Original article

Do alpine plants facilitate each other's pollination? Experiments at a small spatial scale

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ABSTRACT

Short growing seasons, low temperatures, and frequent strong wind classify high mountains as adverse environments, in which pollinator abundance and activity are reduced. In such environments, plants growing in dense stands comprising several species and thus exhibiting larger and more diverse flower displays may profit by attracting more visits from scarce alpine pollinators than do plants that grow alone or in patches only composed of conspecifics. To study whether aggregation of plants increases (facilitation) or decreases (competition) the attraction of pollinators, we measured the rate and numbers with which insects entered experimental plots in the Swiss Alps, and their behaviour at flowers in plots that they entered. The plots contained individuals of the blue-flowering cushion plant *Eritrichium nanum*, either alone or mixed with white- to yellowish-flowering *Saxifraga* species. Pollinators were generally rare: in 55% of 236 observation periods, no pollinators were observed. Over 95% of the pollinators were Diptera. The average probability of observing any insect at all was higher in plots that contained some *Saxifraga* flowers, including mixed plots, than in those containing only *E. nanum* flowers. However, although insects tended to choose *Saxifraga* as the first flower visited in mixed plots, in all other regards their visitation of *Saxifraga* and *E. nanum* flowers in such plots was statistically indistinguishable. We also detected no effect of floral neighbourhood on the frequencies of potentially geitonogamous visits or of transitions among individual plants of the same or different species. Thus, our study suggests that the presence of *Saxifraga* may facilitate visitation to *E. nanum* at larger spatial scales, but gives no evidence for either competition or facilitation at small scales within floral neighbourhoods.

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1. Introduction

Plant species can exert negative, positive, or neutral effects on each other, both directly and indirectly. Direct effects involve the immediate environment of individuals, and are mostly assumed to be negative, i.e., competition for shared and limited resources such as light, water, and nutrients (e.g., Keddy, 2001). However, recent studies suggest that positive interactions, i.e., facilitation, are common in physically adverse environments (Choler et al., 2001; Callaway et al., 2002; Holzapfel et al., 2006). In alpine environments, for instance, experimental removal of neighbouring plants revealed a shift of effects from competition at low elevation to facilitation at high elevation (Choler et al., 2001; Callaway et al., 2002). Neighbouring plants at high elevations can apparently mitigate the negative effects of the abiotic alpine environment (i.e., short growing season, low temperature, strong wind) and thereby enhance each other's growth and reproduction more strongly than these are impaired by competition (Callaway et al., 2002).

Among the possible indirect interactions among individual plants are those involving the service of insect pollinators, which also respond to severe environmental conditions such as those found in the Alpine (Cruden, 1972; Kevan, 1975; Totland, 1993; Garcia-Camacho and Totland, 2009). Reduced pollinator abundance, activity, and diversity at high elevations have been reported in several studies (Schröter, 1926; Cruden, 1972; Arroyo et al., 1982, 2006; Bingham and Orthner, 1998). With limited pollinator services, increasing attractiveness to pollinators may be crucial for the reproduction of high-alpine plants. Compared to single

Table 1
Location of study sites in the Upper Engadine and adjacent valleys of southeastern Switzerland as well as the number of plots established per treatment at each site. For explanation of treatments see Fig. 1.

Site	Name	Longitude/latitude (E/N)	En plots	En + En plots	En + S plots	S + S plots
1	Fuorcla d'Agnel	9°43′00″/46°31′42″	2	2	2	2
2	Fallerfurgga	9°35′18″/46°27′74″	1	1	1	1
3	Forcellina	9°36′75″/46°25′61″	1	1	1	1
4	Margun	9°43′88″/46°30′00″	3	3	3	3
5	Fuorcla Muragl	9°57′00″/46°31′77″	1	1	1	1
6	Pischa	9°59′32″/46°28′64″	3	3	3	3
7	Piz Nair	9°46′80″/46°30′42″	4	4	4	4

individuals or patches of conspecifics, different species growing together might be particularly attractive to pollinators due to their larger and more diverse floral displays, i.e., pollination facilitation (Thomson, 1982; Rathcke, 1983). Contrasting flower shapes, colours, and odors in plant aggregations might be conspicuous to the visual or chemical sensory systems of pollinators, and mixed patches might be visited more often (Thomson, 1978; Sih and Baltus, 1987; Laverty and Plowright, 1988). However, enhanced attractiveness can also have negative consequences if it entails transfer of pollen between species, a form of competition for pollination services (Waser, 1978; Rathcke, 1983; Mitchell et al., 2009). Furthermore, insects may sequentially visit many flowers on plants with large floral displays, leading to geitonogamous selfing, which could reduce the number and fitness of offspring (Charlesworth and Charlesworth, 1987; de Jong et al., 1993). This effect of increased geitonogamy has been shown for some mixtures of species (Thomson, 1978; Brown and Kodric-Brown, 1979; Laverty and Plowright, 1988; Laverty, 1992).

