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The relative importance of positive and negative interactions for pollinator attraction in a plant community

Abstract Plant–pollinator interactions provide ideal frameworks for studying interactions in plant communities. Despite the large potential influence of such interactions on plant community structure, biodiversity and evolutionary processes, we know surprisingly little about the relative importance of positive and negative interactions among plant species for pollinator attraction. Therefore, we explored the relationships between conspecific and heterospecific floral densities and the flower visitation rates of nine plant species mainly visited by bumble bees, and six plant species mainly visited by flies, in a temperate grassland, through stepwise multiple regressions. Significant relationships were interpreted as interactions for pollinator attraction. Our results revealed that positive intra- and interspecific interactions for pollinator attraction were far more frequent than negative ones. Seventeen interspecific interactions were revealed of which 14 were significantly positive, whereas three of four significant intraspecific interactions were positive. Seven species experienced only positive interactions and two species experienced only negative interactions. The results presented here indicate that negative interactions are not necessarily the dominant ecological interaction for pollination among plants within a community, and the study represents a straightforward approach to study intra- and interspecific interactions among multiple species within a community. We discuss

which mechanisms may drive the positive interactions for pollinator attraction and whether this may result in facilitative effects on reproductive success.

Keywords Coexistence · Competition · Facilitation · Floral market · Joint attraction · Magnet-species · Multi-species · Pollination interactions

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Introduction

Ever since Darwin proposed "the struggle for existence" as one of the leading principles of natural selection and evolution (Darwin 1859), scientists have emphasized the role of competition in ecological interactions, and thereby its influence on population dynamics, community structure, and evolutionary processes. Concepts in which negative interactions are an important component, such as competitive exclusion, niche differentiation, and the Lotka–Volterra models, have dominated the theoretical framework of ecology (Bruno et al. 2003). Recently, however, many authors have challenged the view of a predominant importance of competition, through an increasing number of empirical studies showing that facilitation may also be important for ecological and evolutionary processes (Feinsinger 1987; Callaway 1995; Bruno et al. 2003). Competition is certainly influencing species composition and diversity, but coexistence, rather than competitive exclusion, is the rule in ecological communities (Bengtsson et al. 1994; Palmer et al. 2003).

Plant–plant interactions for pollinator attraction, i.e., flower visitation, provide an ideal ecological framework for studying the relative importance of competition and facilitation within plant communities. The visitation frequency to flowers may be important in determining the number of seeds produced in plants that requires animal pollination (e.g., Steffan-Dewenter and Tscharntke 1999; Klein et al. 2003; Morris 2003, but see Kunin 1993). Furthermore, the availability of pollinators and pollen are often limiting factors in the reproduction of plants (Bierzychudek 1981a; Ashman et al. 2004), although

increased pollen availability might as likely affect seed mass as seed quantity (Hegland and Totland 2008). Consequently, pollination is one of the most important aspects of the life-history of flowering plants (Feinsinger 1987). Moreover, pollinators are one of few factors plants compete for that are easily assessed by visual inspection, enabling a relatively easy collection of extensive multi-species data-set on plant–plant interactions.

Pollination in insect-pollinated species is sensitive to several aspects of the ecological context and the local floral density is one of the most important because it may influence pollinator activity (e.g., Thomson 1982; Sih and Baltus 1987; Feinsinger et al. 1991). Both con-specific and heterospecific individuals are potential competitors for pollinators and many earlier works in pollination ecology emphasized that negative interactions for pollinator attraction was one of the most important factors affecting the reproductive success of plants (e.g., Free 1968; Levin and Anderson 1970; Mosquin 1971). Simultaneously, other pollination ecologists argued that plants might also facilitate each other's pollinator visitation (Thomson 1978, 1982; Waser and Real 1979; Rathke 1983). Intra- or interspecific positive interactions occur if the visitation rate to individual flowers increases with the number of conspecific or heterospecific flowers in a patch, i.e., if visitation is directly positively density-dependent (sensu Sih and Baltus 1987; Feinsinger et al. 1991). Analogously, negative interactions occur when there is a negative relationship between per-flower visitation rate and conspecific or heterospecific floral density in a patch. It has been hypothesized that the relationship between floral density and pollination success (i.e., visitation rates or reproductive output) may be unimodal, such that facilitation prevails to a certain level of floral density where competition for pollinator services becomes stronger (Rathke 1983; Feinsinger 1987). Also, some authors expected co-flowering species with similar floral traits or colors to facilitate each other more than those with dissimilar traits or colors (Brown and Kodric-Brown 1979; Bierzychudek 1981b; Schemske 1981).

