



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

Journal:	<i>Ecology Letters</i>
Manuscript ID	ELE-00524-2019
Manuscript Type:	Letters
Date Submitted by the Author:	15-May-2019
Complete List of Authors:	Cagua, Edgar Fernando; University of Canterbury, School of Biological Sciences Marrero, Hugo; Consejo Nacional de Investigaciones Cientificas y Tecnicas Tylianakis, Jason; University of Canterbury, School of Biological Sciences Stouffer, Daniel; University of Canterbury, School of Biological Sciences
Key Words:	interspecific pollen transfer, pollination network, pollen deposition, plant-pollinator interactions, pollination costs and benefits, pollinator sharing, pollination niche, abundance, functional originality, floral visitation

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

Running title: Competition for pollination vs. facilitation

Keywords: abundance, floral visitation, functional originality, interspecific
pollen transfer, plant-pollinator interactions, pollen deposition, pollination
costs and benefits, pollination network, pollination niche, and pollinator
sharing

Type of article: Letter.

Number of words: 153 in abstract; 4,511 in main text.

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

Number of references: 42

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

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

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.

Abstract

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

36 **Introduction**

37 Animal pollination plays a disproportionally important role in food produc-
38 tion and maintenance of global biodiversity (Bascompte & Jordano 2007;
39 Klein *et al.* 2007; Ollerton *et al.* 2011). Alongside the direct benefits of mu-
40 tualisms between plants and their pollinators, biodiversity can be supported
41 as a result of inter-species “facilitation”—the indirect positive feedback loops
42 that exist between plant species that share pollinators or pollinators that
43 share plants (Moeller 2004; Ghazoul 2006; Molina-Montenegro *et al.* 2008;
44 Liao *et al.* 2011). This inter-species facilitation is able to promote species
45 coexistence by offsetting the effects of direct resource competition (Stachow-
46 icz 2001). Indeed, studies at the core of our current theoretical knowledge
47 of mutualisms predict that the maximum number of coexisting species is
48 achieved when the number of shared mutualistic partners is maximised in a
49 community (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 part-
52 ners because there is a trade-off between the benefits gained from maximising
53 the number of partners and the costs of sharing them with other plant species
54 (Waser 1978). It has been clear for a long time that when competition for
55 pollination is strong enough, these costs can make pollination detrimental to
56 plants’ fitness (shown both experimentally and theoretically; Robertson 1895;
57 Lewis 1961; Levin & Anderson 1970). In fact, it can be sufficient to drive
58 ecological differentiation (Caruso 2000; for example by driving the evolution
59 of both traits and reproductive strategies; Mitchell *et al.* 2009). However, it
60 is less clear how exactly this ecological differentiation may, in turn, favour
61 (or hinder) the pollination service.

62 There are two main mechanisms through which competition for pollinators
63 can affect plant fertilization (Morales & Traveset 2008). The first is by

changes in intraspecific pollen transfer. This happens, for example, when plants with more attractive flowers might reduce the number of visits to those less of attractive neighbouring plants, and hence reduce the amount of *conspecific pollen* deposited by animals (Yang *et al.* 2011). The second is via interspecific pollen transfer and occurs when plants share pollination partners. In that case, even receiving a visit might not necessarily translate into fertilization (Campbell & Motten 1985) because a focal plant might receive *heterospecific pollen* or because pollen from the focal plant might be lost to different species. Generally speaking, provided pollen is viable and compatible (de Jong *et al.* 1992; Dafni & Firmage 2000; Ramsey & Vaughton 2000), the higher the quantity of conspecific pollen and its purity (relative to heterospecific pollen), the better the pollination service received by the focal plant. By definition, these two mechanisms of competition occur at the community scale. However, with few exceptions (Aizen & Rovere 2010; Tur *et al.* 2016), most of what we know about them and their relationship with key ecological factors is based on studies with two plant species.

