

LETTER

Evaluating the effects of pollinator-mediated interactions using pollen transfer networks: evidence of widespread facilitation in south Andean plant communities

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Abstract

Information about the relative importance of competitive or facilitative pollinator-mediated interactions in a multi-species context is limited. We studied interspecific pollen transfer (IPT) networks to evaluate quantity and quality effects of pollinator sharing among plant species on three high-Andean communities at 1600, 1800 and 2000 m a.s.l. To estimate the sign of the effects (positive, neutral or negative), the relation between conspecific and heterospecific pollen deposited on stigmas was analysed with GLMMs. Network analyses showed that communities were characterised by the presence of pollen hub-donors and receptors. We inferred that facilitative and neutral pollinator-mediated interactions among plants prevailed over competition. Thus, the benefits from pollinator sharing seem to outweigh the costs (i.e. heterospecific deposition and conspecific pollen loss). The largest proportion of facilitated species was found at the highest elevation community, suggesting that under unfavourable conditions for the pollination service and at lower plant densities facilitation can be more common.

Keywords

Competition, conspecific pollen loss, facilitation, heterospecific pollen deposition, hub-species, interspecific pollen transfer, multi-species, network, pollination interactions, pollinator sharing.

Ecology Letters (2016)

INTRODUCTION

Nearly 87.5% of all flowering plants rely on animals (mainly insects) as vectors for effective pollen transport (Ollerton *et al.* 2011). Most animal-pollinated plants are relatively generalised (Waser & Ollerton 2006; Willmer 2011; Rosas-Guerrero *et al.* 2014) and often there is a high degree of pollinator sharing among co-flowering species in communities. The outcomes of pollinator sharing on plant reproductive performance vary from positive (facilitation), neutral, to negative (competition) (Moragues & Traveset 2005; Bjerknes *et al.* 2007; Morales & Traveset 2008; Hegland *et al.* 2009). However, the costs–benefits of pollinator sharing for plants have been mostly studied using isolated pairs of species, which do not allow generalisations of what pollination-mediated process, facilitation vs. competition, prevails in plant communities (but see Hegland *et al.* 2009; Aizen & Rovere 2010).

By flowering together, flowers of two or more species can experience an increase (facilitation) or decrease (competition) in visitation frequency (e.g. Brown *et al.* 2002; Ghazoul 2006). In any event, a pervasive negative consequence of pollinator sharing is interspecific pollen transfer (IPT), as movements of shared pollinators often result in pollen transfer from anthers of one species to stigmas of another. IPT is common in natural communities as most plants receive heterospecific pollen,

although its contribution to total stigmatic load is highly variable (0–75%) (McLernon *et al.* 1996; Montgomery & Rathcke 2012; Ashman & Arceo-Gómez 2013; Fang & Huang 2013). IPT can imply a reproductive cost in terms of both male and female fitness with potential ecological and evolutionary implications for plant community structure (Feinsinger 1987; Morales & Traveset 2008; Sargent & Ackerly 2008; Mitchell *et al.* 2009; Muchhala *et al.* 2010).

Here, we propose a conceptual framework to indirectly estimate the potential effects of pollinator-mediated interactions at the community level through the study of the relation between heterospecific pollen (HP) and conspecific pollen (CP) deposited on stigmas. Deposition of HP on stigmas might be viewed as a ‘service fee’ that plant species have to pay for the pollination service by shared mutualists, as it can have detrimental reproductive consequences (e.g. stigma clogging, allelopathic effects, ovule usurpation) (Galen & Gregory 1989; Murphy & Aarssen 1995; Brown & Mitchell 2001). An even more important cost associated to pollinator sharing is a reduction in the amount of CP exported by plants and deposited on stigmas because of CP losses on heterospecific stigmas, other floral structures or detachment during pollinator movement and grooming (Murcia & Feinsinger 1996; Flanagan *et al.* 2009; Muchhala & Thomson 2012). The relation between the overall amounts of CP and HP transferred to

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stigmas reflects the balance between plant–plant facilitation via increased visitation and competition via either reduced visitation or CP loss. Thus, it might indicate the relative benefit or cost obtained from pollinator sharing (Fig. 1a–c), that is the sign of the net effect of pollinator-mediated interactions. A positive linear relation between HP and CP deposited on stigmas might be found when sharing pollinators imply an increase in HP deposition, but also in CP deposition (Fig. 1a). This parallel increase might occur, for instance, when the ‘mass effect’ of flowering together or the presence of a particular ‘magnet-species’ attracts more pollinators to the area, increasing the quantity of visits per flower to neighbour plants (Laverty 1992; Moeller 2004; Ghazoul 2006; Molina-Montenegro *et al.* 2008; Liao *et al.* 2011). On the other hand, a negative relation between HP and CP on stigmas might take place when shared pollinators deposit increasing amounts of HP while decreasing CP deposition (Fig. 1b). This effect would be expected when (1) species compete for limited pollinators and the presence of a certain plant species reduces visitation to other co-flowering plants (Brown *et al.* 2002; Mitchell *et al.* 2009; Tscheulin & Petanidou 2013), (2) there are increasing losses of CP during visitation to heterospecific flowers or in more prolonged flights between conspecifics (Mitchell *et al.* 2009; Muchhala & Thomson 2012) or (3) deposition of HP blocks the stigma surface (stigma clogging) preventing adherence of CP grains (Galen & Gregory 1989; Brown & Mitchell 2001; Matsumoto *et al.* 2010; Runquist 2012). Finally, a neutral effect (i.e. no relation between CP and HP receipt) might result when the facilitative effect of flowering via pollinator

attraction balances the negative effects of pollinator sharing, for example via CP loss (Fig. 1c).

