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# Facilitative interactions among co-flowering *Primula* species mediated by pollinator sharing

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**Abstract** We investigated flowering phenology, pollinator visitation and visitor community composition in communities of self-incompatible sympatric *Primula* species in a high-elevation Himalayan ecosystem. Within the tight constraints imposed by short growing seasons in such ecosystems, interactions among co-occurring plants for pollinators may vary from competition to facilitation, depending on the specifics of the system. We found that pollinator community composition changed with elevation in this system: lepidopterans were the dominant visitors at lower elevations (2200–3000 masl), bees (other than bumblebees) dominated at mid-elevations (3000–3800 masl) and bumblebees dominated at higher elevations (3800–4600 masl). However, within an elevation zone, there were no significant differences in pollinators amongst co-occurring *Primula* species. At a focal study site where multiple *Primula* species co-occurred, our results showed that even while the overall flowering periods of these species broadly overlapped, the peak flowering periods of different *Primula* species were temporally segregated. Upon further inferring the nature of interaction amongst co-flowering *Primula* species, we found that plots with higher *Primula* diversity ($\geq 2$ species) and density (80–100 individuals) experienced significantly higher pollinator visitation, compared with plots with single species and low flower densities (40–50 individuals). Our results suggest that in this community of sympatric, self-incompatible *Primula* species, a broadly aggregated, synchronous floral display of multiple species results in pollinator facilitation by attracting a greater number of pollinator visitors. Within this broadly synchronous display, the temporal segregation of peak flowering period of individual species may reduce competition for pollinators and limit heterospecific pollen transfer.

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## Introduction

Many self-incompatible flowering plants depend on insects for cross-pollination (Kearns et al. 1998; Klein et al. 2007), and competition among plants for

pollinator services can drive plant community structure via differentiation of flowering phenologies (Campbell 1985; Stone et al. 1998). The effective pollination and reproductive success of an individual plant is therefore closely linked to its phenology (Primack 1985; English-Loeb and Karban 1992; Ollerton et al. 2011; Sproull et al. 2015). Flowering phenology may be especially critical to successful pollination strategies in regions where multiple self-incompatible plant species co-flower and share pollinators. Co-flowering species may either experience competition for shared pollinators (Campbell 1985; Stone et al. 1998) or pollinator facilitation if co-flowering attracts a significantly higher number and diversity of pollinators (Petanidou et al. 1995; Johnson et al. 2003). Depending on the relative strengths of these processes, co-flowering plant species that share pollinators may experience either increased or decreased reproductive success (Ghazoul 2006; Yang et al. 2007; Grab et al. 2017).

Facilitation amongst synchronously flowering sympatric species occurs if the presence of one species increases the pollinator visitation of another species (Rathcke 1984; Ghazoul 2006; Grab et al. 2017). For example, individuals of self-incompatible and less-attractive *Raphanus raphanistrum* received more pollinator visits when they flowered in combination with attractive co-flowering species (Ghazoul 2006). On the other hand, synchronous flowering may also generally increase heterospecific neighbour density. Where pollinators are shared, this may result in higher rates of heterospecific pollen transfer and reduced seed sets (Campbell 1985; Bell et al. 2005; Flanagan et al. 2010; Morales and Traveset 2008). For instance, Bell et al. (2005) reported that when *Mimulus ringens* and *Lobelia siphilitica* are grown in sympatry, the outcrossing rate of *M. ringens* decreased by 20% and seed set reduced by 37%.

Flowering time divergence may be an important mechanism that can ensure reproductive isolation between sympatric species (Elzinga et al. 2007). By staggering their flowering phenology in time, sympatric species may both avoid competition for pollinator services and reduce the costs of heterospecific pollen deposition, gamete wastage or hybridization (Borchsenius 2002; Aizen and Rovere 2010). Depending on the relative costs and benefits of pollinator sharing, such asynchronous flowering may range from complete asynchrony such that flowering occurs

earlier or later than sympatric species, or partial asynchrony such that only peak flowering times of co-occurring species are segregated (Stone et al. 1998; Raine et al. 2007; Baldock 2011).

