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LETTER

Pollination outcomes reveal negative density-dependence coupled with interspecific facilitation among plants

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Abstract

Pollination is thought to be under positive density-dependence, destabilising plant coexistence by conferring fitness disadvantages to rare species. Such disadvantage is exacerbated by interspecific competition but can be mitigated by facilitation and intraspecific competition. However, pollinator scarcity should enhance intraspecific plant competition and impose disadvantage on common over rare species (negative density-dependence, NDD). We assessed pollination proxies (visitation rate, pollen receipt, pollen tubes) in a generalised plant community and related them to conspecific and heterospecific density, expecting NDD and interspecific facilitation due to the natural pollinator scarcity. Contrary to usual expectations, all proxies indicated strong intraspecific competition for common plants. Moreover interspecific facilitation prevailed and was stronger for rare than for common plants. Both NDD and interspecific facilitation were modulated by specialisation, floral display and pollinator group. The combination of intraspecific competition and interspecific facilitation fosters plant coexistence, suggesting that pollination can be a niche axis maintaining plant diversity.

Keywords

Allee effects, coexistence theory, diversity maintenance, floral display, generalisation, interspecific competition, intraspecific competition, niche partitioning, plant fitness, specialisation.

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INTRODUCTION

Negative density-dependence (NDD), that is, a fitness disadvantage when a species becomes relatively abundant, prevents total dominance in a community (Adler *et al.* 2018). In species-rich tropical plant communities, NDD often fosters coexistence and promotes co-occurrence of rare and abundant species (Murphy *et al.* 2017). The abundant plant species often face higher intraspecific competition for space or abiotic resources and stronger interactions with natural enemies than rare ones, stabilising interspecific competition (Comita *et al.* 2014). Interactions with mutualists such as pollinators are often thought to be under positive density-dependence (PDD), and thus, less likely to contribute to coexistence (Ghazoul 2005). However, intraspecific competition for pollinators is common (Rathcke 1983; Ward *et al.* 2013) and NDD in flower visitation rates could make pollination a driver of plant coexistence in species-rich communities (Benadi & Pauw 2018). In fact, the relationship between pollinator visitation and pollination outcomes is often density-independent (Harder *et al.* 2016). Thus, it is necessary to measure visitation and its outcomes (pollen deposition on stigmas and pollen tubes) to better understand how pollination fosters plant coexistence.

Although NDD may be perceived at the landscape-level, flower abundance influences pollination outcomes at small spatial scales, that is, between neighbouring plants (Nottebrock *et al.* 2017). Plants may exhibit negative or positive intraspecific responses (when high conspecific density attracts less or more pollinators, respectively, Totland 1993), interspecific facilitation (when plants of different species jointly attract more pollinators, Moeller 2004) and interspecific competition (when visitation rates are reduced by plants of other species, Mitchell *et al.* 2009). Moreover, interaction between neighbours for pollination may be widespread and one interaction sign may prevail in a community (Rathcke 1983). Studies with focal plant species have shown that the effect sign of conspecific and heterospecific flower density on pollination is scale-dependent (plot- vs. landscape-level; Hegland 2014; Albrecht *et al.* 2016). Furthermore, plant species may vary in their responses to plot- (Lázaro *et al.* 2014) and landscape-level density (Benadi & Pauw 2018), hampering our ability to extend patterns from focal species to the whole community.

Theoretical models and empirical data suggest a hump-shaped relationship for visitation rates in response to conspecific and heterospecific flower density (Rathcke 1983; Seifan *et al.* 2014; Benadi & Pauw 2018). This is because rare species and low availability of floral resources at the local scale attract few pollinators. Thus, an increase in floral resources at this point generates a strong positive response in visitation rates. Abundant species and extremely high availability of floral resources

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at local scales may lead to strong intra and interspecific competition for pollination, decreasing again the visitation rates (Rathcke 1983). When interspecific competition is prevalent over facilitation, coexistence between rare and abundant plants is only fostered when there is some degree of pollination specialisation in the community. In this situation, specialisation leads intraspecific competition to be stronger than interspecific competition (Pauw 2013; Benadi 2015). Nevertheless, it is unclear which coexistence mechanisms are required to operate in generalised plant communities.

The ecosystems that exhibited flower visitation hump-shaped patterns were characterised by relatively high specialisation and pollinator abundance (Rathcke 1983; Benadi & Pauw 2018). Pollinator scarcity should lead to strong intraspecific competition, potentially generating advantages of rarity (NDD). However, the shape that density-dependence assumes in generalised and pollinator-depauperated communities is unclear. In addition to NDD, prevalence of interspecific facilitation is also expected, as the importance of joint attraction is higher when pollinators are scarce (Moeller 2004; Tur *et al.* 2016). Furthermore, facilitation can foster coexistence if rare plants benefit more than abundant plant species, weakening Allee effects (Feldman *et al.* 2004).

Besides community-level patterns of density-dependence, little is known about the ecological drivers influencing density-dependence and interspecific interactions for pollination. For instance, generalised plant species exhibit higher visitation rates than specialists and may be less prone to exhibit NDD (Benadi & Pauw 2018). Moreover heterospecific neighbours may enhance the diversity of pollinators visiting the focal plant species (Lázaro *et al.* 2009). Attracting a diverse array of visitors should translate into interspecific facilitation for generalised species. Conversely, specialised species may not experience such benefit, and may suffer stronger interspecific competition. Secondly, species that produce few flowers (small floral display) may face disproportional effects from other plants, since changes on pollinator attraction will strongly affect their visitation rates (Carvalheiro *et al.* 2014). We expect these species to be more subjected to density-dependence than species with large floral displays. Lastly, each pollinator functional group (e.g. bees, flies and hummingbirds) may respond differently to floral density (Albrecht *et al.* 2016). Indeed, factors influencing potential plant-plant interactions vary among plants pollinated by these different functional groups of pollinators (Carvalheiro *et al.* 2014; Bergamo *et al.* 2017). However, the possibility that plant specialisation, floral display and pollinator group are associated with the prevalence of NDD vs. PDD or of facilitation vs. competition has never been tested.

