

The pollination trade-off

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Draft Info

Changes

- Now using AICc instead of AIC to evaluate models (no change in results)
- Traits: (*a*) to keep signature of phenology, absolute flower counts (log-transformed) are used instead of relative abundances. Also, now (*b*) columns in the trait matrix for phenology are scaled so that it doesn't count 5 times as much as other traits.
- The absolute/relative/gain terminology was confusing. Now I'm modelling open and bagged pollen counts directly, using the bagged as a sort of control.
- Introduced visit efficacy instead of the share in the pollen pool as a predictor in the model. Turns out to be a better predictor and also incorporates quantitative visitation data which was missing from the previous models.
- Now I use a PCA of the explanatory variables to understand different plant strategies and give a deeper treatment to the facilitation/competition question.

To do

- Spell-check everything & check that reference list is correct.
- Choose journal (the manuscript is written for an interdisciplinary journal).

Questions

Feel free to come back here after you've read the manuscript. Thanks!

- Do you know of a reasonable reference for the claims in page 4, line 52 and page 7, line 150?
- I got feedback that "denote" in page 4, line 74 might be overly formal?
- Hugo. Some journals require publication of data alongside with the paper. Is it OK to consider those? Or you prefer to keep data private?

Abstract

In the context of animal-mediated pollination, sharing pollinators between plant species creates a balancing act between two ecological opposites: mutualism and competition. Sharing pollinators can be beneficial because it allows plant species to harness positive feedback loops between populations. It can also be detrimental to co-flowering plants because pollen can be lost to foreign flowers and stigma surface can be occupied by foreign pollen. However, these detrimental effects of sharing pollinators are poorly understood at the community level because, at this scale, many other factors play a role in shaping species interactions. Specifically, here we quantify the potential negative impact that the number of interacting species can play on the pollination service while accounting for the structure of the interactions, the pollen flows that occur within it, and the traits of the species that integrate the community. We found that there is indeed a trade-off between the number of interacting partners and both the quantity and quality of pollination received by different flowering plants. However, the trade-off's role on pollination service is relatively small when compared to other ecological factors. In particular, competition for pollinators is more strongly shaped by density effects caused by the species abundance and the amount of pollen the plant produces, as well as its functional originality. While sharing pollinators can be detrimental for plant fitness, when scaling up to empirical communities, we show that plants can compensate for these detrimental effects using other ecological mechanisms.

Keywords: X, Y, Z

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; Lopezaraiza-Mikel *et al.*

2007; Hegland *et al.* 2009; Aizen & Roever 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 pollination partners a plant has increases (species degree). 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 quantity 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

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

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

152 Data collection

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

163 Data analysis

164 To evaluate the relationship between heterospecific and conspecific pollen, we used a generalised linear
165 mixed model (GLMM) with a Poisson error distribution in each of our communities (Tur *et al.* 2016). In
166 these models, the number conspecific pollen grains per stigma was the response variable and the number of
167 heterospecific grains the predictor. The slope and intercept of this relationship were allowed to differ between
168 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).

198 Data analysis

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

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

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

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

217 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
218 is the total number of visits performed by *i*, and p_j is the total number of grains carried by *j*. Because the
219 number of interacting species (and therefore the number of shared pollinators), floral abundance, visitation,
220 and pollen production roughly followed a power-law distribution, we log-transformed these three predictors
221 before including them in the model.

222 Finally, functional originality (*iv*) is defined as the distance of a species from the community trait average—the
223 centroid of functional space of the community (Laliberté & Legendre 2010; Coux *et al.* 2016). As phenology
224 has been shown to be a key mechanism of niche differentiation among plants, we also included the plant
225 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.

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 by one of another species in its community.