That is partly so because, at the community scale, the factors that determine the patterns of pollen deposition are tightly intertwined, operate simultaneously, and may lead to emergent phenomena not observed at smaller scales (Flanagan *et al.* 2011). For instance, recent empirical evidence suggests that plants with flowering traits that are “original” relative to others in the community generally have fewer interaction partners (Coux *et al.* 2016). This evidence is aligned with the notion that a species that interacts with few species does so strongly with each of them whereas a species that interacts with a large number of species does so comparatively weakly (Bascompte *et al.* 2006; Vázquez *et al.* 2007; Thébault & Fontaine 2008). If evolutionary specialisation occurs by changing traits to focus on fewer but better partners (Caruso 2000), we should expect a reduction of competition for pollinators in species with “original” traits and an increase of competition in species with

93 a large number of interaction partners (Gibson *et al.* 2012; Carvalheiro *et al.*
94 2014). Alternatively, it might also be the case that abundance (for example in
95 terms of flower or pollen counts) is the dominant force driving pollen transfer
96 (Seifan *et al.* 2014). Abundant plant species might experience a dilution of
97 available pollinators (Feinsinger 1987; Feldman *et al.* 2004) but might also
98 receive more effective visits by capitalising on a larger share of both visits and
99 the pollen carried by pollinators. In this case, a potential reduction in the
100 absolute amount of conspecific pollen received could be compensated by an
101 increase in the amount of conspecific pollen relative to heterospecific pollen.
102 Altogether, it is clear that these ecological factors can indeed shape pollen
103 deposition at the community level. However, their relative importance and
104 how exactly they can minimise competition for pollination—or equivalently,
105 maximise facilitation—in plant populations (across species and communities)
106 has not been determined.

107 Here, we investigate the balance between competition for pollination and
108 facilitation at the community scale using empirical data from eleven plant-
109 pollinator communities in the Argentinian Pampas. First, we estimate the
110 extent to which the net outcome of plants sharing pollinators is facilitation or
111 competition. If facilitation is the primary outcome, we could expect an overall
112 positive relationship between the amount of conspecific pollen deposited in
113 stigmas and the amount of heterospecific pollen (Tur *et al.* 2016). The higher
114 the deposition of conspecific pollen relative to heterospecific, the larger the
115 slope of this relationship. Second, we investigate the relative contribution
116 that four ecological factors have to the pollination service. Specifically, we
117 hypothesize that the quantity and purity of conspecific pollen deposition
118 should decrease for plants that share many pollination partners. However, we
119 also hypothesize that other factors like the plant's functional originality, its
120 relative floral abundance, and the visit effectiveness should have the potential
121 to compensate for this increase in competition. Third and finally, we examine

122 how much the community context influences the way plants use these factors
123 to minimise competition/maximise facilitation. We use these four ecological
124 factors as a proxy of the realised pollination niche of a plant species in
125 their community. Although some plant species might be widespread across
126 multiple locations, competition for pollinators occurs at the community level
127 and hence we predict that pollination niche will be influenced by the local
128 context. If plant strategy is not flexible across the communities in our study,
129 we could expect niches to be more similar within species than across species.
130 On the contrary, if a species' strategy is flexible, we should expect plants to
131 be able to occupy different niches in each community such that intraspecific
132 competition could ultimately be minimised regardless of the context.

133 **Methods**

134 We collected data from eleven co-flowering plant communities and their
135 pollinators in three locations in the Argentinian Pampas. In each location,
136 we sampled two restored and two agricultural fragments, except in one
137 located in the Flooding Pampas, where we were only able to sample one
138 restored fragment due to the lack of available sites.

139 **Competition vs. facilitation**

140 Our first objective was to identify whether the net outcome of plants sharing
141 pollinators at the community level is facilitation or competition. To do that
142 we examine the relationship between heterospecific and conspecific pollen
143 deposited in plant stigmas (Tur *et al.* 2016). This is because heterospecific
144 pollen can be seen as an unavoidable cost that plants must pay for receiving
145 conspecific pollen from shared pollinators. A negative relationship (when
146 shared pollinators increase heterospecific pollen loads and decrease conspecific
147 loads) may indicate that competition for pollination is strong. In contrast,

1
2 148 a positive relationship is what would be observed when facilitation is the
3
4 149 dominant outcome.

5
6
7 150 **Data collection**

8
9
10 151 In each of the studied communities, we quantified pollen deposition in a subset
11
12 152 of plant species between December 2010 and February 2011. This subset
13
14 153 comprised between three and nine common insect-pollinated (entomophilous)
15
16 154 plant species that were flowering during the sampling period (see Figure 1a).
17
18 155 Based on data from previous years (Marrero *et al.* 2014), we chose plant
19
20 156 species such that they cover a wide range on a specialization-generalization
21
22 157 gradient as well as a wide range of abundances. In each of the selected
23
24 158 plants, we removed all flowers leaving only buds that were expected to go
25
26 159 into florescence on the next day. Two days after flowering, we collected all
27
28 160 remaining flowers and counted the number of conspecific and heterospecific
29
30 161 pollen grains in their pistils. More details can be found in Marrero *et al.*
31 162 (2016).