Although the above-mentioned cases refer to quantitative effects of pollinator-mediated interactions, the proposed framework can be expanded to qualitative effects. This can be achieved, for instance, through the study of the relation between the amount of HP deposited on stigmas and the number of CP grains germinated, pollen tubes in the style and/or ultimately seeds sired per CP grain deposited on the stigma. In the case of pollen germination (Fig. 1d–f), a positive relation between HP and the proportion of germinated CP (germination ratio) might occur when the presence of co-flowering species promotes arrival of more pollinators that visit fewer flowers per plant. This will decrease self-pollen deposition (mainly via reduced geitonogamy and pollen incompatibility), while favouring outcross-pollen deposition (Liao *et al.* 2011; Yang *et al.* 2013). On the other hand, a negative relation between HP and CP germination ratio might be found in the opposite scenario (i.e. fewer visitors, but more flowers visited per plant) and when HP causes mechanical or allelopathic inhibition of CP germination (Kanchan & Chandra 1980; Murphy & Aarssen 1995).

In this study, we use this novel and simple conceptual framework to estimate the sign of the effect (i.e. positive, neutral or negative) of pollinator-mediated interactions at a community level, both in terms of pollination quantity and quality. To achieve this goal, germinated and non-germinated CP and HP grains per stigma were counted and identified in co-flowering plant species from three alpine communities at different altitudes (1600, 1800 and 2000 m a.s.l.) in the Patagonian Andes. Using this data we constructed directed plant–plant networks depicting all IPTs in each community (Fang & Huang 2013). These networks are maps of pollinator-mediated interactions among co-occurring plants. Generalised linear mixed models (GLMMs) were used to estimate the sign of (1) the overall quantitative and qualitative effect of all pollinator-mediated interactions on every plant receptor species, and (2) the quantitative and qualitative effect of each pairwise interaction. We also determined the relative frequency of each type of interaction (positive, neutral and negative) in each community, assessing whether the prevalence of facilitative, neutral and competitive pollinator-mediated interactions changes across the altitudinal gradient studied. It has been proposed that facilitation is more common in habitats with adverse abiotic conditions, and that competition at low elevations can shift to facilitation at high elevations (Callaway *et al.* 2002; He *et al.* 2013). In the particular case of pollination, high elevations are harsh environments for insect-pollinated plants as abiotic conditions there (e.g. low temperatures, strong winds, short snow-free growing seasons) limit abundance, diversity and activity of insect pollinators (Arroyo *et al.* 1982; Totland 1993). Changes in pollinator availability can thus affect the direction and magnitude of pollinator-mediated interactions among plants (Lázaro *et al.* 2014; Ye *et al.* 2014). Moreover, pollinator-mediated effects vary also with plant density and flower abundance, so the effect of a focal species may change from facilitation to competition with increasing density (Muñoz & Cavieres 2008; Seifan *et al.* 2014). Therefore, we expect that plant–plant facilitation might be more frequent at

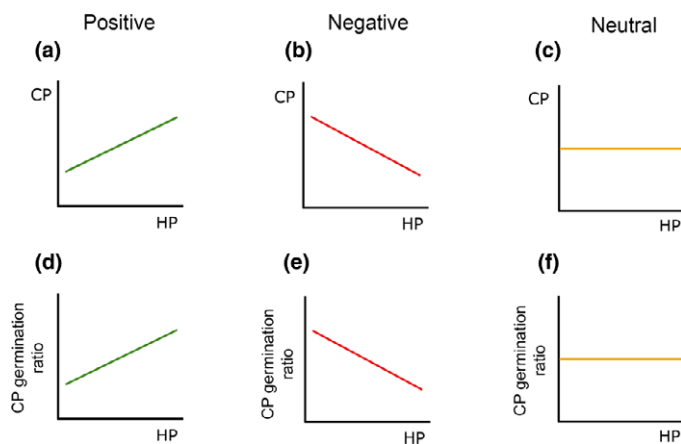


Figure 1 Simple conceptual model for the evaluation of quantitative (a–c) and qualitative (d–f) effects of pollinator-mediated interactions through the study of pollen deposition on stigmas (CP, conspecific pollen, HP, heterospecific pollen). HP transfer to stigmas is assumed to be a consequence of pollinator sharing among plants. Here graph intercept represents the average CP deposition when pollinators are not shared among plants. A positive effect of pollinator sharing (i.e. facilitation) is found when shared pollinators increase HP deposition on stigmas, but also CP deposition (a) and/or the proportion of CP germinated (d). On the other hand, a negative effect of pollinator sharing (i.e. competition) is found when shared pollinators reduce the amount of CP load (b) and/or CP germination ratio (e). Finally, a neutral effect is found when HP deposition does not modify CP deposition (c) and/or CP germination ratio (f).

higher than at lower altitudinal communities because, under limited pollinator services and at lower plant densities, plant benefits obtained from sharing pollinators (e.g. increase in quantity and/or quality of CP deposition) outweigh their resulting costs (i.e. HP deposition and CP loss).

MATERIAL AND METHODS

Study sites and sampling

Field work was conducted at the northern face of Cerro Challhuaco (2101 m) in Nahuel Huapi National Park (San Carlos de Bariloche, Río Negro, Argentina) over the 2010–2011 austral flowering season (from December, after snow melt, to March). A brief description of climate, vegetation and main flower visitors in the study area is provided in Appendix S1. We sampled animal-pollinated plant species from the high-Andean semi-desert at three altitudinal levels above the *Nothofagus pumilio* timberline: (1) 1641 m above sea level (41°16.01' S, 71°18.08' W), (2) 1807 m a.s.l. (41°16.09' S, 71°18.45' W) and (iii) 2101 m a.s.l. (41°16.003' S, 71°19.161' W). Hereafter, we refer to these altitudes as 1600, 1800, and 2000 m, respectively. Each altitudinal level was sampled once a day every 2 weeks during the whole study period (six times in total). **On each sampling day, we identified all flowering plant species in bloom in a 100 m × 25 m transect** per altitudinal level (a total of 48 species were identified, Table S1). At each altitude we randomly selected **five plant individuals per species**, whenever possible, and collected five senescent flowers (i.e. post-anthesis) per individual, which were stored separately in clean eppendorf tubes with ethanol 70% (Harder & Aizen 2004; Jakobsson *et al.* 2008). Later in the laboratory, we counted and identified all heterospecific and conspecific pollen grains (germinated and non-germinated) on stigmas of collected flowers (Appendix S2).

