

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

*E. Fernando Cagua*¹ (*efc29@uclive.ac.nz*)

*Hugo J. Marrero*² (*hugomarrero@gmail.com*)

*Jason M. Tylianakis*¹ (*jason.tylianakis@canterbury.ac.nz*)

*Daniel B. Stouffer*¹ (*daniel.stouffer@canterbury.ac.nz*)

¹ Centre for Integrative Ecology, School of Biological Sciences, University of
Canterbury, Private Bag 4800, Christchurch 8041, New Zealand

² Centro de Recursos Naturales Renovables de las Zonas Semiáridas, CON-
ICET, Camino de la Carrindanga Km. 7, 8000 Bahía Blanca, Argentina

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Author for correspondence: E. Fernando Cagua (+64 20 4026 8153).

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23 Abstract

24 Plant-pollinator interactions are commonly viewed as mutualistic ~~interactions.~~
25 ~~When plants.~~ When plant species share pollinators, however, interspecific
26 pollen transfer occurs and plants can ~~start competing~~ compete for pollination.
27 The extent of competition for pollination and its effects ~~in the~~ on pollination
28 service are not well understood at the community level ~~where;~~ many species
29 interact simultaneously and ~~intertwined factors like~~ multiple factors that
30 might play a role (abundance, visitation, ~~and traits~~ might play a role traits)
31 are often intertwined. By examining comprehensive empirical data, we confirm
32 that competition for pollination is pervasive and is only partially influenced
33 by the number of shared pollinators. Furthermore, the factors that most
34 influence the pollination service ~~the most~~ (abundance and visit effectiveness)
35 also introduce a trade-off between the absolute amount of conspecific pollen
36 received and the amount relative to heterospecific pollen. Most importantly,
37 the ~~way~~ ways plants balance these trade-offs ~~are dependent~~ depend on the
38 community context, as most species showed flexibility ~~on their strategy in~~
39 the strategy they used to cope with competition for pollination. Achieving
40 a better understanding of ~~plant-pollination~~ plant-pollinator communities
41 will require seeing them as ~~both~~ comprising mutualistic and competitive
42 ~~communities~~ interactions.

43 Introduction

44 Animal pollination ~~systems play~~ plays a disproportionally important role
45 in food production and maintenance of global biodiversity (Bascompte &
46 Jordano 2007; Klein *et al.* 2007; Ollerton *et al.* 2011). Alongside the direct
47 benefits of mutualisms between plants and their pollinators, biodiversity
48 can be supported as a result of ~~the~~ inter-species “facilitation”—the indi-
49 rect positive feedback loops that exist between plant species that share
50 pollinators or pollinators that share plants (Moeller 2004; Ghazoul 2006;
51 Molina-Montenegro *et al.* 2008; Liao *et al.* 2011). This inter-species fa-
52 cilitation is able to promote species coexistence by offsetting the effects
53 of direct resource competition (Stachowicz 2001). Indeed, studies at the
54 core of our current theoretical knowledge of mutualisms predict that the
55 maximum number of coexisting species is achieved when the number of
56 shared mutualistic partners is maximised in a community (Bastolla *et al.*
57 2009).

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

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 (~~Ratheke 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