Here we examine flowering phenology and pollinator visitation in sympatric species of the herbaceous, alpine flowering plant genus *Primula*. *Primula* species are self-incompatible, high-elevation specialists with a high diversity of co-occurring species in the high elevations of the Himalayas. We first examine flowering phenology and pollinator visitation of six sympatric *Primula* species along their elevational distributional ranges. Secondly, we investigate changes in pollinator visitation with respect to diversity and the density of co-flowering species. We hypothesized that due to the short growing seasons at high elevations (Rawat and Pangtey 1987; Kudo 1991), sympatric *Primula* species may be constrained to overlap in their flowering phenology such that they experience competition for pollinator services. Alternatively, instead of competition, these species may experience facilitation if synchronous flowering attracts a large number and/or diversity of potential pollinators, provided they do not experience large costs in the form of heterospecific pollen transfer.

## Methods

### Study system

The genus *Primula* L. in the family Primulaceae is a genus of herbaceous flowering plants with an estimated global diversity of 430–500 species (Hu and Kelso 1996; Richards 2003). *Primula* species are restricted in their distribution, occurring in the cool and moist regions of the northern hemisphere (Richards 2003), including North America, Europe, China and the Himalaya, with the majority of species occurring in China and the Himalayan regions (Richards 1993). Our study was conducted in the Eastern Himalayan state of Sikkim (270°20′N, 88°40′E), India along the Lachen and Lachung valley. There are 58 *Primula* species found in the Sikkim Himalaya (Ghosh 1981), making it among the most species-rich sub-regions for this genus (Ghosh 1981; Smith and Fletcher 1948). In the Sikkim Himalaya, *Primula* species are distributed from the low-elevation temperate broad-leaved forest (1700–2700 meters

above sea level (masl) to high-elevation alpine pastures above 4000 masl (Champion and Seth 1968; Polunin and Stainton 1984), with the highest diversity of co-occurring species at the higher elevation. The genus is typically associated with a wide range of insect pollinators including bees, butterflies, and moths (Heslop-Harrison et al. 1981; Kurian and Richards 1997; Richards 2003). *Primula* provides pollen and nectar rewards for the floral visitors (Richards 2003). While there have been extensive studies on the breeding system and phylogeny of the genus *Primula* L. (Bateson and Gregory 1905; Miller et al. 1994; Mast et al. 2006; Jacquemyn et al. 2009; Schmidt-Lebuhn et al. 2012; Zhang et al. 2013) the ecology of *Primula* communities in the wild remains largely understudied (with the exception of a few studies e.g., Richards 1993).

## Population survey

Field surveys were carried out during the growing season from March to September during two consecutive years (2012–2013). In an initial reconnaissance survey, we sampled transects from 1500 to 5000 masl, which represent the lowest and the highest elevation limits of *Primula* species in this region (Hooker 1854; Polunin and Stainton 1984). Based on these surveys, *Primulas* were found to be absent below 2200 masl, therefore, transects below 2200 m were excluded.

We sampled 14 elevation bands between 2200 and 5000 masl in each valley (Lachen and Lachung). Every 200 m we laid three 100 m vertical transects that were 100 m apart from each other. Along each vertical transect, we laid 1 m² quadrats at 1, 25, 50, 75, and 100 m, for a total of 15 quadrats within each 100-m wide elevation band. In each quadrat, the presence or absence of *Primula* species and numbers of individuals of each species was recorded. Transect numbers varied between the two valleys because of differences in habitat conditions and terrain. In total, we sampled 96 transects (Lachen = 54 and Lachung = 42) and 480 quadrats. We chose six *Primula* species which varied in their distribution along elevation gradients in the two valleys. Three species are widely distributed along the elevation gradient (*Primula denticulata* 2223–4400 masl, *Primula sikkimensis* 3500–4632 masl, *Primula capitata* 2966–4432 masl), while the three remaining species occurred at elevations greater than 3500 masl

(*Primula dickieana* 3500–4010 masl, *Primula glomerata* 3800–4400 masl, *Primula primulina* 4320–4667 masl). All six species were observed to co-occur between 3400 and 4600 masl.