Construction of a plant–plant pollen transfer network

Data from pollen deposition on stigmas were used to construct directed unipartite networks depicting HP transfers among plant species for each altitude (i.e. 1600, 1800 and 2000 m). Nodes are plant species and links represent HP transfer from anthers of one species to stigmas of another species. For instance, a link is directed from species *i* to *j* ($i \rightarrow j$) when pollen of species *i* was detected on stigmas of species *j* (*i* is the donor species and *j* is the receptor). The presence of a link in one direction does not entail necessarily the presence of the reverse link. In directed networks, in-degree (k_i^{in}) and out-degree (k_i^{out}) are defined as the number of links incoming and outgoing a focal node *i*, respectively (Newman 2003). Hence, here k_i^{in} measures the number of species from which plant species *i* receives pollen excluding itself, whereas k_i^{out} measures to how many other species *i* donates pollen. The frequency distributions of the number of incoming and outgoing links per node (in-degree and out-degree distributions) were examined for each network. Spearman rank correlation between in- and out-degree of species within each network was calculated ($r_{\text{in-out}}$). A significant positive correlation indicates that species in the network which tend to donate pollen

to many others also tend to receive from many, whereas a negative correlation means ‘successful’ donors are ‘poor’ receptors or vice versa. Species were classified as pollen donors ($k_i^{\text{in}} < k_i^{\text{out}}$), receptors ($k_i^{\text{in}} > k_i^{\text{out}}$) or balanced donor–receptors ($k_i^{\text{in}} = k_i^{\text{out}}$). As chances of receiving or donating pollen to other species might depend to some extent on floral abundances or pollen production, we tested the correlation between these two variables and in- and out-degree (Appendix S3). Moreover, for species sampled in more than one community (Table S1), the correlations between in-degree ($r_{\text{in-in}}$) and out-degree ($r_{\text{out-out}}$) at different communities were calculated to assess whether their role as receptors and donors was consistent across communities.

Because observed HP transfers are a consequence of pollinator sharing among plants, our networks depict all plant–plant pollinator-mediated interactions in communities. The sign of the effect of each interaction on receptor species (positive, neutral or negative) was determined following methods described in the next section. The open-source software Gephi 0.8-beta (<https://gephi.github.io/>) was used for network drawings and package *igraph* (Csardi & Nepusz 2006) in R software (version 2.15, R Development Core Team 2012) for in- and out-degree calculation.

Models for the estimation of pollinator-mediated interactions effect: facilitation, neutrality or competition

Data from pollen deposition on stigmas were used to fit generalised linear mixed-effects models (GLMMs) for estimating (1) whether the overall effect of all pollinator-mediated interactions on each plant receptor species was positive, neutral or negative, and (2) the sign of the effect of each donor species on every receptor species, that is the sign of plant–plant interactions in our networks. All models were fitted separately for each community using the *lmer* function in R package *lme4* (Bates *et al.* 2015). Data and R scripts for all analyses are archived in Figshare doi:10.6084/m9.figshare.2242447.

To assess the first objective, two models were performed: model 1 for quantitative effects of pollinator-mediated interactions and model 2 for qualitative effects (see conceptual framework Fig. 1). Model 1 was a Poisson GLMM with number of CP grains per stigma as response variable, total number of HP grains as predictor (all grains pooled irrespective of the donor species) and sampling date as covariate (factor with six levels indicating the sampling time to partially account for changes in plant and pollinator densities across the flowering season). Plant receptor species and also plant individual were included as random effects (random slope and intercept, and random intercept, respectively). Model 2 was a Binomial GLMM with germination ratio (i.e. number of germinated CP grains/total CP grains deposited) as response variable, total number of HP grains as predictor, sampling date as covariate and plant species as random effect (Appendix S3). Following our conceptual framework (Fig. 1), the slope β_j estimated for each species is an indicator of the quantity or quality effect of pollinator sharing on receptor plant species. We considered this slope to be evidence of an overall positive or facilitative effect when $\beta_j \pm 2\text{SE} > 0$, a neutral effect when $\beta_j \pm 2\text{SE}$ overlapped 0 and of a negative or competitive effect when

$\beta_j \pm 2SE < 0$. The percentage of species experiencing each type of effect was determined for each community (i.e. 1600, 1800 and 2000 m).

For the second objective, two other models were constructed (model 3 for quantitative effects and model 4 for qualitative effects), but this time only considering stigmas with both CP and HP deposition (21% of all observations) and incorporating information from the identity of donor species. Receptor and donor species were included as random effects (random slope and intercept), with donor nested within receptor (Appendix S4). We considered the slope estimation of each combination donor : receptor (β_{ij}) to be evidence of a positive or facilitative plant–plant interaction when $\beta_{ij} \pm 2SE > 0$, a neutral interaction when $\beta_{ij} \pm 2SE$ overlapped 0 and of a negative or competitive interaction when $\beta_{ij} \pm 2SE < 0$. The percentage of each type of interaction was determined for each community.