32
33
34 163 **Data analysis**

35
36
37 164 To evaluate the relationship between heterospecific and conspecific pollen,
38
39 165 we used a generalised linear mixed model (GLMM) with a Poisson error
40
41 166 distribution (following Tur *et al.* 2016). In this model, the number of
42
43 167 conspecific pollen grains per flower was the response variable and the number
44
45 168 of heterospecific grains the predictor variable (the log number of stigmas
46
47 169 sampled was added as an offset term). The slope and intercept of this
48
49 170 relationship were allowed to differ between populations (plant species \times
50
51 171 community), which were modelled as a random effect. Models were fitted
52
53 172 using the function `glmer` from the R package `lme4` 1.1-19 (Bates *et al.*
54 173 2015). A positive slope for a plant population indicates facilitation while a

negative slope competition (Tur *et al.* 2016).

Factors affecting quantity and purity of pollination service

Our second objective was to investigate the relative contribution that different ecological factors have on the mechanisms of pollinator-mediated competition. Generally speaking, we expect that 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 plant's abundance relative to the rest of the community, (*iii*) the mean visit effectiveness—a metric that combines the amount and type of pollen carried by floral visitors and the number of visits it receives from them, and (*iv*) the plant's functional originality (Laliberté & Legendre 2010). See *Data Analysis* section below for more details on these four factors.

Data collection

To obtain the number of shared pollinators for each species, we collected data to construct qualitative and quantitative pollination networks. Qualitative networks were constructed based on ten-hour observations of floral visits in each fragment. Quantitative networks were constructed using two 50 m randomly located transects in each fragment. We counted and collected all floral visitors found in a 2 m wide strip while walking at a pace of 10 m per minute (Memmott 1999; Marrero *et al.* 2014). We visited the transects each month between November 2010 and March 2011. To obtain floral abundance, we counted all units of floral attraction found during an independent sampling of the same transects used to construct the quantitative visitation networks. To estimate visit effectiveness, we need to construct pollen transfer networks

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

Data analysis

To investigate the impact of ecological factors on pollination services, we used two sets of linear mixed models (LMM) with bootstrap resampling. The response variables for these model sets were the number of conspecific and heterospecific pollen grains deposited per stigma in flowers open to animal-mediated pollination. We used LMMs in which pollen loads were log-transformed because these models offered a better fit than equivalent GLMMs with Poisson (or quasi-Poisson) error structure. Models were fitted using the R package *nlme* 3.1-131 (Pinheiro *et al.* 2018).

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

As fixed predictors in the models, we included the four ecological factors

described above. Specifically, we calculated the number of shared pollinators for each plant species by pooling data from the qualitative and quantitative pollination networks. To calculate the plants' relative floral abundance in their community, we aggregated floral counts for each species. We then calculated the mean visit effectiveness of 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 . We log-transformed the number of shared pollinators, floral abundance, and visit effectiveness before including them in the model.

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

To estimate the coefficients, perform model selection, and quantify the associated uncertainty, we used a combination of multi-model inference and bootstrap resampling with 99 replicates. First, we performed model selection using the AICc and determined the likelihood of each candidate model (a particular combination of predictors) by calculating the median ΔAICc (relative to the most likely model) for each bootstrap sample. As we wanted model coefficients from more likely candidate models to carry more weight

in our results, we sampled the coefficients for our factors proportionally to the likelihood of their candidate model. Finally, we used these distributions of the model coefficients to estimate their mean impact on the pollination service (in terms of quantity and purity of conspecific pollen deposition).

Flexibility of plant strategies

Our last objective was to tease apart the plant strategies that might reduce competition and, importantly, how the community context influences these strategies. If community context plays a relatively small role or the species strategy is inflexible, we would expect plants of the same species to fill similar pollination niches across different communities. Alternatively, if the community plays a large role and/or plant strategies are flexible, we should be able to observe differences in the realised niche a plant species occupies across communities. To test this, we first used a principal component analysis (PCA) of the four ecological factors (number of shared pollinators, floral abundance, visit effectiveness, and trait originality). We scaled factors across the whole study to ensure that the PCA space does not change according to the species present in each community. We define a species' niche in a community as its coordinates in PCA space. For each species that was present in two or more communities, we then calculated (*i*) the median distance between the strategies that the species uses in different communities and (*ii*) the area of the convex hull defined by these points in the first two principal components (only for species present in three or more communities). We then compared the magnitude of these two metrics to those obtained with 99 Monte Carlo randomizations in which we replaced the strategy of the focal plant species by that of another randomly selected species in the dataset.

