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

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21 analyses with input from all authors; HJM collected the data; all authors
22 contributed to the study design.

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Abstract

Plant-pollinator interactions are commonly viewed as mutualistic. When plant species share pollinators, however, interspecific pollen transfer occurs and plants can compete for pollination. The extent of competition and its effects on pollination service are understood at the community level; many species interact simultaneously and multiple factors might play a role (abundance, visitation, traits) By examining comprehensive empirical data, we confirm that competition for pollination is pervasive and is only partially influenced by the number of shared pollinators. Furthermore, the factors that most influence the pollination service (abundance and visit effectiveness) also introduce a trade-off between the absolute amount of conspecific pollen received and the amount relative to heterospecific pollen. Most importantly, the ways plants balance these trade-offs depend on the community context, as most species showed flexibility in the strategy they used to cope with competition for pollination. Achieving a better understanding of plant-pollinator communities will require seeing them as comprising mutualistic and competitive interactions.

Introduction

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

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

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₇₂ There are two main mechanisms through which competition for pollinators

₇₃ can affect plant fertilization (Morales & Traveset 2008). The first is by

₇₄ changes in intraspecific pollen transfer. This happens, for example, when

₇₅ plants with ~~distinctively~~ more attractive flowers might reduce the number

₇₆ of visits to those less of attractive neighbouring plants, and hence reduce

₇₇ the amount of *conspecific pollen* deposited by animals (Yang *et al.* 2011).

₇₈ The second is ~~intraspecific~~ via interspecific pollen transfer and occurs when

₇₉ plants share pollination partners. In that case, even receiving a visit might

₈₀ not necessarily translate into fertilization (Campbell & Motten 1985) because

₈₁ a focal plant might receive *heterospecific pollen* or because pollen from the

₈₂ focal plant might be lost to different species. Generally speaking, provided

₈₃ pollen is viable and compatible (de Jong *et al.* 1992; Dafni & Firmage 2000;

₈₄ Ramsey & Vaughton 2000), the higher the ~~amount~~ quantity of conspecific

₈₅ pollen ~~(both in absolute terms and~~ and its purity (relative to heterospecific

₈₆ pollen), the better the pollination service received by the focal plant. ~~These~~

₈₇ By definition, these two mechanisms of competition ~~, by definition,~~ occur

₈₈ at the community scale. However, with few exceptions (~~Rathcke 1988;~~

₈₉ ~~Lopezaraiza-Mikel *et al.* 2007; Hegland *et al.* 2009;~~ Aizen & Rovere 2010;

₉₀ Tur *et al.* 2016), most of what we know about ~~the deposition of conspecific~~

₉₁ ~~and heterospecific pollen—and its relationship to competition vs. facilitation~~

₉₂ ~~in pollination systems—is~~ them and their relationship with key ecological

₉₃ factors is based on studies with two plant species.

₉₄ ~~At~~ That is partly so because, at the community scale, the factors that

₉₅ determine the patterns of ~~conspecific and heterospecific~~ pollen deposition

₉₆ are tightly intertwined, operate simultaneously, and may lead to emergent

₉₇ phenomena not observed at smaller scales (Flanagan *et al.* 2011). For

₉₈ instance, recent empirical evidence suggests that plants with flowering traits

₉₉ that are "original" relative to others in the community generally have fewer

₁₀₀ interaction partners (Coux *et al.* 2016). This evidence is aligned with the

notion that a species ~~which~~ 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 & 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 ~~density~~ 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 also receive more effective visits by capitalising on a larger share of both visits and the pollen 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 pollen relative to heterospecific pollen. Altogether, it is clear that ~~some~~ these ecological factors can ~~influence pollen deposition and that these factors, in the specific context of pollination, could be used to roughly define a species *realised niche* in their community. However, the intertwined nature of these factors makes it hard to determine whether they favour or hinder the pollination service~~ indeed shape pollen deposition at the community level. ~~Moreover~~However, their relative importance ~~has not yet been empirically evaluated in natural plant communities~~and how exactly they can minimise competition for pollination—or equivalently, maximise facilitation—in plant populations (across species and communities) has not been determined.