RESULTS

We counted a total of 57 514 pollen grains (54 937 CP and 2577 HP) on 2987 stigmas revealing an overall number of 264 IPTs among the three communities (Table 1). The highest richness of plant species and IPTs was found in the intermediate community (1800 m). Average total pollen load per stigma was extremely variable among species (range: 0–180.84 grains). CP was identified in *c.* 85% ($n = 2513$) of all stigmas examined, HP was detected in only *c.* 21% ($n = 625$) and no pollen grains in *c.* 14% of stigmas ($n = 426$) (i.e. flowers presumably not visited by pollinators). In general, the amount of HP per stigma was small compared to CP deposition, which for most species represented > 90% of total pollen load per stigma (range: 36.7–100%). The maximum number of HP grains on a stigma was 64 (*Hypochaeris tenuifolia*), whereas the maximum number of different pollen species identified on a single stigma was 7 (*Valeriana carnosa*).

Table 1 Total number of species, stigmas and pollen grains (heterospecific and conspecific) sampled in each community. Interspecific pollen transfers are the total links identified in each plant–plant network. Species within each network were classified as pollen donors, receptors or balanced donor–receptors considering their incoming and outgoing pollen transfers, percentages are indicated in the table. The correlations between in- and out-degree for species within each network are also shown; in all cases values were non-significant (ns)

	1600 m	1800 m	2000 m
No. species	26	34	14
Total no. stigmas	925	1501	561
Total no. pollen grains	18960	29504	9050
Conspecific no. pollen grains	18174	27989	8774
Heterospecific no. pollen grains	786	1515	276
Interspecific pollen transfers	105	130	29
% donor species	48%	41.94%	27.27%
% receptor species	44%	51.61%	63.64%
% donor–receptor species	8%	6.45%	9.09%
In- and out-degree correlation (r_{in-out})	−0.05 ^{ns}	0.33 ^{ns}	−0.05 ^{ns}

In all IPT networks, frequency distributions of species in- and out-degree were heterogeneous and right skewed (Fig. 2). Most species received HP from one or two donors (*c.* 60% species), but a few species acted as hub-receptors and received pollen from many species. For instance, *Valeriana carnosa* (1600 m), *Armeria maritima* (1600 m), *Quinchamalium chilense* (1800 m) and *Leucheria millefolium* (1800 m) all received pollen from > 12 HP donors. A similar pattern was found for pollen donation, with most plant species donating pollen to a few receptors (*c.* 65% of species donate to less than three species) and a few species donating to many (Fig. 2). *Quinchamalium chilense* (1600 m), *Adesmia parviflora* (1800 m) and *Nassauvia pygmaea* (2000 m) showed the highest out-degree in their respective communities. In- and out-degrees were not correlated with floral abundances and pollen production of species (Appendix S3). The proportion of species acting as donors decreased from 48% in the lowest altitudinal network to 27% in the highest one, whereas the proportion of receptors increased with altitude (Table 1). Moreover, hub-receptors were not the same species acting as hub-donors, i.e. species which received pollen from many did not necessarily exported pollen to many species as shown by non-significant correlations between in- and out-degrees of species (Table 1). In-degrees of the same species present in different communities were correlated ($r_{in-in} = 0.64$, $P < 0.001$) but not out-degrees ($r_{out-out} = 0.25$, $P = 0.18$), suggesting that across communities a species identity as HP receptor is less variable than as a donor.

The overall quantitative effect of pollinator-mediated interactions on receptor species (model 1) varied from positive, neutral to negative (Fig. 3a, c, e; Table S2). In two communities (1600 and 2000 m) the effect for most receptors was positive (63 and 75% of species, respectively, Fig. 3a, e). However, in the intermediate altitudinal community (1800 m) neutral effects predominated (59% of species), followed by positive effects of pollinator sharing (33% of species) (Fig. 3c). Interestingly, negative effects for receptor species in terms of pollen quantity (model 1) were rare in all communities (5, 8 and 0% of all species at 1600, 1800 and 2000 m, respectively).

On the other hand, neutral effects prevailed when qualitative effects (model 2) of all pollinator-mediated interactions were evaluated (89, 67 and 62% of receptor species in 1600, 1800 and 2000 m, respectively; Fig. 3b, d, f; Table S2). The percentage of species with positive effects increased with altitude, from 11% at 1600 m, to 17% at 1800 m and 25% of species at 2000 m (model 2). In total, the percentage of species showing positive qualitative effects was nearly twice as high as that of species exhibiting negative effects.

Quantitative effects of pairwise donor : receptor interactions at 1600 and 1800 m (model 3) were predominantly neutral (87 and 79% of all interactions, respectively), followed by positive effects (Fig. 4a, b). A few hub-donor species within each of these two communities (i.e. species donating pollen to many other species) accounted for most positive effects on receptor species. For instance, *Quinchamalium chilense* and *Senecio argyreus* were responsible for more than half of the positive effects on receptor species at 1600 m. Contrary to findings in the two lower communities, positive interactions between