## Flowering phenological patterns

Within each 1 m² quadrat of the population survey from Lachen valley, we randomly selected four individuals of each *Primula* species and marked them to study flowering phenology along the elevation gradient. All marked individuals were observed every 6–8 days throughout the flowering period (March–September). The phenological phases of marked individuals were determined by counting the number of open flowers per inflorescence. In addition, we noted the onset of flowers, flowering duration and flowering peak date where each individual was in full/maximum bloom. For each individual, we calculated the flowering synchrony value. The flowering synchrony for individual $i$ ($X_i$) is a measure of the amount of overlap of individual's flowering days with those of other individuals in the population (here population refers to the elevation bands). Thus, for an individual, the flowering synchrony is a composite measure of the amount of overlap of a given individual's flowering period with those of all individuals in the population (Augspurger 1983). Perfect synchrony is represented by $X = 1$, and no-synchrony or asynchrony by $X = 0$. Synchrony values below 0.5 are considered to be low, between 0.5 and 0.85 are considered medium and above 0.85 are considered high (Augspurger 1981, 1983). Flowering synchrony is calculated as

$$X_i = \left[ \frac{1}{(n-1)} \right] \left( \frac{1}{f_i} \right) \sum e_{j \neq i} \qquad (1)$$

where $X$ indicates the degree of synchrony, $i$ and $j$ represent individuals of same species within a population, $e_j$ is the number of days during which both individuals $i$ and $j$ flower synchronously, $f_i$ is the number of days individual $i$ is in flower and $n$ is the number of individuals in the population.

The amount of overlap of all individuals with each other in the population defines the population synchrony ($Z$), which is equal to the mean of the values of individual synchrony (Augspurger 1983). Population synchrony is determined by

$$Z = \left(\frac{1}{n}\right) \sum X_i \qquad (2)$$

Population synchrony ($Z$) of focal *Primula* species along the elevation gradient was compared with two-way ANOVA (Fujikoshi 1993). All data analyses were performed using the software R 3.1.0 (R Development Core Team 2014).

### Flower visitors

During the peak blooming period (April–August), the composition and abundance of potential pollinators (hereafter flower visitors) were assessed by documenting insects visiting focal *Primula* species. We sampled twelve elevation bands between 2200 and 4600 masl in each valley (Lachen and Lachung). Every 200 m we laid three 2 m$^2$ plots, giving a total of 72 plots (36 plots per valley). We counted the number of open flowers per focal *Primula* species and recorded the pollinator visitation rates for 3 h of observation/day/plot in 10-min intervals, giving a total of 74 h of observations. The time period 07:00–13:00 h was selected because preliminary observations indicated that flower visitors before and after this period were uncommon. All observations were made under favourable weather conditions (sunny days or days with no/little cloud cover), and three observers recorded all flower visitors in each 2 m$^2$ vegetation plot. We categorized flower visitors into five categories: lepidopterans, bumblebees, other bees, flies, and others (wasps, beetles etc.).

The floral visitors along the elevation gradient as well as among *Primula* species were expected to be distinct. We calculated Shannon–Wiener diversity indices for visitor communities along the three elevation zones (i.e., 2200–3000 masl, 3000–3800 masl, and 3800–4600 masl) and compared these using Kruskal–Wallis $H$ tests (Kruskal and Wallis 2012). We also used non-metric multidimensional scaling, implemented in the *vegan* package in R (O'Hara et al. 2013) to compare Bray–Curtis dissimilarities (Bray and Curtis 1957) of the community compositions of flower visitors across elevation zones and across focal *Primula* species.

### Floral diversity and density

The objective of this observational study was to determine whether pollinator visitation increased with respect to diversity of co-flowering species. The study was carried out along the elevation gradient of Lachung valley and all the plots were within an elevation band of 3400–4600 masl where most of the focal species co-occurred. Nine 2 m$^2$ plots were selected for this study, three plots with single focal species, three with two and the remaining three with three co-flowering focal species (Table 1). We used ANOVA to compare the average number of flower visitors visiting the plots with single, two co-occurring and three co-occurring species in 10-min time intervals.