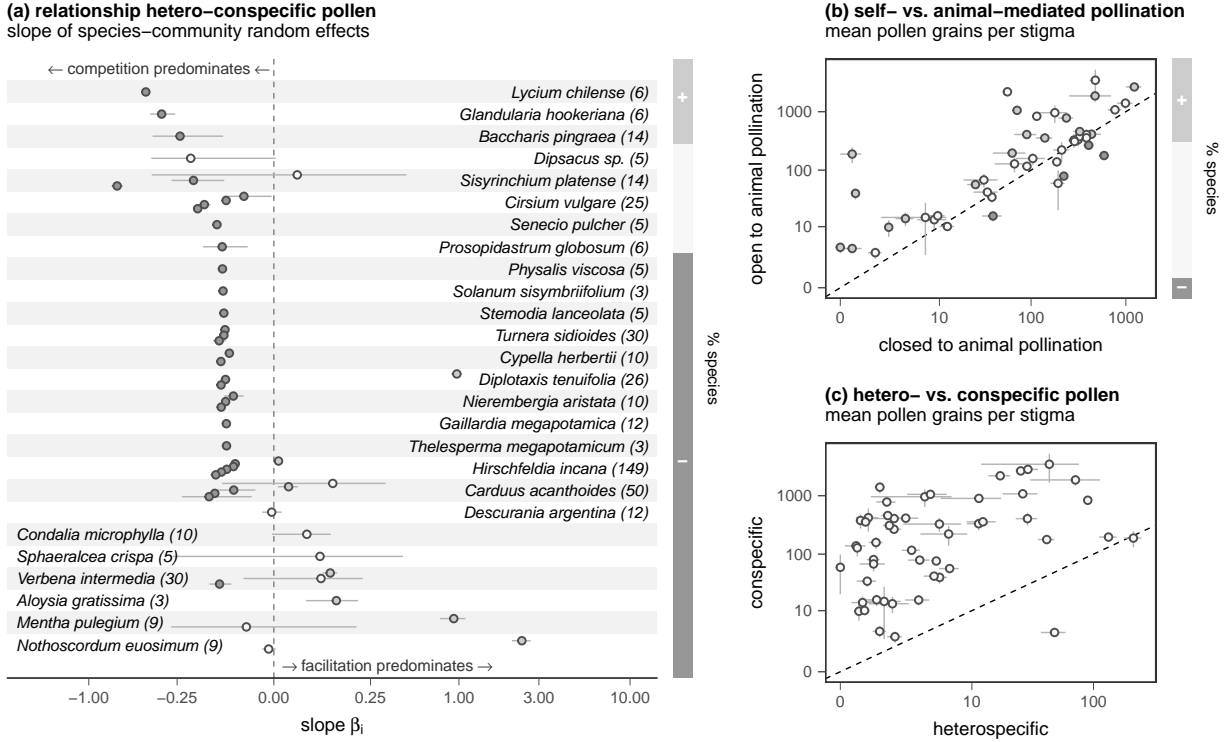


Figure 1: The interplay between the gain on heterospecific and conspecific pollen. Each dot indicates the predicted median gains for a species in its community (which corresponds to the selected random effects in all of our models). The horizontal and vertical bars under each dot indicate the 0.05 bootstrap confidence intervals of the estimates. The solid lines indicate the overall relationship in each of the bootstrap replicates and were calculated by sampling the predictions from 100 conspecific/heterospecific model pairs and estimated the relationship by fitting a standardised major axis (SMA) to each pair (we used the R package smatr 3.4-3, Warton et al. 2012). The dashed line indicates the isoline at which heterospecific pollen is gained at the same rate than conspecific pollen.

Results

Competition vs. facilitation

Effect of ecological factors in the pollination service

Plant strategies

We found that, for both the model sets of conspecific and heterospecific pollen, the random structure that was best supported by the data was the one that included plant species nested in community as the grouping factors (Table S1). When looking at the relative amount of conspecific pollen gained, we observe that only 41% of species in their communities observed a significant increase in conspecific pollen density when comparing open and bagged flowers (Table S2). We also observed a positive relationship between the gain in

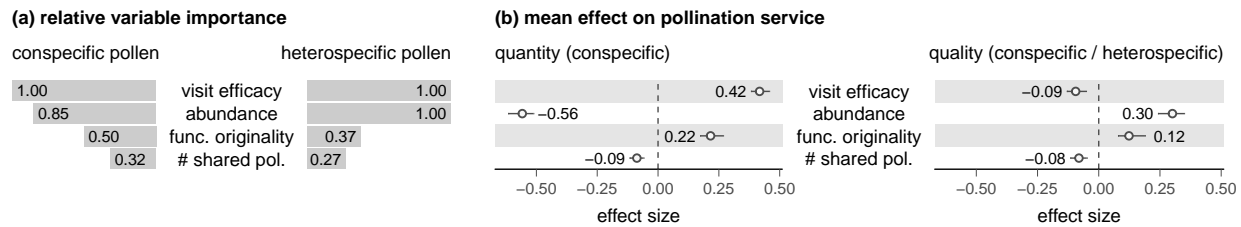


Figure 2: Mean relative effect of ecological variables on the quantity and quality of pollination. Results are shown for values calculated with both the absolute gain in pollen density (abs.) and the gain relative to selfing (rel.). Bootstrap confidence intervals of the mean (at the 0.05 level) are shown in square brackets.