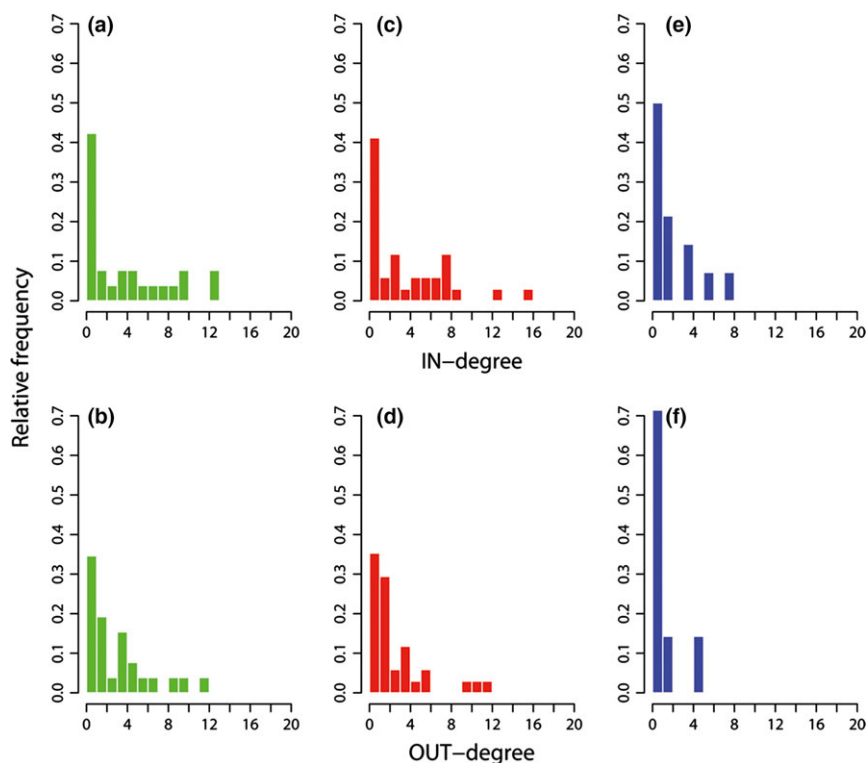


Figure 2 Frequency distributions of species in- and out-degree in the different IPT networks: (a–b) 1600 m network, (c–d) 1800 m network and (e–f) 2000 m network. In-degree distributions represent the pattern of heterospecific pollen receipt on stigmas (HP deposition), whereas out-degree distributions show the pattern of pollen donation to heterospecific stigmas (CP loss). In all cases there is a large number of species receiving from and donating to a small number of species (i.e. low in-degree and out-degree) and a small number of species receiving from and donating to a large number of species (i.e. high in-degree and out-degree).

plants prevailed in the highest altitudinal community (97% of all interactions, Fig. 4c). Thus, the proportion of positive interactions increased with altitude (9, 12 and 97% at 1600, 1800 and 2000 m, respectively).

The sign of the effect of species–pairs interactions changed depending on whether quantitative or qualitative effects were considered (model 3 vs. model 4, Fig. 4). Model 4 showed that neutral effects of IPTs on CP germination ratio predominated in the three communities, followed again by positive effects (Fig. 4d, e, f). The highest percentage of interactions with positive effects (41%) was found at the intermediate altitudinal community.

DISCUSSION

Facilitation seems to prevail over competition in pollinator-mediated interactions among plants in the high-Andean study communities. In general, pollen receptor species showed more positive or neutral than negative effects of pollinator sharing, which neither appears to reduce CP deposition nor decrease CP germination on stigmas. Interestingly, the proportion of species experiencing a facilitative effect was larger at higher than at lower altitudes. This suggests that in environments with extreme pollinator scarcity, the benefits of species co-flowering on pollinator attraction surpass the cost of CP loss. Below we discuss the potential mechanisms explaining these results, their implications and the benefits and limitations of our multi-species approach.

Pollinator-mediated interactions among plants in a multi-species context: a wide range of mechanisms and outcomes

Our study confirms that IPT due to pollinator sharing among co-flowering plants is ubiquitous in natural communities, although HP contribution to total pollen load on stigmas is small on average (McLernon *et al.* 1996; Aizen & Rovere 2010; Montgomery & Rathcke 2012; Ashman & Arceo-Gómez 2013; Fang & Huang 2013). Despite pollinators move frequently between plants and carry pollen from more than one species, only a low proportion of stigmas receives HP grains (Murcia & Feinsinger 1996; Bartomeus *et al.* 2008; Jakobsson *et al.* 2008).

In all communities we found species acting as hubs of interspecific pollen donation or receipt. These species were not those with the highest number of flowers or producing much pollen per flower, although we cannot rule out the influence of other species traits non-evaluated here, such as pollen and stigma stickiness. Surprisingly, hub-receptors were often not hub-donors, as patterns of interspecific pollen donation and receipt were unrelated at the species level. Hub-donors (e.g. *Quinchamalium chilense*, *Senecio argyreus*, *Adesmia parviflora*, *Mulinum echinus*, *Nassauvia pygmaea*) accounted for c. 50% of all interactions with positive quantitative effects in the low- and mid-elevation communities. This suggests that they play a relevant ecological role in attracting pollinators and enhancing visitation to co-occurring plants in the area. Despite effects can be variable depending on receptor identity, hub-donors

