

The pollination trade-off

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Introduction

Animal pollination systems play a disproportionately important role in food production and maintenance of global biodiversity (Bascompte & Jordano 2007; Klein *et al.* 2007; Ollerton *et al.* 2011). Alongside the direct mutualisms between plants and their pollinators, the support to biodiversity can be achieved as a result of inter-species facilitation—the positive feedback loops that exist between plants that share pollinators or pollinators that share plant (Moeller 2004; Ghazoul 2006; Molina-Montenegro *et al.* 2008). Facilitation is able to promote species coexistence because it offsets the effects of direct competition for resources (Stachowicz 2001). Indeed, studies that are fundamental to our current knowledge of mutualism predict that the maximum number of coexisting species—an upper limit to biodiversity—is achieved when the number of mutualistic partners is maximised in a community (Bastolla *et al.* 2009). And yet, not every pollinator species in natural communities interacts with every species of plant.

One of the possible explanations is that sharing a mutualistic partner also has costs (Waser 1978). As soon as there are costs, plants start competing for mutualistic partners, even if this competition is not strong enough to produce a **net** negative effect in fitness. The possible detrimental effects of competition for pollinators have been long recognised (Robertson 1895) and widely documented both experimentally (Lewis 1961) and theoretically (Levin & Anderson 1970). Multiple factors (like the number of shared pollinators, the plants' relative abundance, visitor fidelity, and traits) have been shown to modulate the strength of competition and, in turn, the fitness outcome (Bobisud & Neuhaus 1975; Campbell 1985; Feinsinger 1987; Morales & Traveset 2008; Mitchell *et al.* 2009). It is currently clear that the effects of these factors on fitness have the potential to drive the evolution of flower phenologies, morphologies and reproductive strategies, as well as ecological differentiation (Caruso 2000; Mitchell *et al.* 2009).

The main two mechanisms through which these ecological factors can affect plant fertilization are: (*i*) by reducing the number of conspecific pollen grains on stigmas or (*ii*) by increasing the deposition of heterospecific pollen (Morales & Traveset 2008). For example, plants with more attractive flowers might reduce the number of visits—and hence the amount of conspecific pollen deposited by animals—for those less attractive (Yang *et al.* 2011). We denote this as the *quantity* of the pollination service. More subtly, when plants share pollination partners, even receiving a visit might not translate into fertilization due to interspecific pollen transfer (Campbell & Motten 1985). Interspecific pollen transfer affects the pollination service because a focal plant might receive pollen from a different species, or conversely, pollen from the focal plant might be lost to different species. Generally speaking, the higher the proportion of conspecific relative to heterospecific pollen the higher the *quality* of the pollination service. With few exceptions (Rathcke 1988; Lopezaiza-Mikel *et al.*

2007; Hegland *et al.* 2009; Aizen & Rovere 2010; Tur *et al.* 2016), most of what we know about the quantity and quality of pollination—and its relationship to competition vs. facilitation in pollination systems—is based mostly on studies of two plant species. However, competitive interactions between species pairs do not occur in isolation.

Instead, co-flowering plants often occur in communities in which multiple intertwined factors operate simultaneously and 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 have generally fewer interaction partners (Coux *et al.* 2016). This evidence is aligned with the notion that a species that interacts with few species does so strongly with each of them; in contrast, a species that interacts with a large number of species does so comparatively weakly. If evolutionary specialisation occurs by changing traits to focus on fewer but better partners (Caruso 2000), we should expect a reduction of competition for pollination in species with original traits and an increase in species with a large number of interaction partners (Gibson *et al.* 2012). Alternatively, it might also be the case that flower/pollen density is the dominant force driving pollen transfer (Seifan *et al.* 2014). Abundant plant species might experience a dilution of available pollinators (Feinsinger 1987) but might also receive more effective visits by capitalising on a larger share of both the pollen being transported by pollinators and their visits compared to other species. In this case, a potential reduction in the quantity of pollination (the amount of conspecific pollen received) could be compensated by an increase in the quality of pollination (the amount of conspecific relative to heterospecific pollen received). To complicate things more, autonomous self-pollination can also influence a plant sensitivity to competition for pollination because it can ensure reproduction even in the absence of outcross pollen (Kalisz & Vogler 2003). Altogether, multiple, potentially correlated, factors may act simultaneously. Therefore, understanding the relative importance of these factors and how plant species harness them to minimise competition for pollination within their communities requires extensive data. Both describing the structure of the interactions and the pollen flows that occur within it.