Previous studies of interactions for pollinator attraction have mainly focused on two-species interactions and have rarely examined intra- and interspecific interactions simultaneously (but see Thomson 1982; Caruso 2002; Moeller 2004). Consequently, it is difficult to generalize from existing literature about how plants interact for pollinator attraction at the whole-community level. The insight that most plant species are generalists in their use of pollinators (Waser et al. 1996) implies that plants have a large potential for interactions with each other when attracting pollinators. Authors have demonstrated negative effects (Thomson 1978; Campbell and Motten 1985; Feinsinger et al. 1991), positive effects (Thomson 1978, 1981; Laverty 1992; Moeller 2004; Ghazoul 2006) and no effects (Campbell and Motten 1985; McGuire and Armbruster 1991; Caruso 2002) of heterospecific floral density on pollinator visitation of a focal species. At the intraspecific level, it is commonly observed that dense patches of a flowering species are more attractive to pollinators than scattered plants, probably because foraging costs of pollinators are lower at high floral densities (e.g., Goulson 2003). However, the relationship between conspecific floral density and the visitation rate to flowers varies from positive to negative (e.g., Thomson 1981; Kunin 1997; Totland and Matthews 1998).

Competitive interactions for pollination have been suggested to be an important factor for the evolution of flowering phenologies (Mosquin 1971; Parrish and Bazzaz 1979), flower morphologies (Kodric-Brown and Brown 1979; Caruso 2000) and reproductive strategies (Fishman and Wyatt 1999), but still we know little about the importance of negative interactions for pollinator attraction at the whole community level, and its importance relative to positive interactions. We therefore examined how flower visitation rates of several species were related to heterospecific and conspecific floral densities of co-flowering plant species to assess the relative importance of positive and negative interaction for pollinator attraction in a species-rich temperate grassland community. In particular, we discuss the general expectations that the direction of such pollination interactions should be dependent on floral traits and vary along a gradient of floral densities.

Materials and methods

Study community and data collection

Our study site was a 50×50 m species-rich meadow situated on the border between the boreo-nemoral and south-boreal zone in the inner Sognefjord, west Norway. Thirty-eight insect-pollinated flowering species occurred in the study site, and 27 of these flowered simultaneously in mid-July (unpublished data). Most plant species were mainly visited by flies (Diptera) or bumble bees (*Bombus*) and these two groups dominated the pollinator community (see Hegland and Totland 2005 for more information on the plant and pollinator community). Moreover, plant species had a relatively high generalization level, i.e., median number of flower visiting species to plant species within the community was ten (unpublished data, see also Hegland and Totland 2008).

We collected data from 28 May to 18 August 2003, during 41 days. The period covered the flowering season of most plant species in the community, and thus their main pollination period. To determine the attractiveness to potential pollinators of each plant species, we assessed visitation inside 20 permanent plots of 1.5×1.5 m, randomly positioned at the start of the fieldwork. We restricted the placement of plots to areas where there were no distinct edge effects, i.e., differences in light influx and shading effects, and where the vegetation was similar in height and composition. This design, in combination with the small scale of the study, minimizes the probability that environmental heterogeneity (e.g., water availability, soil nutrients etc.) among plots will affect

the resource availability (e.g., nectar volume) and hence affect pollinator behavior independently of floral density in plots (see Hegland and Boeke 2006 for a Mantel-test of environmental heterogeneity among plots). The 10-min observation periods ($n = 201$) were randomly distributed across the plots throughout the season. We conducted most of the observation periods in calm and dry periods between 10.00 and 16.00. We monitored visitation frequency to each insect-pollinated plant species within the plots by counting the number of insect visits to their flowers or inflorescences (depending on species; hereafter, flowers). After each period, we counted the number of flowers of each species inside the plot to determine the floral density.