Pollination facilitation has been investigated before (Thomson, 1978, 1982; Sih and Baltus, 1987; Moeller, 2004; Ghazoul, 2006; Hansen et al., 2007), but we are unaware of studies in alpine environments. Here we report on a study of the alpine cushion plant *Eritrichium nanum*, with insect-pollinated blue flowers, and its common neighbours, white- to yellowish-flowered *Saxifraga* species (Gams 1975). By observing insects in experimental plots in the Swiss Alps, we could determine (1) whether plots containing both *E. nanum* and *Saxifraga* were approached more often by pollinators than those not containing mixtures, (2) whether insects preferred one or the other species within mixed plots, and (3) whether sequential flower visits on the same individuals of *E. nanum* or *Saxifraga*, potentially leading to geitonogamy, increased in mixed associations.

2. Materials and methods

2.1. Study species and sites

Eritrichium nanum (L.) Gaud. (Boraginaceae) is a long-lived high-alpine cushion plant common at elevations between 2500 and 3000 m a.s.l. in the European Alps (Gams, 1975). Cushions produce bright blue, self-compatible flowers (Wirth et al., 2010), which offer nectar at their base (Zoller et al., 2002). The species is confined to siliceous bedrock and is commonly associated with *Saxifraga exarata* ssp. *exarata* Vill. and *Saxifraga bryoides* L. (Saxifragaceae). These two long-lived *Saxifraga* species are perennial, subalpine to alpine plants (Kaplan, 1995). In contrast to *E. nanum*, their white to yellowish flowers offer nectar that is openly accessible (Kaplan, 1995). Flies are the main pollinators of all these plant species, which flower simultaneously between June and August (Zoller et al., 2002).

We worked in the Upper Engadine and adjacent valleys (Canton of Grisons, southeastern Switzerland) from the middle of June to the end of July 2006. We chose seven study sites with sparse vegetation at elevations between 2770 and 3050 m a.s.l., separated from each other by at least 1 km (Table 1).

2.2. Experimental design and pollinator observation

Depending on the topography and area of the sites, we established different numbers of experimental plots at each site ($n = 60$ plots total; Table 1). Plots were separated by distances of more than 100 m as well as by rocky outcrops, rock terraces, or rugged terrain. Each plot consisted of an inner circle of 0.5 m radius surrounded by an outer ring of 1.5 m radius, the latter containing ten flowering *E. nanum* cushions, but no other flowering species (Fig. 1). Four treatments were established in the inner circle: (1) three *E. nanum* cushions (En; low density), (2) eleven *E. nanum* cushions (En + En; high density), (3) three *E. nanum* cushions with *S. exarata* ssp. *exarata* and *S. bryoides* as neighbours (En + S; high mixed density) and (4) only *Saxifraga* individuals (S + S; high density). Desired numbers of co-flowering plants in the inner circles and in the outer rings of plots were obtained by manually de-flowering all other plants as well as surplus *E. nanum* and *Saxifraga*. We trimmed flowers in the inner circles of plots to produce floral displays that were as similar in size as was practical to achieve; continued opening of flowers, however, led to some variation among plots in overall flower number at any given time.

To explore pollinator-mediated interactions between *E. nanum* and the two *Saxifraga* species as well as potential effects of different plant densities, we observed insects at flowers in the inner circle of each plot during 10-min periods spread nearly evenly across morning (between 0900–1130 h), midday (1130–1400) and afternoon (1400–1630). A total of 236 observation periods resulted in an overall observation duration of ca. 40 h across 20 days. Because of the general scarcity of insect flower visitors in the Alpine (Schröter, 1926; Arroyo et al., 1982, 1985), the usual approach of recording rates of visitation to single flowers or individuals would have resulted in many zero observations. Therefore, we first counted the number of insects found in the inner circle of each plot being observed at the beginning and at the end of each observation period. Second, we focused on the behaviour of single pollinators during each observation period. When the first insect entered a study plot being observed, we followed this insect until it left the study plot. Subsequently, another pollinator was observed and so on until the 10-min period was over. For each visitor being followed, we determined the species identity of the first flower visited (only in treatment En + S), the number of visited flowers per plant species, potential geitonogamy (i.e. the number of transitions from one flower to another flower of the same plant individual) and the number of transitions of visitors between cushions of the same or different species. We also counted the numbers of open flowers of *E. nanum* and *Saxifraga* species in each study plot and recorded the weather conditions in three broad classes (sunny and no wind, cloudy and/or weak wind, and rainy and/or strong wind). Visitors were classified into four broad taxonomic groups: hoverflies (Syrphidae), other flies (Diptera), bees (Hymenoptera), and beetles (Coleoptera).