101 notion that a species ~~which~~that interacts with few species does so strongly
 102 with each of them whereas a species that interacts with a large number
 103 of species does so comparatively weakly (Bascompte *et al.* 2006; Vázquez
 104 *et al.* 2007; Thébault & Fontaine 2008). If evolutionary specialisation
 105 occurs by changing traits to focus on fewer but better partners (Caruso
 106 2000), we should expect a reduction of competition for pollinators in species
 107 with “original” traits and an increase of competition in species with a
 108 large number of interaction partners (Gibson *et al.* 2012; Carvalheiro *et*
 109 *al.* 2014). Alternatively, it might also be the case that ~~density~~abundance
 110 (for example in terms of flower or pollen counts) is the dominant force
 111 driving pollen transfer (Seifan *et al.* 2014). Abundant plant species might
 112 experience a dilution of available pollinators (Feinsinger 1987; Feldman *et*
 113 *al.* 2004) but might also receive more effective visits by capitalising on a
 114 larger share of both visits and the pollen carried by pollinators. In this
 115 case, a potential reduction in the absolute amount of conspecific pollen
 116 received could be compensated by an increase in the amount of conspecific
 117 pollen relative to heterospecific pollen. Altogether, it is clear that ~~some~~these
 118 ecological factors can ~~influence pollen deposition and that these factors,~~
 119 ~~in the specific context of pollination, could be used to roughly define a~~
 120 ~~species realised niche in their community. However, the intertwined nature~~
 121 ~~of these factors makes it hard to determine whether they favour or hinder~~
 122 ~~the pollination service~~indeed shape pollen deposition at the community level.
 123 ~~Moreover~~However, their relative importance ~~has not yet been empirically~~
 124 ~~evaluated in natural plant communities~~and how exactly they can minimise
 125 competition for pollination—or equivalently, maximise facilitation—in plant
 126 populations (across species and communities) has not been determined.
 127 Here, we investigate the balance between competition for pollination and
 128 facilitation at the community scale using empirical data from eleven plant-
 129 pollinator communities in the Argentinian Pampas. First, we estimate the

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

160 Methods

161 We collected data from eleven co-flowering plant communities and their
162 pollinators in three locations in the Argentinian Pampas. ~~These locations are~~
163 ~~distributed across a precipitation gradient with a humid temperate climate~~
164 ~~of the eastern Flooding Pampas becoming drier as one moves inland and~~
165 ~~westward towards the Pampean Grasslands. This precipitation gradient~~
166 ~~generated a natural gradient of network architecture which allowed us to~~
167 ~~examine the generality of our findings.~~ In each location, we sampled two
168 restored and two agricultural fragments, except in one located in the Flooding
169 Pampas, where we were only able to sample one restored fragment due to
170 the lack of available sites.

171 Competition vs. facilitation

172 Our first objective was to identify whether the net outcome of plants sharing
173 pollinators at the community level is facilitation or competition. ~~We use two~~
174 ~~complementary lines of evidence. The first line can be found via~~ To do that
175 we examine the relationship between heterospecific and conspecific pollen
176 deposited in plant stigmas (Tur *et al.* 2016). This is because heterospecific
177 pollen can be seen as an unavoidable cost that plants must pay for receiving
178 conspecific pollen from shared pollinators. A negative relationship (when
179 shared pollinators increase heterospecific pollen loads and decrease conspecific
180 loads) may indicate that competition for pollination is strong. In contrast,
181 a positive relationship is what would be observed when facilitation is the
182 dominant outcome.

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

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.~~

193 **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 ²and counted the number of conspecific and
205 heterospecific pollen grains in their pistils. More details can be found in
206 Marrero *et al.* (2016).

207 **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

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

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

Factors affecting quantity and purity of pollination service

Our second objective was to investigate the relative contribution ~~of different~~
~~factors—that describe the plant competition for pollination niche—to the~~
~~pollination service~~that different ecological factors have on the mechanisms
of pollinator-mediated competition. Generally speaking, ~~in the context of~~
~~competition for pollination,~~ we expect that ~~a~~any factor that increases the
 amount of conspecific pollen deposited in stigmas, both in quantity and
 purity relative to heterospecific pollen, also has a positive effect on the
 pollination service. Specifically, we investigated the effect of (i) a plant's
 number of shared pollinator species, (ii) a ~~plants~~plant's abundance relative
 to the rest of the community, (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~~amount and type of pollen carried by floral visitors and the
 number of visits it receives from them, and (iv) the ~~plants~~plant's functional
 originality (Laliberté & Legendre 2010). See *Data Analysis* section below for
 more details on these four ~~variables~~factors.