In this study, we investigated landscape and plot density-dependence on visitation rates, pollen deposition and pollen tube number in a biodiverse tropical community. We conducted our study in a tropical mountaintop ecosystem characterised by high generalisation and low pollinator visitation rates (Freitas & Sazima 2006; Danieli-Silva *et al.* 2012). To achieve a comprehensive community-wide assessment, we collected data for 67 animal-pollinated plant species. We expected (1) disadvantage of the most abundant species due to intraspecific competition for pollination, generating NDD and (2) positive heterospecific density-dependence (interspecific facilitation) especially for the rare species, both driven by the low availability of pollinators. We predicted that NDD and prevalence of interspecific facilitation would be modulated by plant generalisation, floral display size and pollinator group. Our results showed prevalence of NDD and interspecific facilitation on pollination outcomes, a combination that could foster plant coexistence.

MATERIALS AND METHODS

Study system

The study was conducted in the highland grassland ecosystem (*Campos de altitude*) in the Itatiaia National Park, southeastern Brazil (*c.* 2300 m a.s.l., 22°21' S, 44°40' W). This ecosystem is characterised by marked seasonality, classified as tropical mountain climate (Cwb in Köppen system, Ribeiro *et al.* 2007). Mean annual temperature is 14.4 °C, with minimum temperatures reaching −10 °C, and mean annual precipitation is 2400 mm (Ribeiro *et al.* 2007). Grasses, herbs and shrubs dominate the vegetation, growing in rocky outcrops and shallow soils. More than 150 plant species were previously recorded in the study area (Brade 1956) and our study included the 67 species (45%) for which at least one pollination metric was measured (Table S1).

Field sampling

We collected data in monthly censuses during two consecutive warm and humid seasons (October/2016 to May/2017 and September/2017 to May/2018) totalling 17 censuses. Sampling was conducted in 101 plots of 2 m^2 established on three transects along pre-existing trails in the park. We placed 30–40 plots per transect, with a minimum distance of 50 m between plots, totalling 2 km per transect and 0.02 ha of total area sampled. The minimum distances between plots of distinct transects were 1.2–2.5 km. On each census, we registered the number of individuals flowering and the number of flowers on each individual for all plots. For species with large inflorescences, we estimated the number of flowers per inflorescence. For species with flowers arranged in small capitula or other similar arrangements (i.e., individual flowers with less than one centimetre in size), we used the number of inflorescences as a surrogate of abundance (Benadi & Pauw 2018). Although the amount of resources per flower varied among species, we used abundance as a feasible first approximation of floral resources. Then, we obtained the landscape conspecific density (sum of the number of conspecific flowers of all transects for each census), plot conspecific density (number of conspecific flowers within the plot) and plot heterospecific density (number of heterospecific flowers within the plot). Landscape and plot conspecific densities were not correlated (see Results), indicating within species plot-variation. Therefore, we had to sum up all plots to achieve a comparable measurement of conspecific density over a larger scale and, consequently, broad density-dependent responses.

We registered the visitation rate per focal plant (number of visits/flowers observed/observation duration) via direct observations. We considered only visits with potential for pollination (i.e. when the visitor touched stigmas and anthers). On each monthly census, we observed a random subset of the plots. Each session lasted from 30 to 60 min due to the low visitation rates of this ecosystem (Freitas & Sazima 2006). We observed 4–6 plots per day; the same plot was observed from 1 to 9 times throughout the whole study. Sessions were conducted from 0900 h to 1500 h (peak visitation time) on sunny days. We conducted 134 h of observation for 222 focal plants of 65 plant species (two species were not censused because of their rarity and short flowering, Table S1). At the end of the day, we collected pistils from open flowers of each individual of all 101 plots and stored them in 70% alcohol. We collected 24 samples on average per species, each sample from a different plant individual (Table S1). We selected flowers starting to wilt to guarantee that all potential pollination events could have occurred. We collected 994 pistil samples from 44 species, which had flowers large enough to be manipulated without promoting artificial self-pollination (Table S1). For the other 23 species we could only calculate visitation rates by observing pollinator activity.

Pollen receipt and pollen tubes

To quantify the pollination outcomes, we counted the number of pollen grains on stigmas (pollen receipt – quantitative component of female fitness) and the number of pollen tubes in styles (qualitative component of female fitness) (Alonso *et al.* 2012). We stained pistils following Martin (1959) and performed counting with epifluorescence microscopy. Only conspecific pollen grains were counted (recognised due morphological similarity with a pollen reference collection). Pollen receipt and pollen tubes are commonly used as proxies of the pollinators' contribution to female fitness. Moreover it allows a comparison of quantitative vs. qualitative effects mediated by pollinators (Alonso *et al.* 2012; Tur *et al.* 2016). Plant species vary in pollen receipt and pollen tubes due to intrinsic differences in pollen and pistil traits. To achieve comparable values among species, we calculated z-scores (scaled to a mean of 0 and standard deviation of 1) within species for pollen receipt and pollen tubes.

Statistical analyses

Landscape and plot density-dependence

To assess landscape and plot density-dependence on visitation rate and pollination outcomes, we fitted generalised linear mixed models (GLMMs). For visitation rate (of the focal plant), we used the raw counts as a response variable and included the number of flowers per hour observed as offset, using Poisson error-structure and log link. For pollination outcomes, we used the z-scores of pollen receipt and number of pollen tubes as response variables. Then, each pollination outcome was fit separately using Gaussian error-structure and identity link. All models had the flower count variables (landscape and plot conspecific density; and plot heterospecific density, all log- and z-transformed to improve model convergence) as fixed effects. Observation time was included as fixed effect in the visitation model. We also included interaction terms between plot heterospecific density with landscape and plot conspecific density. Monthly census, focal plant species identity and plot within transect were included as random effects to account for changes in the community over the flowering season. We used two variables to describe plot heterospecific density: one using the total number of heterospecific flowers in the plot, and a second using the number of heterospecific flowers with potential pollinator sharing. Potential pollinator sharing was assumed when the focal and heterospecific plants were pollinated by the same pollinator functional group (e.g. bees, flies, beetles, hummingbirds), determined for each plant species based on observation data. Furthermore, we fitted the same models using quadratic terms for the fixed effects, since hump-shaped relationships are common (Benadi & Pauw 2018). We then compared linear and quadratic models based on their AIC values. We checked multicollinearity between the fixed factors by computing Variation Inflation Factor (VIF). Factors had VIF < 3 in all models, and thus we assumed robustness to collinearity (Zuur *et al.* 2010).

