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Competition and facilitation among plants for pollination: can pollinator abundance shift the plant–plant interactions?

Zhong-Ming Ye · Wen-Kui Dai · Xiao-Fang Jin · Rober W. Gituru · Qing-Feng Wang · Chun-Feng Yang

Abstract We hypothesize interactions among plants for pollination may depend on pollinator abundance, which always varies among years and habitats and has different effects on plant reproductive success. Honeybee-pollinated plants, *Lotus corniculatus*, and its commonly coflowering neighbor, *Potentilla reptans* var. *sericophylla,* were used in a two-year project. We designed six types of plant combinations with different conspecific and interspecific flower densities in 2011 and repeated this in the same site in 2012. Meanwhile, we artificially increased pollinator abundance by hiring beehives only in 2011. Pollinator abundance as well as flower density significantly affected pollination of *L. corniculatus* plants from both the conspecific and interspecific plots. Total number of bees visiting a plot was enhanced by an increase in both the conspecific and interspecific flower densities regardless of high or low pollinator abundance. However, changes in visitation rates and fruit sets in the focal plants when flower densities were increased depended on pollinator abundance. Under high pollinator abundance, an increase in both the conspecific and interspecific flower densities significantly enhanced pollinator visits to *L. corniculatus*. However, under low pollinator abundance, the pollinator visitation rate remained unchanged as conspecific flower density increased, but decreased when there was an increase in interspecific flower density. Coflowering plants enhanced fruit sets of *L. corniculatus* only when the pollinator abundance was high. The findings suggest that the interactions among plants for pollination are influenced not only by a plant density threshold, but also by a pollinator abundance threshold.

Keywords Conspecific flower density · Honey bees · Interspecific flower density · *Lotus corniculatus* · *Potentilla reptans* var. *sericophylla*

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Introduction

When co-occurring plant species overlap in flowering phases and share the major pollinator fauna, pollination interactions among them may be competitive (Waser 1978; Brown et al. 2002; Mitchell et al. 2009;

Takakura et al. 2009; Muchhala and Thomson 2012; Runquist and Stanton 2013), facilitative (Moeller 2004; Moragues and Traveset 2005; Ghazoul 2006; Lopezaraiza-Mikel et al. 2007; Liao et al. 2011; McKinney and Goodell 2011; Sieber et al. 2011), or neutral (Feinsinger 1987; Rathcke 1988; Armbruster and McGuire 1991; McGuire and Armbruster 1991; Wirth et al. 2011). Negative effects could be induced by competing for limited pollinator resources (Campbell and Motten 1985; Chittka and Schurkens 2001; Hochkirch et al. 2012), or interference through heterospecific pollen deposition, which may lead to a reduction in seed yield and/or pollen loss (Feinsinger et al. 1988; Bjerknes et al. 2007; Morales and Traveset 2008; Flanagan et al. 2010). On the other hand, the positive effects could take place when the occurrence of a plant species increases pollinator visits to the coflowering plant, which subsequently contributes to the reproductive success of neighboring individuals (Schemske 1981; Moeller 2004; Ghazoul 2006). Facilitative pollination can be as a result of two or more coflowering plants forming a large and complementary collective floral display (Morales and Traveset 2009). Furthermore, neutral effect occurs when the altered visitation rates are too minimal to affect reproductive success (Totland et al. 2006), or when there is no change in visitation rates and reproduction success of plants when they co-occur with others (Aigner 2004), or there is no change in heterospecific or conspecific pollen deposition (review in Bjerknes et al. 2007). Overall, the pollinator-mediated plant–plant interactions are likely to depend on composition and density of coflowering plants (Feldman et al. 2004). However, the previous studies also suggested that competitive, facilitative, or neutral interactions among plants for pollination should be mainly due to the change of available pollinator resources for the focal plants when flowering alone or coflowering with other plants. Thus, such interactions may also depend on pollinator abundance in a given community.