Here, we explore competition for pollination at the community scale using comprehensive empirical data from eleven plant-pollinator communities in the Argentinian Pampas. First, we ask the extent to which the outcome of animal-mediated pollination is facilitation or competition. If facilitation is the primary outcome we would expect (i) an overall positive relationship between the amount of conspecific pollen deposited in stigmas and the heterospecific pollen (Tur *et al.* 2016) and (ii) a larger amount of conspecific pollen deposited in stigmas when flowers are open to animal pollinators than that due to self-pollination. Second, we investigate the relative contribution that four ecological factors, that together, describe the role of the plant species and the ecological context, have on competition for pollination. We hypothesize that competition for

pollination at the community level should increase as the number of shared pollination partners a plant has increases. However, other factors like the plant's functional originality, its relative abundance, and the visit effectiveness, should have the potential to compensate this increase in competition by improving either the quality or the quality of pollination. Third, and finally, we explore how community influences the way plants use these factors to minimise competition. Although some plant species might be widespread across multiple locations, competition for pollinators occurs at the community level and are hence is likely to be defined by the ecological context. If plant species adopt comparable roles across different communities, we should expect plant strategies to be more similar within species than across species in the study. On the contrary, if species role is flexible, we should expect plants to be able to adopt different strategies in each community such that competition is minimised depending on the context.

Methods

We collected data from eleven co-flowering plant communities and their pollinators in three locations, each in a distinct region of the Argentinian Pampas. These locations are distributed across a precipitation gradient with a humid temperate climate in the eastern Flooding Pampas and becoming drier as one moves inland and westward towards the Pampean Grasslands. Annual mean temperatures range between 14.8 and 44.9°C. In each location, we sampled two restored and two agricultural fragments, except in the Flooding Pampas, where due to the lack of available sites, we were only able to sample one restored fragment.

Competition vs. facilitation

Our first objective is to identify whether, at the community level, the net outcome of animal-mediated pollination is facilitation or competition. The first line of evidence can be found in the relationship between heterospecific and conspecific pollen deposited in plant stigmas (Tur *et al.* 2016). This is so because heterospecific pollen can be seen as a cost that plants must pay for receiving conspecific pollen from shared pollinators. A negative relationship (when shared pollinators increase heterospecific pollen loads and decrease conspecific loads) may indicate that competition for pollination is strong. This negative relationship could arise, for example, when another, more dominant species, monopolizes a limited number of pollinators (Mitchell *et al.* 2009), when heterospecific pollen deposited in the stigma interferes with deposition of conspecific pollen (Runquist 2012), or when conspecific pollen is lost to heterospecific stigmas (Mitchell *et al.* 2009; Muchhala & Thomson 2012). In contrast, a positive relationship is what should be observed if

101 facilitation is the dominant outcome. For example, when the abundance of shared pollinators is positively
102 influenced by floral resources and these positive effects ripple through the mutualistic network in a chain of
103 positive feedback loops (Liao *et al.* 2011).

104 The second line of evidence could be obtained by examining the difference between the amount conspecific
105 pollen deposited in flower stigmas *with* and *without* animal-mediated pollination. Self-pollination can be
106 favourable to plant reproduction when competition for pollination is strong because it provides insurance
107 against a poor pollination service (Kalisz & Vogler 2003). If competition for pollination is sufficiently strong,
108 then the amount of conspecific pollen deposited in flower stigmas when animal pollination is prevented could
109 be higher than when floral visits are allowed. In contrast, the opposite pattern may indicate that plants
110 benefit from animal-mediated pollination—even a small difference between outcross and self-pollen may be
111 important to plant fitness (???). This is particularly so for species that are not self-fertile or those in which
112 self-fertilization is rarely effective due to a temporary separation in the maturation of the sexes (dichogamy).

