we included the four ecological factors described above.

Specifically, we calculated the number of shared pollinators for each plant species by pooling

data from the qualitative and quantitative pollination networks. To calculate the plants'

relative floral abundance in their community, we aggregated floral counts for each species.

We then calculated the mean visit potential of pollinator species *i* to plant species *j* as

$$o_{ij} = rac{v_{ij}}{v_i} rac{p_{ji}}{p_j}$$
)

where v_{ij} is the observed number of visits by i to j, p_{ji} is the number of pollen grains from jattached to i, v_i is the total number of visits performed by i, and p_j is the total number of 167 grains carried by j. We log-transformed the number of shared pollinators, floral abundance, 168 and visit potential before including them in the model. 169 Finally, functional originality is defined as the distance of a species from the community trait 170 average—the centroid of functional space of the community (Laliberté and Legendre 2010, 171 Coux et al. 2016). To include phenological variation, we treated floral abundance in each 172 of the survey months (November to March) as a "trait" in the canalysis. To account for the 173 non-independence of floral counts and weight all traits equally, we assigned a weight of 1/5 to 174 these abundances (one for each month). We scaled all traits before calculating the centroid 175 of the functional space and calculated the species-specific functional coordinates using the R do we ever say or explain why we do this?

package FD 1.0-12 (Laliberté et al. 2014). Finally, we scaled all four factors to have a zero mean and unit variance.

To estimate the coefficients, perform model selection, and quantify the associated uncertainty, 179 we used a combination of multi-model inference and bootstrap resampling with 99 replicates. 180 First, we performed model selection using AICc and determined the likelihood of each 181 candidate model (a particular combination of predictors) by calculating the median $\Delta AICc$ 182 (relative to the most likely model) for each bootstrap sample. As we wanted model coefficients 183 from more likely candidate models to carry more weight in our results, we sampled the 184 coefficients for our factors proportionally to the likelihood of their candidate model. Finally, 185 we used these distributions of the model coefficients to estimate their mean impact on the 186 pollination service (in terms of quantity and purity of conspecific pollen deposition). 187

188 Flexibility of plant strategies

Our second objective was to tease apart whether and how these factors that might affect 189 pollen deposition might change across communities species are present. If community context 190 plays a relatively small role, or species are inflexible in regards to these factors, we would 191 expect plants of the same species to fill similar pollination niches across different communities. 192 Alternatively, if the community plays a significant role and plant species are flexible, we 193 should be able to observe differences in the realised niche a plant species occupies across communities. To test this, we first used a principal component analysis (PCA) of the four 195 ecological factors (number of shared pollinators, floral abundance, visit potential, and trait 196 originality). We scaled factors across the whole study to ensure that the PCA space does 197 not change according to the species present in each community. We define a species' (niche 198 in a community as its coordinates in PCA space. For each species that was present in two 199 or more communities, we then calculated (i) the median distance between the strategies 200 that the species uses in different communities and (ii) the area of the convex hull defined by 201

> niche or Strategy are they the Same

these points in the first two principal components (only for species present in three or more communities). We then compared the magnitude of these two metrics to those obtained with 99 Monte Carlo randomizations in which we replaced the strategy of the focal plant species by that of another randomly selected species in the dataset.

$_{ iny 106}$ Results

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Factors affecting quantity and purity of pollination service

examined the potential roles played in pollen deposition by four ecological factors (number of shared pollinators, abundance, mean visit potential, and functional originality). 209 We found that our models of pollen deposition had high explanatory power (the coefficient of 210 determination R² ranged between 0.76 and 0.93) although a large portion of the explanatory 211 power came from the random effects (Table S3). As determined by AICc, the random 212 structure best supported by the data was the one that fit intercept for each species in 213 each community (as opposed to a common intercept for each species irrespective of the 214 community to which they belong). This structure was best for both the models of conspecific 215 and heterospecific pollen (Table S4). 216 Of the four factors we considered, we found that a plant's mean visit potential and relative 217

floral abundance were the most important at predicting pollen deposition in plant stigmas
(Fig. 1a). 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 S5).

[Figure 1 about here.]

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 Leposition

with an increase in conspecific pollen were also associated with an increase in heterospecific pollen deposition. Specifically, the plants' mean visit potential had a positive effect on pollen 226 deposition (Fig. 1b). However, the effect size was slightly larger for heterospecific than for 227 conspecific pollen. This larger effect indicates that, although there is a positive association 228 between visit potential and the quantity of pollen deposition, there is a negative relationship 229 with its purity (Fig. 1c). In contrast, a plants' relative floral abundance negatively affected its 230 deposition quantity, but the mean difference between the coefficients in the models indicates 231 positive association with purity (Fig. 1c). The third most important factor, functional 232 originality, had a positive, although comparatively smaller, association with both the quantity 233 and purity. Finally, the number of shared pollinators had negative and neutral associations 234 with conspecific and heterospecific pollen, respectively, but these impacts were small when 235 compared to the other factors. Although the ecological factors were positively correlated (Fig. 236 S2), the collinearity between predictors did not qualitatively affect our findings (Fig. S3).