Currently, conservation biologists and ecologists are paying increasing attention to declines in pollinator resources and the ecological consequences of this in this changing world (Kearns et al. 1998; Biesmeijer et al. 2006; Potts et al. 2010). Undoubtedly, changing pollinator abundance is an important environmental factor influencing plant reproductive success (Steffan-Dewenter and Tscharntke 1999; Utelli and Roy 2000; Molina-Freamer et al. 2003; Hanley et al. 2011;

Lazaro et al. 2013). However, few experimental studies directly investigate whether and how pollinator abundance affects plant–plant pollination interactions. Moragues and Traveset (2005) found that effects of alien *Carpobrotus* spp. on pollination of four native species alternated from negative, positive, to neutral. They then postulated that interactions among coflowering plants for pollination might be not constant, but depend on the ecological circumstances, such as pollinator abundance, composition, or flower density of co-occurring plants, and these could fluctuate year by year (see also Bjerknes et al. 2007; Lazaro et al. 2013). Rathcke (1983) hypothesized that facilitation and competition among plants for pollination should depend on a threshold of plant density or size. Facilitation would occur under the threshold, but shift to competition beyond the threshold and this has been proved by later field investigations (see Ghazoul 2006; Feldman 2008; Munoz and Cavieres 2008). Seemingly, the studies were based on a stable level of pollinator abundance. Since pollinator abundance may change spatio-temporally, we hypothesize that competition and facilitation among plants for pollination may also depend on a threshold of pollinator abundance.

To test the hypothesis, we artificially created two levels of pollinator abundance and investigated the effects of conspecific and interspecific flower densities on pollination of a focal plant. *Lotus corniculatus* L. (Fabaceae), Birdsfoot trefoil, a common herb in meadows of Southwestern China is used as the focal plant; while the coflowering plant is *Potentilla reptans* var. *sericophylla* (Rosaceae). This coflowering plant system is found in different community contexts. Moreover, fruit set of *L. corniculatus* varies substantially among communities (Z.-M. Ye, unpublished data). We hypothesize that the abundance of pollinators may work in conjunction with *P. reptans* var. *sericophylla* plants in affecting pollination success of *L. corniculatus*. We designed a two-year experiment where pollinator abundance was artificially maintained at a high level in 2011 and at a low level in 2012. In both years, we used the same experimental arrays of plant compositions and flower densities at the same site. Our specific objectives were: (1) to detect the effects of conspecific flower densities on pollination of the focal species; (2) to test the competition-facilitation effects of coflowering *P. reptans* var. *sericophylla* in pollination of the focal species; and (3)

to ascertain whether and how pollinator abundance affects pollinator-mediated plant–plant interactions.

Materials and methods

Study species and site

Lotus corniculatus is a perennial herb, and occurs mainly in grasslands and heaths in Europe, Asia, and Northern Africa (Jones and Turkington 1986). A plant usually has 2–20 inflorescences each comprising 1–5 yellow flowers. The height of the inflorescence ranges from 5 to 15 cm. Reproduction in the species exclusively depends on insect pollinators. Self-pollination under natural circumstances is considered impossible (Ollerton 1993; Ollerton and Lack 1998). The rewards provided by the flowers are both the pollen and nectar. Although it has been observed that bumble bees are the main pollinators of *L. corniculatus* in Europe (Jones and Turkington 1986; Pellissier et al. 2012), in natural populations from Yunnan Himalaya, the main visitors are honey bees (*Apis mellifera*). When foraging on a flower, the pollinator imposes a pressure on the keel and causes the staminal column to act as a piston, which allows pollen to be deposited on the ventral surface of the insect as well as the stigma (Pellissier et al. 2012). Such a pollination process tends to resulting in a mixed stigmatic pollen load with self and outcross pollen. *P. reptans* var. *sericophylla* is a perennial stoloniferous herb with yellow, actinomorphic flowers, borne on a 5–10 cm peduncle growing from the stolon. The flower mainly provides nectar to attract pollinators. In Northwest Yunnan province, *P. reptans* var. *sericophylla* is the common species coflowering with *L. corniculatus*. Flowering periods of the two species overlap considerably. *A. mellifera* is the main pollinator visiting flowers of both species at the study site. The study was carried out during June to July in 2011 and 2012 at a hillside meadow (27°51′56″N, 99°41′32″E, 3278 m), in Shangri-La county, Northwest of Yunnan province, China.