2.3. Statistical analysis

We analyzed presence/absence of visitors in plots during observation periods across treatments with logistic regression using JMP 7.0.1 (SAS, Cary, USA). To all other data, general linear models were applied using SPSS 14.0 (SPSS, Chicago, USA). The effect of treatment on the mean number of visitors at the beginning
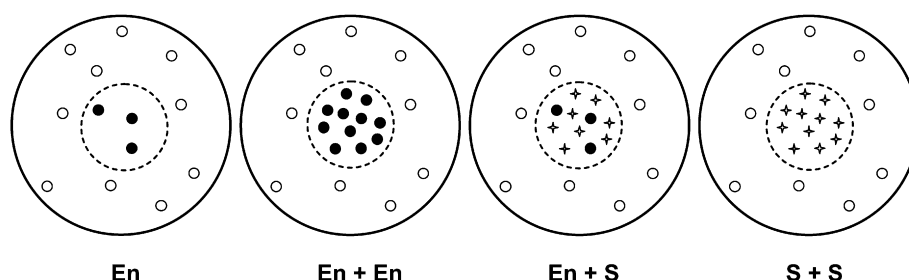
Fig. 1. Design of experimental plots. The solid circles indicate the outer rings (radius 1.5 m) that define plots, and the smaller dashed circles indicate the inner circles (radius 0.5 m) that received one of four different treatments. Black dots represent *Eritrichium nanum* and crosses represent *Saxifraga* individuals. En: three *E. nanum*; En + En: 11 *E. nanum*; En + S: three *E. nanum* with *Saxifraga* species; S + S: *Saxifraga* individuals only. Open dots represent ten *E. nanum* cushions in the outer ring.

and at the end of an observation period was tested with post hoc Bonferroni pairwise comparisons. Table 2 gives an overview of the statistical approaches, dependent variables, data transformations, factors and covariates used. We always started with full models, but in cases where the interaction terms were not significant, we dropped them from analysis. Examination of residuals indicated no deviations from normal distribution.

3. Results

3.1. Attractiveness of study plots

Of 366 insects observed to visit flowers, 0.5% were bees and 2% beetles, while the remaining 97.5% were flies, including 3% hover-flies. We saw no visitors at all in 129 of the 236 10-min observation periods (55%). The probability of observing visitors varied across the seven study sites (Table 1), with the highest value (visitors seen in 73% of observation periods) at site 4, somewhat lower values (ca. 50%) at sites 1 and 7, and the lowest values (ca. 33%) at the four remaining sites. The probability of observing visitors declined significantly under rainy weather conditions with strong wind (Table 2a; Fig. 2c), while it increased with the total number of open flowers in a study plot (Table 2a). Finally, abundance of visitors significantly increased with increasing number of flowers per plot (Table 2a).

The probability of seeing any visitors at all during an observation period was significantly higher in plots including *Saxifraga* species (treatments En + S and S + S) than in the treatments containing *E. nanum* alone (Fig. 2a, Table 2a). When we averaged the numbers of insects present at the beginning and at the end of the 10-min period in the 107 observation periods with insects present, however, this average was significantly greater only in plots with *Saxifraga* alone (treatment S + S; Fig. 2b, Table 2b); all other treatments (including En + S) were statistically indistinguishable. Treatment S + S also had the highest total number of visitors, and it was visited by all four insect groups (Fig. 2d).

