

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

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Running title: The pollination trade-off

Keywords: Competition, facilitation, interspecific pollen transfer, conspe-
cific, pollen deposition, multi-species, plant-pollinator interaction, pollination
trade-off, pollination costs, networks (up to 10).

Type of article: Letter.

Number of words: 154 in abstract; 4,999 in main text.

Number of displays: 3 figures; 0 tables; 0 text boxes.

Number of references: 39

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Data accessibility: Data supporting the results will be accessible in an
appropriate data repository after publication. The data DOI will be included
here.

Author contributions: EFC wrote the manuscript and performed all
analyses with input from all authors; HJM collected the data; all authors
contributed to the study design.

20 Abstract

21 Plant-pollinator interactions are commonly viewed as mutualistic interac-
22 tions. When plants share pollinators, however, interspecific pollen transfer
23 occurs and plants can start competing. The extent of competition for polli-
24 nation and its effects in the pollination service are not well understood at
25 the community level where species interact simultaneously and intertwined
26 factors like abundance, visitation, and traits might play a role. By examining
27 comprehensive empirical data, we confirm that competition for pollination is
28 pervasive. Furthermore, the factors that influence the pollination service the
29 most (abundance and visit effectiveness) also introduce a trade-off between
30 the absolute amount of conspecific pollen and the amount relative to het-
31 erospecific pollen. Most importantly, the way plants balance these trade-offs
32 are dependent on the community context as most species showed flexibility
33 on their strategy used to cope with competition for pollination. Achieving
34 a better understanding of plant-pollination communities will require seeing
35 them as both mutualistic and competitive communities.

36 Introduction

37 Animal pollination systems play a disproportionally important role in food
38 production and maintenance of global biodiversity (Bascompte & Jordano
39 2007; Klein *et al.* 2007; Ollerton *et al.* 2011). Alongside the direct mutualisms
40 between plants and their pollinators, biodiversity can be supported as a result
41 of the inter-species “facilitation”—the indirect positive feedback loops that
42 exist between plant species that share pollinators or pollinators that share
43 plants (Moeller 2004; Ghazoul 2006; Molina-Montenegro *et al.* 2008; Liao *et*
44 *al.* 2011). This inter-species facilitation is able to promote species coexistence
45 by offsetting the effects of direct resource competition (Stachowicz 2001).
46 Indeed, studies at the core of our current theoretical knowledge of mutualisms
47 predict that the maximum number of coexisting species is achieved when
48 the number of shared mutualistic partners is maximised in a community
49 (Bastolla *et al.* 2009).

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

63 There are two main mechanisms through which competition for pollinators

64 can affect plant fertilization (Morales & Traveset 2008). The first is in-
65 traspecific pollen transfer. This happens, for example, when plants with
66 distinctively attractive flowers might reduce the number of visits to those less
67 attractive neighbouring plants, and hence reduce the amount of *conspecific*
68 *pollen* deposited by animals (Yang *et al.* 2011). The second is intraspecific
69 pollen transfer and occurs when plants share pollination partners. In that
70 case, even receiving a visit might not necessarily translate into fertilization
71 (Campbell & Motten 1985) because a focal plant might receive *heterospecific*
72 *pollen* or because pollen from the focal plant might be lost to different species.
73 Generally speaking, the higher the amount of conspecific pollen (both in
74 absolute terms and relative to heterospecific pollen) the better the pollination
75 service received by the focal plant. These two mechanisms of competition,
76 by definition, occur at the community scale. However, with few exceptions
77 (Rathcke 1988; Lopezaraiza-Mikel *et al.* 2007; Hegland *et al.* 2009; Aizen &
78 Rovere 2010; Tur *et al.* 2016), most of what we know about the deposition
79 of conspecific and heterospecific pollen—and its relationship to competition
80 vs. facilitation in pollination systems—is based on studies with two plant
81 species.

82 At the community scale, the factors that determine the patterns of conspecific
83 and heterospecific pollen deposition are tightly intertwined, operate simulta-
84 neously, and may lead to emergent phenomena not observed at smaller scales
85 (Flanagan *et al.* 2011). For instance, recent empirical evidence suggests
86 that plants with flowering traits that are “original” relative to others in the
87 community generally have fewer interaction partners (Coux *et al.* 2016). This
88 evidence is aligned with the notion that a species which interacts with few
89 species does so strongly with each of them whereas a species that interacts
90 with a large number of species does so comparatively weakly. If evolutionary
91 specialisation occurs by changing traits to focus on fewer but better partners
92 (Caruso 2000), we should expect a reduction of competition for pollinators in

93 species with “original” traits and an increase of competition in species with
94 a large number of interaction partners (Gibson *et al.* 2012; Carvalheiro *et al.*
95 2014). Alternatively, it might also be the case that density (for example in
96 terms of flower or pollen counts) is the dominant force driving pollen transfer
97 (Seifan *et al.* 2014). Abundant plant species might experience a dilution of
98 available pollinators (Feinsinger 1987) but might also receive more effective
99 visits by capitalising on a larger share of both visits and the pollen carried
100 by pollinators. In this case, a potential reduction in the absolute amount
101 of conspecific pollen received could be compensated by an increase in the
102 amount of conspecific pollen relative to heterospecific pollen. Altogether,
103 it is clear that some ecological factors can influence pollen deposition and
104 that these factors, in the specific context of pollination, could be used to
105 roughly define a species *realised niche* in their community. However, the
106 intertwined nature of these factors makes it hard to determine whether they
107 favour or hinder the pollination service at the community level. Moreover,
108 their relative importance has not yet been empirically evaluated in natural
109 plant communities.