In the second observational study, run simultaneously with the above study, the objective was to determine whether pollinator visitation rates increased with increasing density of co-flowering species. Eighteen 2 m$^2$ plots were selected, nine with low flower density (40–50 flowering individuals) and nine with high flower density (80–100 flowering individuals). For each plot, 3 h of observations were recorded in 10-min time intervals on a single day, between 7:00 and 13:00 h. We used ANOVA to compare the average number of flower-visiting in plots with low and high flower densities.

## Results

### Flowering phenology: onset of flowers, flowering duration, flowering peak and synchrony

We observed a gradual delay in onset of the flowering of focal *Primula* species with increasing elevation along their elevational distribution ranges. The flowering of focal *Primula* species along the elevation gradient began in early March and ended by September. The timing of flowering differed among species at different elevations (Fig. 1a). The flowering began earlier at lower elevations (the first week of March) than at higher elevations (the second week of June). The average flowering duration of plants was 2–3 weeks at each elevation band.

Given that most of the *Primula* species in this system occurred at high elevation with short flowering periods, we observed overlap in the flowering period

**Table 1** Observational study of pollinator visitation was conducted along the elevation gradient of Lachung valley and all the plots were within the elevation zone of 3400–4600 masl, where most of the focal species co-occurred

| Plant diversity | Replicate number | Total plant/plot | Species name | Species number | Floral visitors | | | | | Visitation rate |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Lepidopteron | Other bees | Bumblebees | Flies | Other insects | |
| Single species | 1 | 150 | *P. glomerata* | 150 | 0 | 0 | 7 | 6 | 9 | 0.146667 |
| Single species | 2 | 163 | *P. primulina* | 163 | 0 | 0 | 0 | 16 | 10 | 0.159509 |
| Single species | 3 | 154 | *P. capitata* | 154 | 0 | 0 | 6 | 7 | 11 | 0.155844 |
| Two species | 1 | 152 | *P. sikkimensis* | 79 | 4 | 0 | 2 | 12 | 13 | 0.392405 |
| | | | *P. capitata* | 73 | 0 | 0 | 4 | 6 | 7 | 0.232877 |
| Two species | 2 | 150 | *P. primulina* | 76 | 1 | 0 | 5 | 14 | 16 | 0.473684 |
| | | | *P. capitata* | 75 | 0 | 2 | 12 | 6 | 4 | 0.32 |
| Two species | 3 | 151 | *P. sikkimensis* | 79 | 0 | 8 | 6 | 8 | 11 | 0.417722 |
| | | | *P. glomerata* | 71 | 0 | 2 | 11 | 7 | 7 | 0.380282 |
| Three species | 1 | 162 | *P. sikkimensis* | 57 | 7 | 1 | 3 | 13 | 12 | 0.631579 |
| | | | *P. capitata* | 59 | | 6 | 12 | 1 | 3 | 0.372881 |
| | | | *P. primulina* | 46 | 3 | 3 | 2 | 3 | 10 | 0.456522 |
| Three species | 2 | 164 | *P. sikkimensis* | 52 | 0 | 0 | 3 | 15 | 11 | 0.557692 |
| | | | *P. capitata* | 66 | 0 | 11 | 10 | 4 | 8 | 0.5 |
| | | | *P. glomerata* | 46 | 0 | 3 | 7 | 9 | 9 | 0.608696 |
| Three species | 3 | 151 | *P. sikkimensis* | 47 | 3 | 0 | 7 | 12 | 11 | 0.702128 |
| | | | *P. primulina* | 60 | 1 | 0 | 13 | 5 | 2 | 0.35 |
| | | | *P. capitata* | 44 | 6 | 0 | 7 | 4 | 5 | 0.5 |

Plots with greater plant diversity ($\geq 2$ *Primula* species) attracts higher floral visitor ($p < 0.05$ ANOVA) compared to plots with single plant species. The total number of the plants in each plot is between 150 and 164, and the number of individuals per species is approximately the same

among co-occurring species (3400–4600 masl, Fig. 1a), with at least two species flowering at the same time. However, temporal segregation or phenological displacement of peak flowering period was observed among co-flowering species (Fig. 1b). Data on peak flowering times of the *Primula* species over two valleys for the year 2013 are shown in Fig. 1b; we observed temporal separation in peak flowering times where peak flowering of *P. denticulata* was the third and the fourth weeks of April; followed by *P. dickieana*—the third and the fourth weeks of May; *P. sikkimensis*—the first and the second week of June; *P. glomerata*—the forthth week of June and the first week of July; *P. primulina*—the third and the fourth weeks of July and *P. capitata*—the fourth week of July and the first week of August (Fig. 1b).