Results

Competition vs. facilitation

We first examined the degree of facilitation/competition in natural communities. Specifically, we examined the slope of the relationship between the quantities of heterospecific and conspecific pollen deposited on stigmas of each species in a community. Overall, we found that neither net facilitation nor net competition dominates (Table S1). Indeed, we found that the proportions of species that experienced a statistically significant positive or negative relationship between heterospecific and conspecific pollen were very similar (35% and 37%, respectively; Figure 1; 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 herbertyi*, *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 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 S1).

Factors affecting quantity and purity of pollination service

We then examined the potential roles played in pollen deposition by four ecological factors (number of shared pollinators, abundance, mean visit effectiveness, and functional originality). We found that our models of pollen deposition had high explanatory power (the coefficient of determination R^2 ranged between 0.76 and 0.93) although a large portion of the explanatory

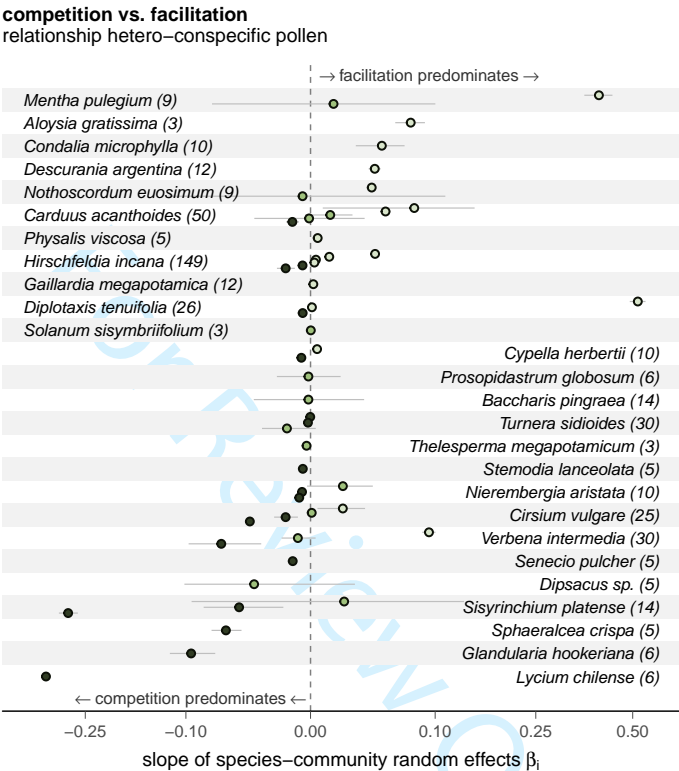


Figure 1: Competition vs. facilitation at the community level. Points indicate the estimated slopes for the relationship between the amount of heterospecific and conspecific pollen deposited per stigma across species in each of their communities. Statistically significant negative slopes (darkest shade) 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. Error bars correspond to \pm the standard error (SE).

power came from the random effects (Table S3). As determined by AICc, the random structure best supported by the data was the one that fit an intercept for each species in each community (as opposed to a common intercept for each species irrespective of the community to which they belong). This structure was best for both the models of conspecific and heterospecific pollen (Table S4).

Of the four factors we considered, we found that a plant's mean visit effectiveness and relative floral abundance were the most important at predicting pollen deposition in plant stigmas (Figure 2a). Surprisingly, the number of shared pollinators was comparatively unimportant, particularly for models of heterospecific pollen deposition, as it was only ever included in models with relatively large AICc values (Table S5).

We found that the relationship between each of the ecological factors and pollen deposition was similar for both conspecific and heterospecific pollen. That is, strategies that were associated with an increase in conspecific pollen were also associated with an increase in heterospecific pollen deposition. Specifically, the plants' mean visit effectiveness had a positive effect on 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 of pollen deposition, there is a negative relationship with its purity (Figure 2c). In contrast, a plants' relative floral abundance negatively affected its deposition quantity, but the mean difference between the coefficients in the models indicates a positive association with purity (Figure 2c). The third most important factor, functional originality, had a positive, although comparatively smaller, association with both the quantity and purity. Finally, the number of shared pollinators had negative and neutral associations with conspecific and heterospecific pollen, respectively, but these impacts were small when compared to the other factors. Although the ecological factors

337 were positively correlated (Figure S2), the collinearity between predictors
338 did not qualitatively affect our findings (Figure S3).