110 Here, we investigate competition for pollination at the community scale using
111 empirical data from eleven plant-pollinator communities in the Argentinian
112 Pampas. First, we estimate the extent to which the net outcome of plants
113 sharing pollinators is facilitation or competition. If facilitation is the primary
114 outcome, we could expect two things. On the one hand, we could expect
115 an overall positive relationship between the amount of conspecific pollen
116 deposited in stigmas and the amount of heterospecific pollen (Tur *et al.* 2016).
117 The higher the deposition of conspecific pollen relative to heterospecific, the
118 larger the slope of that relationship. On the other, we could also expect a
119 larger amount of conspecific pollen deposited in stigmas when flowers are open
120 to animal pollinators than what is deposited due to self-pollination. Second,
121 we investigate the relative contribution that four ecological factors have

on the pollination service. Specifically, we hypothesize that competition, measured as the quantity of conspecific pollen deposition and its purity (relative to heterospecific pollen), should increase for plants that share many pollination partners. However, we also hypothesize that other factors like the plant's functional originality, its relative 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. 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 be influenced by the local context. If plant strategy is not flexible across communities, 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 be minimised regardless of the context.

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 the Flooding Pampas, where we were only able to sample one restored fragment due to the lack of available sites.

149 **Competition vs. facilitation**

150 Our first objective was to identify whether the outcome of plants sharing
151 pollinators at the community level is facilitation or competition. We use two
152 complementary lines of evidence.

153 The first line can be found via the relationship between heterospecific and
154 conspecific pollen deposited in plant stigmas (Tur *et al.* 2016). This is
155 because heterospecific pollen can be seen as an unavoidable cost that plants
156 must pay for receiving conspecific pollen from shared pollinators. A negative
157 relationship (when shared pollinators increase heterospecific pollen loads and
158 decrease conspecific loads) may indicate that competition for pollination is
159 strong. In contrast, a positive relationship is what would be observed when
160 facilitation is the dominant outcome.

161 The second line of evidence can be obtained by examining the difference
162 between the amount of conspecific pollen deposited in flower stigmas *with*
163 and *without* animal-mediated pollination. Self-pollination can be favourable
164 to plant reproduction when competition for pollination is strong because it
165 provides insurance against poor pollination service (Kalisz & Vogler 2003).
166 If competition is sufficiently strong, then the amount of conspecific pollen
167 deposited in flower stigmas when animal pollination is prevented should be
168 higher than when animal pollination is allowed. In contrast, the opposite
169 pattern may indicate that plants benefit from having pollen delivered directly
170 to the stigma by animals.

171 **Data collection**

172 In each of the studied communities, we quantified pollen deposition in a subset
173 of plant species between December 2010 and February 2011. This subset
174 comprised between three and nine common insect-pollinated (entomophilous)
175 plant species that were flowering during the sampling period (see Figure 1a).

176 We chose plant species such that they cover a wide range on a specialization-
177 generalization gradient as well as a wide range of abundances. In each of the
178 selected plants, we removed all flowers leaving only buds that were expected
179 to go into florescence on the next day. Approximately a quarter of these buds
180 were bagged to prevent animal pollination. Two days after inflorescence, we
181 collected all remaining flowers' and counted the number of conspecific and
182 heterospecific pollen grains in their pistils. More details can be found in
183 Marrero *et al.* (2016).

184 **Data analysis**

185 To evaluate the relationship between heterospecific and conspecific pollen,
186 we used a generalised linear mixed model (GLMM) with a Poisson error
187 distribution (Tur *et al.* 2016). In this model, the number of conspecific pollen
188 grains per flower was the response variable and the number of heterospecific
189 grains the predictor (the number of stigmas sampled was added as an offset
190 term). The slope and intercept of this relationship were allowed to differ
191 between plant species within each community, which were modelled as a
192 random effect. Models were fitted using the function `glmer` from the R
193 package `lme4` 1.1-19 (Bates *et al.* 2015). A positive slope for a plant-
194 community combination might indicate facilitation while a negative slope
195 might indicate competition (Tur *et al.* 2016).

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

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

201 Our second objective was to investigate the relative contribution of different
202 factors—that describe the plant competition for pollination niche—to the
203 pollination service. Generally speaking, in the context of competition for
204 pollination, we expect that a factor that increases the amount of conspecific
205 pollen deposited in stigmas, both in quantity and purity relative to heterospe-
206 cific pollen, also has a positive effect on the pollination service. Specifically,
207 we investigated the effect of (*i*) a plant’s number of shared pollinator species,
208 (*ii*) a plants abundance relative to the rest of the community, (*iii*) the mean
209 visit effectiveness—a metric that combines the share of pollen that a plant
210 species is able to place on each of their floral visitors and the number of visits
211 it receives from them, and (*iv*) the plants functional originality (Laliberté &
212 Legendre 2010). See *Data Analysis* section below for more details on these
213 four variables.