The average values of individual flowering synchrony for all the focal species were low in most of the elevation bands ($< 0.5$) with few exceptions (medium synchrony between 0.5 and 0.63). Population flowering synchrony ($Z$, which was the mean of values of individual synchrony) ranged from low to medium 0.3–0.63 (Fig. 2).

Visitation patterns: elevation gradient, floral diversity, and density

Flowers of *Primula* species attracted numerous insect visitors. A total of 2682 visitors were observed on 33,990 flowering individuals. Lepidopterans, bumblebees, other bees, and flies were the primary visitors of focal *Primula* species across the elevation gradient. Flower visitor abundance varied across elevation, with
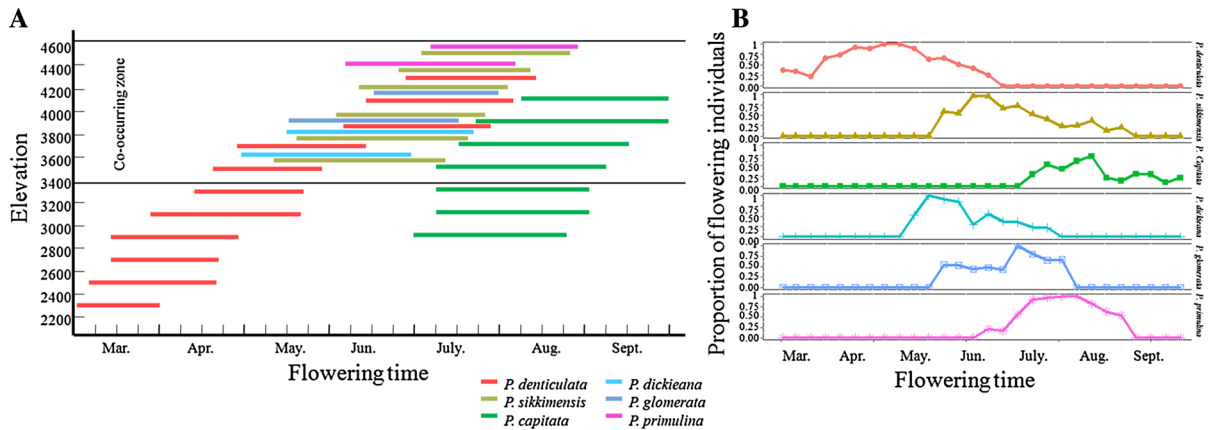
Fig. 1 The onset of flowers, flowering duration and peak flowering of focal *Primula* species. **a** Elevational differences in flowering date of focal *Primula* species during spring–summer seasons (2012–2013). The horizontal bars refer to the duration of flowering in each elevation band. **b** Segregated peak flowering of six focal *Primula* species within an elevation zone of 3400–4600 masl, where they co-occurred
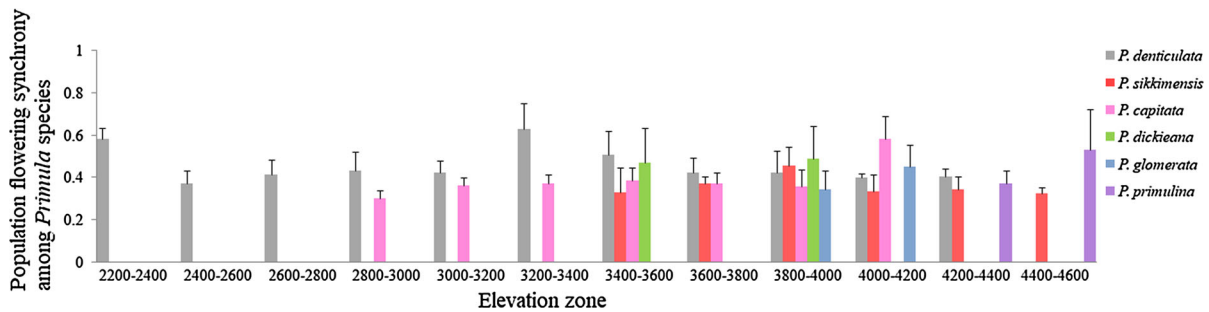