339 **Flexibility of plant strategies**

340 We used a PCA of the analysed species to investigate whether plants' realised
341 pollination niche is similar across communities or whether they are flexible
342 and therefore a reflection of the community context. The first two PCA
343 components explained 75% of the total variance (Figure 3a). The first
344 component was dominated by visit effectiveness and relative abundance while
345 the second component was dominated by the number of shared pollinators
346 and the plant's functional originality. When we locate the species that were
347 sampled in more than one community in the first two PCA components
348 (Figure 3b), we observe that the niches of any given species do not tend to be
349 close to each other. Indeed, when we measured the median distance between
350 the plants' coordinates, we found that it was only significantly smaller than
351 that of randomisations for only two of the twelve species analysed (Figure
352 3c).

353 **Discussion**

354 Our results suggest that community context plays a central role in deter-
355 mining the net cost or benefit of sharing pollinators. First, we found that
356 pollinator sharing can lead to both net facilitative and net competitive effects
357 to plant species in a community. Second, we found that multiple ecological
358 factors can modulate the intensity of competition; however, conspecific and
359 heterospecific pollen deposition are tightly coupled and this creates a clear
360 trade-off between the quantity and purity of pollination (Thomson *et al.*
361 2019). Third, we found that the way these factors influence competition
362 is strongly shaped by the community context. That is, if these factors

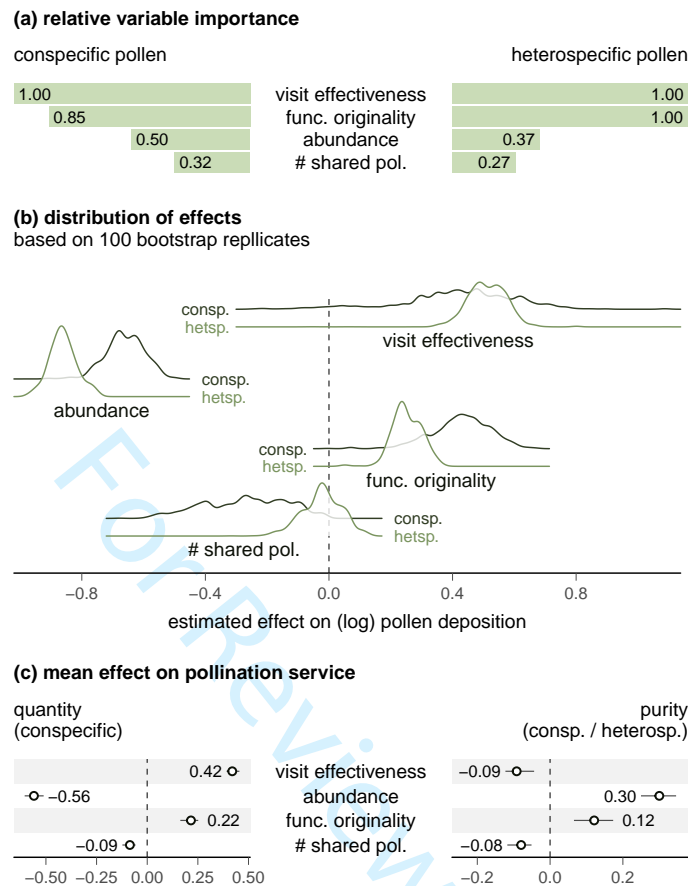


Figure 2: Effect of strategies to minimise competition in the pollination service. (a) The plant's visit effectiveness and relative floral abundance are the most important factors determining the deposition of conspecific and heterospecific pollen. Meanwhile, the number of shared pollinators was generally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