Here, we investigate the balance between competition for pollination and facilitation at the community scale using empirical data from eleven plant-pollinator communities in the Argentinian Pampas. First, we estimate the

extent to which the net outcome of plants sharing pollinators is facilitation or competition. If facilitation is the primary outcome, we could expect ~~two things. On the one hand, we could expect~~ an overall positive relationship between the amount of conspecific pollen deposited in stigmas and the amount of heterospecific pollen (Tur *et al.* 2016). The higher the deposition of conspecific pollen relative to heterospecific, the larger the slope of ~~that relationship. On the other, we could also expect a larger amount of conspecific pollen deposited in stigmas when flowers are open to animal pollinators than what is deposited due to self-pollination.~~ this relationship. Second, we investigate the relative contribution that four ecological factors have ~~on~~ to the pollination service. Specifically, we hypothesize that ~~competition, measured as the quantity~~ the quantity and purity of conspecific pollen deposition ~~and its purity (relative to heterospecific pollen), should increase~~ should decrease for plants that share many pollination partners ~~.~~ However, we also hypothesize that other factors like the plant's functional originality, its relative floral abundance, and the visit effectiveness should have the potential to compensate for this increase in competition. Third and finally, we examine how much ~~does~~ the community context influences the way plants use these factors to minimise competition~~.~~/maximise facilitation. We use these four ecological factors as a proxy of the realised pollination niche of a plant species in their community. Although some plant species might be widespread across multiple locations, competition for pollinators occurs at the community level and hence we predict ~~the competition for pollination niche to~~ that pollination niche will be influenced by the local context. If plant strategy is not flexible across ~~communities~~the communities in our study, we could expect niches to be more similar within species than across species~~in the study~~. On the contrary, if a species' strategy is flexible, we should expect plants to be able to occupy different niches in each community such that ~~competition could~~ intraspecific competition could ultimately be minimised regardless of the context.

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Methods

We collected data from eleven co-flowering plant communities and their pollinators in three locations in the Argentinian Pampas. ~~These locations are distributed across a precipitation gradient with a humid temperate climate of the eastern Flooding Pampas becoming drier as one moves inland and westward towards the Pampean Grasslands. This precipitation gradient generated a natural gradient of network architecture which allowed us to examine the generality of our findings.~~ 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.

Competition vs. facilitation

Our first objective was to identify whether the net outcome of plants sharing pollinators at the community level is facilitation or competition. ~~We use two complementary lines of evidence. The first line can be found via~~ To do that we examine the relationship between heterospecific and conspecific pollen deposited in plant stigmas (Tur *et al.* 2016). This is because heterospecific pollen can be seen as an unavoidable 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. In contrast, a positive relationship is what would be observed when facilitation is the dominant outcome.

~~The second line of evidence can be obtained by examining the difference between the amount of conspecific pollen deposited in flower stigmas *with* and *without* animal-mediated pollination. Self-pollination can be favourable to plant reproduction when competition for pollination is strong because it~~

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187 ~~provides insurance against poor pollination service (Kalisz & Vogler 2003).~~
188 ~~If competition is sufficiently strong, then the amount of conspecific pollen~~
189 ~~deposited in flower stigmas when animal pollination is prevented should be~~
190 ~~higher than when animal pollination is allowed. In contrast, the opposite~~
191 ~~pattern may indicate that plants benefit from having pollen delivered~~
192 ~~directly to the stigma by animals.~~

Data collection

194 In each of the studied communities, we quantified pollen deposition in a subset
195 of plant species between December 2010 and February 2011. This subset
196 comprised between three and nine common insect-pollinated (entomophilous)
197 plant species that were flowering during the sampling period (see Figure 1a).
198 ~~We~~ Based on data from previous years (Marrero *et al.* 2014), we chose plant
199 species such that they cover a wide range on a specialization-generalization
200 gradient as well as a wide range of abundances. In each of the selected
201 plants, we removed all flowers leaving only buds that were expected to go
202 into florescence on the next day. ~~Approximately a quarter of these buds~~
203 ~~were bagged to prevent animal pollination.~~ Two days after inflorescence, we
204 collected all remaining flowers ~~'~~ and counted the number of conspecific and
205 heterospecific pollen grains in their pistils. More details can be found in
206 Marrero *et al.* (2016).