113 Data collection

114 In each of the studied communities, we quantified pollen deposition in a subset of plant species between
115 December 2010 and February 2011. This subset comprised of between three and nine common insect-pollinated
116 (entomophilous) species that were flowering during the sampling period (see Figure 1a). We chose plant
117 species such that they cover a wide range on a specialization-generalization gradient as well as a wide range
118 of abundances. Briefly, in each of the selected plants, we removed all flowers leaving only buds that were
119 expected to go into florescence on the next day. Approximately a quarter of these buds were bagged to
120 prevent animal pollination. Two days after inflorescence, we counted the pollen grains in the remaining
121 flowers' pistils, classified them between conspecific and heterospecific pollen, and calculated the number of
122 pollen grains per stigma in each flower. More details about the study sites and data collection and laboratory
123 protocols can be found in Marrero *et al.* (2016).

124 Data analysis

125 To evaluate the relationship between heterospecific and conspecific pollen, we used a generalised linear
126 mixed model (GLMM) with a Poisson error distribution in each of our communities (Tur *et al.* 2016). In
127 these models, the number conspecific pollen grains per stigma was the response variable and the number of
128 heterospecific grains the predictor. The slope and intercept of this relationship were allowed to differ between
129 plant species, which were modelled as a random effect. Models were fitted using the function `lmer` from the

R package `lme4` 1.1-19 (Bates *et al.* 2015) To compare the conspecific pollen deposited with and without animal-mediated pollination, we performed a Mann-Whitney U test of the number of conspecific pollen grains per stigma between un-bagged and bagged flowers for each of the studied species in a community.

Effect of ecological factors in the pollination service

Our second objective is to investigate the relative contribution that different factors that describe the plants' role and its ecological context have on the pollination service. Specifically, we investigate the effect of (i) the number of shared pollinators, (ii) the plants relative abundance, (iii) the mean visit effectiveness—a metric that combines the share of pollen that a plant species is able to place on each of their floral visitors and the number of visits it receives from them, and (iv) the plants functional originality. Here, we define visit effectiveness of the pollinator species i to plant species j as the proportion between the visits of i to j and all visits of i , multiplied by the proportion between the number of pollen grains of j attached to individuals of i and all pollen attached to individuals of i .

Data collection

To obtain the number of shared pollinators for each species (i), we collected data to construct qualitative and quantitative pollination networks. Qualitative networks were constructed based on two-hour observations of floral visits in each fragment. Quantitative networks were constructed using two 50 m randomly located transects in each transect. We counted and collected all floral visitors found in a 2 m wide strip while walking at a pace of 10 m per minute (Memmott 1999; Marrero *et al.* 2014). We visited the transects each month between November 2010 and March 2011. To obtain plant abundance (ii), we counted all units of floral attraction found during an independent sampling of the same transects used to construct the quantitative visitation networks. To estimate visit effectiveness (iii), in addition to the visitation networks we need to construct pollen transfer networks. To construct the transfer networks we examined the pollen loads present on the collected floral visitors (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 whenever 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 (iv) that relate to plant type (herb, shrub, climber), life cycle (annual, perennial), flower colouration, and whether the species is native in the study region. More details about the study sites, data collection, and laboratory protocols can be found in Marrero *et al.* (2014 and 2017).

159 Data analysis

160 We investigate the impact of the ecological factors on the pollination services using two metrics: the quantity
161 and the quality of pollination. Here we define the quality of pollination as the amount of conspecific pollen
162 and the quality of pollination as the amount of conspecific pollen *relative* to heterospecific pollen. To construct
163 these metrics we use two sets of linear mixed models (LMM) in which the response variables are the number
164 of conspecific and heterospecific pollen grains deposited per stigma in flowers open to animal-mediated
165 pollination. In general, using LMMs in which pollen loads were log-transformed (Figure S1) offered better
166 results than a GLMM with Poisson (or quasipoisson) error structure. Models were fitted using the R package
167 `nlme` 3.1-131 (Pinheiro *et al.* 2018).