Determinants of density-dependence

We investigated ecological determinants of density-dependence. For this, we used a subset of 37 species for which we had enough pollen receipt and pollen tubes sample sizes per species (at least 8 samples from different individuals, Table S1). We did not use visitation rates since few species had enough sample size for this variable. For landscape-level conspecific density-dependence, we restricted our analysis to 28 species that had flower counts over several months, and thus, enough variation in flowering density (Table S1). We fit two GLMMs: the first with pollen receipt and the second with pollen tubes as response variables. All models had landscape conspecific density, plot conspecific density, plot heterospecific density (with potential pollinator sharing), their interactions, and monthly census as fixed effects. We log transformed all flower count variables due their skewed distribution. Focal plant species was included as a random effect (random slope and intercept), as well as plot within transect. We extracted the slope (β) per species from the models as evidence for the sign of density-dependence and interspecific interactions for pollinators (following Tur *et al.* 2016). We considered evidence of landscape- and plot-level advantages of abundance (PDD), or interspecific facilitation when $\beta \pm 2SE > 0$, evidence of landscape- and plot-level advantages of rarity (NDD), or interspecific competition when $\beta \pm 2SE < 0$, and no overall effect when $\beta \pm 2SE$ overlapped 0. In these models, we could extract the slope separately for each plant species. Thus, we preferred to use the response variables of pollen receipt and tube counts without z-transformation, fitting models with Poisson error-structure and link log. Then, we calculated the percentage of interaction signs per species for each response. The overall effect was calculated by weighted meta-analysis (with the inverse of the variance as weight) using the slope of each species as effect size and its associated error as the standard error (Hedges & Olkin 1985).

To investigate which factors modulate density-dependence, we classified each species into three attribute categories: (1) *functional specialisation*: specialised (pollinated by one functional group – bees, or flies, etc.) vs. generalised (pollinated by more than one group, Ollerton *et al.* 2007). (2) *Floral* *display size*: small (individuals displaying < 25 open flowers) vs. large (> 25 open flowers) (Fig. S1) and (3) *main pollinator group* (bees, flies or hummingbirds), considering the group that accounted for the majority of visits (> 70%) to the plant species. Appendix S1 contains details on plant classification. Then, we used these attributes as moderators in weighted fixed-effects meta-analytical models. We applied *post hoc* contrasts to inspect the differences within categories. We also calculated the proportion of species with positive, negative and no effects for all categories. All GLMMs were fitted with the R-package *lme4* (Bates *et al*. 2015) and meta-analytical procedures were done with the R-package *metafor* (Viechtbauer 2010).

RESULTS

We registered 4455 visits to 6267 observed flowers. Visitation rates were relatively low with less than one visit per flower per hour on average (0.85 ± 1.92 visits.flower^{-1}.hour^{-1}). We counted 19 345 conspecific pollen grains on stigmas, with 19.46 ± 40.47 grains on average per stigma and 12 965 pollen tubes, with 13.06 ± 23.80 tubes on average per style.

The effect of conspecific density depended on spatial scale and on heterospecific density (i.e. interactions between variables were significant, Table 1). The effect of landscape conspecific density was mostly negative, being most accentuated when heterospecific density was high (Fig. S2a, c, e). This gives strength to the expectation that rare species had advantages (negative density-dependence, NDD). Positive effects were only detected for visitation rate when heterospecific density was high (Fig. S2a). The effect of plot conspecific density was only negative for visitation rate and only when heterospecific density was low (Fig. S2b, d, f). Thus, contrary to expectations, the effect of plot conspecific density was mostly positive, revealing advantages of abundance (positive density-dependence, PDD). The effect of heterospecific density depended on conspecific density (Table 1). The increase of heterospecific density increased the different pollination metrics when landscape conspecific density was low (Fig. 1a, c, e) and when plot conspecific density was high (Fig. 1b, d, f). This suggests that facilitative effects were stronger at low landscape (rare species) and high plot conspecific density (abundant species).

The effect of heterospecific density disappeared when we considered the density of all species regardless of pollinator sharing (Table S2). The models with quadratic terms had higher AIC values than the linear models, indicating that linear relationships provided a better fit (Tables S3 and S4). Flower count variables were weakly correlated (Tables S5 and S6), allowing us to interpret their effects separately.

Determinants of density-dependence

The effects detected when running analyses per species reinforced the overall effects: prevalence of landscape-level NDD (advantages of rarity), plot-level PDD (advantages of abundance) and interspecific facilitation (Tables S7–S9, Fig. 2, Fig. S3). The proportions of species showing each effect also generally followed these patterns, with most species showing landscape-level NDD, plot-level PDD and interspecific facilitation (Tables S10–S12, Fig. 3). Exceptions were 11 species showing landscape-level NDD and PDD on pollen tubes and 15 species showing interspecific facilitation and neutral effects on pollen tubes (Fig. 3).

The prevalence of density-dependence was modulated by functional specialisation, floral display and pollinator group as expected (Table 2, Fig. 2). The exception was the lack of effect of floral display for landscape density-dependence on pollen tubes. The direction of landscape density-dependence varied between attribute categories: as expected, generalists showed no landscape density-dependence, while specialists showed landscape-level NDD on pollen receipt (χ^2 = 18.81, P < 0.001). For pollen tubes, generalists showed landscape-level PDD, while specialists showed landscape-level NDD (χ^2 = 28.96, P < 0.001). Regarding floral display, species with large displays exhibited landscape-level PDD, while small display ones showed landscape-level NDD on pollen receipt (χ^2 = 122.08, P < 0.001). There was no landscape-level density-dependence on pollen tubes for either group (χ^2 = 0.05, P = 0.832). Between pollinator groups, bee- and fly-pollinated plants had no landscape density-dependence on pollen receipt and showed similar effects (χ^2 = 0.46, P = 0.500), while both were different from the prevalent landscape-level NDD of hummingbird-pollinated plants (χ^2 = 22.87, P < 0.001 and χ^2 = 15.94, P < 0.001 respectively). For pollen tubes all pollinator groups differed: bee-pollinated plants had no landscape density-dependence, while the magnitude of the landscape-level NDD effect differed between fly- and hummingbird-pollinated plants.