214 **Data collection**

215 To obtain the number of shared pollinators for each species, we collected data
216 to construct qualitative and quantitative pollination networks. Qualitative
217 networks were constructed based on two-hour observations of floral visits
218 in each fragment. Quantitative networks were constructed using two 50 m
219 randomly located transects in each fragment. We counted and collected all
220 floral visitors found in a 2 m wide strip while walking at a pace of 10 m per
221 minute (Memmott 1999; Marrero *et al.* 2014). We visited the transects each
222 month between November 2010 and March 2011. To obtain plant abundance,
223 we counted all units of floral attraction found during an independent sampling
224 of the transects used to construct the quantitative visitation networks. To
225 estimate visit effectiveness we need to construct pollen transfer networks
226 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. 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 we used two sets of linear mixed models (LMM) with bootstrap resampling. The response variables for these model sets were the number of conspecific and heterospecific pollen grains deposited per stigma in flowers open to animal-mediated pollination. We used LMMs in which pollen loads were log-transformed (Figure ??) because these models offered a better fit than a GLMM with Poisson (or quasipoisson) 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 predictors in the models, we included the four ecological variables 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 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 pollinator species i to plant species j as

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

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 the number
of shared pollinators, floral abundance, visitation, and pollen production
roughly followed a power-law distribution, we log-transformed these three
predictors 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, we
treated plant 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 (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 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

280 using the AICc and determined the likelihood of each candidate model (a
281 particular combination of predicting variables) by calculating the median
282 ΔAICc (relative to the most likely model) for each bootstrap sample. As
283 we wanted model coefficients from more likely candidate models to carry
284 more weight in our results, we sampled the coefficients for our variables
285 proportional to the likelihood of its candidate model. Finally, we used these
286 distributions of the model coefficients to estimate their mean impact on the
287 pollination service (in terms of quantity and purity of conspecific pollen
288 deposition).

289 **Flexibility of plant strategies**

290 Our last objective was to tease apart the plant strategies that might reduce
291 competition and, importantly, how the community context influences these
292 strategies. If community context plays a relatively small role or the species
293 strategy is inflexible we would expect plants of the same species to fill similar
294 competition for pollination niches across different communities. Alternatively,
295 if the community plays a large role and plants strategies are flexible, we
296 should be able to observe differences in the realised niche a plant species
297 occupies across communities. First, we used a principal component analysis
298 (PCA) of the four ecological variables. We scaled variables across the whole
299 study to ensure that the PCA space does not change according to the species
300 present in each community. We define a species' niche in a community as
301 its coordinates in PCA space. For each species that was present in two or
302 more communities, we then calculated (*i*) the median distance between the
303 strategies that the species uses in different communities and (*ii*) the area of
304 the convex hull defined by these points in the first two principal components
305 (only for species present in three or more communities). We then compared
306 the magnitude of these two metrics to those obtained with 99 Monte Carlo
307 randomizations in which we replaced the strategy of the focal plant species

308 by that of another randomly selected species in the dataset.