Fig. 2 Population flowering synchrony of focal *Primula* species. Bars represent population synchrony ($Z$) values ± SD. $x$-axis represent populations in 12 elevation zones and $y$-axis represent population flowering synchrony among six focal *Primula* species

greater abundance at higher elevation zones (3000–3800 and 3800–4600 masl) compared to lower-elevation zones at 2200–2800 masl (Fig. 3). We also observed that Lepidopterans were the dominant visitors at the lower-elevation zones, replaced by bees (other than bumblebees) at mid-elevation and bumblebees at higher elevation zones (Fig. 3). The Shannon-Weiner diversity index of flower visitors in high-elevation zones was also more diverse than at lower-elevation zones (Fig. 4, Kruskal–Wallis $H$ test: $H = 15.23$ (2, $N = 36$), $p < 0.05$). Community composition of flower visitors also differed significantly among elevation zones (Fig. 5a; PERMANOVA: $F = 180.94$, df = 2, $p = 0.001$), where the lower-levation zone with negative NMDS axis one score was correlated with lepidopterans, while mid-elevation with positive NMDS axis one score corresponded with bees and other insects and the higher elevation with
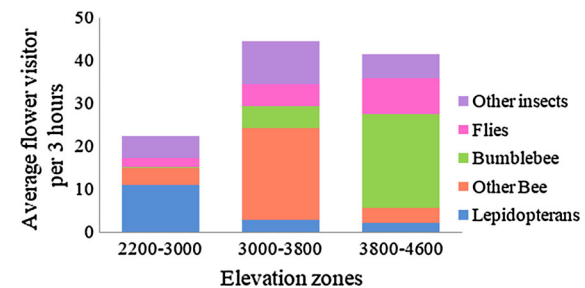


Fig. 3 Relative flower visitors' abundance in focal *Primula* species along an elevation gradient. Average floral visitor abundance observed per 3-h sampling period in six *Primula* species from three elevation zones (2200–3000, 3000–3800 and 3800–4600 masl) were grouped into five categories: lepidopterans, bumblebees, other bees, flies, and others (wasps, beetles etc.)

positive NMDS axis one score corresponded to bumblebees and flies (Fig. 5a). However, no significant differences in community composition of flower
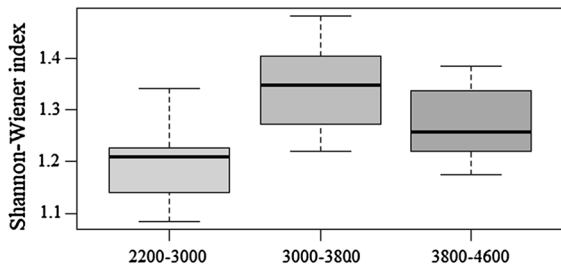
**Fig. 4** Shannon–Wiener diversity of flower visitors of *Primula* species. Shannon–Wiener diversity of flower visitors for three elevation zones are based on Shannon–Wiener diversity measures for plots in each elevation zones. Boxes represent the interquartile range (25th–75th percentile). The line represents the median and whiskers are the furthest data points within 1.5 times the interquartile range

visitors (Fig. 5b; PERMANOVA: $F = 141.68$, df = 5, $p = 0.169$) were observed among focal *Primula* species in the zone where they co-occurred.