Experimental design

Plot establishment

Our study site was a 300 m × 800 m plain area, which was dominated by *L. corniculatus* and *P. reptans* var. *sericophylla*. This area could be divided into two areas 50 m apart. One was mainly occupied by *L. corniculatus*, and the other one hosted the two plants with almost equal composition. Experimental arrays of conspecific and interspecific flower densities were established in the two defined areas. All pollination observations were conducted in randomly selected plots with three replicates for each type of varying flower densities. Each plot consisted of an inner 1 m × 1 m quadrat surrounded by an outer 3 m × 3 m quadrat, with the latter used as a transition region. The whole plot was controlled with same plant composition and flower density. Distance between any two plots was more than 10 m. Data on pollination and reproductive success were strictly collected from the inner 1 m × 1 m quadrat.

To detect the effects of conspecific flower densities on pollination of the focal species, we set up three conspecific plot types with different numbers of *L. corniculatus* inflorescences within each 1 m × 1 m quadrat, namely, (1) 60 inflorescences (L60), (2) 120 inflorescences (L120), and (3) 240 inflorescences (L240). Additionally, to compare the abilities of the two species in attracting pollinators, a treatment was also set up in which 1 m × 1 m quadrats within a plot contained 120 *P. reptans* var. *sericophylla* flowers (P120). To test the competition–facilitation effects of coflowering plants in pollination of the focal species, we established two interspecific arrays of different numbers of *L. corniculatus* inflorescences and *P. reptans* var. *sericophylla* flowers within each 1 m × 1 m quadrat, namely, (1) 60 inflorescences and 60 flowers (L60P60) and (2) 10 inflorescences and 60 flowers (L10P60). Each plot type had three replicates. We removed any other flowering plant species in each plot. Additionally, to maintain the exact numbers of inflorescences of *L. corniculatus* and/or flowers of *P. reptans* var. *sericophylla* within each plot, we also removed surplus *L. corniculatus* inflorescences and/or *P. reptans* var. *sericophylla* flowers every morning in the course of the field investigations. We set up these plots in both 2011 and 2012.

Levels of pollinator abundance

To detect the effects of pollinator abundance on plant–plant pollination interactions, we set up different abundances of honeybees between 2011 and 2012. To create different levels of pollinator abundance, we employed a beekeeper to erect beehives of *A. mellifera*

to provide supplementary pollination service in 2011. The beehives were placed 100 m away from our study site. In 2012, however, beehives were restricted to 5 km away from the study site. To detect any differences in pollinator abundance between the 2 years, we compared pollinator frequency in all plots between the 2 years. The number of visiting bees per plot within an hour was 16.62 ± 4.44 in 2011 vs. 8.98 ± 1.96 in 2012 ($t = 3.06$, d.f. $= 34$, $P = 0.004$). Other insects such as bumblebees and leaf-cutting bees were occasional visitors and were not taken into account in this study.

Pollination observation

We used two indexes to evaluate pollinator attraction in each plot type. First, to detect any changes in pollinator attraction among different plots, we noted total number of bees visiting an inner quadrat during an observation period. Second, to compare the potential differences in pollinator service to the focal plants, we investigated visitation rates within an inner quadrat during an observation period. The observation period spanned 10 min and was conducted on fine days from 0900 h to 1630 h. At least 30 observation periods were conducted for each plot in each year. To ensure that the data in each plot were collected at the same time on each day, we designed an observation schedule so that each plot had the same replicates at any time of day during field investigations of each year.

The total number of bees per plot referred to the cumulative numbers of bees visiting any flowers from the inner quadrat within a 10 min period. The value was multiplied by six to represent visits per hour. The visitation rate of the focal species was estimated by the ratio of the number of visited flowers to the total number of open flowers of *L. corniculatus* within each 10 observation period. The value was also presented as per hour. Values of total number of bees and visitation rates were at plot level.

Reproductive success

Considering fluctuation in environmental conditions, fruit set rather than seed set would be more suitable to directly reflect pollination service. Moreover, Ollerton (1993) indicated that seeds per fruit in *L. corniculatus* remained unchanged in response to resource level and hand-pollination treatments. Therefore, we used fruit set as an indicator for the estimation of reproductive success of *L. corniculatus* in this study (see also Cussans et al. 2010). When establishing each plot, we marked at least 30 inflorescences in bud stage and recorded the number of flowers in each inflorescence. Fruit set represented the percentage of fruits with at least one seed to total number of flowers. We used plot-level means for all subsequent analyses.