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

172 As predictors in the models, we included the four ecological variables described above. Specifically, we
173 calculated the number of shared pollinators for each plant species (*i*) by pooling data from the qualitative
174 and quantitative pollination networks. This variable is strongly correlated to the number of animal species a
175 plant interacts with (the species degree). To calculate the plants' relative abundance in their community (*ii*),
176 we simply aggregated floral counts for each species. We then calculated the mean visit effectiveness (*iii*). As
177 explained before, we define the effectiveness of a visit by pollinator species *i* to plant species *j* as

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

178 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
179 is the total number of visits performed by *i*, and p_j is the total number of grains carried by *j*. Because the
180 number of interacting species (and therefore the number of shared pollinators), floral abundance, visitation,
181 and pollen production roughly followed a power-law distribution, we log-transformed these three predictors
182 before including them in the model.

183 Finally, functional originality (*iv*) is defined as the distance of a species from the community trait average—the
184 centroid of functional space of the community (Laliberté & Legendre 2010; Coux *et al.* 2016). As phenology
185 has been shown to be a key mechanism of niche differentiation among plants, we also included the plant
186 abundance in each of the survey months (November to March) as an additional trait in our analysis. This

approach allowed us to integrate the originality in phenological niche alongside the originality on other functional traits. However, because floral counts across months are not independent, we assigned them a weight of 1/5 such that phenology has an equal weight as other traits. We scaled all traits prior to calculating the centroid of the functional space and calculated the species-specific functional coordinates using the R package `FD 1.0-12` (Laliberté *et al.* 2014). Finally, to facilitate comparison across the four continuous explanatory variables in our models, we rescaled them all to have a zero mean and unitary variance.

To estimate the coefficients and to perform model selection and the associated uncertainty, we used a combination of multi-model inference and bootstrap resampling with one hundred replicates. First, we performed model selection using the AICc and determined the likelihood of each candidate model (a particular combination of predicting variables) 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 variables proportional to the likelihood of its candidate model. We “shrank” the estimates coefficient of potentially unimportant variables by setting its estimate to 0 when the variable was not included in the model. Finally, we used these distributions of the model coefficients to estimate their impact on the quantity and quality of pollination. For the quantity of pollination, we simply calculated the mean value of a sample of the conspecific pollen loads. For the quality of pollination, we calculated the mean difference between a sample of the distribution of the effects of conspecific pollen and a sample of those of heterospecific pollen gain. Again, here we used bootstrap resampling to estimate the uncertainty around these means.

Flexibility of plant strategies

Our last objective is to tease apart the strategies that plants might use to reduce competition and, importantly, how the community context influences these strategies. If community context plays a relatively small role, we should expect plants to adopt similar strategies across different communities. Alternatively, if the community plays a large role, we should be able to observe differences in the strategy a plant species across communities. We first use a principal component analysis (PCA) of the four ecological variables. We define the species strategy in a community as its coordinates in PCA space. For each species that was present in two or more communities, we then calculate (i) the median distance between the strategies that the species uses different communities, and (ii) the area of the convex hull defined by these points in the first two principal components. We then compare these two metrics to those obtained with 99 Monte Carlo randomizations in which we replace the strategy of the focal plant species by one of another species in the dataset.