Plots with higher species diversity ($\geq 2$ species) showed a significantly higher average number of floral visitors compared to single species plots (Fig. 6a; ANOVA: $F$ (2, 6) = 74.209, $p = 0.001$). Post hoc comparisons using the Tukey HSD test (Tukey 1949) indicated that the mean scores for the plots with different *Primula* species diversity were significantly different (single species: $M = 23.33$, SD = 2.52; two co-occurring species: $M = 56$, SD = 6.56; three co-occurring species: $M = 81.67$, SD = 7.37). We also observed a significantly higher average number of flower visitors in plots with higher flower density compared with plots with low flower density (Fig. 6b; ANOVA: $F$ (1, 56) = 25.44, $p = 0.001$). Insect

visitation rates were more than three times greater in high-density plots versus low-density plots. At relatively low flower density (40–50 flowering individuals), we observed less than 0.1 average number of flower visitors per open flower during 10 min of observation. However, the average number of flower visitors per open flower in higher density plots (80–100 flowering individuals) was observed to be greater than 0.3.

## Discussion

Sympatric flowering plants can respond to competition for shared pollinators by adjusting their flowering phenology (Campbell 1985; Stone et al. 1998). Our study suggests that pollinator-mediated facilitation may occur when sympatric *Primula* species with substantially overlapping flowering phenologies attract a greater number and/or diversity of potential pollinators. However, a potential cost of simultaneous flowering in sympatric species is the potential for the increased heterospecific pollen transfer. The temporal staggering of peak flowering period, as seen in this study, may limit heterospecific pollen transfer among sympatric species and thus act as an effective reproductive isolation mechanism (Grant 1992, 1994a, b; Hodges and Arnold 1994; Husband and Sabara 2004).

The sequential flowering of sympatric plant species is a commonly observed phenomenon and allows sympatric species to temporally segregate their use of pollinators and thereby reduce competition for a
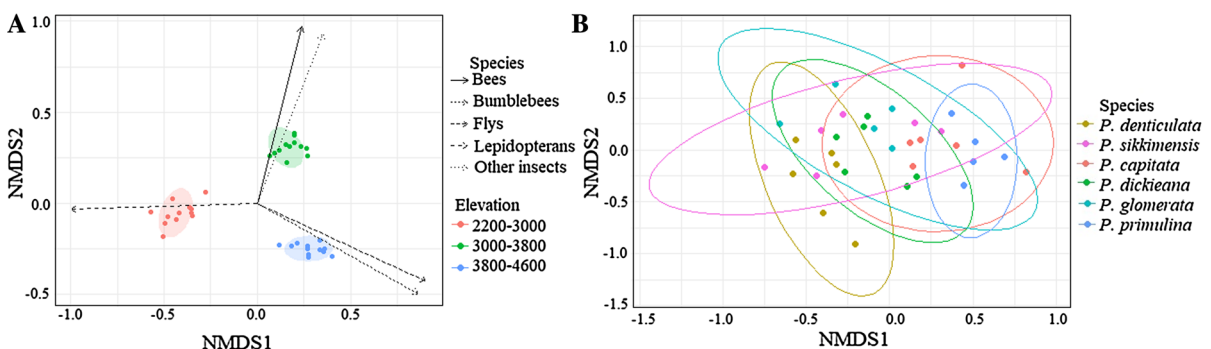


**Fig. 5** Non-metric multidimensional scaling using Bray–Curtis dissimilarity distances. A distance matrix of flower visitor community composition using the Bray–Curtis index was used to form a non-metric multidimensional scaling plot. Plots that are closer in ordination space have more similar flower visitor

community composition. **a** Community composition among elevation zones, where ellipses represent groupings by elevation zones using 0.95 confidence interval. **b** Community composition among focal *Primula* species, where ellipses represent grouping by species using 0.95 confidence interval
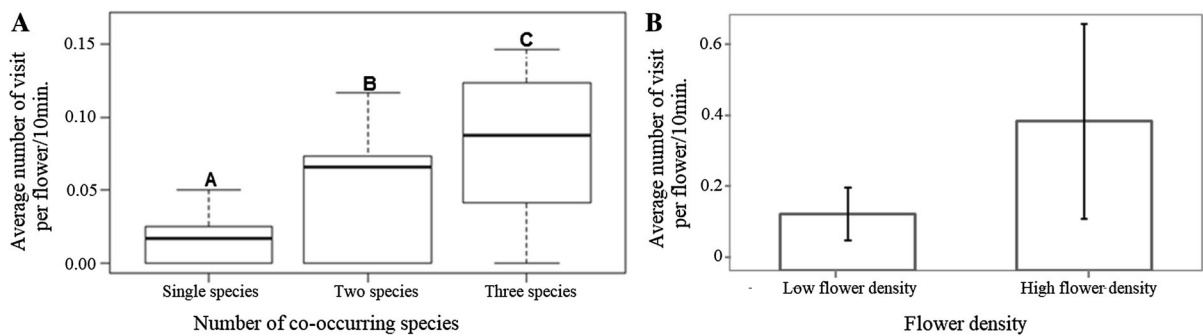
Fig. 6 An average number of flower visitors per flower per 10-min interval. **a** Flower visitors number in single species, two co-occurring species, and three co-occurring species plots. The boxes in the graph with different alphabets A, B, and C represent significant differences. **b** Flower visitors number in low flower density and high flower density plots