Hand-pollination experiment

To detect whether reproductive success of the focal plants fluctuated between 2011 and 2012 due to potential changes in abiotic factors, we manipulated the same hand-pollination treatments on enclosed flowers and compared the fruit set between the two studied years. Additionally, we tried to test the effects of outcross pollen loads on fruit set of the plants. Considering the fact that it is difficult to emasculate *L. corniculatus* flowers because the anthers are concealed by the keel, we, therefore, conducted hand-pollination with self pollen and with mixed pollen load consisting of self and outcross pollen grains. In each year, 60 inflorescences were labeled and bagged before opening, and then hand-pollinated 2 days later. Self-pollination was completed by pushing the keel imitating the visitor's behavior on the flowers that causes the pollen spouting and coming into contact with the stigma (30 inflorescences). For mixed-pollination, pollen grains from another plant were added to the protruded stigma after the pushing treatment (30 inflorescences). Hand-pollinations were conducted twice a day and continued until flowers wilted. Fruit set was calculated as the percentage of the number of fruits to flowers per inflorescence.

Statistical analysis

All statistical analyses were carried out in SPSS 16.0, and significance was defined at level of $P = 0.05$. We used two-way ANOVA to test the effects of pollination treatments and years on fruit set of the focal species under a fixed model. To detect the differences in pollinator attraction between *L. corniculatus* and *P. reptans* var. *sericophylla*, total number of bees in plots L60, L120, L240, and P120 was tested by one-way ANOVA in both 2011 and 2012. Post hoc tests (Tukey HSD) were used for multiple comparisons if one-way ANOVA revealed significant differences.

In this study, we seek to determine whether pollinator abundance and flower density affected the three dependent variables, namely, the total number of bees within a plot, visitation rate, and fruit set of the focal species. For each of the variables under both the conspecific and interspecific experimental design, two-way ANOVA was used in a fixed model, in which the pollinator abundance was indicated by year 2011 (high) and 2012 (low), and the flower density was regarded as different plot types. To evaluate effects of flower densities on each dependent variable, three types of plots, namely, L60, L120, and L240 were used for analyses at conspecific level, while L60, L60P60, and L10P60 were used for interspecific level. In each year and under conspecific and interspecific experimental design, Tukey HSD was applied to multiple comparisons for each of the dependent variables among plots with different flower densities when one-way ANOVA revealed significant differences. Values of all the three variables were at the plot level. Original data on total number of bees visiting a plot and visitation rate to the focal plants were transformed by logarithmic transformations $[\log(x + 1)]$, while those of fruit set were transformed by arcsine transformations.

Results

Results of hand-pollination indicated that fruit set of *L. corniculatus* differed significantly between self-pollination and mixed-pollination, but showed no difference between the 2 years (Table 1). Fruit set under mixed-pollination was higher than that under self-pollination (51.8 ± 12.0 % vs. 19.6 ± 6.5 %, mean ± SD, data combined across 2 years). Results showed that the total number of bees visiting plots L60, L120, L240, and P120 differed significantly in both 2011 ($F_{3,8} = 31.16$, $P < 0.0001$) and 2012 ($F_{3,8} = 10.81$, $P = 0.003$).

Table 1 Two-way ANOVA analyses of the effects of artificial pollination treatments (self- and mixed pollination) and years (2011 and 2012) on fruit sets of *Lotus corniculatus* under fixed model

Source	d.f.	F	P
Treatment	1, 109	21.01	<0.001
Year	1, 109	0.023	0.880
Treatment × year	1, 109	0.000	0.986
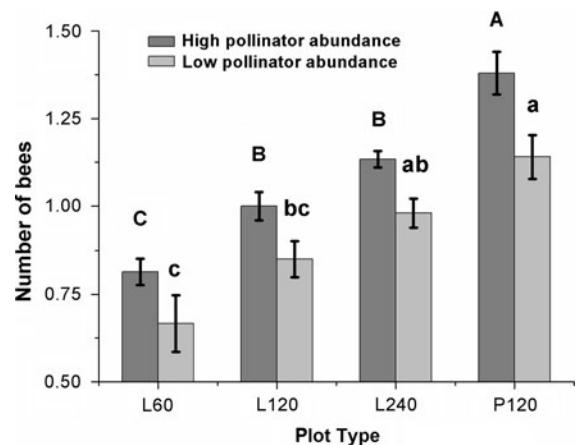
Fig. 1 Comparison of pollinator attraction between *Potentilla reptans* var. *sericophylla* and *Lotus corniculatus* under both the high and low pollinator abundance. Three plot types with different flower densities of *L. corniculatus* (L60, L120, and L240), and one plot type of *P. reptans* var. *sericophylla* (P120) were compared. Sites with *different letters* have significant differences at $P < 0.05$ (*capital and lowercase letters* were represented for results of multiple comparisons under high and low pollinator abundance, respectively). Data were transformed by logarithmic transformations $[\log(x + 1)]$. Bars are mean ± 1SE