Results

Competition vs. facilitation

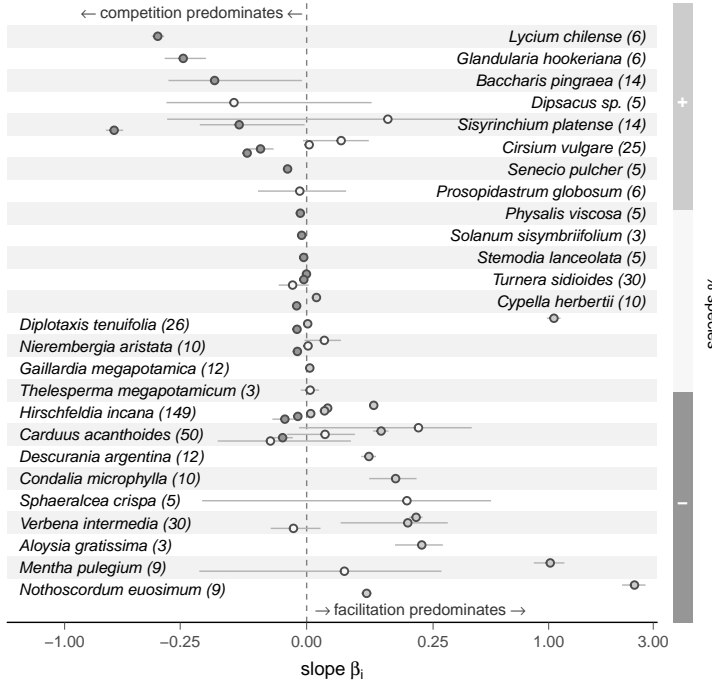
We first examined the relationship between the heterospecific and conspecific pollen deposited on stigmas of a species in a community. We found that the overall slope of the relationship was positive (Table SXX), but a large proportion of plants experienced a negative or no significant relationship or a between heterospecific and conspecific pollen (37% and 30% respectively; Figure 1a). 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, four of species sampled in multiple communities (*Cypella herbertii*, *Diplotaxis tenuifolia*, *Hirschfeldia incana*, and *Carduus acanthoides*) showed evidence that facilitation (positive relationships) predominates in some communities while competition (negative relationships) predominates in others. Furthermore, although there was wide variation in the slope of the relationship between heterospecific and conspecific pollen, plants, in almost all cases, had more conspecific than heterospecific pollen deposited on their stigmas (Figure 1b).

Second, we compared the amount of conspecific pollen deposited on flowers that were open to animal-mediated pollinators with those that were closed. Here again, we found large differences between plants. Specifically, the difference was non-significant for 56% of plants, 35% had significantly more pollen when open, and the remaining 9% had significantly less pollen when open ($\alpha = 0.05$, Mann-Whitney U tests; Figure 1c). Variation within species was slightly smaller and only two species (*H. incana* and *C. acanthoides*) had both significantly positive and negative differences.

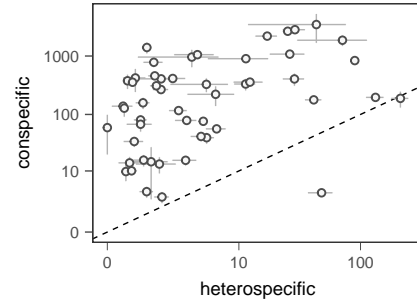
Effect of ecological factors in the pollination service

We then examined the role that four ecological variables (number of shared pollinators, abundance, mean visit effectiveness, and functional originality) play on pollen deposition and, by extension, in the quantity and quality of pollination. We found that the linear mixed models of pollen deposition used had high explanatory power. The conditional coefficient of determination $R^2_{(c)}$ of the most parsimonious models (those with the lowest AICc) ranged between 0.87 and 0.93 (mean of 0.91) for the bootstrap replicates of the conspecific pollen models and between 0.76 and 0.87 (mean 0.8) for the models of heterospecific pollen (Nakagawa & Schielzeth 2013). A large portion of this explanatory power came from the random effects, particularly for models of conspecific pollen. The marginal coefficient of determination $R^2_{(m)}$, which describes the proportion of variance explained for the fixed variables alone, ranged between 0.06 and 0.14 (mean 0.09) for the conspecific

(a) relationship hetero–conspecific pollen
slope of species–community random effects