Contrary to expectations, plot-level PDD (advantages of abundance) prevailed for all attribute categories, with distinct effect sizes (Fig. 2). Lastly, the direction of interspecific interactions varied between attribute categories (Fig. 2): as expected, generalists were facilitated, while competition prevailed for specialists on pollen receipt (χ^2 = 270.88, P < 0.001) and pollen tubes (χ^2 = 79.54, P < 0.001). Facilitation prevailed for both species with large displays and small displays. However, on pollen receipt, the effects were stronger for large displays (χ^2 = 14.90, P < 0.001), while both groups were facilitated in similar strength on pollen tubes (χ^2 = 0.03, P = 0.862). Finally, facilitation on pollen receipt prevailed in all pollinator groups. Bee- and fly-pollinated plants had similar positive effects (χ^2 = 0.91, P = 0.340), both higher than hummingbird-pollinated plants (χ^2 = 31.72, P < 0.001 and χ^2 = 7.87, P = 0.005 respectively). For pollen tubes, facilitation remained prevalent in bee-pollination and changed to neutral for fly-pollination, although both showed similar overall effect (χ^2 = 2.96, P = 0.085). In contrast to results on bees (χ^2 = 22.84, P < 0.001) and flies (χ^2 = 18.07, P < 0.001), competition was prevalent for hummingbird-pollination.

DISCUSSION

We found negative density-dependence in visitation and pollination outcomes, indicating advantages of rare species when compared to abundant ones. Landscape-level NDD was stronger at high heterospecific density. Therefore, interspecific interactions played a critical role in generating advantages of rarity in pollination. Interspecific competition from highly

Table 1 GLMM coefficients of the visitation rate (Poisson error structure), pollen receipt and pollen tubes (Gaussian error structure) models

	Visitation rate		Pollen receipt		Pollen tubes	
Fixed effects	β ± SE	χ^2 (*P*-value)	β ± SE	χ^2 (*P*-value)	β ± SE	χ^2 (*P*-value)
Landscape conspecific density	**−0.34 ± 0.03**	**4.20 (0.022)**	**−0.09 ± 0.04**	**4.21 (0.040)**	−0.08 ± 0.04	3.69 (0.053)
Plot conspecific density	**−0.11 ± 0.20**	**13.66 (<0.001)**	**0.15 ± 0.04**	**15.54 (<0.001)**	**0.17 ± 0.04**	**18.14 (<0.001)**
Heterospecific density	**0.91 ± 0.02**	**22.23 (<0.001)**	**0.10 ± 0.03**	**9.19 (0.002)**	**0.09 ± 0.03**	**8.76 (0.003)**
Landscape conspecific density * Heterospecific density	**−0.22 ± 0.20**	**20.79 (<0.001)**	**−0.04 ± 0.04**	**6.85 (0.011)**	**−0.05 ± 0.04**	**6.44 (0.027)**
Plot conspecific density * Heterospecific density	**−0.17 ± 0.21**	**35.87 (<0.001)**	**0.10 ± 0.04**	**6.08 (0.014)**	**0.08 ± 0.04**	**4.13 (0.042)**
Observation time	**−0.10 ± 0.08**	**5.11 (0.024)**	-	-	-	-

Landscape conspecific density was estimated as the sum of conspecific flowers at landscape-level whereas plot conspecific density was measured as the number of conspecific flowers at plot level. Heterospecific density refers to the total number of heterospecific flowers at plot level (with potential pollinator sharing). β = effect estimate, SE = standard error, χ^2 = equivalent *F* statistic. Bold values indicate significant effects at $P < 0.05$.

Random effect among-group variances: visitation rate model – 0.10 for monthly census, 0.11 for plant species and 0.17 for plot within transect. Pollen receipt model – 0.07 for monthly census, 0.02 for plant species and 0.04 for plot within transect. Pollen tubes model – 0.07 for monthly census, 0.01 for plant species and 0.04 for plot within transect.

abundant heterospecifics could lead to disadvantages to rare species and destabilise plant coexistence (Pauw 2013), but instead, we found facilitation for all outcomes. We argue that interspecific facilitation contributed to generate NDD because rare species benefited more from heterospecific neighbours than abundant ones (see Fig. 1a, c and e). Facilitation can only foster coexistence if rare species benefit disproportionately in relation to the abundant species (Soliveres *et al.* 2015). Thus, plants' pollination niches may represent an axis stabilising plant interspecific competition (Benadi & Pauw 2018; Lanuza *et al.* 2018; Johnson & Bronstein 2019). Nevertheless, landscape-level NDD was only marginally significant for pollen tubes. Some abundant species, although receiving less pollen, may have received enough to produce as many viable pollen tubes as rare species. Even though the benefit of rarity is weak when measured in terms of pollen tubes, the fact that landscape-level NDD is stronger at high heterospecific density and facilitation was stronger for rare species than common ones, may still contribute to plant coexistence.

High conspecific density at the plot-level was linked to a decline in visitation rates, but to an increase in pollen receipt and pollen tubes. These contrasting results may be explained by previous evidence on pollen carryover: low visitation rates at high conspecific density still lead to higher pollen carryover on pollinators and, consequently, to more pollen deposited per stigma than at low conspecific density (Robertson 1992). Interestingly, plot-level advantages of rarity (NDD) in visitation were stronger at low heterospecific density. This suggests that at the plot-level, intraspecific competition in visitation occurs when interspecific interactions are weaker. The plot-level advantages of abundance (PDD) in pollen receipt and pollen tubes were also reinforced at high heterospecific density and due to stronger benefits from heterospecific neighbours to abundant species. Such relationships could destabilise interspecific competition, leading to the exclusion of rare species (Heystek & Pauw 2014; Nottebrock *et al.* 2017). However, our results show that plot-level advantages of abundance are compensated at the landscape-level. While high density at the plot-level promotes better pollination outcomes, high density at the landscape-level may cause pollinator dilution and result in more flowers left unpollinated (Hegland 2014).