Multiple comparisons revealed that plot P120 had the highest visiting frequencies (Fig. 1).

Effects of conspecific flower densities on pollination of *L. corniculatus*

Under high pollinator abundance, total number of bees visiting a plot differed significantly among plot types (Table 2). Multiple comparisons indicated that total number of visiting bees was enhanced by an increase in the density of flowers (Fig. 2a). Similarly, visitation rates varied significantly among different plots (Table 2) and increased from low to high flower densities (Fig. 2b). However, conspecific flower densities did not significantly affect fruit set (Table 2; Fig. 2c). Under low pollinator abundance, conspecific flower densities significantly increased total number of bees visiting a plot, but did not affect visitation rate and fruit set of the focal species (Table 2; Fig. 2).

Effects of coflowering plant on pollination of *L. corniculatus*

Under high pollinator abundance, total number of bees visiting a plot differed significantly among plots L60,

Table 2 One-way ANOVA on the effects of conspecific and interspecific flower densities on the three dependent variables, namely, total number of bees visiting a plot, pollinator visitation rate, and fruit set of *Lotus corniculatus* in each of the 2 years with different pollinator abundance

Variable	d.f.	Conspecific flower density				Interspecific flower density			
		High pollinator abundance		Low pollinator abundance		High pollinator abundance		Low pollinator abundance	
		F	P	F	P	F	P	F	P
Total number of bees	2, 6	22.15	0.002	7.00	0.027	153.76	<0.001	11.11	0.010
Visitation rates	2, 6	77.36	<0.001	1.94	0.224	25.93	0.001	6.74	0.029
Fruit set	2, 6	4.07	0.076	0.11	0.895	8.44	0.018	1.00	0.421

Plots L60, L120 and L240 were used for detecting effects of conspecific flower density while plots L60, L60P60 and L10P60 were used for detecting effects of interspecific flower density

L60P60, and L10P60 (Table 2). Multiple comparisons revealed that compared to L60, adding flowers of *P. reptans* var. *sericophylla* significantly enhanced pollinator attraction in the plot (Fig. 3a). Considering visitation rate of the focal species in a given plot, there were significant differences among the three plot types (Table 2); L60P60 had the highest value, while the other two types showed no difference (Fig. 3b). Changes in fruit set among different plots displayed a similar pattern when compared with visitation rates (Table 2; Fig. 3c). Under low pollinator abundance, total number of bees visiting a plot differed significantly among the three plot types (Table 2). Compared to L60, L60P60, and L10P60 had more visiting bees (Fig. 3a). However, although visitation rate showed significant differences among plots (Table 2), this reduced in L60P60 and L10P60, contrary to what was observed in L60 (Fig. 3b). No significant differences were detected in fruit sets among the three types of plots (Table 2; Fig. 3c).

Effects of pollinator abundance on pollinator-mediated plant–plant interactions

Two-way ANOVA indicated that under experimental arrays of conspecific flower densities, the total number of bees visiting a plot was significantly affected by pollinator abundance and flower density, but there was no significant influence when their interaction was considered. A similar pattern was found under experimental arrays of interspecific flower densities (Table 3). Visitation rate to the focal species was significantly influenced by both pollinator abundance and flower densities, as well as their interactions under

experimental arrays of both the conspecific and interspecific flower densities (Table 3). Both pollinator abundance and flower density enhanced total number of bees visiting a plot and visitation rate of the focal species. Additionally, fruit set was significantly affected by both pollinator abundance and flower density under experimental arrays of interspecific, but not conspecific flower densities (Table 3).