Data analysis

208 To evaluate the relationship between heterospecific and conspecific pollen,
209 we used a generalised linear mixed model (GLMM) with a Poisson error
210 distribution (following Tur *et al.* 2016). In this model, the number of
211 conspecific pollen grains per flower was the response variable and the num-
212 ber of heterospecific grains the predictor ~~(the~~ variable (the log number of

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²¹³ stigmas sampled was added as an offset term). The slope and intercept of
²¹⁴ this relationship were allowed to differ between ~~plant species within each~~
²¹⁵ ~~community~~populations (plant species × community), which were modelled
²¹⁶ as a random effect. Models were fitted using the function `glmer` from
²¹⁷ the R package `lme4 1.1-19` (Bates *et al.* 2015). A positive slope for
²¹⁸ a ~~plant-community combination might indicate~~ plant population indicates
²¹⁹ facilitation while a negative slope ~~might indicate~~ competition (Tur *et al.*
²²⁰ 2016).

²²¹ ~~To compare the conspecific pollen deposited with and without animal-mediated~~
²²² ~~pollination, we followed the same approach as above. In this case, however,~~
²²³ ~~the predictor was the treatment (whether the flower was bagged or~~
²²⁴ ~~unbagged) instead of the number of heterospecific grains.~~

²²⁵ **Factors affecting quantity and purity of pollination service**

²²⁶ Our second objective was to investigate the relative contribution ~~of different~~
²²⁷ ~~factors that describe the plant competition~~for pollination niche ~~to the~~
²²⁸ ~~pollination service~~that different ecological factors have on the mechanisms
²²⁹ of pollinator-mediated competition. Generally speaking, ~~in the context of~~
²³⁰ ~~competition for pollination,~~ we expect that ~~a~~ any factor that increases the
²³¹ amount of conspecific pollen deposited in stigmas, both in quantity and
²³² purity relative to heterospecific pollen, also has a positive effect on the
²³³ pollination service. Specifically, we investigated the effect of (*i*) a plant's
²³⁴ number of shared pollinator species, (*ii*) a ~~plants~~ plant's abundance relative
²³⁵ to the rest of the community, (*iii*) the mean visit effectiveness—a metric
²³⁶ that combines the ~~share of pollen that a plant species is able to place on~~
²³⁷ ~~each of their~~ amount and type of pollen carried by floral visitors and the
²³⁸ number of visits it receives from them, and (*iv*) the ~~plants~~ plant's functional
²³⁹ originality (Laliberté & Legendre 2010). See *Data Analysis* section below for
²⁴⁰ more details on these four ~~variables~~factors.

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Data collection

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

Data analysis

To investigate the impact of ecological factors on pollination ~~service~~ 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

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and heterospecific pollen grains deposited per stigma in flowers open to animal-mediated pollination. We used LMMs in which pollen loads were log-transformed ~~(Figure ??)~~ because these models offered a better fit than ~~a GLMM~~ equivalent GLMMs with Poisson (or ~~quasipoisson~~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).

As fixed predictors in the models, we included the four ecological ~~variables~~ 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 ~~simply~~ aggregated floral counts for each species. We then calculated the mean visit effectiveness ~~. We define the effectiveness of a visit by~~ of pollinator species i to plant species j as

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

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

Finally, functional originality is defined as the distance of a species from the community trait average–the centroid of functional space of the community (Laliberté & Legendre 2010; Coux *et al.* 2016). To include ~~phenology~~phenological variation, we treated ~~plant~~ floral abundance in each of the survey months (November to March) as a "trait" in our analysis. To account for the non-independence of floral counts and weight all traits equally, we assigned ~~the abundances~~ a weight of 1/5 to these abundances (one for each month)~~compared to other functional 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~~ we scaled all four factors to have a zero mean and unitary variance.