The effect of plot-level heterospecific density was consistently positive for all variables measured, indicating that interspecific facilitation in pollinator attraction also leads to benefits in pollination outcomes. There were no relationships with heterospecific density regardless of pollinator sharing, reinforcing the idea that interactions via pollinator sharing among neighbours accounted for this pattern. Although the identity of the heterospecific neighbour can determine the outcome of plant-plant interactions (Arceo-Gómez *et al.* 2019), overall heterospecific density was shown to affect the pollination of a single species (Albor *et al.* 2019). The prevalence of interspecific facilitation is expected when pollinators are scarce (Rathcke 1983), which was demonstrated experimentally (Lázaro *et al.* 2014) and in pollinator-depauperate communities (Tur *et al.* 2016). In these communities, plant species are under scarce pollination environments and, thus, jointly benefit from increases in pollinator attraction. The combination of interspecific facilitation with stronger benefits for rare species, and intraspecific competition is thought to maintain biodiversity (Feldman *et al.* 2004). Interestingly, we found empirical evidence for such mechanisms in a relatively generalised community, despite the theoretical requirement of niche partitioning (pollination specialisation) for NDD (Pauw 2013; Benadi 2015). We propose that strong facilitation fosters coexistence in generalised communities. In this scenario, the reduced pollination partitioning due to generalisation generates positive effects in rare species while abundant species are prevented from dominating due to intraspecific competition. This assumption still needs theoretical and experimental exploration.

We found evidence for linear relationships instead of the predicted theoretical hump-shaped patterns in pollinator visitation (Benadi & Pauw 2018). Also in alpine systems, linear relationships between visitation rates or seed set with flower conspecific and heterospecific density have been detected (Hegland *et al.* 2009; Lázaro *et al.* 2013). We attributed this to the low availability of pollinators, a feature shared by alpine communities and the tropical highland grassland studied here. In such systems, increases in conspecific floral resources are not followed by the same magnitude of increasing in visitation rates (Arroyo *et al.* 1985), generating negative linear relationships. Moreover high heterospecific density will