241 Data collection

242 To obtain the number of shared pollinators for each species, we collected data
243 to construct qualitative and quantitative pollination networks. Qualitative
244 networks were constructed based on two-hour observations of floral visits
245 in each fragment. Quantitative networks were constructed using two 50 m
246 randomly located transects in each fragment. We counted and collected all
247 floral visitors found in a 2 m wide strip while walking at a pace of 10 m
248 per minute (Memmott 1999; Marrero *et al.* 2014). We visited the transects
249 each month between November 2010 and March 2011. To obtain ~~plant~~
250 floral abundance, we counted all units of floral attraction found during an
251 independent sampling of the same transects used to construct the quantitative
252 visitation networks. To estimate visit effectiveness, we need to construct
253 pollen transfer networks in addition to the visitation networks. To do this,
254 we examined the pollen loads present on the floral visitors collected (Marrero
255 *et al.* 2017). When the pollen count on an individual animal was estimated
256 to be less than 2,000 grains, we identified every grain to the species level
257 when possible and to pollen complexes when it was not. When the pollen
258 count was above 2,000 grains, we classified ~~approx.~~ approximately 50% of
259 pollen and total pollen counts were extrapolated (Bosch *et al.* 2009). Finally,
260 we also recorded morphological traits that relate to plant type (herb, shrub,
261 climber), life cycle (annual, perennial), flower colouration, phenology, and
262 whether the species is native in the study region. More details can be found
263 in Marrero *et al.* (2014 and 2017).

264 Data analysis

265 To investigate the impact of ecological factors on pollination ~~service~~ services,
266 we used two sets of linear mixed models (LMM) with bootstrap resampling.
267 The response variables for these model sets were the number of conspecific

268 and heterospecific pollen grains deposited per stigma in flowers open to
 269 animal-mediated pollination. We used LMMs in which pollen loads were
 270 log-transformed (~~Figure ??~~) because these models offered a better fit than
 271 ~~a GLMM equivalent GLMMs~~ with Poisson (or ~~quasipoisson~~ quasi-Poisson)
 272 error structure. Models were fitted using the R package `nlme` 3.1-131
 273 (Pinheiro *et al.* 2018).

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

280 As fixed predictors in the models, we included the four ecological ~~variables~~
 281 factors described above. Specifically, we calculated the number of shared
 282 pollinators for each plant species by pooling data from the qualitative and
 283 quantitative pollination networks. To calculate the plants' relative floral
 284 abundance in their community, we ~~simply~~ aggregated floral counts for each
 285 species. We then calculated the mean visit effectiveness ~~—We define the~~
 286 ~~effectiveness of a visit by of~~ pollinator species i to plant species j as

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

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

294 Finally, functional originality is defined as the distance of a species from
 295 the community trait average—the centroid of functional space of the
 296 community (Laliberté & Legendre 2010; Coux *et al.* 2016). To include
 297 ~~phenology~~phenological variation, we treated ~~plant~~floral abundance in each
 298 of the survey months (November to March) as a “trait” in our analysis.
 299 To account for the non-independence of floral counts and weight all traits
 300 equally, we assigned ~~the abundances~~ a weight of 1/5 to these abundances
 301 (one for each month)~~compared to other functional traits~~. We scaled all
 302 traits prior to calculating the centroid of the functional space and calculated
 303 the species-specific functional coordinates using the R package FD 1.0-12
 304 (Laliberté *et al.* 2014). Finally, ~~to facilitate comparison across the four~~
 305 ~~continuous explanatory variables in our models, we rescaled them all~~we
 306 scaled all four factors to have a zero mean and unitary variance.

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

319 **Flexibility of plant strategies**

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

322 strategies. If community context plays a relatively small role or the species
 323 strategy is inflexible, we would expect plants of the same species to fill similar
 324 ~~competition for~~ pollination niches across different communities. Alternatively,
 325 if the community plays a large role and ~~plants-/or plant~~ strategies are flexible,
 326 we should be able to observe differences in the realised niche a plant species
 327 occupies across communities. ~~First, we~~ To test this, we first used a principal
 328 component analysis (PCA) of the four ecological ~~variables~~ factors (number of
 329 shared pollinators, floral abundance, visit effectiveness, and trait originality).
 330 We scaled ~~variables~~ factors across the whole study to ensure that the PCA
 331 space does not change according to the species present in each community.
 332 We define a species' niche in a community as its coordinates in PCA space.
 333 For each species that was present in two or more communities, we then
 334 calculated (*i*) the median distance between the strategies that the species
 335 uses in different communities and (*ii*) the area of the convex hull defined by
 336 these points in the first two principal components (only for species present in
 337 three or more communities). We then compared the magnitude of these two
 338 metrics to those obtained with 99 Monte Carlo randomizations in which we
 339 replaced the strategy of the focal plant species by that of another randomly
 340 selected species in the dataset.