Precise species determination is difficult when observing visitation to flowers of many species simultaneously (see above), but information on pollinator sharing may be decisive to understand whether plant species competes for pollinators. Therefore, we used data from an accompanying sampling during 2003 and 2004 within the same community to estimate the degree of pollinator sharing between species. Using the sample of 3417 insect visitors determined to species level visiting all flowering species within the community we could investigate which pollinator species visited which plant species (see Hegland and Totland 2008 for details on transect walks). In total, 11 species of bumble bees and 133 species of diptera were determined (see Sect. "Acknowledgements") within the study community in 2003 (unpublished data; see shortened species list in Supplementary Appendix 4).

Data analysis

Primary data analysis

We focused our analysis on plant species whose pollinator assemblage mainly consisted of bumble bees (generally more than 80% of visits by bumble bees, except *Knautia arvensis*: 59%, and *Campanula rotundifolia*: 70%) and flies (more than 75% of visits by flies, except *Leucanthemum vulgare*: 59%; all numbers at group level). This choice was influenced by the fact that these pollinator groups are considered important pollinators in temperate ecosystems, and that they are relatively easy to observe. Furthermore, our sample sizes were large enough for plant species visited by these groups of pollinators to perform regression analysis (number of observation periods ranged between 31 and 189, depending on species).

Floral densities of each species (i.e., number of flowers in the 1.5×1.5 m plot) were predictors and flower visitation rate to each species (i.e., number of pollinator visits per flower during 10 min) was the response variable in multiple linear regression analyses. The use of a standardized measure for visitation (i.e., visitation rates) corrects for potential biases due to density variation in time and space. In most relationships the variance in the response variable increased with the values of the predictor variable, and therefore we used a quasi-Poisson distribution (a standard Poisson distribution could not be used because the response variables are not integers). To find the best model explaining the variation in flower visitation rates as influenced by conspecific and heterospecific floral density we applied stepwise regression with both backward elimination and forward selection ($P < 0.01$ for inclusion and $P < 0.05$ for deletion) starting with the maximum model (Crawley 2002). Because the likelihood is not formally defined for quasi-Poisson models, Akaike Information Criterion (Crawley 2002) is not available, and we therefore used an *F*-test in the stepwise procedure. The floral densities of predictor species generally showed low intercorrelations (all $r < 0.4$; see Supplementary Appendix 1A, B) and the variance inflation factor (VIF) only rarely was > 3. In the three cases where we observed a VIF >3 the variables causing this high VIF were removed and analyses redone, but reanalysis never changed which variables were included in the final model. Furthermore, there were no clear indications of unimodal relationships when inspecting the relationships between floral densities and visitation rates with scatterplots and this warrants our use of linear models.

The numbers of negative and positive relationships in the final model were used as an indication of the relative importance of negative and positive interactions at the plant community level (sensu Sih and Baltus 1987). An interaction for pollinator attraction was thus defined as a significant ($P < 0.05$) negative or positive relationship between the conspecific or heterospecific floral density in the plot (i.e., the predictors) and the flower visitation rate of a species (i.e., the responses). The observational design and subsequent regression analysis we used are probably one of the best ways to assess interactions among multiple species, as replicated experimental manipulations of multi-species assemblages would be more or less unrealistic at the community level. However, we stress that this is a correlational approach and that the results should be interpreted with care. To avoid unreliable results in the multiple regressions, we only included plant species as response species if they occurred in more than 30 observation periods. From this sub-set of plant species, we only used those that had at least 15 observation periods where pollinators actually visited flowers to ensure variation in the response variable. With this preselection, we ended up with nine response species mainly visited by bumble bees and six response species mainly visited by flies. All zero-visits were included and each period was treated as an independent observation in the analysis. Predictor species were all species mainly visited by the same pollinator group and with a minimum of 20% plot co-occurrence with the response species. Some species are only included as predictors and not as response species and the number of predictor species may vary among the separate regressions.