3.2. Behaviour of visitors

We followed a total of 321 individual insects visiting flowers in the experimental plots. The ranking of the total numbers of visitors followed in each of the four treatments resembled that for the mean numbers of visitors at the beginning and end of each observation period: 31 visitors in treatment En, 47 in En + En, 123 in En + S and 120 in S + S. In treatment En + S, *E. nanum* was chosen as the first flower visited by only 14 insects (11.4%), whereas *Saxifraga* was first approached in the remaining 109 cases (88.6%). However, we detected no significant difference in any other aspect of insect behavioural response to the two species that we analyzed (Table 2c–h). The mean percentage of flowers visited per 10-min

period was equivalent for *E. nanum* and *Saxifraga* ($10.4 \pm 1.4\%$ versus $10.4 \pm 0.9\%$ SE), although the percentage of *Saxifraga* flowers visited increased in good weather and with increasing numbers of flowers in a plot (Table 2d, f). The mean numbers of *E. nanum* and *Saxifraga* flowers visited while we followed individual insects were also very similar (respectively 7.3 ± 1.0 and 7.5 ± 0.9), and so were the mean numbers of potentially geitonogamous visits (i.e. average number of flowers visited on the same plant after the first flower of that plant had been visited; 5.5 ± 0.9 in both cases). The mean number of potentially geitonogamous visits to *Saxifraga* flowers varied across the seven study sites, with a range of about two to ten flowers visited per plant on average. We also detected some significant site × treatment interactions (Table 2d, e, g). Pollinators rarely moved between individuals of the same or different species. We only saw ten insects flying between *E. nanum* cushions (3.1% of all insects observed), only 29 between *Saxifraga* cushions (9%), and only four between *E. nanum* and *Saxifraga* cushions (1.2%).

4. Discussion

The absence of pollinators from about half of our observations agrees with other reports of low pollinator presence and activity at high elevations (e.g., Bingham and Orthner, 1998; Arroyo et al., 2006). This is not surprising: one is immediately struck by the relative rarity of insects when ascending from a species-rich meadow at 2000 m in the Alps to a wind-blown scree slope at 3000 m. The rapidly changing and severe weather conditions at higher elevations strongly reduce insect flight.

One potential consequence of this scarcity of pollinators is that plants growing in aggregations with other species and flowering simultaneously might attract more pollinators. Our results with *E. nanum* and *Saxifraga* spp., however, present a more complex picture. Plots containing *E. nanum* alone attracted visitors less often than treatments containing *Saxifraga*, including those with a mixture of *Saxifraga* and *E. nanum*. However, when we look at those plots that did attract insects, the numbers of insects did not differ significantly among treatments. Thus the earlier hypothesis of Zoller et al. (2002) that *Saxifraga* species attract pollinators away from *E. nanum* was not confirmed when one considers mixtures of the species as neighbours. Competition between neighbouring *E. nanum* and *Saxifraga* via interspecific transfer of pollen (e.g., Mitchell et al., 2009) also seems unlikely, given how rarely we observed insects flying from one species to another.

It certainly is possible that we were observing two apparently contradictory effects. First, the presence of some *Saxifraga* in a plot might send some sensory signal that attracts insects at a higher rate (or provide a reward that causes them to return at a higher rate) than is the case when no *Saxifraga* flowers are present. Once insects arrive, however, they appear not to prefer *Saxifraga* relative to *E. nanum*. That this latter "neutral" interaction (Rathcke, 1983)

Table 2
Overview of statistically analyzed variables, data transformation, treatments (Fig. 1), statistical methods, covariables and factors as well as P-values for those effects that are significant.

Data	Data type [transformation]	Treatments	Statistical method[a]	Covariable [transformation]	Factors	Interaction	Significant effects	Chi^2	F-value	P
Attractiveness of plots										
(a) Presence of visitors	0 or 1 per plot	En En + En En + S S + S	LR	Flowers per plot [log] Weather	Study site (random) Treatment (fixed) Time (fixed)		Treatment Study site Weather Total number of flowers	20.738 20.373 7.896 12.563		0.001 0.002 0.019 0.001
(b) Number of visitors	Average number of visitors per plot [log + 1]	En En + En En + S S+ S	GLM	Fowers per plot [log] Weather	Study site (random) Treatment (fixed) Time (fixed)	Study site × treatment	Treatment Total number of flowers		6.464$_{3, 23.667}$ 4.059$_{1, 81}$	0.002 0.047
Behaviour of visitors										
(c) Percentage of En flowers visited	Number of En flowers visited over total number of En flowers [log + 1]	En En + En En + S	GLM	Weather	Study site (random) Treatment (fixed) Time (fixed)	Study site × treatment				
(d) Percentage of S flowers visited	Number of S flowers visited over total number of S flowers [log + 1]	En + S S + S	GLM	Weather	Study site (random) Treatment (fixed) Time (fixed)	Study site × treatment	Weather Study site × treatment		5.252$_{1, 80}$ 3.788$_{6, 80}$	0.025 0.002
(e) Number of En flowers visited	Mean number of visited En flowers per visitor [log + 1]	En En + En En + S	GLM	Number of En flowers per plot [log + 1] Number of S flowers per plot [log + 1] Weather	Study site (random) Treatment (fixed) Time (fixed)	Study site x treatment	Study site x treatment		2.778$_{8, 68}$	0.010
(f) Number of S flowers visited	Mean number of visited S flowers per visitor [log + 1]	En + S S + S	GLM	Number of En flowers per plot [log + 1] Number of S flowers per plot [log + 1] Weather	Study site (random) Treatment (fixed) Time (fixed)	Study site x treatment	Number of S flowers per plot		6.076$_{1, 78}$	0.016
(g) Geitonogamy of En cushions	Mean geitonogamous visits per visitor [log + 1]	En En + En En + S	GLM	Number of En flowers per plot [log + 1] Number of S flowers per plot [log + 1] Weather	Study site (random) Treatment (fixed) Time (fixed)	Study site x treatment	Study site x treatment		2.910$_{8, 68}$	0.007
(h) Geitonogamy of S cushions	Mean geitonogamous visits per visitor [log + 1]	En + S S + S	GLM	Number of En flowers per plot [log + 1] Number of S flowers per plot [log + 1] Weather	Study site (random) Treatment (fixed) Time (fixed)	Study site x treatment	Study site		10.118$_{6, 5.642}$	0.008