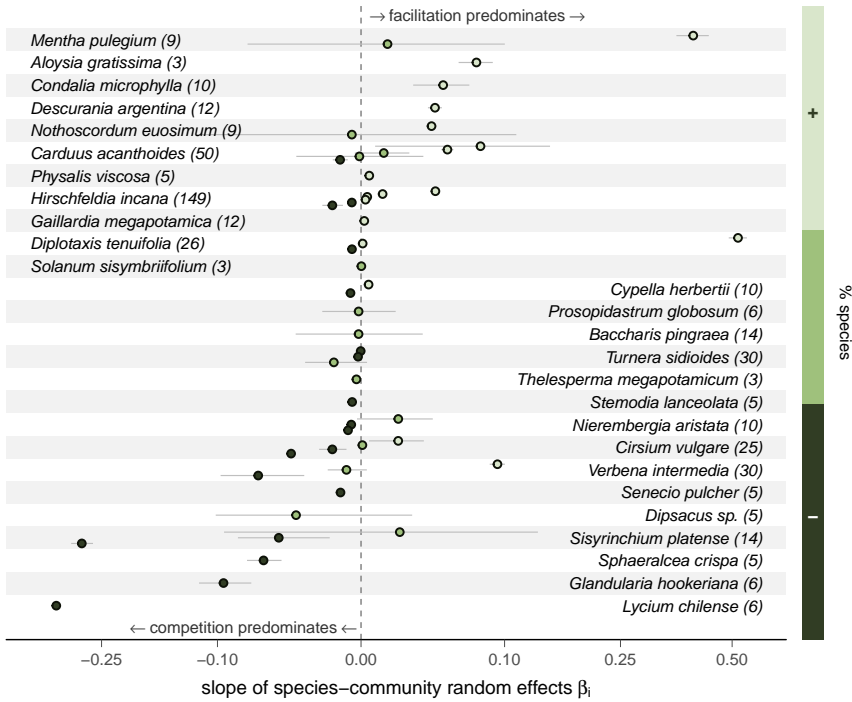
309 Results

310 Competition vs. facilitation

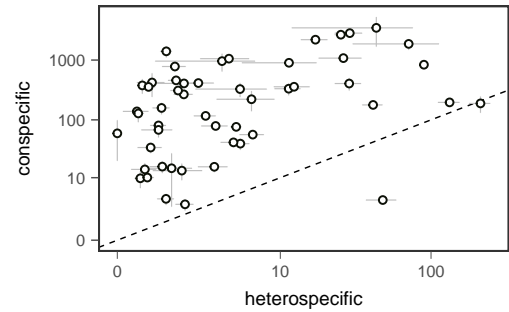
311 We first examined the degree of facilitation/competition in natural commu-
312 nities. Specifically, we examined the slope of the relationship between the
313 heterospecific and conspecific pollen deposited on stigmas of each species
314 in a community. We found that overall neither facilitation nor competition
315 dominates (Table S1). Indeed, we found that the proportion of species
316 that experienced a statistically significant positive or negative relationship
317 between heterospecific and conspecific pollen than negative was very similar
318 (35% and 37%, respectively; Figure 1a; Table S2). Most of the variation be-
319 tween plants in a facilitation-competition gradient was driven by differences
320 *between* species; however, we also observed some important differences *within*
321 species. For instance, six of the species sampled across multiple communities
322 (*Carduus acanthoides*, *Cirsium vulgare*, *Cypella herbertii*, *Diploaxis tenuifo-*
323 *lia*, *Hirschfeldia incana*, and *Verbena intermedia*) showed evidence that the
324 same species, can experience facilitation (positive relationships) in some com-
325 munities and competition (negative relationships) in others. Interestingly,
326 although there was a wide variation in the slope of the relationship between
327 heterospecific and conspecific pollen almost all plants had more conspecific
328 than heterospecific pollen deposited on their stigmas (Figure 1b).

329 Second, we compared the amount of conspecific pollen deposited on flowers
330 that were open to animal-mediated pollinators with that of those that were
331 closed. Here, we again found large differences between plants but with a clear
332 tendency to find more pollen in open flowers (Table S3). Specifically, 66%
333 of plants had more pollen when open and 15% had less pollen when open
334 (the difference was statistically non-significant for the remaining 19%; Figure

(a) competition vs. facilitation – criterion #1
relationship hetero–conspecific pollen



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



(c) competition vs. facilitation – criterion #2
self– vs. animal–mediated pollination

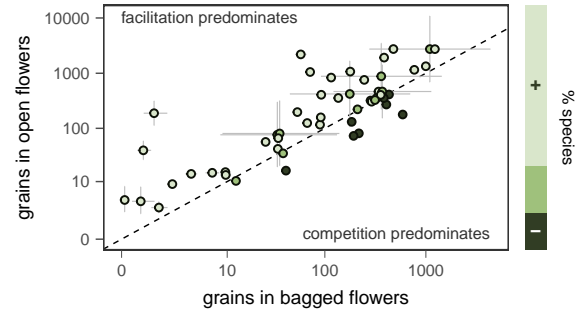


Figure 1: Competition vs. facilitation at the community level. (a) According to the first criterion we used, some species experience more competition for pollination than others. Points indicate the estimated slopes for the relationship between the amount of heterospecific and conspecific pollen deposited per stigma across species in their communities. Statistically significant negative slopes (darkest shade) indicate that plants experience competition for animal-mediated pollination, while significantly positive slopes (lightest shade) indicate that facilitation is the predominant outcome. The number of plants analysed for each species is shown within brackets next to the species name. (b) Despite the variety of slopes, overall plants had more conspecific than heterospecific pollen deposited in their stigmas. (c) 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 bars correspond to \pm the standard error (SE).

335 1c; Table S4). Variation within species was slightly smaller and only four
336 species (*C. acanthoides*, *C. vulgare*, *H. incana*, and *Sisyrinchium platense*)
337 had both positive and negative differences.

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

339 We then examined the potential roles played by four ecological variables
340 (number of shared pollinators, plant abundance, mean visit effectiveness,
341 and functional originality) play in pollen deposition. We found that our
342 models of pollen deposition had high explanatory power (the coefficient of
343 determination R^2 ranged between 0.76 and 0.93) although a large portion
344 of the explanatory power came from the random effects (Table S5). As
345 determined by AICc, the random structure best supported by the data was
346 the one that fit an intercept for each species in each community (as opposed
347 to a common intercept for each species irrespective of the community they
348 belong to). This structure was best for both the models of conspecific and
349 heterospecific pollen (Table S6).

350 Of the four variables, we considered, we found that a plant's mean visit
351 effectiveness and abundance were the most important ecological variables
352 predicting pollen deposition in plant stigmas (Figure 2a). Surprisingly, the
353 number of shared pollinators was comparatively unimportant, particularly
354 for models of heterospecific pollen deposition, as it was only ever included in
355 models with relatively large AICc values (Table S7).

356 We found that the relationship between each of the ecological factors and
357 pollen deposition was similar for both conspecific and heterospecific pollen.
358 That is, strategies that were associated with an increase in conspecific pollen
359 were also associated with an increase in heterospecific pollen deposition.
360 Specifically, the plants' mean visit effectiveness had a positive effect on
361 pollen deposition (Figure 2b). However, the effect size was slightly larger

for heterospecific than for conspecific pollen. This indicates that, although there is a positive association between visit effectiveness and the quantity pollen deposition, there is a negative relationship with its purity (Figure 2c). In contrast, a plants' relative abundance had a negative effect on the pollen deposition quantity, but the mean difference between the coefficients in the models indicates a positive association with the purity (Figure 2c). The third most important variable, functional originality, had a positive, although comparatively smaller, association with both the quantity and purity. Finally, the number of shared pollinators had a negative and neutral association with conspecific and heterospecific pollen, but these impacts were small when compared to the other variables.