In addition to the results of the aforementioned statistical analyses, we present the degree of pollinator sharing between plant species that appears to interact

for pollinator services. Pollinator sharing was calculated as the number of shared pollinator species (bumble bee or fly species, respectively) divided by the total number of pollinator species visiting the responding species. These species numbers were based on the transect walks (see above) and varied between 12.5 and 100% sharing for bumble bee-visited plant species and 11.8–85.7% for fly-visited species.

Evaluating potential autocorrelation and the use of multiple tests

Three factors may cause problems for our statistical testing. First, the structure of the data does not necessarily follow the assumed quasi-Poisson distribution. Second, repeated sampling of some plots may be seen as pseudoreplication and cause inflated P-values. Third, phenology, or temporal autocorrelation, may cause a correlation between insect activity and flowering abundance and again inflate P-values. All these three factors may cause our final models to contain more, or alternatively fewer, variables than would be granted in the absence of the factors. To evaluate the potential effect of these factors on the number of variables found in the final models, three sets of randomizations were made (Supplementary Appendix 3, including detailed explanations). For all three sets, visitation rates were resampled randomly without replacement and new models were made with the same stepwise procedure as described above with the randomized visitation rates as response variable. In the first set of randomizations, no restrictions were put on the permutations that only accounted for the distribution of the variables. In the second set of randomizations, only observations within the same plots were randomized accounting for spatial autocorrelation in the data. In the third set of randomizations, only observations within the same day were randomized accounting for temporal autocorrelation in the data. Each set was permuted 1,000 times and the number of predictor variables in each randomized final model was counted for each permutation. The mean number of variables included in the final model from these permutations was compared to the number of variables included in the original models (Supplementary Appendix 3). For those response species where spatial or temporal autocorrelation could be suspected, based on the simulations, we performed an additional Mantel-test to assess whether visitation rates was autocorrelated (see Supplementary Appendix 3 for specifications). All data analyses were performed using R version 2.2.1.

Results

Interactions for pollinator attraction in bumble bee-visited plants

Heterospecific floral density affected flower visitation rate of all response species, although to a varying degree (Table 1). Of the 17 statistically significant interspecific relationships ($P < 0.05$), 14 were positive and three were negative. Six species, *Campanula rotundifolia*, *Centaurea jacea*, *Clinopodium vulgare*, *Euphrasia stricta*, *Prunella vulgaris* and *Trifolium repens* only experienced significant positive relationships with other species' floral density (one to four species); two species, *Hypericum maculatum* and *Trifolium pratense*, only experienced significant negative relationships with heterospecific floral density (one species); whereas *Knautia arvensis* had both positive and negative relationships with other species' floral density.

The conspecific floral density was important for the flower visitation rate of three species, *Campanula rotundifolia*, *Clinopodium vulgare* and *Trifolium pratense* (Table 1). The visitation rate of the two former species showed a significant positive relationship with conspecific density, indicating intraspecific facilitation for pollinator attraction. Visitation rate to the latter species showed a negative relationship with its own density, which might indicate intraspecific competition for pollinator attraction. The flower visitation rate to the six other plant species mainly visited by bumble bees showed no significant relationship with conspecific floral density.

In total, 11 bumble bee species were observed in the study community by means of transect walks in 2003 and 2004. The total number of bumble bee species visiting different plant species varied from two to eight. The degree of pollinator sharing among responding species and predictor species were in general very high and average 77.5% (see Table 1 for interaction specific degrees).

Interactions for pollinator attraction in fly-visited plants

Heterospecific floral density significantly affected flower visitation rate of only one response species, *Galium verum*, which showed a positive relationship with the floral density of two other species (Table 2). The conspecific floral density had significant impact on the flower visitation rate of only one species, *Galium verum*, and this intraspecific interaction was positive (Table 2). The flower visitation rate to the five other species was not significantly related to their own floral density.