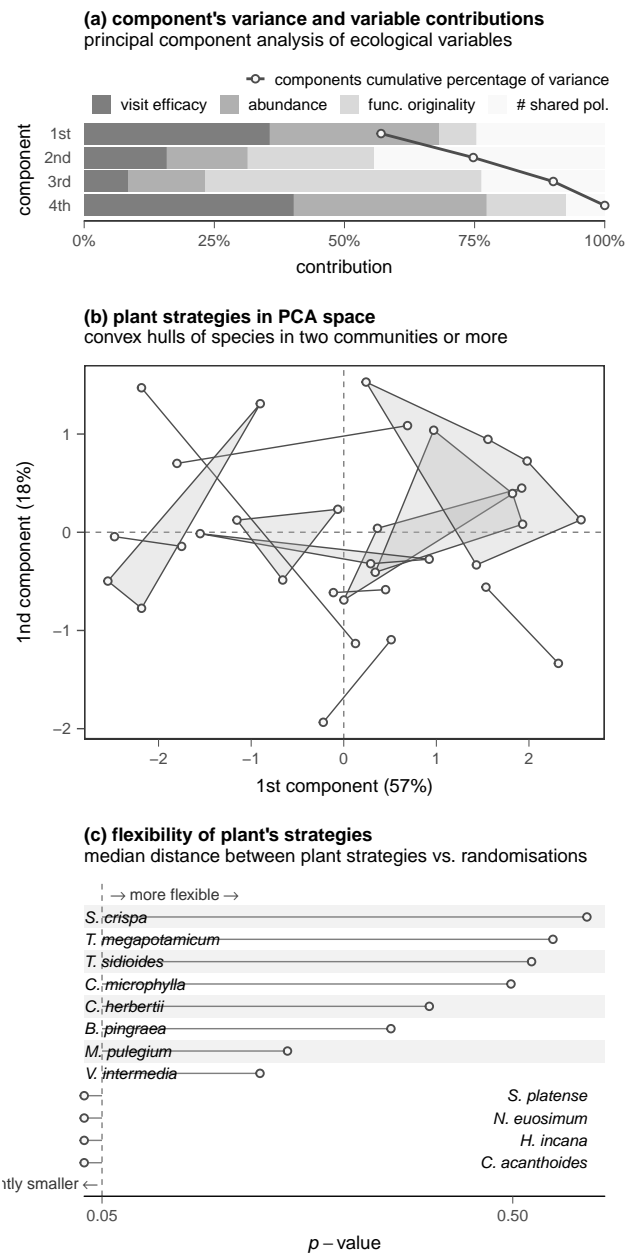


Figure 3: PCA results.

heterospecific pollen and both the relative and absolute gain of conspecific pollen (Figure 1). The slope of the relationship is such that across plant species in their communities heterospecific pollen is gained slower than the absolute amount of conspecific pollen but faster than the amount of conspecific pollen relative to the potential selfing.

In addition, AIC scores of the candidate model sets indicated that the species' share in the pollen pool, the functional originality, and the species relative abundance were the most important variables determining the gain in both conspecific and heterospecific pollen (Figure ??). Note that relative abundance plays a more important role determining the gain in heterospecific pollen than the gain in both the absolute and relative amounts of conspecific pollen. Surprisingly, the species degree was comparatively less important for predicting pollen gain as it was only included in models with relatively large AICc values (Table S3).

Overall we observed that species degree and abundance had a negative relationship with the gain of both absolute and relative conspecific pollen (Figure ??). Functional originality had a weak negative relationship with the absolute gain of conspecific pollen but a small positive effect on the relative gain. The plant's share in the community pollen pool, had opposite effects, with a positive relationship with the absolute gain and a negative relationship with the relative gain of conspecific pollen. Although relative abundance, degree, and the share in the pollen pool 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).