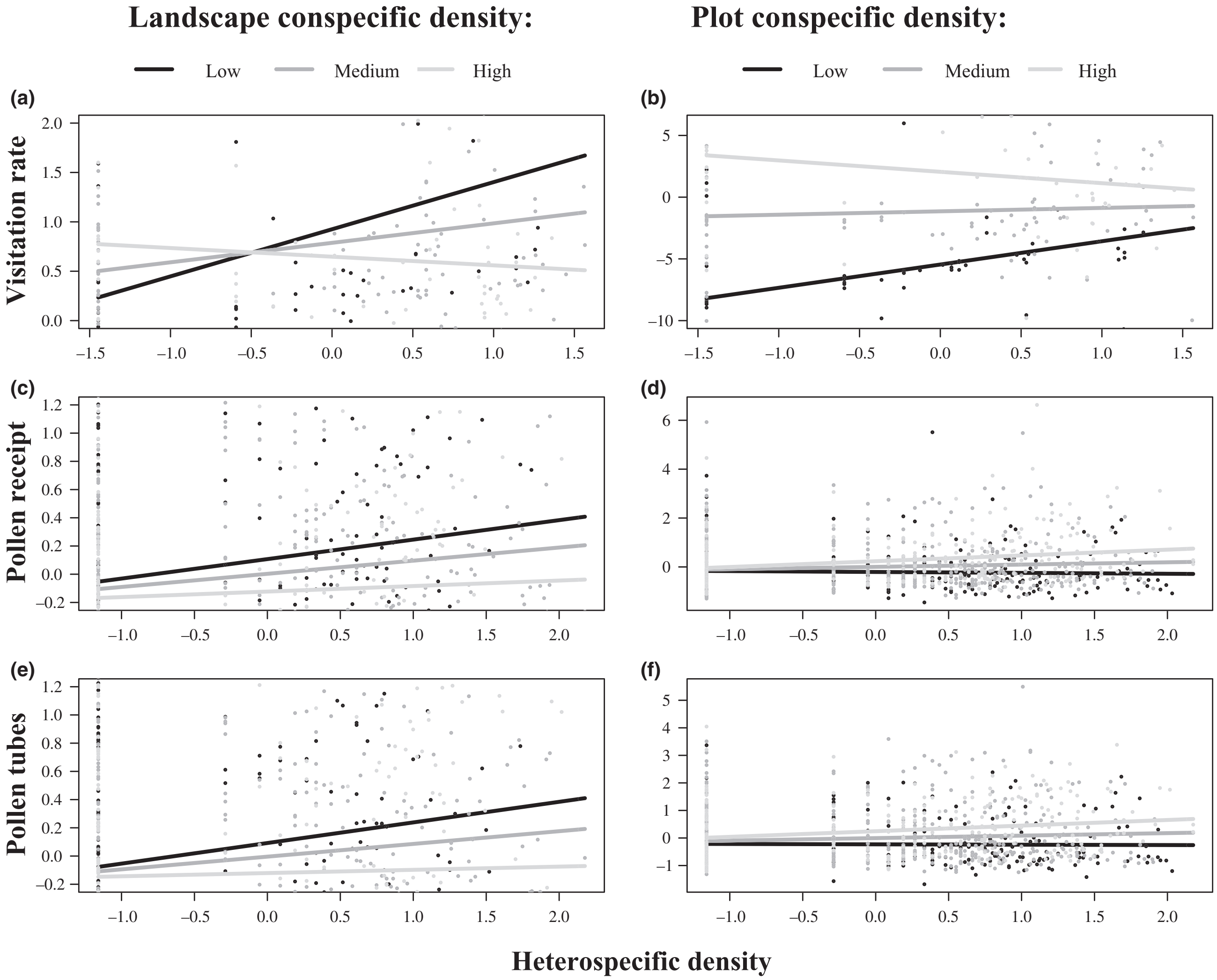
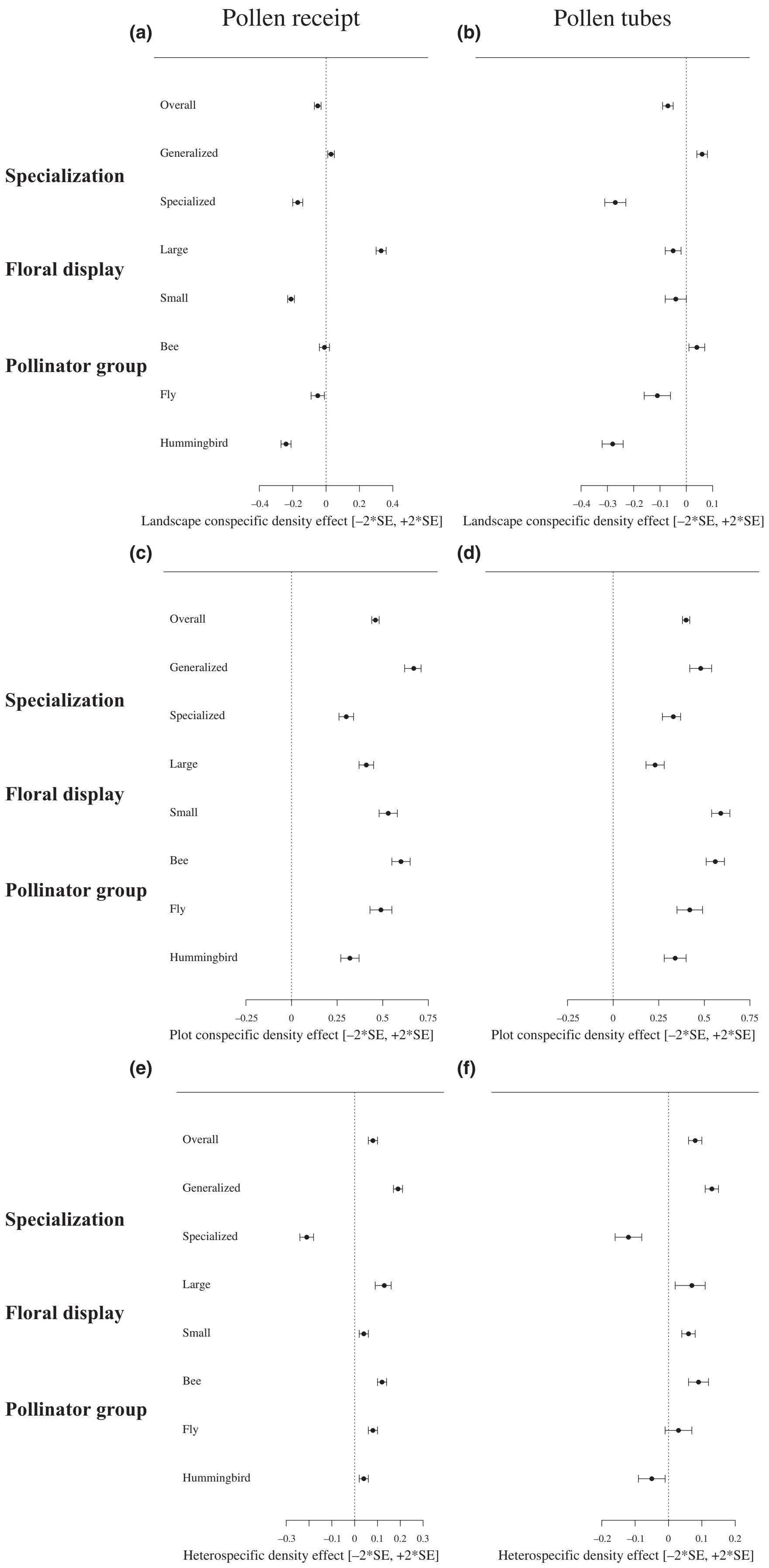


Figure 1 Interactive effects between heterospecific density with landscape conspecific density (left panels) and with plot conspecific density (right panels) on visitation rates and pollination outcomes. Each dot represents the partial residuals (after removing variation explained by other variables in each model) for each focal plant species-date combination (panels a and b) and individual stigma samples (panels c–f). Black dots and lines represent the heterospecific density effect for species with low landscape and plot conspecific density (below the first quartile), dark grey for species with intermediate landscape and plot conspecific density (between the first and third quartile) and light grey for high landscape and plot conspecific density (above the third quartile). Visitation rates are on visits.flower^{-1}.hour^{1}. The variables 'pollen receipt' and 'pollen tubes' were z-transformed (within plant species) to achieve comparable values among different species.

still lead to increases in pollinator abundance in the area and benefits of joint attraction, in contrast to the expected interspecific competition generating hump-shaped patterns.

We included only immediate pollination outcomes and, thus, proximately linked to the contribution of pollination to plant coexistence. However, we acknowledge that seed set is commonly used as a fitness proxy in coexistence studies. By comparing immediate outcomes and subsequent fitness estimates, one may assess how pollination influences plant coexistence across the reproductive dynamics of the community.

Figure 2 Estimated slopes (βj ± 2 SE) for the effect of landscape conspecific density, plot conspecific density and plot heterospecific flower density (with potential pollinator sharing at the plot level) on a, c, and e) pollen receipt (quantitative female component) and b, d, and f) pollen tubes (qualitative female component). Since all predictor variables were centred, the slopes represent effects when the other predictor in the interaction is average. We interpreted as positive effects (landscape- and plot-level positive density-dependence and interspecific facilitation) when βj ± 2 SE > 0, negative (landscape- and plot-level negative density-dependence and interspecific competition) when βj ± 2 SE < 0 and neutral when βj ± 2 SE overlapped 0. Specialisation category includes species pollinated by one pollinator group and generalisation by more than one group (i.e. functional specialisation *sensu* Ollerton et al. 2007). Floral display size categories were based on the distribution of open flowers per species in the community (Fig. S1). Small display includes species with < 25 open flowers per individual and large 25 flowers. Pollinator group categories were based on the main pollinator group visiting the species. Some species had two groups visiting in similar proportions and were thus represented in both categories (e.g. bees and flies).