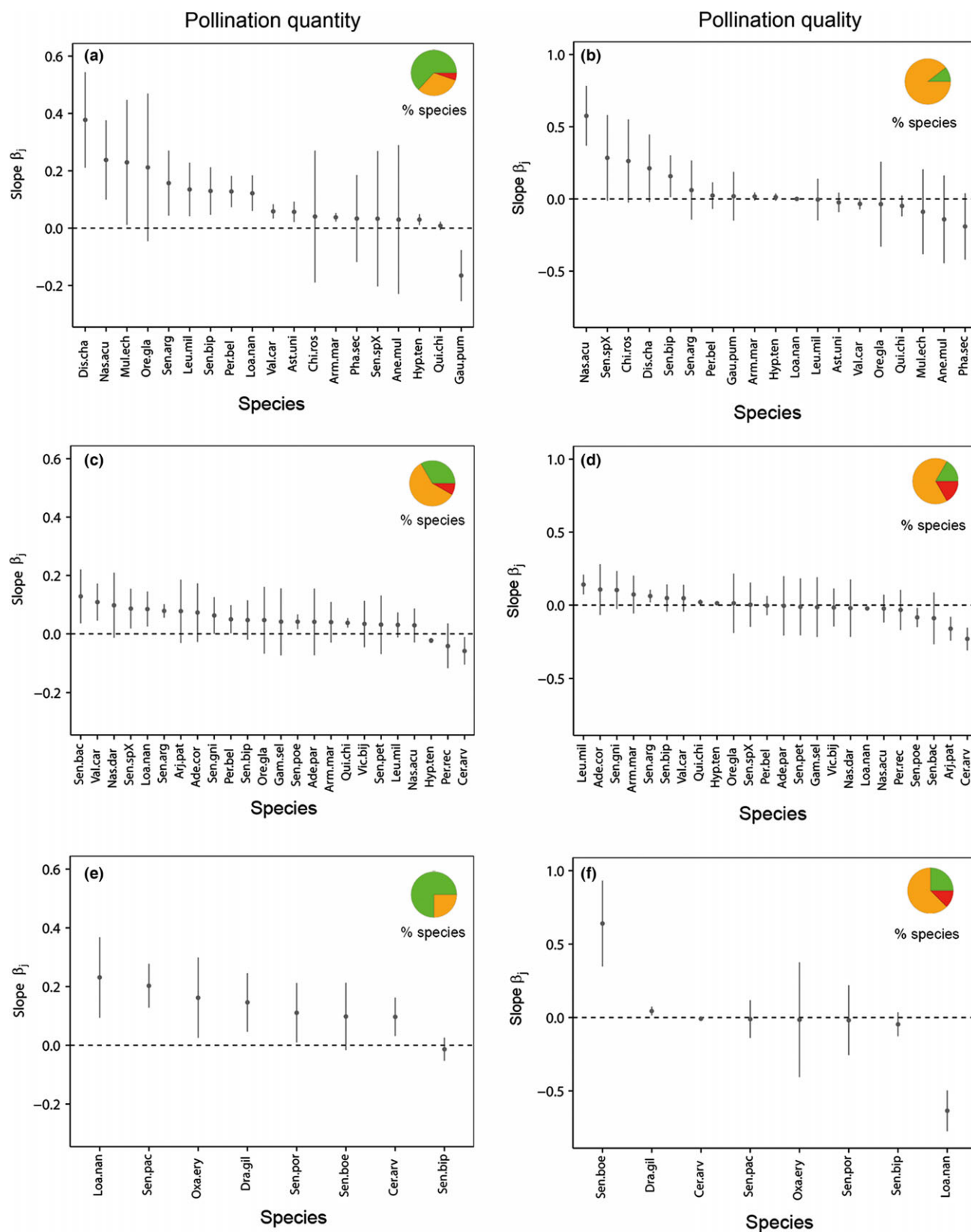


Figure 3 Estimated slopes ($\beta_j \pm 2SE$) for the effect of HP deposition on CP deposition ('pollination quantity'), and the effect of HP deposition on the proportion of CP grains germinated ('pollination quality') for each receptor plant species at the three high-Andean semi-desert communities studied: (a–b) 1600 m, (c–d) 1800 m and (e–f) 2000 m. Coloured pie charts represent the percentage of species in each case which undergo an overall facilitative (green), neutral (orange) or competitive (red) effect from sharing pollinators with other plants in the community. Results from both models show that facilitation is more common than competition in these communities.