Overall, collinearity did not affect our findings qualitatively. Although relative abundance, the number of shared pollinators, and the visit effectiveness were all positively correlated (Figure S1), the effect each had on conspecific pollen was similar among models that included all or just some of these three explanatory variables (Figure S2). One exception was visit-effectiveness, which exhibits a positive association with the relative amount of conspecific pollen under some variable combinations. Nevertheless, these differences were observed only in model specifications with relatively low AICc support.

Flexibility of plant strategies

We used a PCA of the analysed species to investigate whether plants' realised niche of competition for pollination 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 changes in 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

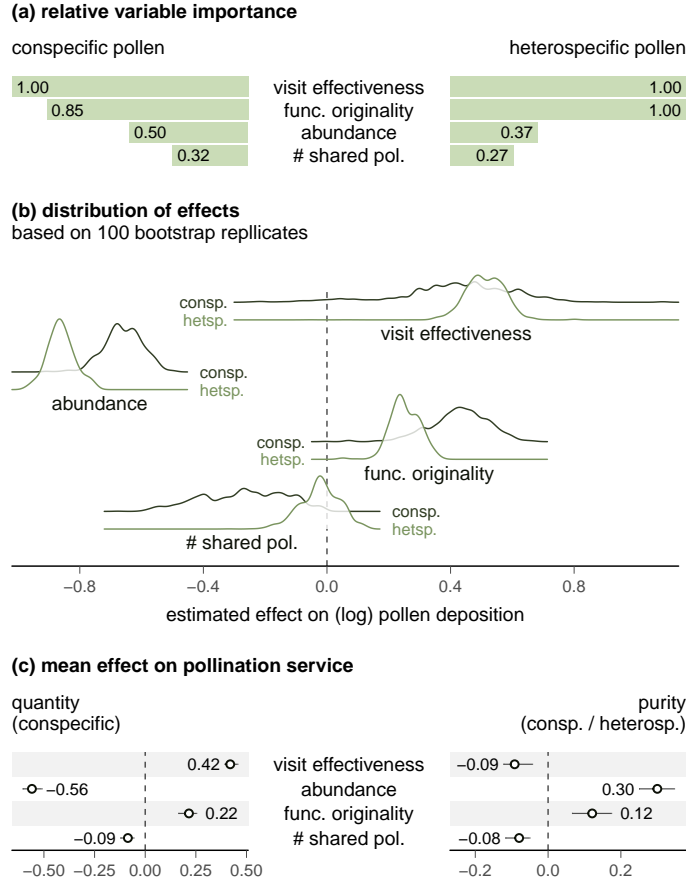


Figure 2: Effect of strategies to minimise competition in the pollination service. (a) The plant's visit effectiveness and relative abundance are the most important variables determining the deposition of conspecific and heterospecific pollen. Meanwhile, the number of shared pollinators was relatively unimportant. The graph shows the relative variable importance calculated as the sum of the Akaike weights of the candidate models that included the variable. (b) The association between ecological variables 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 abundance and the number of shared pollinators had a negative association. The plot shows the distribution of the effects (across 99 bootstrap replicates) of the four ecological variables for conspecific 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).