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



(c) self– vs. animal-mediated pollination
mean pollen grains per stigma

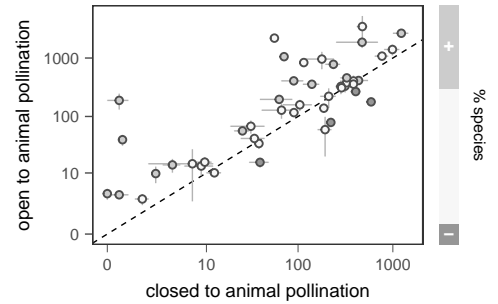


Figure 1: Competition vs. facilitation at the community level. (a) Some species experience more competition for pollination than others. Points indicate the estimated slopes for the relationship between the amount of heterospecific and conspecific pollen deposited per stigma across species in their communities. Negative slopes indicate that plants experience competition for animal-mediated pollination, while positive slopes 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) Generally, plants also had more pollen deposited in their stigmas when they were open to animal-mediated pollination than when they were closed. However, in the majority of cases, the difference is not large enough to be statistically significant at the 0.05 level. In all plots, error bars correspond to \pm the standard error (SE).

models and between 0.21 and 0.35 (mean 0.27) for the heterospecific models.

We tested two random structures. As determined by the AICc, the random structure best supported by the data was the one that fits an intercept for each species in a community independently (as opposed to an 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 SXX).

Out of the four variables we explored, we found that the plants' mean visit effectiveness and its 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 included in models with relatively large AICc values.

We found that the relationship between each of the ecological factors and pollen deposition was similar for both conspecific and heterospecific pollen. This is, factors that were associated with an increase (or a decrease) in conspecific pollen, were also associated with an increase (or a decrease) in heterospecific pollen deposition. Specifically, the plants' mean visit effectiveness had a positive effect on pollen deposition (Figure 2b). The positive association with conspecific pollen indicates a positive effect on the quantity of pollination. However, the difference between the coefficient that relates visit effectiveness to heterospecific and conspecific pollen deposition suggests a negative, but marginal, relationship of this variable and our definition of the quality of the pollination service (Figure 2c). Contrastingly, the plants' relative abundance had a negative effect in pollen deposition (and consequently the quantity of pollination), but the difference between the coefficients in the models of conspecific and heterospecific pollen indicates a considerable positive impact on the quality of pollination. The third most important variable, functional originality, had a positive, although comparatively smaller, association with both the quantity and quality of pollination. Finally, the number of shared pollinators had a negative association with the quantity and quality of pollination, but these impacts were small when compared to all other ecological factors. Although relative abundance, the number of shared pollinators, and the visit effectiveness were positively correlated (Figure S3), the effect that each of them had on conspecific pollen was relatively similar among models that included all or just some of these three explanatory variables (Figure S4).

Flexibility of plant strategies

We used a PCA of the analysed species to investigate whether plants strategy are similar across communities or whether they are flexible, and therefore able to adapt to the community context. The first two PCA components explained 75% of the total variance (Figure 3a). The first component was dominated by changes