Discussion

Although pollinator-mediated autonomous selfing can occur in *L. corniculatus* due to the special floral architecture (Pellissier et al. 2012), hand-pollination with mixed pollen grains significantly enhanced fruit set. The results indicated that the import of pollen from other individuals transferred by pollinators is beneficial for reproductive success of the species. Additionally, hand-pollination experiments on bagged flowers revealed no differences in fruit set between the 2 years, which suggested that in our study system, the reproductive success of *L. corniculatus* was mainly affected by pollinator service rather than any other environmental factors.
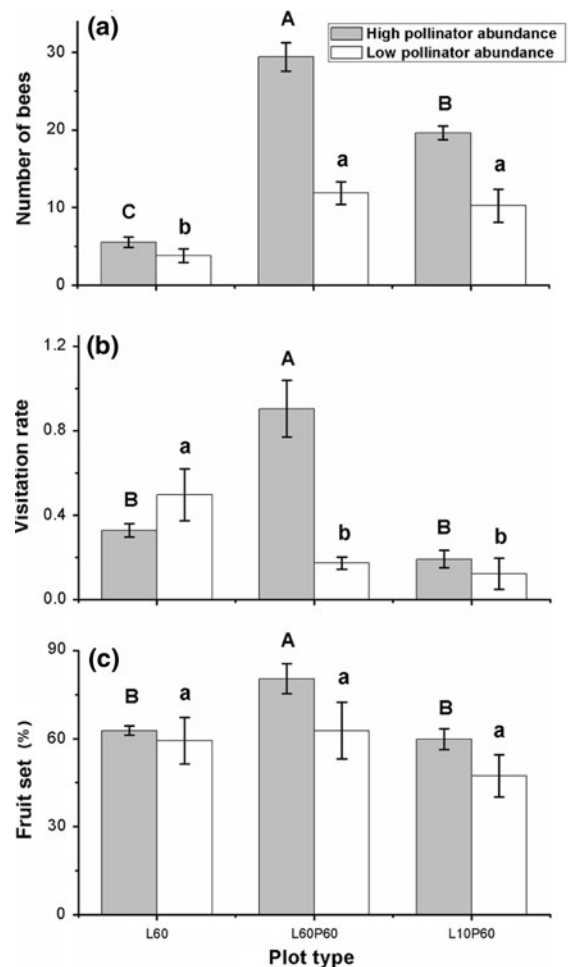
Effects of conspecific flower densities on pollination of *L. corniculatus*

Generally, pollinators may be more likely to forage patches with high plant densities than those with low densities (Kunin 1993; Steffan-Dewenter and Tscharntke 1999), and may visit fewer flowers within low-density patches (Sih and Baltus 1987). Kunin
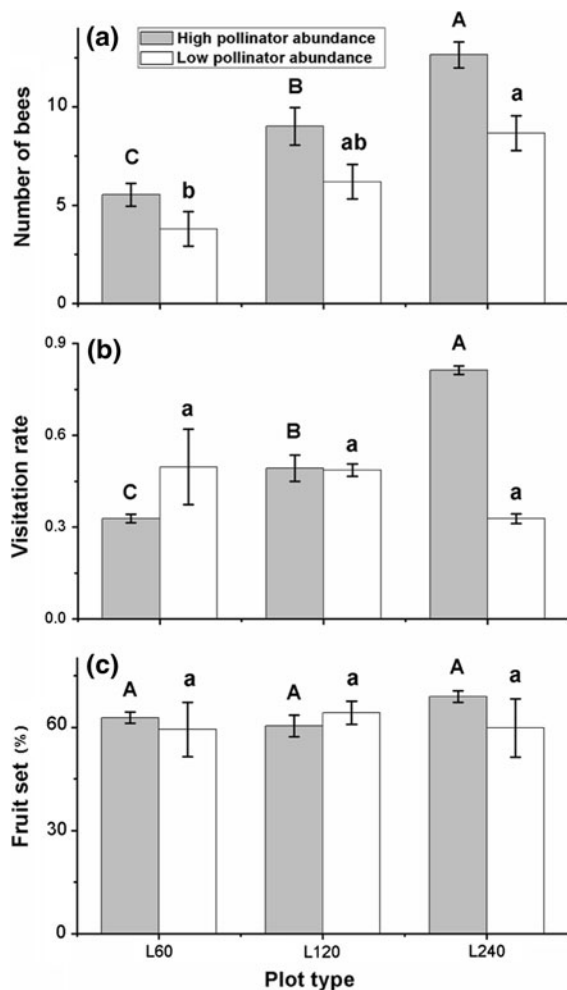
Fig. 2 Differences in the three dependent variables, namely, total number of bees visiting a plot (**a**), pollinator visitation rate (**b**), and fruit set (**c**) of *Lotus corniculatus* among different plots with differently conspecific flower densities (L60, L120, and L240) under both the high and low pollinator abundance. Data on total number of bees and visitation rate were transformed by logarithmic transformations [log(x + 1)], while those of fruit set were transformed by arcsine transformations. Sites with *different letters* have significant differences at $P < 0.05$ (*capital and lowercase letters* were represented for results of multiple comparisons under high and low pollinator abundance, respectively). Bars are mean ± 1 SE