In total, 133 Diptera species were observed in the study community by means of transect walks. The total number of Diptera species visiting the different response species varied from 7 to 51. The degree of pollinator sharing for both significant interspecific interactions was 45%.

Discussion

Positive interactions, both inter- and intraspecific, for pollinator attraction (i.e., flower visitation rate) were

Table 1 Relationships between the flower visitation rate of bumble bees to focal plants (response) and conspecific and heterospecific floral density (predictors)

	Flower visitation rate to (response)								
	Campanula rotundifolia	*Centaurea jacea*	*Clinopodium vulgare*	*Euphrasia stricta*	*Hypericum maculatum*	*Knautia arvensis*	*Prunella vulgaris*	*Trifolium pratense*	*Trifolium repens*
Floral density of (predictor)									
Campanula rotundifolia	+2.46*	ns	ns	+2.92** (100%)	−2.00* (75%)	+2.33* (63%)	+2.29* (83%)	ns	ns
Centaurea jacea	−1.57()	ns	ns	ns	ns	+2.49* (88%)	ns	ns	ns
Clinopodium vulgare	ns	ns	+2.46*	ns	ns	ns	ns	ns	ns
Euphrasia stricta	ns	ns	ns	ns	ns	ns	ns	ns	+2.76** (75%)
Hypericum maculatum	ns	ns	ns	ns		ns			
Knautia arvensis	ns	ns		ns	ns		ns	ns	ns
Prunella vulgaris	ns	+2.47* (75%)	ns	ns	ns	−1.34()	+2.23* (83%)	−1.98*	ns
Trifolium pratense	+3.23** (80%)	ns	+3.30** (100%)	+3.16** (0.75%)		ns	ns	ns	ns
Trifolium repens	ns		+4.58*** (100%)	ns	ns	ns	ns	ns	ns
Lotus corniculatus	ns		+2.13* (50%)	ns	ns	−2.06* (38%)	ns	ns	ns
Polygala vulgaris	ns	ns	ns	ns	ns	ns	ns	ns	ns
Observation periods	103	41	73	120	95	31	84	164	54
Null deviance	46.33	56.83	30.37	15.88	56.7	87.17	51.15	65.65	19.75
Residual deviance	38.84	51.4	21.87	13.34	53.57	45.79	46.46	62.92	17.33
F-value	7.90	4.96	8.04	8.21	4.79	7.94	3.84	5.51	5.07
P-value (*F*)	0.0007	0.032	0.0001	0.0005	0.031	0.0002	0.026	0.02	0.028
Dispersion	0.474	1.095	0.352	0.154	0.653	1.303	0.611	0.496	0.478

The *values* show the relative importance of competitive (−) and facilitative (+) interactions for those species that are included in the final model for bumble bee attraction in the temperate grassland community, Rudsviki, Kaupanger, western Norway

Stepwise multiple regressions, with backward elimination, (*P* < 0.05 for deletion) and forward selection (*P* < 0.01 for inclusion) starting with full model, using flower visitation rate (bumble bee visits per flower per 10 min) as response to conspecific (*shaded grey*) and heterospecific floral densities (number of flowers within 1.5 × 1.5 m plots). Statistically significant relationships (i.e., referring to *t*-test of coefficient: *P < 0.05, **P < 0.01, ***P < 0.001, and () > 0.1) are specified with *t*-values for comparability between species, while not significant relationships are denoted *ns*. When using a quasi-Poisson distribution the *t*-test and *F*-test will sometimes produce deviating results, and we here follow the *F*-tests when making the models and only use the *t*-values as indication of relative strengths of the different predictor variables. Negative *t*-values indicate a competitive (−) interaction and positive values indicate a facilitative (+) interaction for pollinator attraction. Some species are only included as predictors and not as response species and the number of predictor species may vary among the separate regressions. *Open spaces* show that the predictor species did not fulfill the selection criteria. The degree of pollinator sharing between the responding species and the predictor species (interspecific interaction), simply calculated as the number of shared species divided by the total number of species visiting the responding species, is given as a percentages. Null deviance, residual deviance, *F*-value, *P*-value, and dispersion parameter (degree of over- or underdispersion) are given for final significant models (see Sect. "Materials and methods" for further details)