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

Flexibility of plant strategies

Our last objective was to tease apart the plant strategies that might reduce competition and, importantly, how the community context influences these

strategies. If community context plays a relatively small role or the species strategy is inflexible, we would expect plants of the same species to fill similar ~~competition for~~ pollination niches across different communities. Alternatively, if the community plays a large role and ~~plants~~ /or plant strategies are flexible, we should be able to observe differences in the realised niche a plant species occupies across communities. ~~First, we~~ To test this, we first used a principal component analysis (PCA) of the four ecological ~~variables~~ factors (number of shared pollinators, floral abundance, visit effectiveness, and trait originality). We scaled ~~variables~~ factors across the whole study to ensure that the PCA space does not change according to the species present in each community. We define a species' niche in a community as its coordinates in PCA space. For each species that was present in two or more communities, we then calculated (i) the median distance between the strategies that the species uses in different communities and (ii) the area of the convex hull defined by 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.

Results

Competition vs. facilitation

We first examined the degree of facilitation/competition in natural communities. Specifically, we examined the slope of the relationship between the quantities of heterospecific and conspecific pollen deposited on stigmas of each species in a community. ~~We found that overall neither facilitation nor~~ Overall, we found that neither net facilitation nor net competition dominates (Table S1). Indeed, we found that the ~~proportion~~ proportions of

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species that experienced a statistically significant positive or negative relationship between heterospecific and conspecific pollen ~~than negative was~~ were very similar (35% and 37%, respectively; Figure 1a; Table S2). Most of the variation between plants in a facilitation-competition gradient was driven by differences *between* species; however, we also observed some important differences *within* species. For instance, six of the species sampled across multiple communities (*Carduus acanthoides*, *Cirsium vulgare*, *Cypella herbertii*, *Diplotaxis tenuifolia*, *Hirschfeldia incana*, and *Verbena intermedia*) showed evidence that the same species, can experience facilitation (positive relationships) in some communities and competition (negative relationships) in others. Interestingly, although there was ~~a~~ wide variation in the slope of the relationship between heterospecific and conspecific pollen, almost all plants had more conspecific than heterospecific pollen deposited on their stigmas (Figure ~~1b~~S1).

~~Second, we compared the amount of conspecific pollen deposited on flowers that were open to animal-mediated pollinators with that of those that were closed. Here, we again found large differences between plants but with a clear tendency to find more pollen in open flowers (Table ??). Specifically, 66% of plants had more pollen when open and 15% had less pollen when open (the difference was statistically non-significant for the remaining 19%; Figure 1c; Table ??). Variation within species was slightly smaller and only four species (C. acanthoides, C. vulgare, H. incana, and Sisyrinchium platense) had both positive and negative differences.~~

Factors affecting quantity and purity of pollination service

We then examined the potential roles played in pollen deposition by four ecological ~~variables~~ factors (number of shared pollinators, ~~plant~~ abundance, mean visit effectiveness, and functional originality)~~play in pollen deposition~~. We found that our models of pollen deposition had high explanatory power
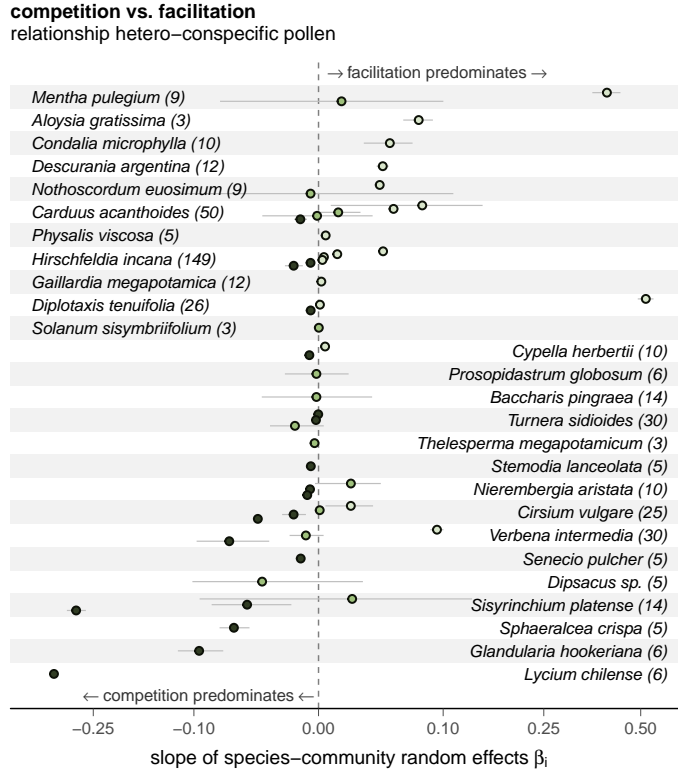
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competition vs. facilitation
relationship hetero–conspecific pollen