The gain in heterospecific pollen was negatively related to the species abundance but positively to the species' share in the pollen pool, functional originality, and degree (Figure ??). Compared to the models of conspecific pollen, the collinearity in the explanatory variables had a larger impact in the models of heterospecific pollen. For instance, when the species abundance was not accounted for, both the species' share in the pollen pool and its functional originality have a negative relationship with the gain in heterospecific pollen (Figure S4).

Using the results from the models of conspecific and heterospecific pollen gain we then examined the relationship between the explanatory variables and the quantity and quality of pollination (Figure 2). Degree, had a negative, albeit relatively small, effect on both the quantity and quality of pollination. The species relative abundance has a large positive effect to the quality of pollination accompanied by a relatively smaller negative impact on the quantity. Finally, the plant's functional originality and its share in the pollen pool have a moderate positive impact on its quantity but also a negative impact on the quality.

Discussion

- We did find a trade-off between the number of partners a species interacts with and the mutualistic service. Interacting with more species alone is often accompanied by a decreases in both the quantity and quality of pollination.
- However, the effect and importance of this trade-off is comparatively small when considering other factors that describe the species niche and its ecological settings.
- We found that animal pollination only brings a small amount of extra conspecific pollen (compared selfing) if any. This relatively small difference is probably very important because, first, some plants simply aren't self-fertile, even if their own pollen gets deposited on the stigma. Second, in some flowers there is temporary separation in the maturation of the sexes (dichogamy) that favours cross-pollination as, evolutionary, it has been shown to be a better strategy than cloning.
- Overall it seems like density seems to be a dominant force behind pollen transfer. If you have many individuals of your species, you get fewer visits (dilution of the pollinators flying around), which is reflected in a smaller amount of deposited pollen. We show that abundant plants also tend to comprise a greater component of the pollen source pool and so the end result is that get more conspecific pollen per visit than heterospecific pollen.
- Our result of the comparatively weak effect of the mutualistic trade-off is important because it is fundamentally related to the way we understand and mathematically represent mutualistic systems. Some of the most widely used theoretical models of pollination account for the negative effects of mutualism by adjusting the mutualistic benefit of an interaction so that it can be negatively affected by the number of mutualistic partners—the species degree. This approach, considerably simplifies the mathematical treatment of competition for pollinators. However we show that care must be taken because the negative effects of the mutualistic trade-off in both the quantity and quality of pollination can be offset by density mechanisms. Species with large degrees also tend be abundant and prolific pollen producers.

Interspecific pollen transfer is the most important factor underpinning competition for pollinators (Campbell & Motten 1985)

Traits are determined by competition for pollination – Caruso 2000

, all while accounting for the traits of the species that integrate the community. extent to which plants employ relative contribution and the interplay of each factor requires First, that plants might use different strategies to reduce competition for pollination. Second that the effect of coorelated factors in the quality

and quantity of pollination (like generalism, its relative abundance, and visitation frequency; Sargent & Otto 2006) might balance each other.

Interspecific pollen transfer was responsible for reduction in set set for one species but loss of conspecific pollen was responsible for another – Campbell and Motten 1985

Plant species vary greatly on the extent to which each of these two mechanisms can affect fertilisation (Campbell & Motten 1985), a large plant

Competition can also be mediated by pollinator density, not just plant density (Ye *et al.* 2014)

Check Flanagan *et al.* (2011) for discussion on the effects when one thinks about communities.

Traits can have a role only with High abundances, where being dominant can be bad for other plants in communities. Abundance is important in small species number systems (Muñoz & Cavieres 2008)

Plants have mechanisms that prevent heterospecific pollen deposition. Bartomeus *et al.* (2008) show that even when a plant dominates the pollen transfer network other species might not receive lots of heterospecific pollen (Bartomeus *et al.* 2008; Flanagan *et al.* 2010)

Pollen limitation is inversely related to abundance, but high abundance is also related to mate limitation (Moeller 2004)

Competition also depends on the spatial extent (Cariveau & Norton 2009)

Facilitation is still controversial? (Feldman *et al.* 2004)

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