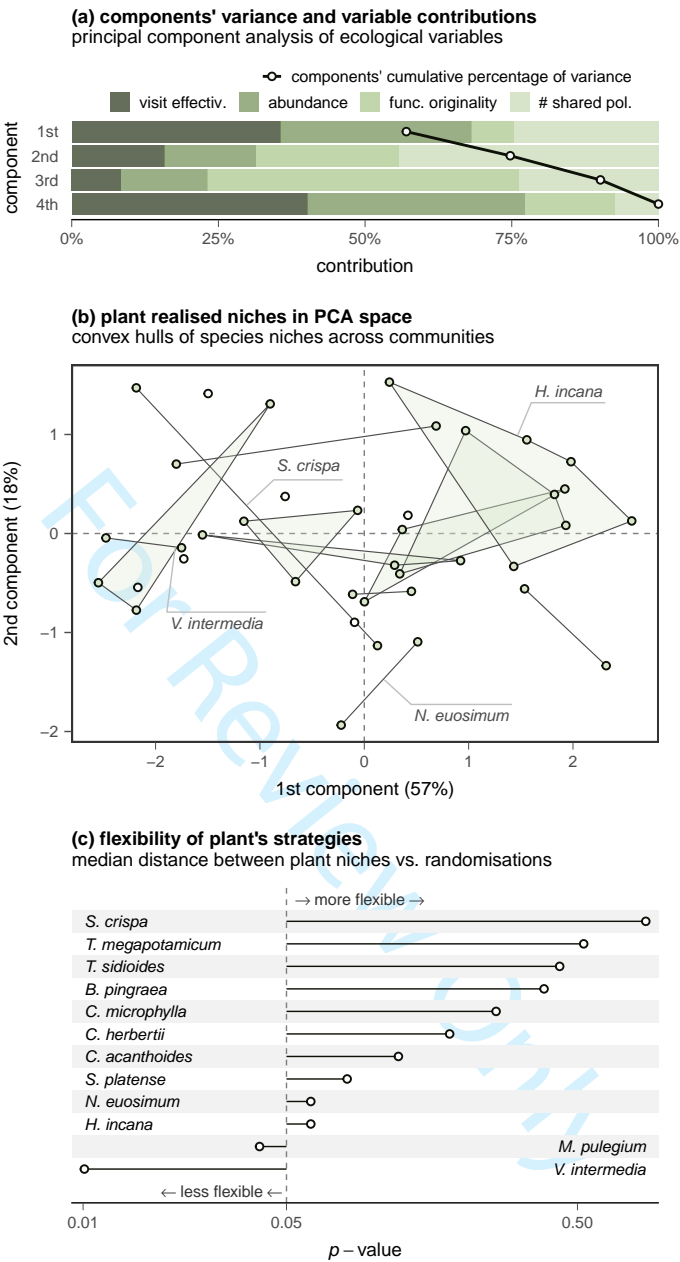


Figure 3: The flexibility of plant strategies. (a) The two first components explain a large proportion of the total variance. (b) When plants that were sampled in more than one community are plotted in terms of these two components, we observe that their points—which represent the strategy (the particular combination of ecological factors) of that species in 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 two of the examined species had strategies that were less flexible than would be expected at random.

collectively define a species' pollination niche, the same plant species can occupy dramatically different niches depending on the community to which it belongs.

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

In the short term, being a specialist and sharing no pollinators might reduce competition (Muchhala *et al.* 2010) and hence be preferable, not only due to costs to male fitness (Morales & Traveset 2008; Muchhala & Thomson 2012), but also because, as we show here, sharing pollinators reduces both the quantity and purity of the conspecific pollen deposited. However, over long periods of time, there could be a risk associated with a specialist plant having few pollinators (Ricketts 2004). To ensure long-term survival, it is thus likely that plants also need to balance this risk with the costs of sharing pollinators (Aizen *et al.* 2012). One possible solution is to share pollinators *and* have original traits—as we show that trait originality is generally beneficial to pollen deposition and it is commonly thought that species that are further

from others in trait space benefit from reduced competition. Yet, there are two possible caveats to this strategy that highlight the interrelatedness of the ecological factors. First, in a mutualism context, it is also possible that trait originality could come at the cost of being less ‘apparent’ to pollinators (Reverté *et al.* 2016). Second, the negative relationship between originality and generalism (Carvalho *et al.* 2014) has been shown to depend on plant abundance (Coux *et al.* 2016), with generalist species being able to also have original traits only when they are abundant enough to provide a valuable reward to make visiting worthwhile to pollinators.