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

377 (the coefficient of determination R^2 ranged between 0.76 and 0.93) although a

378 large portion of the explanatory power came from the random effects (Table

379 S3). As determined by AICc, the random structure best supported by the

380 data was the one that fit an intercept for each species in each community (as

381 opposed to a common intercept for each species irrespective of the community

382 ~~they belong to~~to which they belong). This structure was best for both the

383 models of conspecific and heterospecific pollen (Table S4).

384 Of the four ~~variables,~~ factors we considered, we found that a plant's mean

385 visit effectiveness and relative floral abundance were the most important

386 ~~ecological variables~~ at predicting pollen deposition in plant stigmas (Figure

387 2a). Surprisingly, the number of shared pollinators was comparatively

388 unimportant, particularly for models of heterospecific pollen deposition, as

389 it was only ever included in models with relatively large AICc values (Table

390 S5).

391 We found that the relationship between each of the ecological factors and

392 pollen deposition was similar for both conspecific and heterospecific pollen.

393 That is, strategies that were associated with an increase in conspecific pollen

394 were also associated with an increase in heterospecific pollen deposition.

395 Specifically, the plants' mean visit effectiveness had a positive effect on

396 pollen deposition (Figure 2b). However, the effect size was slightly larger

397 for heterospecific than for conspecific pollen. This indicates that, although

398 there is a positive association between visit effectiveness and the quantity

399 of pollen deposition, there is a negative relationship with its purity (Fig-

400 ure 2c). In contrast, a plants' relative ~~abundance had a negative effect on~~

401 ~~the pollen~~ floral abundance negatively affected its deposition quantity, but

402 the mean difference between the coefficients in the models indicates a pos-

403 itive association with ~~the~~ purity (Figure 2c). The third most important

404 ~~variable~~factor, functional originality, had a positive, although comparatively

405 smaller, association with both the quantity and purity. Finally, the number

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of shared pollinators had negative and neutral associations with conspecific and heterospecific pollen, respectively, but these impacts were small when compared to the other factors. Although the ecological factors were positively correlated (Figure S2), the collinearity between predictors did not qualitatively affect our findings (Figure S3).