341 Results

342 Competition vs. facilitation

343 We first examined the degree of facilitation/competition in natural com-
 344 munities. Specifically, we examined the slope of the relationship between
 345 the quantities of heterospecific and conspecific pollen deposited on stigmas
 346 of each species in a community. ~~We found that overall neither facilitation~~
 347 ~~nor~~ Overall, we found that neither net facilitation nor net competition dom-
 348 inates (Table S1). Indeed, we found that the ~~proportion~~ proportions of

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

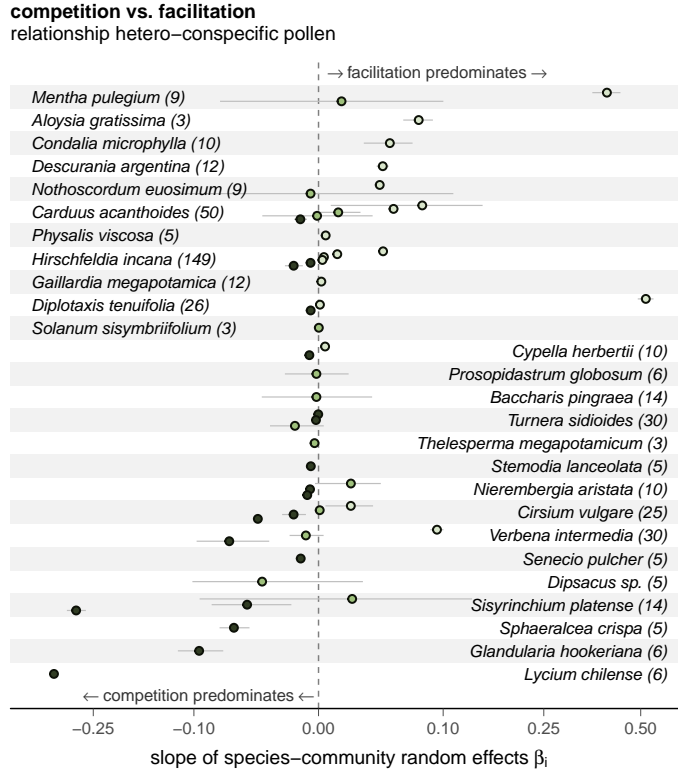


Figure 1: Competition vs. facilitation at the community level. (a) According to the first criterion we used, some species experience more competition for pollination than others. Points indicate the estimated slopes for the relationship between the amount of heterospecific and conspecific pollen deposited 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 \pm 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

406 of shared pollinators had ~~a~~ negative and neutral ~~association~~ associations
407 with conspecific and heterospecific pollen, respectively, but these impacts
408 were small when compared to the other ~~variables~~.

409 ~~Overall, collinearity did not affect our findings qualitatively. Although~~
410 ~~relative abundance, the number of shared pollinators, and the visit~~
411 ~~effectiveness were all factors. Although the ecological factors were~~ positively
412 correlated (Figure S2), the ~~effect each had on conspecific pollen was similar~~
413 ~~among models that included all or just some of these three explanatory~~
414 ~~variables~~ collinearity between predictors did not qualitatively affect our
415 findings (Figure S3). ~~One exception was visit effectiveness, which exhibits~~
416 ~~a positive association with the relative amount of conspecific pollen under~~
417 ~~some variable combinations. Nevertheless, these differences were observed~~
418 ~~only in model specifications with relatively low AICc support.~~