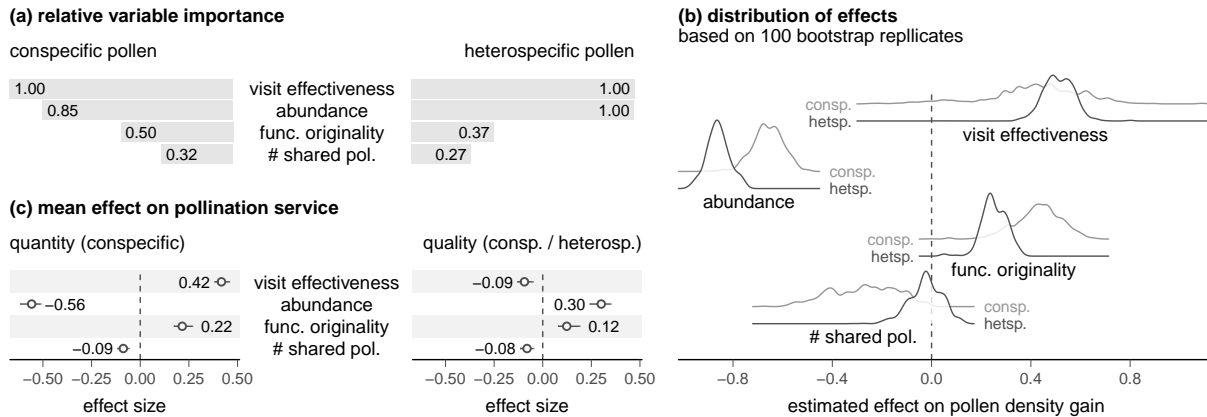


Figure 2: **Effect of ecological factors in the pollination service.** (a) The plant's visit effectiveness and relative abundance are the most important variables determining the deposition of conspecific and heterospecific pollen. Meanwhile, the number of shared pollinators was relatively unimportant. 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 of ecological variables on heterospecific pollen tended to be aligned with its association on 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 (top panel) and heterospecific pollen (bottom panel). Results are only shown for models that included explanatory variable. (c) The end result of these associations is that only the plants' functional originality has a positive impact on both the quantity and quality of pollination. The plot shows the model averaged mean effect (\pm SE) of the four analysed ecological variables in the quantity and quality of pollination.

on the visit effectiveness and the 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 the first two PCA components (Figure 3b), we observe that the strategies of a species do not seem to be close to each other. Indeed, when we measured the median distance between the plants coordinates we found that it was significantly smaller than that of randomisations for only one of all analysed species (Figure 3c).

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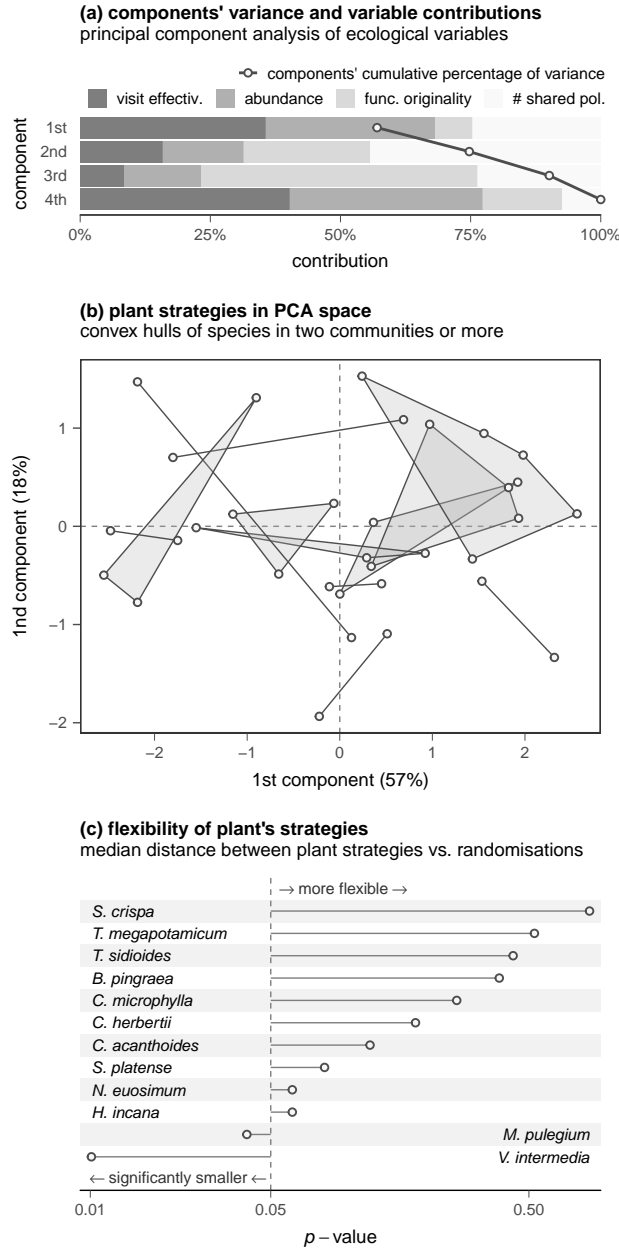


Figure 3: **The flexibility of plant strategies.** (a) The two first components explain a large proportion of the total variance. (b) When plants that were sampled in more than one community are plotted with these two components, we observe that points, which represent the strategy (the particular combination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

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