Flexibility of plant strategies

We used a PCA of the analysed species to investigate whether plants' realised pollination niche is similar across communities or whether they are flexible and therefore a reflection of the community context. The first two PCA components explained 75% of the total variance (Figure 3a). The first component was dominated by visit effectiveness and relative abundance while the second component was dominated by the number of shared pollinators and the plant's functional originality. When we locate the species that were sampled in more than one community in the first two PCA components (Figure 3b), we observe that the niches of any given species do not tend to be close to each other. Indeed, when we measured the median distance between the plants' coordinates, we found that it was only significantly smaller than that of randomisations for only two of the twelve species analysed (Figure 3c).
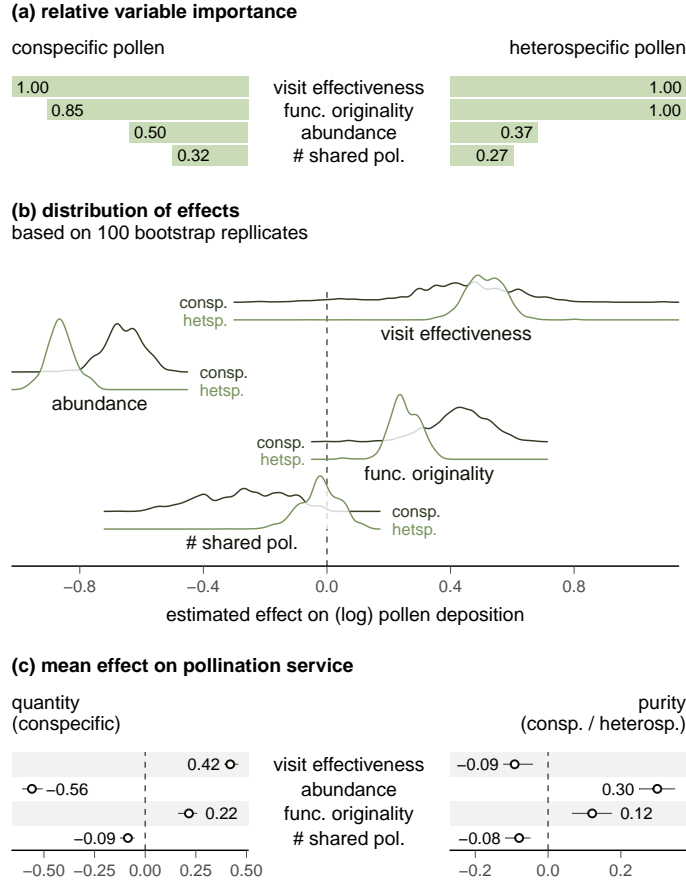
18

(a) relative variable importance

conspecific pollen   heterospecific pollen

1.00		visit effectiveness		1.00
0.85		func. originality		1.00
	0.50	abundance	0.37	
	0.32	# shared pol.	0.27	

(b) distribution of effects
based on 100 bootstrap repllicates

consp.
hetsp.
visit effectiveness

consp.
hetsp.
abundance

consp.
hetsp.
func. originality

consp.
hetsp.
shared pol.

−0.8   −0.4   0.0   0.4   0.8

estimated effect on (log) pollen deposition

(c) mean effect on pollination service

quantity   purity
(conspecific)   (consp. / heterosp.)

	0.42 visit effectiveness	−0.09	
−0.56	abundance		0.30
	0.22 func. originality	0.12	
−0.09	# shared pol.	−0.08	

−0.50 −0.25 0.00 0.25 0.50   −0.2   0.0   0.2

Figure 2: Effect of strategies to minimise competition in the pollination service. (a) The plant's visit effectiveness and relative floral abundance are the most important ~~variables~~ factors determining the deposition of conspecific and heterospecific pollen. Meanwhile, the number of shared pollinators was ~~relatively unimportant~~generally less important. The graph shows the relative ~~variable~~ importance calculated as the sum of the Akaike weights of the candidate models that included the ~~variable~~selected factor. (b) The association between ecological ~~variables~~ factors and heterospecific pollen tended to align with their association with conspecific pollen. Visit effectiveness and functional originality had a positive association with pollen deposition, while 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 ~~variables~~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).

(a) components' variance and variable contributions
principal component analysis of ecological variables

(b) plant realised niches in PCA space
convex hulls of species niches across communities