419 Flexibility of plant strategies

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

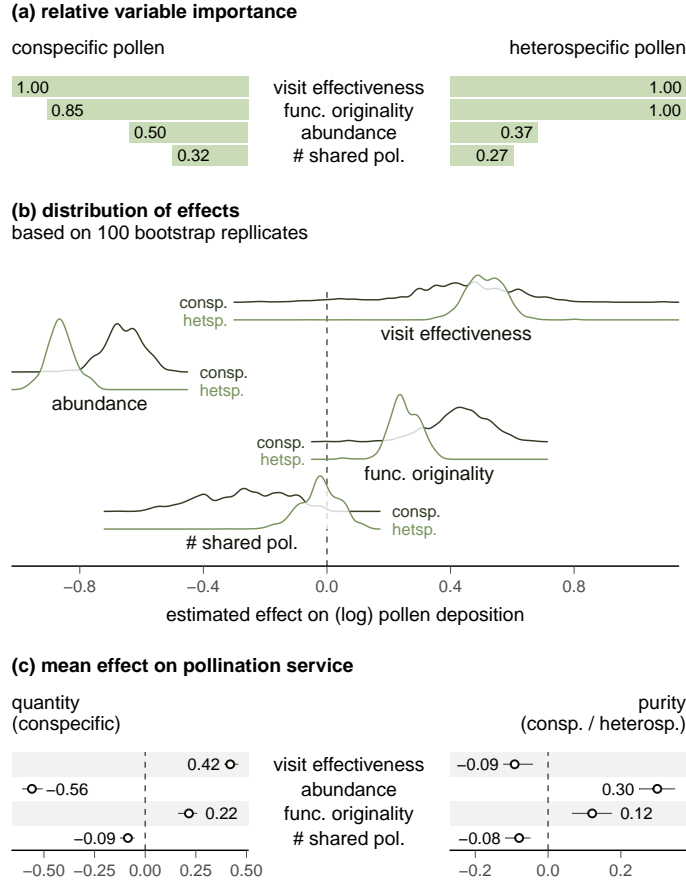


Figure 2: Effect of strategies to minimise competition in the pollination service. (a) The plant's visit effectiveness and relative floral abundance are the most important ~~variables~~ factors determining the deposition of conspecific and heterospecific pollen. Meanwhile, the number of shared pollinators 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).