Fig. 3 Differences in the three dependent variables, namely, total number of bees visiting a plot (**a**), pollinator visitation rate, (**b**) and fruit set (**c**) of *Lotus corniculatus* among different plots with differently interspecific flower densities (L60P60, L10P60) under both the high and low pollinator abundance. L60 is used as a control group. Data on total number of bees and visitation rate were transformed by logarithmic transformations [log(x + 1)], while those of fruit set were transformed by arcsine transformations. Sites with *different letters* have significant differences at $P < 0.05$ (*capital and lowercase letters* were represented for results of multiple comparisons under high and low pollinator abundance, respectively). Bars are mean ± 1 SE

(1997) also demonstrated that plant density had strong effects on both the visitation and reproductive success in *Brassica kaber*. Moreover, our study revealed that the effects of flower densities on pollination success were not invariable, but depended on pollinator abundance. *L. corniculatus* plants in plots with higher flower densities received more pollinators under high

pollinator abundance. However, no relationships were found between the visitation rates and flower densities when pollinator abundance was low. There were no differences in fruit sets among plots with different flower densities in both 2 years. This may be attributed to the fact that differences in pollinator visitation among plots were not large enough to translate into significant differences in fruit set.

Table 3 Two-way ANOVA analyses of the effects of pollinator abundance and flower density (conspecific and interspecific) on the three dependent variables, namely, total number of bees visiting a plot, pollinator visitation rate, and fruit set of *Lotus corniculatus* under a fixed model

Source	d.f.	Conspecific						Interspecific					
		Total number of bees		Visitation rate		Fruit set		Total number of bees		Visitation rate		Fruit set	
		F	P	F	P	F	P	F	P	F	P	F	P
Pollinator abundance	1	13.99	0.003	5.63	0.035	0.33	0.577	36.58	<0.001	10.60	0.007	4.71	0.050
Flower density	2	21.33	<0.001	3.96	0.050	0.23	0.797	58.44	<0.001	12.53	0.001	4.60	0.033
Pollinator abundance × flower density	2	0.001	0.999	18.71	<0.001	0.73	0.502	2.25	0.148	15.73	<0.001	0.84	0.455

High and low levels of pollinator abundance were indicated by the 2 years. Plots L60, L120, and L240 were used for detecting effects of conspecific flower density, while plots L60, L60P60, and L10P60 were used for detecting effects of interspecific flower density

Competition-facilitation effects of coflowering plant on pollination of *L. corniculatus*

Although the effects of interspecific plants on pollination of a coflowering plant have been frequently demonstrated as competitive (reviewed in Mitchell et al. 2009), several studies have shown that an increase in the density of the coflowering species could promote pollinator visitation or reproductive success for the focal plant species, if it can exclude the pollen interference (Duffy and Stout 2008; Sieber et al. 2011). In an experimental study, Munoz and Cavieres (2008) found that the invasive *Taraxacum officinale* (Asteraceae) positively affected pollination of two native species (*Hypochaeris thrincioides* and *Perezia carthamoides*) at low densities. The facilitation shifted to competition with the increasing densities of the invasive plants; so that both the pollinator visitation and reproductive success of the focal species decreased. Therefore, it has been concluded that facilitation and competition among interspecific plants for pollination depend on the density of the coflowering species (see also Rathcke 1983). The findings of our study are in agreement with the above conclusion. In 2011 (high pollinator abundance), when the proportion of *P. reptans* var. *sericophylla* individuals was the same as the proportion of *L. corniculatus* (plot L60P60), the focal plants experienced higher pollinator visitation rates and fruit sets when compared to plot L60. However, both the pollinator visitation rates and fruit sets did not increase when the proportion of the focal plants was reduced (plot L10P60). In plots of this type, coflowering *P. reptans* var. *sericophylla* seemed to have a neutral effect on the pollination of *L. corniculatus*.