(c) flexibility of plant's strategies
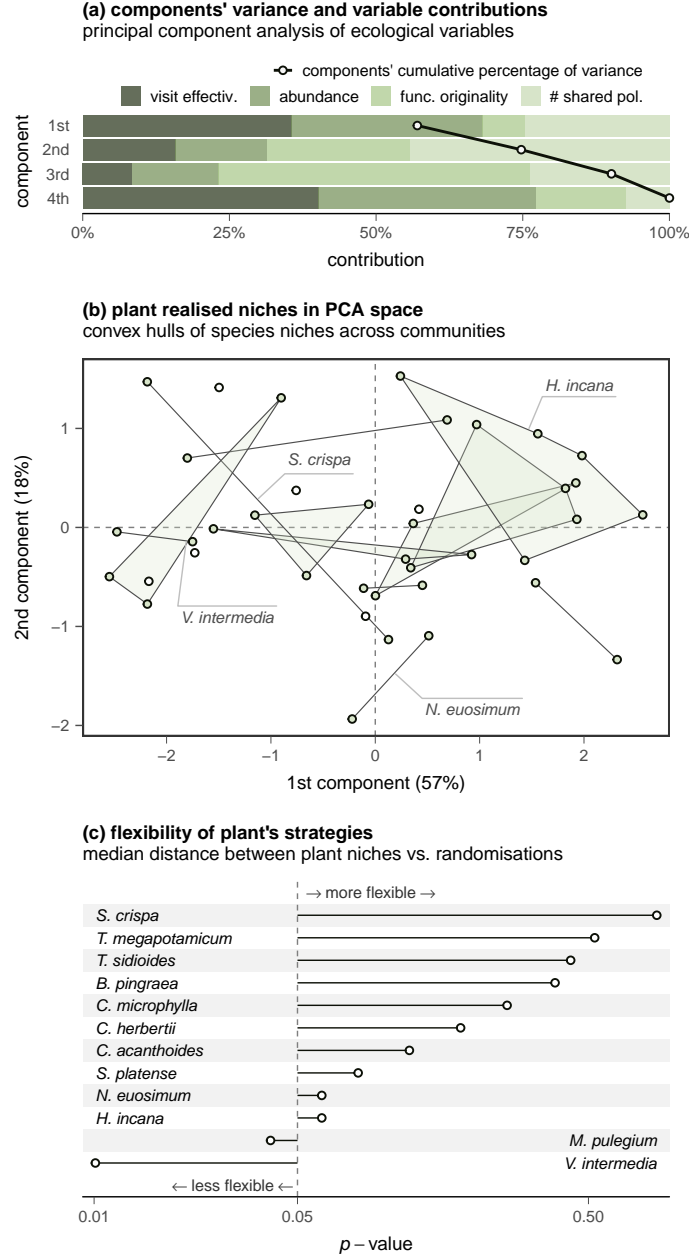median distance between plant niches vs. randomisations

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~~ in terms of these two components, we observe that their points, ~~,~~ which represent the strategy (the particular combination of ecological ~~variables~~factors) of ~~a~~ that species in ~~a~~ 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 ~~one~~ two of the examined species had strategies that were ~~more tightly connected~~ less flexible than ~~what~~ would be expected at random.

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Discussion

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

The criterion we used to identify the effect of animal-mediated pollination suggested that neither facilitation nor competition are dominant in pollination communities. A previous study showed that, in diverse pollination communities, sharing pollinators does not necessarily translate to net competition (Tur *et al.* 2016). The overall extent of facilitation/competition of pollination communities can depend on factors like the adversity of the environment (Callaway *et al.* 2002; Tur *et al.* 2016) or how disturbances affect pollinator populations (Stavert *et al.* 2017). However, why some species experience more competition than others was not understood. Although we were unable to measure the fitness outcomes, here we show that the coexistence of facilitative and competitive effects of animal-mediated pollination can be at least partially explained by trade-offs in the pollination service–both the short and the long term. These trade-offs arise when plants simultaneously maximise the deposition of conspecific pollen

and ~~simultaneously minimising~~ minimise that of heterospecific pollen~~both in the short and the long term~~.