Flexibility of plant strategies

ILLA We used a PCA of the ecological factors-species matrix to investigate whether plants' "strategy 239 towards pollen deposition is similar across communities or whether they are flexible and 240 therefore a reflection of the community context. The first two PCA components explained 241 75% of the total variance (Fig. 2a). The first component was dominated by visit potential 242 and relative abundance while the second component was dominated by the number of shared 243 pollinators and the plant's functional originality. When we locate the species that were 244 sampled in more than one community in the first two PCA components (Fig. 2b), we observe 245 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 247 significantly smaller than that of randomisations for only two of the twelve species analysed (Fig. 2c).

Discussion

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Our results suggest that community context plays a central role in determining the pollen 252 deposition dynamics and ultimately the net cost or benefit of sharing pollinators. First, we 253 found that multiple ecological factors can modulate the quality of the pollination service; 254 however, conspecific and heterospecific pollen deposition are tightly coupled and this creates a 255 clear trade-off between the quantity and purity of pollination (Thomson et al. 2019). Second, 256 we found that the way these factors shape pollen deposition for a species could be dramatically 257 different across communities. For instance, while in a particular community a plant species 258 could show high levels of pollinator sharing and relatively low trait differentiation, the same 259 species in another community can have relatively high trait differentiation and low levels 260 of pollinator sharing. Our findings highlight that trade-offs can at least partially explain 261 the coexistence of facilitative and competitive effects of animal-mediated pollination in the 262 pollination service both the short and the long term. 263 The trade-offs involved in attaining high-quality pollination service (and more broadly between 264 facilitation and competition) are likely to arise when plants simultaneously maximise the 265 deposition of conspecific pollen and minimise that of heterospecific pollen. In the short 266 term, being a specialist and sharing no pollinators might reduce competition (Muchhala et al. 267 2010) and hence be preferable, not only due to costs to male fitness (Morales and Traveset 268 2008, Muchhala and Thomson 2012), with also Williamse, as we show here, sharing pollinators 269 reduces both the quantity and purity of the conspecific pollen deposited. However, over long 270 periods of time, there could be a risk associated with a specialist plant having few pollinators 271 (Ricketts 2004). To ensure long-term survival, it is thus likely that plants also need to balance 272 this risk with the costs of sharing pollinators (Aizen et al. 2012). One possible solution is 273

to share pollinators and have original traits—as we show that trait originality is generally 274 beneficial to pollen deposition and it is commonly thought that species that are further from 275 others in trait space benefit from reduced competition. Yet, there are two possible caveats to 276 this strategy that highlight the interrelatedness of the ecological factors. First, in a mutualism 277 context, it is also possible that trait originality could come at the cost of being less 'apparent' to pollinators (Reverté et al. 2016). Second, the negative relationship between originality and generalism (Carvalheiro et al. 2014) has been shown to depend on plant abundance (Coux et al. 2016), with generalist species being able to have original traits only when they are also abundant enough to provide a valuable reward to make visiting worthwhile to pollinators. 282 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 287 pollen (Fang and Huang 2016). 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 290 and abundance (Feldman et al. 2004, Muñoz and Cavieres 2008, Morales and Traveset 2008), 291 but they also suggest that (because visitation, pollen production and abundance are usually 292 correlated; Sargent and Otto 2006) balancing the pros and cons of sharing pollinators at the 293 community level is not trivial and might even be partially responsible for the diversity of 294 plant-pollinator communities (Benadi and Pauw 2018).] — | dowt zet this. 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 formathers, fitness can instead be limited by the amount of conspecific 297 pollen (Campbell and Motten 1985, Arceo-Gómez et al. 2019). Alternatively, plant species

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can also differ substantially in the extent to which self- vs. outcross-pollen differ in their 300 value for fertilization. The difference can be particularly relevant for species that are not 301 self-fertile or those in which self-fertilization is rarely effective due to a temporary separation 302 in the maturation of the sexes (dichogamy).

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Importantly, we show here that the balances between costs and benefits are determined not 304 only by species identity but also by the community to which plants belong. Specifically, most 305 plant species appear to be flexible enough to adopt markedly different niches in different 306 communities. From an evolutionary perspective, our results suggest that selection for a 307 particular strategy might say something about the community in which a species has typically 308 inhabited during its evolutionary history. Furthermore, from a more applied perspective, 309 flowering plants are sometimes introduced to attract pollinators on other nearby plants. On 310 the one hand, our results suggest that introduced plants that increase the relative originality 311 of natives (e.g. through distinct phenology) might have positive effects (Gibson et al. 2012). 312 On the other, because different niches can lead to different outcomes across communities, 313 our results also highlight the difficulties involved in predicting whether the introduced plant 314 species will facilitate or compete with neighbours (Bartomeus et al. 2008). Other factors that 315 we were unable to measure (e.g. pollinator behaviour and densities or the spatial context) 316 have also been shown to play a role in the outcome of animal-mediated pollination (Cariveau 317 and Norton 2009, Flanagan et al. 2011, Ye et al. 2014, Thomson et al. 2019). Nevertheless, 318 our results indicate that the strategies a plant might use to successfully minimise competition 319 for pollination (or maximise facilitation) must be determined relative to other species in the 320 community, rather than an absolute property of the species itself. 321