shared resource (Listabarth 1996; Henderson et al. 2000a, b; Borchsenius 2002; Barfod et al. 2011; Giorgis et al. 2015). The observed staggering of peak flowering periods of sympatric *Primula* species in this study (Fig. 1b) may likewise serve to increase the likelihood of successful pollination by reducing competition for pollinator visitation. Flowers in peak flowering periods tend to have greater possibilities of being fertilized (Trammell and Peterson 1978; Rodrí-guez-Pérez and Traveset 2016), and the observed differences in peak flowering periods of focal species may be especially significant for reproductive isolation.

Plots with higher plant diversity (≥ 2 co-occurring species) experienced significantly increased flower visitation compared to plots with single focal species (Fig. 6a). These data suggest a facilitative interaction among co-occurring *Primula* species where plots with greater floral diversity experienced greater numbers of insect visitors. Further, floral densities were also important, and plots with higher densities, irrespective of species composition, experienced higher visitation rates. Thus, in addition to higher floral diversity, higher floral densities were also important for attracting more floral visitors. Higher pollinator visitation rates may generally be associated with higher seed sets (Vidal et al. 2010; Osada et al. 2004), although we do not have the data to test this in our study. Most previous studies that provide evidence for facilitative interactions among congeners do so for those with similar floral structures (Moeller 2004; Gross et al. 2000) where it is not possible to determine whether pollinators failed to distinguish between species. However, a study on *Raphanus raphanistrum*

demonstrated an increase in pollinator visitation rates when it occurred with one or more species with different floral forms and colours (Ghazoul 2006). Similarly, our study provides evidence for facilitative interactions among sympatric focal *Primula* species with similar as well as different floral structures and colours.

Our results suggest that the pollinator-mediated facilitation amongst sympatric *Primula* species may occur through several mechanisms. First, facilitation may occur when the aggregated floral displays in plots of higher density and species diversity attract greater numbers of floral visitors compared to plots with single focal species and lower densities. Second, facilitation may indirectly occur if staggered peak flowering reduces competition for pollinator services, and flowers thereby experience higher rates of pollen deposition during these peaks. These patterns suggest that sympatric *Primula* species in this high-elevation ecosystem may benefit each other by providing a broadly continuous and aggregated flower display over the growing season that collectively attracts more potential pollinators, even while the segregation in peak flowering times may allow them to temporally partition pollinators for short periods. Such a strategy may be optimal in the stressful abiotic environments with compressed growing seasons that are character-istic of high-elevation ecosystems (Bertness and Callaway 1994; Callaway and Walker 1997).

In conclusion, our results clearly indicate that the timing of flowering in sympatric *Primula* species has consequences for the pollinator services in these self-incompatible plants. While the broad temporal convergence of flowering times across species enabled

higher visitation rates overall, the finer-scale temporal segregation of species' flowering peaks likely limited losses from heterospecific pollen deposition. All of these responses suggest a fine-tuning of flowering phenology in these communities with the tightly constrained growing season in this high-altitude system. With high-altitude, alpine ecosystem being susceptible to potentially rapid and significant climate shifts; it is likely that such finely tuned plant–pollinator changes may be strongly affected. Indeed, our results provide further evidence that critical plant–pollinator interactions are particularly vulnerable to disruption in high-elevation mountain communities due to the significant impacts of climate change in these ecosystems (Beniston 2005; IPCC 2007).

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