Pollen receipt
Pollen tubes
(a)
(b)
Overall
Specialization
Generalized
Specialized
Floral display
Large
Small
Pollinator group
Bee
Fly
Hummingbird
−0.4
−0.2
0
0.2
0.4
Landscape conspecific density effect [−2*SE, +2*SE]
−0.4
−0.3
−0.2
−0.1
0
0.1
Landscape conspecific density effect [−2*SE, +2*SE]
(c)
(d)
Overall
Specialization
Generalized
Specialized
Floral display
Large
Small
Pollinator group
Bee
Fly
Hummingbird
−0.25
0
0.25
0.5
0.75
Plot conspecific density effect [−2*SE, +2*SE]
−0.25
0
0.25
0.5
0.75
Plot conspecific density effect [−2*SE, +2*SE]
(e)
(f)
Overall
Specialization
Generalized
Specialized
Floral display
Large
Small
Pollinator group
Bee
Fly
Hummingbird
−0.3
−0.1
0
0.1
0.2
0.3
Heterospecific density effect [−2*SE, +2*SE]
−0.2
−0.1
0
0.1
0.2
Heterospecific density effect [−2*SE, +2*SE]

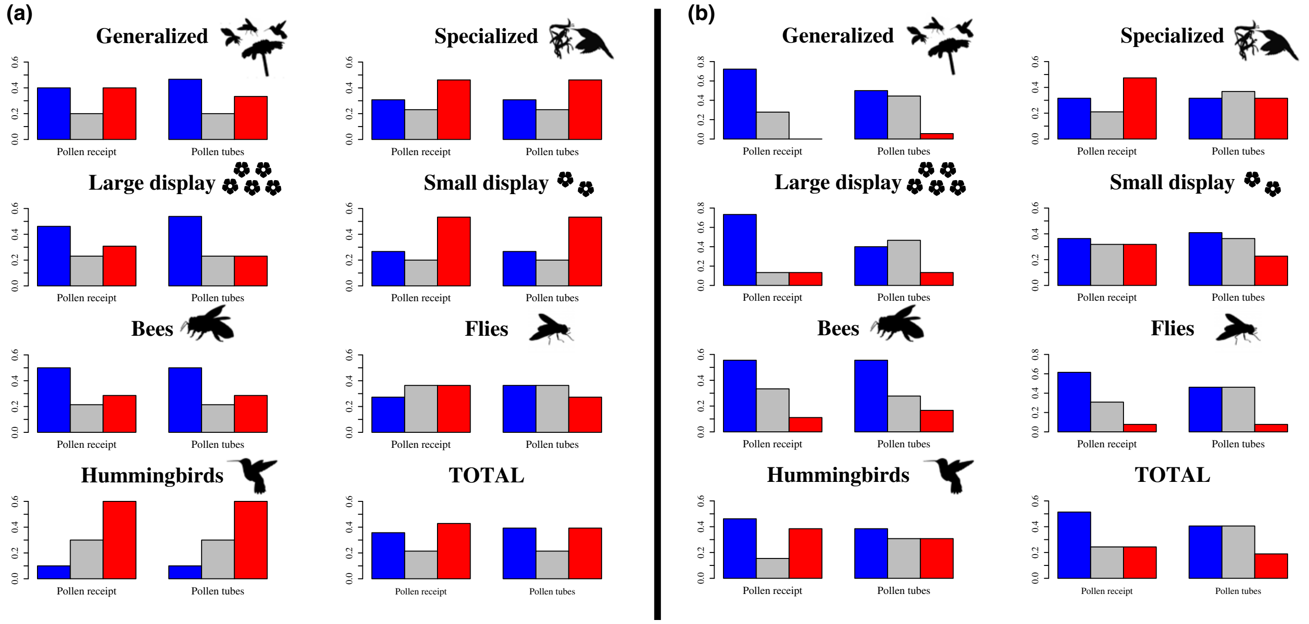


Figure 3 Coloured bar charts represent the proportion of each landscape-level density-dependence sign (a) and interspecific interaction sign (b) in the community and per each plant attribute category. Blue represents positive effects (evidence of landscape-level positive density-dependence or interspecific facilitation), grey neutral effects, and red negative effects (evidence of landscape-level negative density-dependence or interspecific competition). Specialisation category includes species pollinated by one pollinator group and generalisation by more than one group (i.e. functional specialisation *sensu* Ollerton et al. 2007). Floral display size categories were based on the distribution of open flowers per species in the community (Fig. S1). Small display includes species with < 25 open flowers per individual and large 25 flowers. Pollinator group categories were based on the main pollinator group visiting the species. Some species had two groups visiting in similar proportions and were thus represented in both categories (e.g. bees and flies).

Table 2 Meta-analytical coefficients of the analyses with the slopes per species

	Pollen receipt			Pollen tubes		
Attribute category	Landscape conspecific density	Plot conspecific density	Heterospecific density	Landscape conspecific density	Plot conspecific density	Heterospecific density
Functional specialisation	**29.48** ***P* < 0.001**	**1000.48,** ***P* < 0.001**	**196.74** ***P* < 0.001**	**46.74** ***P* < 0.001**	**428.80** ***P* < 0.001**	**42.12** ***P* < 0.001**
Floral display	**112.07** ***P* < 0.001**	**882.45** ***P* < 0.001**	**58.01** ***P* < 0.001**	0.82 *P* = 0.36	**496.93** ***P* < 0.001**	**10.05,** ***P* = 0.002**
Pollinator group	**57.83,** ***P* < 0.001**	**1104.23,** ***P* < 0.001**	**31.84** ***P* < 0.001**	**46.41,** ***P* < 0.001**	**663.62,** ***P* < 0.001**	**18.60** ***P* < 0.001**

Slopes were extracted from the pollen receipt and pollen tubes' (Poisson error structure) models using landscape conspecific density, plot conspecific density and heterospecific density as fixed effects. Landscape conspecific density was estimated as the sum of conspecific flowers at landscape-level whereas plot conspecific density was measured as the number of conspecific flowers at plot level. Heterospecific density refers to the total number of heterospecific flowers at plot level (with potential pollinator sharing). Values indicate QM coefficients and associated P levels for each attribute category on each model. Bold values indicate significant effects at $P < 0.05$.