Overall, using empirical data on pollen deposition, we show that at the community level that sharing pollinators has a smaller effect on pollen deposition than what we expected based on 323 experimental studies with a handful species. Other factors that underpin community dynamics (abundance, traits, visitation) also influence patterns of pollination quantity and purity. The

interrelatedness of these factors, and the flexibility of species to position themselves within these factors means that their contributions to the quality of the pollination service should not these factors means that their contributions to the quality of the pollination service should not and cannot be understood in isolation. All factors we analysed involve substantial trade-offs in pollen deposition in the short and likely also in the long term. These trade-offs emphasise the competitive nature of pollination. However, many of the widely used theoretical models of plant-pollinator communities do not account for the adverse effects of sharing pollinators (but see Rohr et al. 2014 and similar). We propose that achieving a better understanding of species coexistence and how pollination support plant biodiversity will require seeing them as both mutualistic and competitive communities (Johnson and Bronstein 2019).

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467 List of Figures

1	Effect of ecological factors on the pollination service. (a) The plant's visit	
	potential and relative floral abundance are the most important factors deter-	
	mining 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)	23
2	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	
		0.4

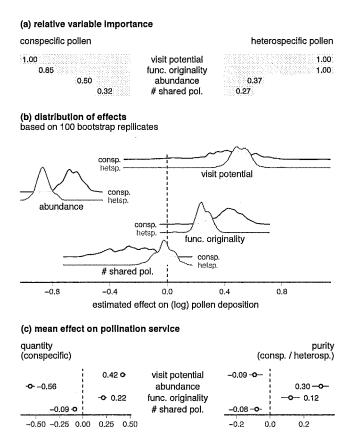


Figure 1: Effect of ecological factors on the pollination service. (a) The plant's visit potential and relative floral abundance are the most important factors determining the deposition of conspecific and heterospecific pollen. Meanwhile, the number of shared pollinators was generally less important. 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 (± SE of 99 bootstrap replicates).

(black line)

(green line)

can/should you make one dashed?

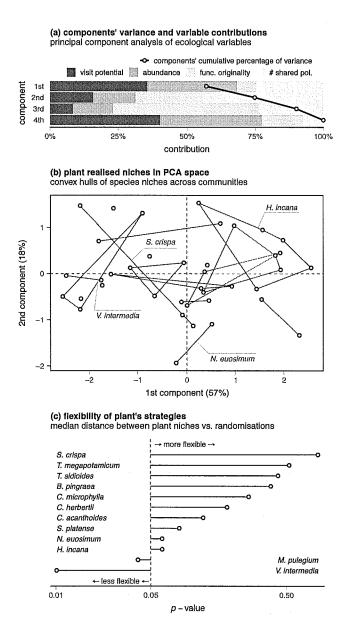


Figure 2: The flexibility of plant strategies. (a) The two first components explain a large proportion of the total variance. (b) When plants that were sampled in more than one community are plotted in terms of these two components, we observe that their points which represent the strategy (the particular 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.

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

Supplementary information

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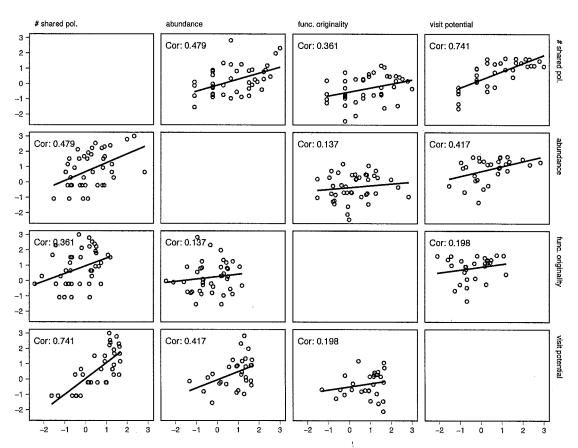


Figure S2: Correlation between the explanatory variables included in the statistical models.



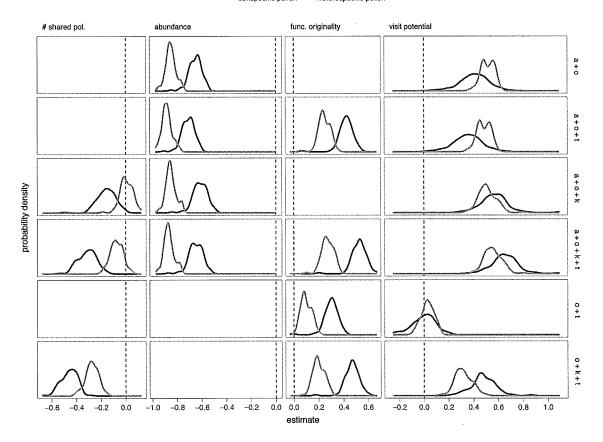


Figure S3: Distribution of effect estimates for models of conspecific and heterospecific pollen density gain. Model formulas have been abbreviated: a for abundance, k for the number of shared pollinators, o for the visit potential, and t for functional originality. Only candidate formulas with a $\Delta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