Visit effectiveness (high pollen and visits) and floral abundance, which were the most important predictors of pollen deposition here, introduced an even more explicit trade-off between gaining conspecific pollen and avoiding heterospecific pollen. Receiving high visitation increases conspecific pollen deposition but increases heterospecific pollen deposition to a greater extent—even when the visitors are likely to carry a high proportion of conspecific pollen (Fang & Huang 2016). Contrastingly, being abundant reduces the amount of conspecific pollen deposited and simultaneously reduces heterospecific pollen at a faster rate. Our results corroborate the importance that two-species studies have ascribed to visitation and abundance (Feldman *et al.* 2004; Morales & Traveset 2008; Muñoz & Cavieres 2008), but 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, 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 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, we show here that the balances between costs and benefits are determined not only by species identity but also by the community to which plants belong. Specifically, most plant species appear to be flexible enough to adopt markedly different niches in different communities. From an evolutionary perspective, our results suggest 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 (or maximise facilitation) must be determined relative to other species in the community, rather than an absolute property of the species itself.

Overall, pollination communities might not necessarily be the paradigmatic mutualistic communities we often believe. Instead, we confirm that plant

competition is pervasive in pollination communities. The potential strategies to minimise competition are likely to involve strong trade-offs in the pollination service both in the short and long-term. Most remarkably, despite large differences in the quantity and purity of conspecific pollen deposition among species, our results provide solid evidence that competition for pollination is inherently a community process and the same species can occupy different niches in different communities. Many of the widely used 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).

Acknowledgements

We thank Jamie Stavert, Bernat Bramon Mora, Laís Maia, and Michelle Marraffini for feedback and valuable discussions. We also thank Cátedra de Botánica General, Facultad de Agronomía, Universidad de Buenos Aires, the Agrasar and Bordeu families, and the University of Buenos Aires, for logistical support and permission to conduct this study at estancias Anquilóo, Las Chilcas and San Claudio, respectively. Fieldwork was supported by grants PICT 08–12504 and 0851. EFC acknowledges the support from the University of Canterbury Doctoral Scholarship and a New Zealand International Doctoral Research Scholarship administered by New Zealand Education.DBS and JMT acknowledge the support of Rutherford Discovery Fellowships (RDF-13-UOC-003 and UOC-1002) and the Marsden Fund Council (UOC-1705), administered by the Royal Society of New Zealand Te Apārangi.

References

- Aizen, M.A. & Roever, A.E. (2010). Reproductive interactions mediated by flowering overlap in a temperate hummingbird-plant assemblage. *Oikos*, 119, 696–706.
- Aizen, M.A., Sabatino, M. & Tylianakis, J.M. (2012). Specialization and Rarity Predict Nonrandom Loss of Interactions from Mutualist Networks. *Science*, 335, 1486–1489.
- Arceo-Gómez, G., Kaczorowski, R.L., Patel, C. & Ashman, T.-L. (2019). Interactive effects between donor and recipient species mediate fitness costs of heterospecific pollen receipt in a co-flowering community. *Oecologia*.
- Bartomeus, I., Vilà, M. & Santamaría, L. (2008). Contrasting effects of invasive plants in plant-pollinator networks. *Oecologia*, 155, 761–770.
- Bascompte, J. & Jordano, P. (2007). Plant-Animal Mutualistic Networks: The Architecture of Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 38, 567–593.
- Bascompte, J., Jordano, P. & Olesen, J.M. (2006). Asymmetric Coevolutionary Networks Facilitate Biodiversity Maintenance. *Science*, 312, 431–433.
- Bastolla, U., Fortuna, M.A., Pascual-García, A., Ferrera, A., Luque, B. & Bascompte, J. (2009). The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature*, 458, 1018–1020.
- Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67, 1–48.
- Benadi, G. & Pauw, A. (2018). Frequency dependence of pollinator visitation rates suggests that pollination niches can allow plant species coexistence. *Journal of Ecology*, 106, 1892–1901.
- Bosch, J., Martín González, A.M., Rodrigo, A. & Navarro, D. (2009). Plant-

pollinator networks: Adding the pollinator's perspective. *Ecology Letters*,
12, 409–419.

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

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

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

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

Carvalho, L.G., Biesmeijer, J.C., Benadi, G., Fründ, J., Stang, M. &
Bartomeus, I. *et al.* (2014). The potential for indirect effects between
co-flowering plants via shared pollinators depends on resource abundance,
accessibility and relatedness. *Ecology Letters*, 17, 1389–1399.

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

Dafni, A. & Firmage, D. (2000). Pollen viability and longevity: Practical,
ecological and evolutionary implications. *Plant systematics and evolution*,
222, 113–132.