Determinants of landscape and plot density-dependence

The landscape-level advantages of rarity (NDD) hold when accounting for only intraspecific changes in density. Thus, several species experienced disadvantages when they became abundant, making community-level Allee effects unlikely (Lachmuth *et al.* 2018). The low pollinator availability in this community likely strengthened intraspecific competition and fostered NDD (Ye *et al.* 2014). As expected, specialists showed landscape-level NDD, since it is more likely that specialised plants have stronger intraspecific competition for the same pollinator species (Johnson *et al.* 2012). Conversely, for generalists, some individuals may be 'rescued' by pollinator species that plants compete for less frequently (Ghazoul 2005). Regarding floral display, patterns matched expectations based on pollinator behavior. Pollinator foraging models have shown that flowers on plant species with small displays are visited less per plant when at high density, potentially generating NDD, while species with large displays are visited less per plant at low density, diminishing pollen receipt and favoring PDD (Ohashi & Yahara 2001). The landscape density-dependence disappeared for pollen tubes. This can be explained by the same pollinator foraging models: at high density, geitonogamy decreases for small-display species while it increases for large-display species (Ohashi & Yahara 2001). Thus, the pollination quality may counteract the density-dependence on pollen receipt.

Advantages of abundance (PDD) were often reported for both bee- and fly-pollinated plants (Ghazoul 2005; Inouye *et al.* 2015). Hummingbird-pollinated plants were shown to be under low (Caruso 1999) and strong intraspecific competition (Aldrich & Hamrick 1998), leading to no clear expectation about density-dependence. The low pollinator abundance may be similar across pollinator groups in our field site, leading to intraspecific competition within each of these pollination guilds, and to the observed lack of density-dependence for bee- and landscape-level NDD for fly- and hummingbird-pollinated species.

Pollination outcomes often increase with conspecific floral density at small spatial scales (Essenberg 2012), consistent with the plot-level PDD found for all attribute categories. This has been used to explain why pollination generates Allee effects and destabilises plant coexistence (Lachmuth *et al.* 2018). However, landscape-level advantages of rarity (NDD) prevailed, creating a scale-dependent relationship between pollination outcomes and floral abundance. Our results stress the importance of broader evaluations to assess the contribution of pollination to plant coexistence.

The fact that prevalence of interspecific facilitation also depended on plant attribute categories could be explained by functional mechanisms. Moreover, no interspecific interactions prevailed in qualitative outcomes for some categories, suggesting that some functional mechanisms lead to facilitation and competition to be equally represented (Thomson *et al.* 2019). Most facilitated species were generalists, which interact with a diverse array of pollinators. Heterospecific patches often attract a high diversity of pollinators (Lázaro *et al.* 2009), making benefits of joint attraction of distinct pollinators more likely to occur for generalists. All competitive effects were represented in specialised species. In general, specialists strongly depend on their pollinators (Vázquez *et al.* 2009). Thus, pollinator preference for an attractive heterospecific neighbour will negatively impact the pollination of specialists, as they cannot rely on alternative pollinators. Facilitation prevailed for both display categories, with large display species accounting for most of the change to neutral on pollen tubes. Although large displays benefit from high pollinator attraction, they also incur high levels of geitonogamy (Klinkhamer & de Jong 1993). Thus, the benefit of interspecific facilitation in pollinator attraction may be partly offset by costs of self-pollen deposition in species with large displays.

Regarding pollinator groups, bee-pollinated plants showed prevalence of facilitation on both pollination outcomes. We attribute this to the strong positive responses of bees to increases in floral densities at the local scale (Kunin 1997; Makino *et al.* 2007). Moreover, bees often show floral constancy even in heterospecific patches (Gegear & Laverty 2001; Lázaro *et al.* 2009), which maintains the visit quality. Facilitation on pollen receipt prevailed for fly-pollinated plants but showed no facilitation on pollen tubes. Although these plants were primarily pollinated by flies, many were also visited by other insect groups at low proportions. Thus, these plants tend to be generalised in the studied community and may benefit from pollinator sharing. However, flies may not be as constant as bees (Inouye *et al.* 2015), which may offset the benefits of higher attraction in fly-pollinated plants. Hummingbird-pollinated plants experienced facilitation and competition in similar proportions. Previous studies suggested an interplay of facilitation and competition on hummingbird-pollinated plant communities (Wolowski *et al.* 2017; Bergamo *et al.* 2018), and our results confirm that both interaction signs are similarly important for these plants.

CONCLUSION

Pollination success was greatest when a plant was rare on a landscape scale but occurred in locally dense patches of conspecific or heterospecific flowers. The combination of negative density-dependence (NDD, advantage of rarity) detected at the landscape scale and interspecific facilitation detected at the local scale found here reduces interspecific competition and fosters plant coexistence. In this context, the benefit of positive interspecific interactions would maintain rare species in the community at the same time that abundant species are prevented from reaching total dominance due to intraspecific competition. We provided empirical evidence that pollination is a component of a species' niche, playing an important role in assembling communities. Moreover, we identified ecological drivers of conspecific density-dependence and interspecific interactions for pollination, namely functional specialisation, floral display size and pollinator group. Our feasible, community-wide methodology may be useful for exploring other communities in the same way, as more data from different communities would allow us to better understand mechanisms of coexistence and maintenance of biodiversity in ecological communities.

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AUTHORSHIP

PJB, MW and MS conceived the project idea. PJB and NSS collected data. PJB, MW and AT designed data analyses. PJB wrote the first draft and all authors provided input and approved the final manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Figshare Repository: https://doi.org/10.6084/m9.figshare.9938438.

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