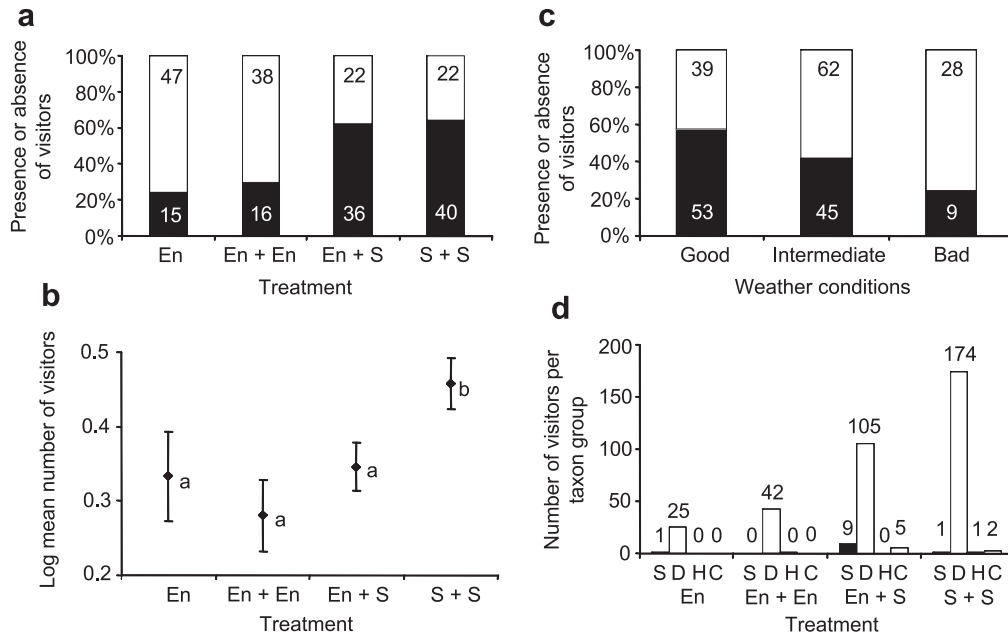[a] LR: logistic regression; GLM: general linear model.

Fig. 2. Effects of treatments and weather conditions on the attractiveness of experimental plots to insect visitors. (a) Percentages of 236 observation periods during which pollinators were present (filled) or absent (open) per treatment. (b) Log mean number of insect visitors (±SE) per observation period and treatment, taken from averages of numbers of visitors seen at the beginning and end of each period (excluding observation periods where no visitors were observed). Different lower-case letters indicate significant differences between treatments according to Bonferroni pairwise comparisons ($\alpha \leq 0.05$). (c) Percentages of observation periods during which pollinators were present (filled) or absent (open) as a function of weather conditions (good = sunny and no wind; intermediate = cloudy and/or weak wind; adverse = rainy and/or strong wind). (d) Total number of insect visitors of different taxa per treatment across all observation periods (S: Syrphidae; D: other Diptera; H: Hymenoptera; C: Coleoptera). Numbers within the histograms in (a) and (c) indicate the numbers of observation periods. Numbers in (d) give the number of observed insect visitors. For treatment abbreviations see Fig. 1.

appears to dominate is suggested by results of a study on seed set in the same system and conducted in the same region (Wirth et al., in press), which detected no positive or negative effects of *Saxifraga* on the numbers of seeds produced by *E. nanum* cushions.