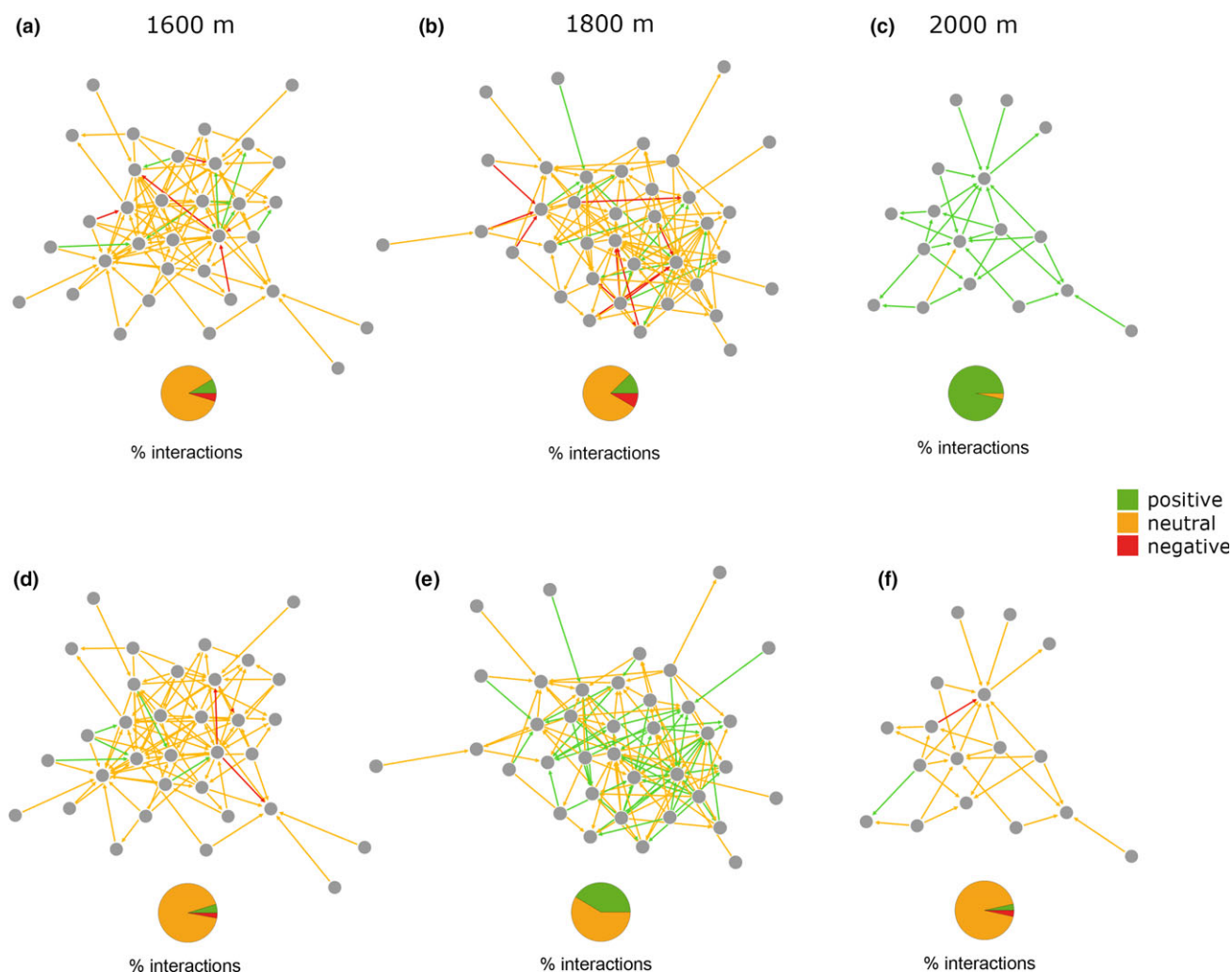


Figure 4 Plant-plant networks of the three communities studied (altitudinal levels: 1600, 1800 and 2000 m) from the high-Andean semi-desert. Nodes are plant species and links (i.e. arrows) among them represent HP transfers due to interspecific movements of shared pollinators. The arrows indicate the direction of pollen transfer from one species (donor) to another (receptor). Colours represent the sign of the quantitative effect estimated with model 3 (a, b, c) and the qualitative effect estimated with model 4 (d, e, f) of each particular plant-plant interaction. Pie charts show the percentage of each type of interactions (positive, neutral or negative) in each community.

with common positive effects on receptor species may be viewed as ‘magnet-species’ of the communities (Laverly 1992). The magnitude of influence on receptors probably depends on how important the donor is as resource (e.g. nectar and pollen), accessibility of such resource and phylogenetic proximity to receptor species (Carvalho *et al.* 2014). On the other hand, hub-receptors can be considered as the generalist plants of the community (Fang & Huang 2013). Interestingly, the role of a species as a receptor (in-degree) was quite consistent across communities, whereas its role as a donor (out-degree) was not. This finding suggests that patterns of HP receipt are influenced by species-specific floral morphological traits (Caruso 2000; Montgomery & Rathcke 2012), whereas patterns of HP donation are more community specific and largely influenced by diversity and traits of co-flowering species as well as by pollinators’ preferences and behaviour.

The fact that some species act more as donors and others as receptors implies different selective pressures and potential

evolutionary consequences (Feinsinger 1987). For donors, the fitness costs from pollinator sharing mainly occur through male fitness reduction via CP loss on heterospecific stigmas (pollen misplacement), whereas for receptors effects on female fitness should be stronger through either diminished CP or increased HP deposition (Johnson *et al.* 2005; Morales & Traveset 2008; Muchhala & Thomson 2012). Although we did not measure effects of IPT on male fitness, they are an unavoidable consequence of CP loss with probably a higher magnitude than effects on female fitness, which are more contingent upon the occurrence of pollen limitation (Campbell & Motten 1985; Murcia & Feinsinger 1996; Flanagan *et al.* 2009; Aizen & Rovere 2010; Muchhala & Thomson 2012).

Pollination plant-plant interactions occur through two main interconnected mechanisms: (1) changes in flower visitation rates and (2) changes in pollination quantity and quality (Mitchell *et al.* 2009). In the high-Andean study communities, the net outcome of these mechanisms was neutral for many

species, but pollinator-mediated facilitative effects prevail over competitive effects. In a different multi-species approach, Hegland *et al.* (2009) reported also more facilitation than competition for visitation among plant species in a temperate grassland. The combination of particularly rewarding hub-species and aggregations of multiple species flowering together may increase pollinator attraction (Lavery 1992; Moeller 2004; Ghazoul 2006; Molina-Montenegro *et al.* 2008), thus benefiting most plants with an increase in visits which deposit CP. Increasing visitation via hub-species or multi-species attraction effects also involves increased HP deposition, a process which might counteract the above-mentioned benefits. Nevertheless, we observed that HP deposition only occurred in a relatively small fraction of stigmas and, for most species, in amounts probably not large enough to entail detrimental effects (Morales & Traveset 2008). Nevertheless, effects are likely to vary with pollen and stigma characteristics of both donors and receptors (e.g. pollen size, stigma area), plant mating systems, phylogenetic relatedness or arrival time of HP relative to CP (Caruso & Alfaro 2000; Ashman & Arceo-Gómez 2013; Fang & Huang 2013).

Interestingly, the sign of particular pollinator-mediated interactions and their incidence changed depending on whether quantity or quality effects were considered. In general, facilitative effects were more common in terms of quantity than quality. Pollinator sharing might translate into an increase in CP deposition per flower, but quality of this CP load (Aizen & Harder 2007) might depend on the degree of kinship (self vs. outcross) between pollen and target stigma (Mitchell *et al.* 2009; Liao *et al.* 2011). Although 66.6% of plant species in our communities have mechanisms (e.g. dichogamy, dioecy, herkogamy, self-incompatibility) to reduce or even avoid autogamy (Table S1), a fraction of CP deposited on their stigmas might come from either the same flower or other within-individual flowers (geitonogamy). Under both scenarios, a negative relation might be detected between HP and CP germination ratio whenever self-pollen: (1) germinates less or slower than outcross pollen (e.g. Aizen *et al.* 1990; Montalvo 1992), (2) does not germinate in sporophytic self-incompatible species (e.g. Galen *et al.* 1989; Waser & Price 1991; de Jong *et al.* 1993) or (3) its germination is affected by HP deposition (Arceo-Gómez & Ashman 2014). Perhaps more pollination quality effects might have been detected if, for instance, pollen-tube survival rather than germination rates had been measured because pollen-tube growth is a better indicator of genetically and environmentally driven pollen–pistil interactions (e.g. Souto *et al.* 2002). Despite the larger paucity of pollination quality than quantity effects detected here, there was also a trend for the former to reflect facilitation rather than competition.