Table 2 Relationships between the flower visitation rate of flies to focal plants (response) and conspecific and heterospecific floral density (predictors)

	Flower visitation rate to (response)					
	Galium uliginosum	*Galium verum*	*Leucanthemum vulgare*	*Plantago lanceolata*	*Potentilla erecta*	*Ranunculus acris*
Floral density of (predictor)						
Galium uliginosum	ns	ns	ns	ns	ns	ns
Galium verum	ns	+2.78**	ns	ns	ns	ns
Leucanthemum vulgare	ns	+2.34* (45%)	ns	ns	ns	ns
Plantago lanceolata	ns	ns	ns	ns	ns	ns
Potentilla erecta	ns	+5.42*** (45%)	ns	ns	ns	ns
Ranunculus acris	ns	ns	ns	ns	ns	ns
Galium album	ns	ns	ns	ns	ns	−0.99()
Galium boreale	ns	ns	ns	ns	ns	ns
Observation periods	52	121	52	108	189	65
Null deviance	2.38	9.6	20.31	9.6	35.45	20.4
Residual deviance		6.62				18.49
F-value		12.45				4.69
P-value (*F*)	ns	<0.0001	ns	ns	0.072	0.034
Dispersion	0.114	0.08	0.546	0.234	0.23	0.408

The *values* show the relative importance of competitive (−) and facilitative (+) interactions for those species that are included in the final model for fly attraction in the temperate grassland community, Rudsviki, Kaupanger, western Norway

Notes: see Table 1

more numerous than negative interactions, both regarding the total number of interactions (17 vs. 4) and the number of species (8 vs. 3) involved in the interactions. Seven species experienced only positive interactions, whereas two experienced only negative interactions. Comparing our results to the randomization tests, performed to control for how many relationships may occur by chance only (Supplementary Appendix 3A, B), clearly showed that the observed models had more significant relationships than expected by chance for bumble bee visitation and a bit fewer predictors than expected for fly visitation. In only two of those five response species for which we could suspect temporal or spatial autocorrelation based on the simulations, did a Mantel-test indicate any autocorrelation among the visitation rates, thus the overall result appears to be valid. Moreover, the randomization tests revealed that we should not expect the observed three-fold of positive versus negative interactions in bumble bee-pollinated plants (see Supplementary Appendix 3 for details).

Even though it has been suggested that interspecific facilitation for pollination may be a rare phenomenon (Feldman et al. 2004; Bell et al. 2005), we found a higher number of interspecific positive interactions than negative interactions for pollinator attraction. Only three out of 15 species experienced interspecific negative effects on pollinator attraction, while eight species experienced positive effects from heterospecific floral density. Other studies involving more than one pair of species have shown that all types of interactions often occur simultaneously within a community (Feinsinger et al. 1991; Grabas and Laverty 1999; Moragues and Traveset 2005). Our results underline the importance of multi-species studies to determine the relative importance of different types of interactions. Investigations on pairs of species do not necessarily include all the interactions that plant species are experiencing, and they may be inflicted by the choice of study species, i.e., researcher bias, thus making it difficult to draw conclusions about the importance of the interactions beyond the two species studied.