Neutral interactions have been reported in other studies of pollinator number and behaviour (Armbruster and McGuire, 1991; McGuire and Armbruster, 1991; Feldman, 2008). The two studies by Armbruster and McGuire resemble ours by taking place in an adverse pollination environment, the arctic tundra of interior Alaska. In contrast, most other studies of pollinator visitation patterns have been carried our in more benign environments and have provided evidence for either positive or negative interactions among co-flowering species (e.g. Waser, 1978; Thomson, 1978, 1982; Feinsinger et al., 1991; Laverty, 1992; Brown et al., 2002; Johnson et al., 2003; Moeller, 2004; Bell et al., 2005; Ghazoul, 2006; Muñoz and Cavieres, 2008; Peter and Johnson, 2008).

Even though the plant species in our study did not measurably influence rates of visitation to neighbouring flowers and even though interspecific pollen transfer was unlikely, high pollinator attractiveness might have harmful effects if it enhances geitonogamous self-pollination and thus leads to loss of fitness in the offspring (Bell et al., 2005; Mitchell et al., 2009). However, we detected no influence of mixed plant associations, higher plant densities, or higher numbers of open flowers on potentially geitonogamous visits in either *E. nanum* or *Saxifraga* spp. To be sure, we observed only a few potentially geitonogamous visits overall, and so potentially had low statistical power to detect any significant effect. However, our results find some parallels in the literature. For example, Bell et al. (2005) recorded pollinator visits to *Mimulus ringens* growing with or without *Lobelia siphilitica*, and detected no difference in geitonogamous visits between treatments. Robertson and Macnair (1995) showed that *Myosotis colensoi* was not visited by more pollinators in a proportional way when offering larger floral displays, just as we found with its relative *E. nanum*. In

contrast, several studies have detected enhanced geitonogamous visits with increasing numbers of open flowers per plant (de Jong et al., 1992, 1993; Karron et al., 2004; Mitchell et al., 2004; Ishii and Harder, 2006), or decreasing geitonogamous visits with increasing plant density (Feldman, 2006).

In complex natural landscapes, in which plants of different species are not distributed uniformly in space, the precise way in which pollinators respond to different aggregations of flowers will determine what patterns of visitation we may observe and whether they appear as facilitative or competitive. The relevant behavioural responses of pollinators include the likelihood that a single insect will perceive a patch of flowers and approach it, as well as how this individual will forage within and among individual plants of one or more species once there. Moreover, the responses must be combined across insects of the same and different species, which may or may not respond independently of one another. These individual and combined responses in a spatially complex environment may be thought of as analogues of the functional and numerical responses postulated by Holling (1959). It is tempting to speculate on how features of the high alpine — severe physical conditions, scarcity of plants, dominance of flies as pollinators, etc. — might elicit the visitation patterns that we detected, and how features at lower elevations might elicit other patterns explaining reports of clear competition or facilitation among neighbouring plants. However, speculation at this point is of little value: too little is yet known about the frequency of facilitative, neutral, and competitive interactions among plants mediated through pollination in different environments, and too little is also known about insect sensory perception and cognition, especially beyond a few species of social bees (Chittka and Raine, 2006), and in particular for alpine flies (A. Ssymank and J. Ziegler, personal communications).

The mechanism by which individual and collective behaviour of pollinators leads to fitness outcomes for plants, and how these

mechanisms might depend on taxonomic and other aspects of plants and animals, are rich areas for future exploration. In pursuit of this goal the further interaction of fields such as plant ecology and cognitive behavioural biology (e.g., Chittka and Thompson, 2001) is likely to be especially fruitful. In addition, an explicit consideration of spatial scale will be an important part of future exploration. The fact that we did not detect interactions between *E. nanum* and *Saxifraga* spp. at the scale of neighbouring plants does not preclude interactions at larger spatial scales, as indeed is suggested by the greater rate at which insects entered plots containing some *Saxifraga*. Removing *Saxifraga* from the overall landscape might therefore strongly alter the identity of insects present and their rate of visitation to *E. nanum*. The logistical difficulty of manipulating plants or the sensory cues that they present on any but small scales has so far kept us and other researchers from investigating such possible landscape-wide effects in a more complete way.

Acknowledgements

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