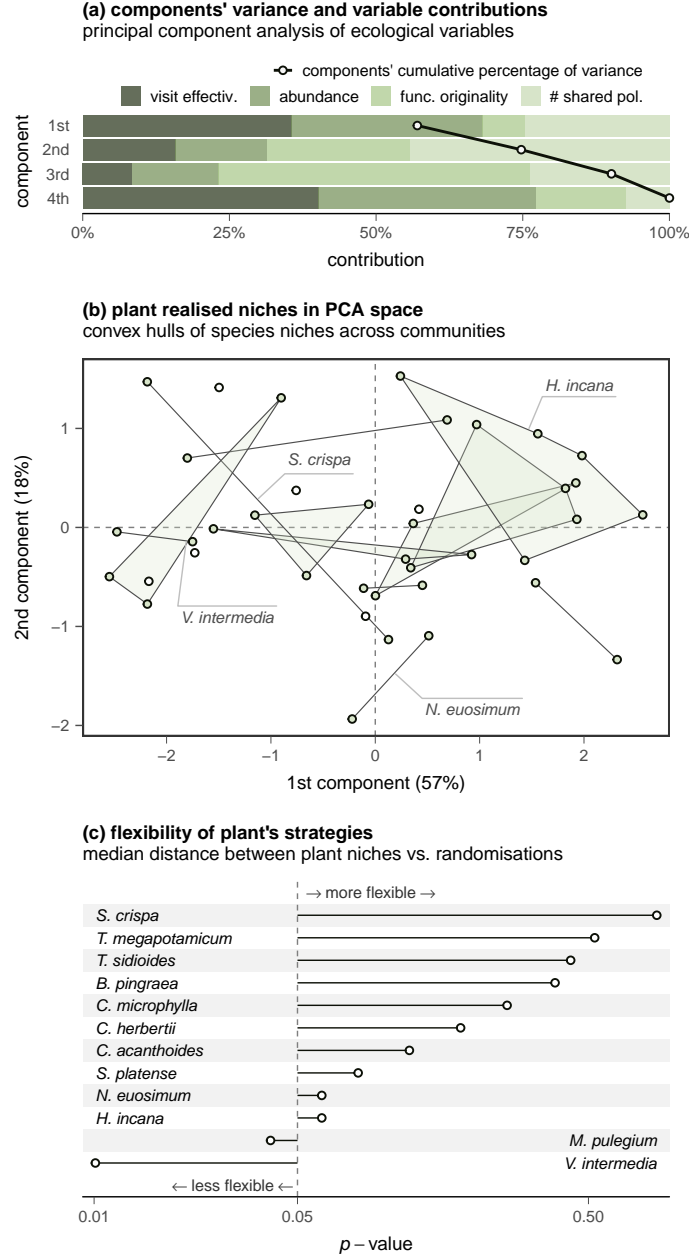


Figure 3: The flexibility of plant strategies. (a) The two first components explain a large proportion of the total variance. (b) When plants that were sampled in more than one community are plotted with-in terms of these two components, we observe that their points, — which represent the strategy (the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

433 Discussion

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

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

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

464 In the short term, being a specialist and sharing no pollinators might reduce
465 competition (Muchhala *et al.* 2010) and hence be preferable, not only due to
466 costs to male fitness (Morales & Traveset 2008; Muchhala & Thomson 2012),
467 but also because, as we show ~~that here,~~ sharing pollinators reduces both
468 the quantity and purity of the conspecific pollen deposited. However, over
469 long periods of time, there could be a risk associated with a specialist plant
470 having ~~no pollinators. Hence, is likely that to ensure long term survival, few~~
471 pollinators (Ricketts 2004). To ensure long-term survival, it is thus likely
472 that plants also need to balance this risk with the costs of sharing pollinators
473 (Aizen *et al.* 2012). One possible solution is to share pollinators *and* have
474 original traits—as we show that trait originality is generally beneficial to
475 pollen deposition and it ~~'s~~ is commonly thought that species that are further
476 from others in trait space benefit from reduced competition. Yet, there are
477 two possible caveats to this strategy that highlight the interrelatedness of
478 the ecological factors. First, in a mutualism context, it is also possible that
479 trait originality could come at the cost of being less ‘apparent’ to pollinators
480 (Reverté *et al.* 2016). Second, the negative ~~;~~ relationship between originality
481 and generalism (Carvalho *et al.* 2014) has been shown ~~depend on the~~
482 ~~plant's~~ to depend on plant abundance (Coux *et al.* 2016), with generalist
483 species being able to also have original traits only when they are abundant
484 enough to provide a valuable reward to make ~~it worth~~ visiting worthwhile
485 to pollinators.

486 Visit effectiveness (high pollen and visits) and floral abundance, which
487 were the most important predictors of pollen deposition ~~;~~ involved here,
488 introduced an even more explicit trade-off between gaining conspecific pollen
489 and avoiding heterospecific pollen. ~~On the one hand, receiving~~ Receiving
490 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 other~~Contrastingly, being abundant reduces the amount of
~~heterospecific pollen deposited but this comes at the expense of a noticeable~~
~~reduction in the amount of conspecific pollen~~conspecific pollen deposited
~~and simultaneously reduces heterospecific pollen at a faster rate.~~ Our re-
sults 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 others~~species~~,
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~~
~~the community plants belong to~~by 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~~

~~generalists in their communities while others (Orchidaceae) are known to~~
~~be more commonly specialised (Johnson & Steiner 2000).~~ From an evolu-
 tionary 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 polli-
 nation service both in the short and long-term. Most remarkably, despite
 large differences ~~on~~ in the quantity and purity of conspecific pollen depo-
 sition among species, our results provide solid evidence that competition
 for pollination is inherently a community process and the same species can
 occupy different niches in different communities. Many of the widely used

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

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