Numerous studies have demonstrated that coflowering plant species act as competitors for pollination against the focal plant when it exhibits stronger pollinator attraction compared to the focal one (Brown et al. 2002; Larson et al. 2006; Mitchell et al. 2009). Studies have also shown that in the course of competition for pollinators, focal plants experience a decrease in pollinator visits and an increase in inbreeding mating (Ellstrand and Elam 1993; Bell et al. 2005; Jakobsson et al. 2009; but see Wirth et al. 2011). In this study, *P. reptans* var. *sericophylla* flowers are more attractive than those of *L. corniculatus*. However, both the pollinator visitation rates and fruit sets of the focal plant in plot L60P60 were higher than those in plot L60 when pollinator abundance was high. Thus, *P. reptans* var. *sericophylla* plants could facilitate pollination of *L. corniculatus* if pollinator abundance was great enough. In summary, coflowering *P. reptans* var. *sericophylla* plants helped to recruit more pollinators to the plot due to their strong pollinator attraction. On the one hand, *L. corniculatus* plants lost some pollinators when coflowering with *P. reptans* var. *sericophylla* due to its relatively weak pollinator attraction when there are few pollinators. On the other hand, when pollinators were abundant; they were surplus for *P. reptans* var. *sericophylla* and might shift to flowers of *L. corniculatus* and facilitate pollination.

Effects of pollinator abundance on pollinator-mediated plant–plant interactions

The majority of the literature on plant–plant pollination interactions report competitive effects (Mitchell et al. 2009). Recently, facilitative interactions have been theoretically and experimentally demonstrated in coflowering plants (Feldman et al. 2004; Mitchell et al. 2009). Moreover, Rathcke (1983) suggested that the outcome of pollination interaction among plants might depend on plant density. For example, facilitation could shift to competition with an increase in plant density. Lazaro and Totland (2010) revealed that the interactions between *T. officinale* and its neighbors for pollination depended on population circumstances such as the pollinator spectrum. Moreover, Moragues and Traveset (2005) found that the pollination in invasive *Carpobrotus* spp. displayed substantial variation when coflowering with four native species, and therefore, suggested pollination interactions among plants may depend greatly on the ecological circumstances, for example, pollinator abundance. Actually, pollinator abundance should be changeable in different habitat and affect plant reproductive success (Steffan-Dewenter and Tscharntke 1999). Although the results of pollination interactions among plants must be alterable and depend on community context (Lazaro et al. 2013), there are few experimental studies that have directly focused on pollinator abundance and how it affects pollination interactions.

Our study demonstrated that positive and negative effects of *P. reptans* var. *sericophylla* on pollination of *L. corniculatus* shifted depending on pollinator abundance. In both years with high and low pollinator abundance, *P. reptans* var. *sericophylla* displayed a higher ability in pollinator attraction compared to *L. corniculatus*. In addition, plots with high flower densities (conspecific or interspecific) tended to attract more pollinators in both years. However, the correlation between flower densities and visitation rates, and fruit sets of the focal species revealed different patterns between the 2 years due to the varying pollinator abundances. Under high pollinator abundance, visitation rates of the focal species were enhanced by the increase in flower densities (conspecific or interspecific) as were fruit set for the high density interspecific treatment. However, they did not benefit from high flower densities under low pollinator abundance. Particularly, pollinator visitation

to flowers of the focal species decreased with an increase in interspecific flower densities. The findings indicated that the plant–plant pollination interactions relied not only on the plant density threshold (Rathcke 1983), but also on a pollinator abundance threshold. For the species with weak pollinator attraction, the influence of neighbors on pollination success depended on pollinator abundance; facilitation occurred beyond a threshold of pollinator abundance. but shifted to competition below the threshold.

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