Oecologia (2014) 174:217–226
DOI 10.1007/s00442-013-2756-y

PLANT-MICROBE-ANIMAL INTERACTIONS - ORIGINAL RESEARCH

# Does the invasive *Lupinus polyphyllus* increase pollinator visitation to a native herb through effects on pollinator population sizes?

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Received: 4 April 2013 / Accepted: 17 August 2013 / Published online: 6 September 2013

**Abstract** Invasive plants may compete with native species for abiotic factors as light, space and nutrients, and have also been shown to affect native pollination interactions. Studies have mainly focused on how invasive plants affect pollinator behaviour, i.e. attraction of pollinators to or away from native flowers. However, when an invasive plant provides resources utilized by native pollinators this could increase pollinator population sizes and thereby pollination success in natives. Effects mediated through changes in pollinator population sizes have been largely ignored in previous studies, and the dominance of negative interactions suggested by meta-analyses may therefore be biased. We investigated the impact of the invasive *Lupinus polyphyllus* on pollination in the native *Lotus corniculatus* using a study design comparing invaded and uninvaded sites before and after the flowering period of the invasive. We monitored wild bee abundance in transects, and visit rate and seed production of potted *Lotus* plants. Bumblebee abundance increased 3.9 times in invaded sites during the study period, whereas it was unaltered in uninvaded sites. Total visit rate per *Lotus* plant increased 2.1 times in invaded sites and decreased 4.4 times in uninvaded sites. No corresponding change in seed production of *Lotus* was found. The increase in visit rate to *Lotus* was driven by an increase in solitary bee visitation, whereas mainly bumblebees were observed to visit the invasive *Lupinus*. The mechanism by which the invasive increases pollinator visit rates to *Lotus* could be increased availability of other flower resources for solitary bees when bumblebees forage on *Lupinus*.

**Keywords** Pollination · Wild bees · Flower resources · Seed production · Agricultural landscape

## Introduction

Pollinator diversity and density are declining in agricultural landscapes and may impose severe threats to the pollination of plants (Kearns et al. 1998; Goulson et al. 2008). The disruption of plant-pollinator interactions is suggested to be further accelerated by species invasions (Traveset and Richardson 2006; Montero-Castaño and Vilà 2012), and there has been a growing interest in recent years in how invasive plants affect pollination of natives. Invasive plant species are frequently visited by native pollinators (e.g. Tepedino et al. 2008; Nienhuis et al. 2009; Woods et al. 2012), and are often highly integrated in the pollination networks in their new habitats (Memmott and Waser 2002; Bartomeus et al. 2008b; Vilà et al. 2009). Pollinator utilization of nectar and pollen produced by invasive plants may result in competition for pollinators between native and invasive plant species during the flowering period of the invasive species (e.g. Chittka and Schürkens 2001; Brown et al. 2002; Totland et al. 2006), but could also increase the carrying capacity for pollinator populations and thereby increase pollinator abundance and facilitate pollination of natives flowering outside the flowering period of the invasive species.

Communicated by Christina Marie Caruso.

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Food sources can be a limiting factor for pollinator populations, especially in areas with intensive agriculture (Kearns et al. 1998; Carvell et al. 2006; Potts et al. 2010), and in such landscapes invasive plants could actually increase the availability of pollen and nectar and thereby strengthen pollinator populations. Increased pollinator abundance has been documented close to areas with high levels of flower resources such as semi-natural habitats (Öckinger and Smith 2007; Ricketts et al. 2008), gardens (Goulson et al. 2002; Osborne et al. 2008; Samnegård et al. 2011) and flowering crops (Westphal et al. 2003, 2006; Herrmann et al. 2007). The presence of an abundant rewarding invasive species could have similar positive effects on the carrying capacity for pollinator populations by increasing the availability of food resources, and native plants in invaded areas may then benefit from more pollinator visits. So far, most studies of how invasive plants affect pollination of native species have focused on effects mediated through changes in pollinator behaviour, i.e. attraction of pollinators to or away from native flowers (e.g. Chittka and Schürkens 2001; Brown et al. 2002; Lopezaraiza-Mikel et al. 2007), and there is limited information on how often effects are mediated through changes in pollinator population sizes. Interactions between invasive and native plants mediated through effects on pollinator population sizes have, to our knowledge, not been explicitly investigated before, but have been suggested as a possible mechanism for positive interactions among native and invasive plants (Bjerknes et al. 2007; Nienhuis et al. 2009; Stout and Morales 2009).