The flower density of species had unequal effects on visitation rate of other species. For example, *Campanula rotundifolia, Trifolium pratense* and *Trifolium repens* each affected the flower visitation rates of three or more other species, whereas several species affected only one or no other species' visitation rate (see Tables 1, 2). The three species with strong effects on multiple other species were all among the most frequently visited in the year of study and also among the species with the largest visual displays (Hegland and Totland 2005). It is possible that species with such traits, i.e., large flowers/inflorescences, high densities and/or large reward production, act as "magnets" in patches where they occur (sensu Laverty 1992), to a greater extent than others. Simultaneously, pollinators may act as optimal foragers and show a "hot-spot response" (sensu Thomson 1981) to patches of high floral density, and thus large quantities of food (Goulson 2003; Hegland and Boeke 2006). Frequent interspecific switching by individual bumble bees (Laverty 1994; Gegear and Laverty 1998), which commonly occurred in our study community (unpublished data) can be one way these "magnet"-species facilitate the visitation to other plant species.

Three out of 15 plant species experienced positive effects of conspecific floral density on the visitation rate; one experienced a negative effect, whereas the other 12 species encountered no effect of conspecific floral density. Other studies have often found that flower

visitation rate to plant species, especially by bumble bees, increases with conspecific floral density (Thomson 1978, 1981; Sih and Baltus 1987; Kunin 1997; but see Totland and Matthews 1998), and that increased visitation rate may result in increased reproductive output in some species (Laverty 1992; Kunin 1997; Steffan-Dewenter and Tscharntke 1999). Thus, such positive density effects of conspecifics may be linked to decreased pollen limitation due to increased mating possibilities through effects on pollinator attraction, degree of heterospecific pollination or selfing rates (Ashman et al. 2004).

The relationships between floral density, both heterospecific and conspecific, and pollination success (i.e., visitation rates or reproductive output) have often been suggested to be unimodal (Rathcke 1983; Feinsinger 1987). At low floral densities, there is low visitation to flowers because of low attractiveness to pollinators. With increasing floral resources, the attractiveness of the patch increases so that visitation rate also increases until a certain point where the available floral resources may saturate the pollinator pool and the visitation rate starts decreasing with increased floral density. Our results from a semi-natural species-rich meadow suggest that floral densities (Appendix S2) most often are within a range where the pollinator pool is not saturated because most relationships tend to be linear. In our case, the relationships also tend to be in the positive range of the unimodal curve; thus positive interactions for pollinator attraction are more common than negative interactions. Plants thus experience a positive effect of clustering, probably a density-dependent effect of "joint attraction" (sensu Moeller 2004). It is possible that the positive interactions for pollinator attraction are strongest among species with similar flower colors, because pollinators, such as bumble bees, may not differentiate between different plant species with similar colors (e.g., Laverty 1994; Goulson 2000). In our study, many of the strongest significant interspecific relationships between floral densities and visitation rates are among plant species with similar floral colors, for example purple, that may also appear similar to insects (e.g., Proctor et al. 1996). The degree of pollinator sharing among interacting species in our study community appears high and such sharing has been seen as a premise for competitive interactions. However, it appears that the positive responding species in our study have the highest degree of pollinator sharing (Table 1), showing that positive interactions may occur also among species sharing pollinator services.

As we have no data on the reproductive output of the response species, we cannot assess the effects of our predominantly positive interactions for pollinator attraction on plants fitness. The positive effects of "joint attraction" may for example be counteracted by heterospecific pollination (Waser 1978, i.e., reduced pollen quality) or pollen wastage (Stout et al. 1998, i.e., reduced pollen quantity) that may reduce both male and female fitness. However, different pollen placement on the body of pollinators or other mechanisms that prevent heterospecific pollen to exert stigma blocking (e.g., Feinsinger 1987; Caruso 2002) may reduce the extent to which such negative effects occur. Another negative effect may occur if individual plants experience increased floral numbers and subsequent higher visitation rates. Such increased intra-plant visitation may potentially increase geitonogamous pollination and cause higher selfing rates that may negatively affect reproductive success. The high number of positive interactions for pollinator attraction in our study community makes it conceivable that some of the species experienced positive subsequent effects on the reproductive success, even if some effects were dampened by changes in pollen quantity or quality. This study may encourage future studies to take a multi-species approach to evaluate central ecological questions. A potential extension of our study focus would be to supplement visitation observations with data on fruit production from many species within a community.

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