In the short term, being a specialist and sharing no pollinators might reduce competition (Muchhala *et al.* 2010) and hence be preferable, not only due to costs to male fitness (Morales & Traveset 2008; Muchhala & Thomson 2012), but also because, as we show ~~that~~ here, sharing pollinators reduces both the quantity and purity of the conspecific pollen deposited. However, over long periods of time, there could be a risk associated with a specialist plant having ~~no pollinators . Hence, is likely that to ensure long term survival,~~ few pollinators (Ricketts 2004). To ensure long-term survival, it is thus likely that plants also need to balance this risk with the costs of sharing pollinators (Aizen *et al.* 2012). One possible solution is to share pollinators *and* have original traits—as we show that trait originality is generally beneficial to pollen deposition and it ~~'s~~ is commonly thought that species that are further from others in trait space benefit from reduced competition. Yet, there are two possible caveats to this strategy that highlight the interrelatedness of the ecological factors. First, in a mutualism 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 ~~depend on the plant 's~~ to depend on plant abundance (Coux *et al.* 2016), with generalist species being able to also have original traits only when they are abundant enough to provide a valuable reward to make ~~it worth~~ visiting worthwhile to pollinators.

Visit effectiveness (high pollen and visits) and floral abundance, which were the most important predictors of pollen deposition ~~, involved~~ here, introduced an even more explicit trade-off between gaining conspecific pollen and avoiding heterospecific pollen. ~~On the one hand, receiving~~ Receiving high visitation increases conspecific pollen deposition but increases het-

erospecific pollen deposition to a greater extent—even when the visitors are likely to carry a high proportion of conspecific pollen (Fang & Huang 2016). On the otherContrastingly, being abundant reduces the amount of heterospecific pollen deposited but this comes at the expense of a noticeable reduction in the amount of conspecific pollenconspecific pollen deposited and simultaneously reduces heterospecific pollen at a faster rate. Our results corroborate the importance that two-species studies have ascribed to visitation and abundance (Feldman *et al.* 2004; Morales & Traveset 2008; Muñoz & Cavieres 2008). But importantly,, but they also suggest that (because visitation, pollen production and abundance are usually correlated; Sargent & Otto 2006) balancing the pros and cons of sharing pollinators at the community level is not trivial and might even be partially responsible for the diversity of plant-pollinator communities (Benadi & Pauw 2018).

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

Importantly, here we show we show here that the balances between cost costs and benefits are determined not only by species identity but also on by the community plants belong toby the community to which plants belong. Specifically, most plant species appear to be flexible enough to adopt markedly different niches in different communities. Although there are many exceptions, some plant families (Asteraceae for example) are often

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generalists in their communities while others (Orchidaceae) are known to be more commonly specialised (Johnson & Steiner 2000). From an evolutionary perspective, our results suggest that that selection for a particular strategy might say something about the community in which a species has typically inhabited during its evolutionary history. Furthermore, from a more applied perspective, flowering plants are sometimes introduced to attract pollinators on other nearby plants. On the one hand, our results suggest that introduced plants that increase the relative originality of natives (e.g. through distinct phenology) might have positive effects (Gibson *et al.* 2012). On the other, because different niches can lead to different outcomes across communities, our results also highlight the difficulties involved in predicting whether the introduced plant species will facilitate or compete with neighbours (Bartomeus *et al.* 2008). Other factors that we were unable to measure (e.g. pollinator behaviour and densities or the spatial context) have also been shown to play a role in the outcome of animal-mediated pollination (Cariveau & Norton 2009; Flanagan *et al.* 2011; Ye *et al.* 2014; Thomson *et al.* 2019). Nevertheless, our results indicate that the strategies a plant might use to successfully minimise competition for pollination must be (or maximise facilitation) must be determined relative to other species in the community, rather than an absolute property of the species itself.

Overall, pollination communities might not necessarily be the paradigmatic mutualistic communities we often believe. Instead, we confirm that plant competition is pervasive in pollination communities. The potential strategies to minimise competition are likely to involve strong trade-offs in the pollination service both in the short and long-term. Most remarkably, despite large differences on in the quantity and purity of conspecific pollen deposition among species, our results provide solid evidence that competition for pollination is inherently a community process and the same species can occupy different niches in different communities. Many of the widely used

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theoretical models of plant-pollinator communities do not account for the negative effects of sharing pollinators (but see Rohr *et al.* 2014 and similar). However, achieving a better understanding of species coexistence and how plant biodiversity is supported by pollination communities will require seeing them as both mutualistic and competitive communities (Johnson & Bronstein 2019).

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