Community-wide studies are important to address whether the overall effect of simultaneous pollinator sharing among multiple species is a linear additive or, alternatively, a non-additive combination of pairwise interactions' effects alone (Mitchell *et al.* 2009; Flanagan *et al.* 2011). Our findings suggest the latter, at least for the sign of the overall effect. This might occur if HP from diverse donors interacts synergistically or antagonistically on stigmas (Arceo-Gómez & Ashman 2011). Even when the overall effect is similar to the addition

of pairwise effects, it does not imply that the underlying competitive or facilitative mechanisms involved are the same (Flanagan *et al.* 2011).

Other factors not considered in our study (e.g. pollen and stigma traits, rewards, pollinator foraging behaviour, plant spatial distribution), or factors for which we only partially controlled in our models (e.g. pollinator's fluctuation in time or intraspecific variation), might influence IPT patterns and generate positive/negative relations between CP and HP without implying any facilitative or competitive processes among co-flowering species. However, overall, these sources of variation might indeed tend to decouple the relation between CP and HP rather than reinforce a positive or negative trend. For instance, intraspecific variation in rewards, number of flowers or density of conspecifics can generate small-scale spatial foraging patterns of pollinator individuals, potentially leading to heterogeneous (quantity and quality) CP transfer in space (Leiss & Klinkhamer 2005; Makino *et al.* 2007; Dupont *et al.* 2014). More rewarding or attractive plants within a population are likely to receive more visits per unit time, what should increase both CP and HP deposition (Ohashi & Yahara 2001; Cartar 2004). However, HP transfer might depend on the distribution of co-flowering species in the area, being more likely when heterospecifics are closer than when they are farther away. Also, a parallel increase in CP and HP in more rewarding or attractive plants might neither occur if, as expected, pollinators probe more flowers within plants in longer visit bouts. A similar effect might be expected in relation to temporal (e.g. daily) variation in visitation rates, where the number of flowers visited per plant could be inversely related to pollinator density. In addition, short-term variability in pollinator abundance might not be reflected in total pollen deposition because of the long flower longevity characteristic of alpine plants (Arroyo *et al.* 1985).

Why is plant–plant pollination facilitation more common at higher altitudes?

The proportion of species receiving a facilitative effect from pollinator sharing was larger at 2000 m than in the two communities below. This is consistent with the proposal that facilitation is more common in habitats with adverse conditions, as reported for nurse effects (Callaway *et al.* 2002). High elevations are severe environments where the potential for pollinator sharing increases; this is because, under low visitation rates, plants are expected to generalise to minimise pollen left undispersed in anthers (Muchhala *et al.* 2010). Moreover, plants in such habitats might be more prone to pollen limitation (but see García-Camacho & Totland 2009) and hence more likely to benefit from neighbour plants attracting pollinators. This benefit seems to be higher than the cost of CP loss associated to pollinator sharing. However, the effect of joint attraction of pollinators is a function of population density or relative abundance of floral resources (Feinsinger 1987). In general, pollinator-mediated facilitation is expected to occur at low–intermediate floral densities, but it turns into competition at relatively high densities (Feinsinger 1987; Moeller 2004; Muñoz & Cavieres 2008; Seifan *et al.* 2014). In

our communities, floral density decreased with altitude. Thus, at the highest altitude, several species growing nearby in patches could contribute to a 'mass effect' of concentration of pollinators. By contrast, at the lower altitudinal communities – in which patch sizes were larger – a dilution effect might occur because the pollinator pool becomes saturated and visits per flower decline (Feinsinger 1987). Nevertheless, the high proportion of species–pairs interactions with positive quantitative effects at 2000 m did not translate into positive qualitative effects. Because of limited floral resources and a sparse plant distribution, insects might visit more flowers per plant (Galloway *et al.* 2002) and deposit poor quality CP.

Concluding remarks

This work provides a feasible and practical multi-species approach to estimate the potential consequences of pollinator sharing in plant communities through the study of IPT. Nevertheless, the particular ecological mechanisms backing up observational inferences need further exploration. The role of competition for pollination has been frequently emphasised, but our results suggest that facilitative interactions among plant species might be predominant, particularly in habitats with challenging conditions for the pollinator service.

ACKNOWLEDGEMENTS

We thank Cecilia Ezcurra for help with plant identifications, Agustina di Virgilio for assistance with field sampling and Lucas Garibaldi for advice with statistical analyses and R scripts. We also acknowledge the editor and three anonymous reviewers for providing valuable comments on an earlier version of this manuscript. Administración de Parques Nacionales Argentina provided permission to work at the study sites. This research was funded by the Argentina National Research Council for Research (PIP 01623), the National Fund for Research (PICT 01300), the National University of Comahue (B152/04) and Programa Iberoamericano de Ciencia y Tecnología para el Desarrollo (CYTED Project 409AC0369). CT received an FPU grant from the Spanish Ministry of Education.

AUTHORSHIP

MAA designed the study. AS and CT collected samples in the field and AS analysed them in the laboratory. CT conducted data analyses with assistance of MAA. CT wrote the first draft of the manuscript and all authors contributed substantially to revisions.

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Editor, José María Gómez

Manuscript received 8 October 2015

First decision made 6 November 2015

Second decision made 20 January 2016

Manuscript accepted 4 February 2016

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