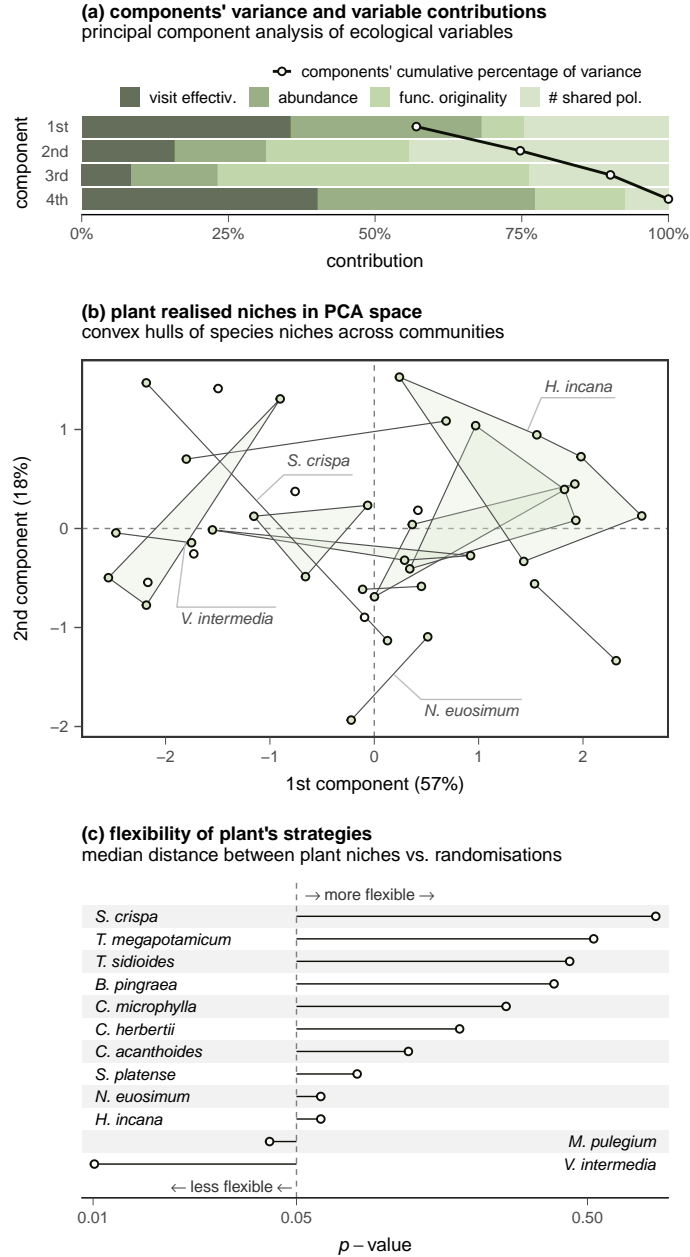


Figure 3: The flexibility of plant strategies. (a) The two first components explain a large proportion of the total variance. (b) When plants that were sampled in more than one community are plotted with these two components, we observe that points, which represent the strategy (the particular combination of ecological variables) of a species in a community do not seem to be grouped by plant species. (c) This was confirmed using Monte Carlo randomizations of the median distance between strategies of a plant species. Only one of the examined species had strategies that were more tightly connected than what would be expected at random.

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 analysed species (Figure 3c).

Discussion

Our results suggest that community context plays a central role in determining net cost or benefit of sharing pollinators. First, we found that pollinator sharing can lead to both overall facilitative and 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 therefore there is 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, this is, if collectively these factors are used to define a niche of competition for pollination, the same plant species can occupy dramatically different niches depending on the community it belongs to.

Both of the criteria we used to identify the effect of animal-mediated pollination suggested the same outcome: 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.

417 Here we show that the coexistence of facilitative and competitive effects of
418 animal-mediated pollination can be at least partially explained by the trade-
419 offs plants have to undergo when maximising the deposition of conspecific
420 pollen and simultaneously minimising that of heterospecific pollen both in
421 the short and the long term.

422 In the short term, being a specialist and sharing no pollinators might reduce
423 competition (Muchhala *et al.* 2010) and hence be preferable, as we show that
424 sharing pollinators reduces both the quantity and purity of the conspecific
425 pollen deposited. However, over long periods of time, there could be a risk
426 associated with a specialist plant having no pollinators. Hence, is likely that
427 to ensure long term survival, plants also need to balance this risk with the
428 costs of sharing pollinators. One possible solution is to share pollinators *and*
429 have original traits—as we show that trait originality is generally beneficial
430 to pollen deposition and it’s commonly thought that species that are further
431 from others in trait space benefit from reduced competition. Yet, there are
432 two possible caveats to this strategy that highlight the interrelatedness of
433 the ecological factors. First, in a mutualism context, it is also possible that
434 trait originality could come at the cost of being less ‘apparent’ to pollinators
435 (Reverté *et al.* 2016). Second, the negative, relationship between originality
436 and generalism (Carvalho *et al.* 2014) has been shown depend on the
437 plant’s abundance (Coux *et al.* 2016), with generalist species being able to
438 also have original traits only when they are abundant enough to provide a
439 valuable reward to make it worth to pollinators. Visit effectiveness (high
440 pollen and visits) and abundance, which were the most important predictors
441 of pollen deposition, involved an even more explicit trade-off between gaining
442 conspecific pollen and avoiding heterospecific pollen. On the one hand,
443 receiving high visitation increases conspecific pollen deposition but increases
444 heterospecific pollen to a greater extent—even when the visitors are likely to
445 carry a high proportion of conspecific pollen (Fang & Huang 2016). On the

other, 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. 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, 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 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 that the balances between cost and benefits are determined not only by species identity but also on the community plants belong to. 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 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 plant might use to minimise competition for pollination must be relative to other species in the community, rather than an absolute property of the species.

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 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 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

504 mutualistic and competitive communities (Johnson & Bronstein 2019).

505 Acknowledgements

506 We thank Bernat Bramon, Laís Maia, and Michelle Marraffini for feedback
507 and valuable discussions. We also thank Cátedra de Botánica General,
508 Facultad de Agronomía, Universidad de Buenos Aires. The Agrasar and
509 Bordeu families, and the University of Buenos Aires, for logistical support
510 and permission to conduct this study at estancias Anquilóo, Las Chilcas
511 and San Claudio, respectively. Fieldwork was supported by grants PICT
512 08–12504 and 0851. EFC acknowledges the support from the University of
513 Canterbury Doctoral Scholarship and a New Zealand International Doctoral
514 Research Scholarship administered by New Zealand Education.DBS and
515 JMT acknowledge the support of a Rutherford Discovery Fellowship and
516 the Marsden Fund Council, both administered by the Royal Society of New
517 Zealand Te Apārangi.

518 References

- 519 Aizen, M.A. & Rovere, A.E. (2010). Reproductive interactions mediated by
520 flowering overlap in a temperate hummingbird-plant assemblage. *Oikos*, 119,
521 696–706.
- 522 Arceo-Gómez, G., Kaczorowski, R.L., Patel, C. & Ashman, T.-L. (2019).
523 Interactive effects between donor and recipient species mediate fitness costs
524 of heterospecific pollen receipt in a co-flowering community. *Oecologia*.
- 525 Bartomeus, I., Vilà, M. & Santamaría, L. (2008). Contrasting effects of
526 invasive plants in plant-pollinator networks. *Oecologia*, 155, 761–770.
- 527 Bascompte, J. & Jordano, P. (2007). Plant-Animal Mutualistic Networks:

528 The Architecture of Biodiversity. *Annual Review of Ecology, Evolution, and*
529 *Systematics*, 38, 567–593.

530 Bastolla, U., Fortuna, M.A., Pascual-García, A., Ferrera, A., Luque, B. &
531 Bascompte, J. (2009). The architecture of mutualistic networks minimizes
532 competition and increases biodiversity. *Nature*, 458, 1018–1020.