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

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

Feldman, T.S., Morris, W.F. & Wilson, W.G. (2004). When can two plant

- species facilitate each other's pollination? *Oikos*, 105, 197–207.
- Flanagan, R.J., Mitchell, R.J. & Karron, J.D. (2011). Effects of multiple competitors for pollination on bumblebee foraging patterns and *Mimulus Ringens* reproductive success. *Oikos*, 120, 200–207.
- Ghazoul, J. (2006). Floral diversity and the facilitation of pollination. *Journal of Ecology*, 94, 295–304.
- Gibson, M.R., Richardson, D.M. & Pauw, A. (2012). Can floral traits predict an invasive plant's impact on native plant-pollinator communities? *Journal of Ecology*, 100, 1216–1223.
- Johnson, C.A. & Bronstein, J.L. (2019). Coexistence and competitive exclusion in mutualism. *Ecology*, e02708.
- de Jong, T.J., Waser, N.M., Price, M.V. & Ring, R.M. (1992). Plant size, geitonogamy and seed set in *Ipomopsis aggregata*. *Oecologia*, 89, 310–315.
- Klein, A.-M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A. & Kremen, C. *et al.* (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, 274, 303–313.
- Laliberté, E. & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91, 299–305.
- Laliberté, E., Legendre, P. & Shipley, B. (2014). *FD: Measuring functional diversity from multiple traits, and other tools for functional ecology*. R package version 1.0-12.
- Levin, D.A. & Anderson, W.W. (1970). Competition for pollinators between simultaneously flowering species. *The American Naturalist*, 104, 455–467.
- Lewis, H. (1961). Experimental Sympatric Populations of *Clarkia*. *The*

554 *American Naturalist*, 95, 155–168.

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

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

562 Marrero, H.J., Torretta, J. & Medan, D. (2014). Effect of land use intensi-
563 fication on specialization in plant-floral visitor interaction networks in the
564 Pampas of Argentina. *Agriculture, Ecosystems & Environment*, 188, 63–71.

565 Marrero, H.J., Torretta, J.P., Vázquez, D.P., Hodara, K. & Medan, D.
566 (2017). Exotic plants promote pollination niche overlap in an agroecosystem.
567 *Agriculture, Ecosystems & Environment*, 239, 304–309.

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

570 Mitchell, R.J., Flanagan, R.J., Brown, B.J., Waser, N.M. & Karron, J.D.
571 (2009). New frontiers in competition for pollination. *Annals of Botany*, 103,
572 1403–1413.

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

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

578 Morales, C.L. & Traveset, A. (2008). Interspecific pollen transfer: Magnitude,
579 prevalence and consequences for plant fitness. *Critical Reviews in Plant*

580 *Sciences*, 27, 221–238.

581 Muchhala, N. & Thomson, J.D. (2012). Interspecific competition in pol-
582 lination systems: Costs to male fitness via pollen misplacement: Pollen
583 misplacement. *Functional Ecology*, 26, 476–482.

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

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

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

593 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. (2018).
594 *Nlme: Linear and Nonlinear Mixed Effects Models*. R package version
595 3.1-137.

596 Ramsey, M. & Vaughton, G. (2000). Pollen quality limits seed set in
597 *Burchardia Umbellata* (Colchicaceae). *American Journal of Botany*, 87,
598 845–852.

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

602 Ricketts, T.H. (2004). Tropical Forest Fragments Enhance Pollinator Activity
603 in Nearby Coffee Crops. *Conservation Biology*, 18, 1262–1271.

604 Robertson, C. (1895). The philosophy of flower seasons, and the phaenological
605 relations of the entomophilous flora and the anthophilous insect fauna. *The*

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

606 *American Naturalist*, 29, 97–117.

607 Rohr, R.P., Saavedra, S. & Bascompte, J. (2014). On the structural stability
608 of mutualistic systems. *Science*, 345, 1253497.

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

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

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

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

621 Thébault, E. & Fontaine, C. (2008). Does asymmetric specialization differ
622 between mutualistic and trophic networks? *Oikos*, 117, 555–563.

623 Thomson, J.D., Fung, H.F. & Ogilvie, J.E. (2019). Effects of spatial pattern-
624 ing of co-flowering plant species on pollination quantity and purity. *Annals*
625 *of Botany*, 123, 303–310.

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

630 Vázquez, D.P., Melián, C.J., Williams, N.M., Blüthgen, N., Krasnov, B.R. &
631 Poulin, R. (2007). Species Abundance and Asymmetric Interaction Strength

in Ecological Networks. *Oikos*, 116, 1120–1127.

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

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

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