533 Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting Linear
534 Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67, 1–48.

535 Benadi, G. & Pauw, A. (2018). Frequency dependence of pollinator visitation
536 rates suggests that pollination niches can allow plant species coexistence.
537 *Journal of Ecology*, 106, 1892–1901.

538 Bosch, J., Martín González, A.M., Rodrigo, A. & Navarro, D. (2009). Plant-
539 pollinator networks: Adding the pollinator’s perspective. *Ecology Letters*,
540 12, 409–419.

541 Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J. &
542 Michalet, R. *et al.* (2002). Positive interactions among alpine plants increase
543 with stress. *Nature*, 417, 844–848.

544 Campbell, D.R. & Motten, A.F. (1985). The Mechanism of Competition for
545 Pollination between Two Forest Herbs. *Ecology*, 66, 554–563.

546 Cariveau, D.P. & Norton, A.P. (2009). Spatially contingent interactions
547 between an exotic and native plant mediated through flower visitors. *Oikos*,
548 118, 107–114.

549 Caruso, C.M. (2000). Competition for Pollination Influences Selection on
550 Floral Traits of *Ipomopsis aggregata*. *Evolution*, 54, 1546–1557.

551 Carvalheiro, L.G., Biesmeijer, J.C., Benadi, G., Fründ, J., Stang, M. &
552 Bartomeus, I. *et al.* (2014). The potential for indirect effects between
553 co-flowering plants via shared pollinators depends on resource abundance,

554 accessibility and relatedness. *Ecology Letters*, 17, 1389–1399.

555 Coux, C., Rader, R., Bartomeus, I. & Tylianakis, J.M. (2016). Linking
556 species functional roles to their network roles. *Ecology Letters*, 19, 762–770.

557 Fang, Q. & Huang, S.-Q. (2016). A paradoxical mismatch between in-
558 terspecific pollinator moves and heterospecific pollen receipt in a natural
559 community. *Ecology*, 97, 1970–1978.

560 Feinsinger, P. (1987). Effects of plant species on each others pollination: Is
561 community structure influenced? *Trends in Ecology & Evolution*, 2, 123–126.

562 Feldman, T.S., Morris, W.F. & Wilson, W.G. (2004). When can two plant
563 species facilitate each other’s pollination? *Oikos*, 105, 197–207.

564 Flanagan, R.J., Mitchell, R.J. & Karron, J.D. (2011). Effects of multiple
565 competitors for pollination on bumblebee foraging patterns and *Mimulus*
566 *Ringens* reproductive success. *Oikos*, 120, 200–207.

567 Ghazoul, J. (2006). Floral diversity and the facilitation of pollination.
568 *Journal of Ecology*, 94, 295–304.

569 Gibson, M.R., Richardson, D.M. & Pauw, A. (2012). Can floral traits predict
570 an invasive plant’s impact on native plant-pollinator communities? *Journal*
571 *of Ecology*, 100, 1216–1223.

572 Hegland, S.J., Grytnes, J.-A. & Totland, Ø. (2009). The relative importance
573 of positive and negative interactions for pollinator attraction in a plant
574 community. *Ecological Research*, 24, 929–936.

575 Johnson, C.A. & Bronstein, J.L. (2019). Coexistence and competitive
576 exclusion in mutualism. *Ecology*, e02708.

577 Johnson, S.D. & Steiner, K.E. (2000). Generalization versus specialization
578 in plant pollination systems. *Trends in Ecology & Evolution*, 15, 140–143.

579 Kalisz, S. & Vogler, D.W. (2003). Benefits of autonomus selfing under

580 unpredictable pollinator environments. *Ecology*, 84, 2928–2942.

581 Klein, A.-M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham,
582 S.A. & Kremen, C. *et al.* (2007). Importance of pollinators in changing
583 landscapes for world crops. *Proceedings of the Royal Society B: Biological*
584 *Sciences*, 274, 303–313.

585 Laliberté, E. & Legendre, P. (2010). A distance-based framework for mea-
586 suring functional diversity from multiple traits. *Ecology*, 91, 299–305.

587 Laliberté, E., Legendre, P. & Shipley, B. (2014). *FD: Measuring functional*
588 *diversity from multiple traits, and other tools for functional ecology*. R
589 package version 1.0-12.

590 Levin, D.A. & Anderson, W.W. (1970). Competition for pollinators between
591 simultaneously flowering species. *The American Naturalist*, 104, 455–467.

592 Lewis, H. (1961). Experimental Sympatric Populations of *Clarkia*. *The*
593 *American Naturalist*, 95, 155–168.

594 Liao, K., Gituru, R.W., Guo, Y.-H. & Wang, Q.-F. (2011). The presence of co-
595 flowering species facilitates reproductive success of *Pedicularis Monbeigiana*
596 (Orobanchaceae) through variation in bumble-bee foraging behaviour. *Annals*
597 *of Botany*, 108, 877–884.

598 Lopezaraiza-Mikel, M.E., Hayes, R.B., Whalley, M.R. & Memmott, J. (2007).
599 The impact of an alien plant on a native plant-pollinator network: An
600 experimental approach. *Ecology Letters*, 10, 539–550.

601 Marrero, H., Medan, D., Zarlavsky, G. & Torretta, J. (2016). Agricultural
602 land management negatively affects pollination service in Pampean agro-
603 ecosystems. *Agriculture, Ecosystems & Environment*, 218, 28–32.

604 Marrero, H., Torretta, J. & Medan, D. (2014). Effect of land use intensi-
605 fication on specialization in plant-floral visitor interaction networks in the

606 Pampas of Argentina. *Agriculture, Ecosystems & Environment*, 188, 63–71.

607 Marrero, H.J., Torretta, J.P., Vázquez, D.P., Hodara, K. & Medan, D.
608 (2017). Exotic plants promote pollination niche overlap in an agroecosystem.
609 *Agriculture, Ecosystems & Environment*, 239, 304–309.

610 Memmott, J. (1999). The structure of a plant-pollinator food web. *Ecology*
611 *Letters*, 2, 276–280.

612 Mitchell, R.J., Flanagan, R.J., Brown, B.J., Waser, N.M. & Karron, J.D.
613 (2009). New frontiers in competition for pollination. *Annals of Botany*, 103,
614 1403–1413.

615 Moeller, D.A. (2004). Facilitative interactions among plants via shared
616 pollinators. *Ecology*, 85, 3289–3301.

617 Molina-Montenegro, M.A., Badano, E.I. & Cavieres, L.A. (2008). Positive
618 interactions among plant species for pollinator service: Assessing the “magnet
619 species” concept with invasive species. *Oikos*, 117, 1833–1839.

620 Morales, C.L. & Traveset, A. (2008). Interspecific pollen transfer: Magnitude,
621 prevalence and consequences for plant fitness. *Critical Reviews in Plant*
622 *Sciences*, 27, 221–238.

623 Muchhala, N., Brown, Z., Armbruster, W.S. & Potts, M.D. (2010). Compe-
624 titution Drives Specialization in Pollination Systems through Costs to Male
625 Fitness. *The American Naturalist*, 176, 732–743.

626 Muñoz, A.A. & Cavieres, L.A. (2008). The presence of a showy invasive
627 plant disrupts pollinator service and reproductive output in native alpine
628 species only at high densities: Invasive impacts on native species pollination.
629 *Journal of Ecology*, 96, 459–467.

630 Ollerton, J., Winfree, R. & Tarrant, S. (2011). How many flowering plants
631 are pollinated by animals? *Oikos*, 120, 321–326.

632 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. (2018).

633 *Nlme: Linear and Nonlinear Mixed Effects Models*. R package version
634 3.1-137.

635 Rathcke, B. (1988). Interactions for pollination among coflowering shrubs.
636 *Ecology*, 69, 446–457.

637 Reverté, S., Retana, J., Gómez, J.M. & Bosch, J. (2016). Pollinators show
638 flower colour preferences but flowers with similar colours do not attract
639 similar pollinators. *Annals of Botany*, 118, 249–257.

640 Robertson, C. (1895). The philosophy of flower seasons, and the phaenological
641 relations of the entomophilous flora and the anthophilous insect fauna. *The*
642 *American Naturalist*, 29, 97–117.

643 Rohr, R.P., Saavedra, S. & Bascompte, J. (2014). On the structural stability
644 of mutualistic systems. *Science*, 345, 1253–1257.

645 Sargent, R.D. & Otto, S.P. (2006). The role of local species abundance in
646 the evolution of pollinator attraction in flowering plants. *The American*
647 *Naturalist*, 167, 67–80.

648 Seifan, M., Hoch, E.-M., Hanoteaux, S. & Tielbörger, K. (2014). The
649 outcome of shared pollination services is affected by the density and spatial
650 pattern of an attractive neighbour. *Journal of Ecology*, 102, 953–962.

651 Stachowicz, J.J. (2001). Mutualism, facilitation, and the structure of ecolog-
652 ical communities. *BioScience*, 51, 235–246.

653 Stavert, J.R., Pattemore, D.E., Gaskett, A.C., Beggs, J.R. & Bartomeus,
654 I. (2017). Exotic species enhance response diversity to land-use change but
655 modify functional composition. *Proceedings of the Royal Society B: Biological*
656 *Sciences*, 284, 20170788.

657 Thomson, J.D., Fung, H.F. & Ogilvie, J.E. (2019). Effects of spatial pattern-
658 ing of co-flowering plant species on pollination quantity and purity. *Annals*

659 of *Botany*, 123, 303–310.

660 Tur, C., Sáez, A., Traveset, A. & Aizen, M.A. (2016). Evaluating the effects
661 of pollinator-mediated interactions using pollen transfer networks: Evidence
662 of widespread facilitation in south Andean plant communities. *Ecology*
663 *Letters*, 19, 576–586.

664 Waser, N.M. (1978). Interspecific pollen transfer and competition between
665 co-occurring plant species. *Oecologia*, 36, 223–236.

666 Yang, S., Ferrari, M.J. & Shea, K. (2011). Pollinator behavior mediates
667 negative interactions between two congeneric invasive plant species. *The*
668 *American Naturalist*, 177, 110–118.

669 Ye, Z.-M., Dai, W.-K., Jin, X.-F., Gituru, R.W., Wang, Q.-F. & Yang, C.-F.
670 (2014). Competition and facilitation among plants for pollination: Can
671 pollinator abundance shift the plant-plant interactions? *Plant Ecology*, 215,
672 3–13.