Meta-analyses have suggested that negative effects of invasive plants on the pollination success of native species predominate (Bjerknes et al. 2007; Morales and Traveset 2009), but the data to support this conclusion are still limited. Indeed, invasive plant species often have characteristics that should make them attractive to pollinators and thereby severe competitors for pollination. Many invasive plants have been introduced for ornamental purposes (Lambdon et al. 2008), have large, showy and highly rewarding flowers, and once established often occur in large abundances in their new habitats (Sakai et al. 2001). However, the apparent dominance of negative interactions could also be caused by a bias in the response variables typically considered. Invasive plants can affect native pollination in three main ways: by effects on pollinator behaviour, i.e. attracting pollinators to or away from native plants (Grabas and Laverty 1999; Chittka and Schürkens 2001; Brown et al. 2002; Totland et al. 2006; Lopezaraiza-Mikel et al. 2007; Muñoz and Cavieres 2008; Kandori et al. 2009; Nienhuis et al. 2009; Dietzsch et al. 2011); by heterospecific pollen transfer or by pollen loss (Grabas and Laverty 1999; Brown et al. 2002; Moragues and Traveset 2005; Larson et al. 2006; Bartomeus et al. 2008a; Jakobsson et al. 2008; Mitchell et al. 2009); and through effects on the sizes of pollinator populations. This third mechanism has perhaps the largest potential for facilitation of native pollination, but has been little studied and therefore not been included in metaanalyses. It is interesting to note that the properties that potentially make invasive plants severe competitors for pollinators, such as high production of pollen and nectar, and high abundance, may indirectly affect the pollination of native plants positively through effects on pollinator population sizes, at least outside the flowering period of the invasive species. The predominance of negative interactions between invasive and native species has been questioned before. Jakobsson et al. (2009) suggested that the small distances used between invaded and uninvaded sites in many studies (often just 5-50 m) precluded the detection of a positive ‘magnet species effect’ (e.g. Lopezaraiza-Mikel et al. 2007; Nielsen et al. 2008). Thus, even if natives growing together with an invasive receive fewer visits than those at a small distance, they may still receive more visits than natives further away if the invasive attracts pollinators to the area. Vilà et al. (2009) noted that negative impacts could be overestimated because native study species suspected to be affected negatively by an invader (for example due to morphological similarities) are frequently selected for study, and in comparisons of invaded and uninvaded networks they found no differences in number of visits and interactions to native plants.

During the flowering period of an invasive it is difficult to separate facilitation of native pollination mediated through a positive effect on pollinator population size from that mediated by the magnet species effect, i.e. the attraction of pollinators into an area. However, unlike the latter mechanism, positive effects on the size of local pollinator populations should be detected also as increased pollination success of species flowering after the invasive. Such facilitation of pollination of later flowering species by highly rewarding species flowering earlier in the season has been demonstrated among native plant species (Waser and Real 1979). A general problem when comparing invaded and uninvaded sites is that they may differ also in other respects than invasion status. One way to reduce this problem is to study seasonal changes in pollinator abundance within sites and compare these changes between invaded and uninvaded sites. In this study we examine the hypothesis that the invasive *Lupinus polyphyllus* increases wild bee population sizes and thereby pollination success of the native *Lotus corniculatus* after the flowering period of the invasive species. We use a study design where we monitor wild bee abundance in transects, and visit rate and seed production of potted native individuals in invaded and uninvaded sites before and after the flowering period of the invasive.

## Materials and methods

### Study species

*Lupinus polyphyllus* Lindl. (Fabaceae) is a species of North American origin which is naturalized and common along road verges in Sweden. It is spreading in Europe (Kowarik 2003) and has recently been observed to colonize semi-natural grasslands in Finland (Anonymous 2005). It is a common invader in the study region in southwestern Sweden, and has been noted as one of the top ten invasive pests by the local County Administrative Board (Frisborg 2009). We used the native *Lotus corniculatus* L. (Fabaceae) as the target species because it depends on insect visitation for fertilization (McGregor 1976 and references therein) and shares pollinators with *Lupinus polyphyllus*. The main natural flowering period of *L. corniculatus* ranges from the end of May until the end of July. Both species are perennial herbs with closed zygomorphic flowers aggregated in inflorescences, and they are mainly pollinated by bumblebees and solitary bees (Pettersson et al. 2004). The species are hereafter referred to by genus names for brevity.

*Lotus* plants were raised from seeds of Swedish origin (Pratensis, Lönashult, Sweden) in an experimental garden outside Lysekil, southwestern Sweden, in 2010. An investigation of the reproductive system of the experimental plants showed that they were self-incompatible and thus depended on cross-pollination for fruit and seed production. Four treatments were performed: bagging, bagging combined with assisted self-pollination, bagging combined with cross-pollination, and open-pollinated control. The treatments were performed at the branch level, i.e. an individual plant received all four treatments but on different branches, and all flowers on treated branches were subjected to treatment ($n = 15$ plants). Cross-pollen was collected from at least eight donors, mixed and transferred by a small brush every 1–2 days depending on weather conditions. No seeds were produced by bagged non-pollinated *Lotus* flowers; bagged flowers with assisted self-pollination also had a median of 0 seeds (although four of 72 flowers produced seeds); bagged and cross-pollinated flowers had a median of seven seeds; and open-pollinated control flowers had a median of 9.6 seeds (Kruskal–Wallis test, $\chi^2 = 49.57$, $df = 3$, $P < 0.01$).

### Experimental design

The study was performed in summer 2011 in southwestern Sweden (58°22′N; 11°30′E) in four naturally invaded sites with very large populations of *Lupinus* (1,600–7,000 flowering stems, invaded areas ranging from 0.3 to 1 ha) and four uninvaded sites with a more or less *Lupinus*-free zone within a radius of 800 m. Sites were selected to be as similar as possible except for the difference in *Lupinus* abundance. They were all situated in an open agricultural landscape in immediate vicinity to a road, and invaded and uninvaded sites were scattered evenly throughout the landscape. Ten potted individuals of *Lotus* were placed in the road verge at each site: (1) during 2 weeks just before the flowering period of *Lupinus* (17 May to 3 June), and (2) during 2 weeks immediately after the flowering period of *Lupinus* (11–26 July). The potted plants were arranged in rectangular arrays, with an inter-plant distance of around 10 cm. In invaded sites the arrays were placed in the part of the road verge most central with respect to the *Lupinus* population. Inflorescences exposed to pollinators during the experimental period were marked ($n = 7$–10 per individual) and the number of flowers in each inflorescence was counted. Single *Lotus* flowers are open for around 1 week, but marked inflorescences contained buds in various degree of openness, so flowers on marked branches were exposed for pollination during the whole 2-week period.

To examine if *Lupinus* has a general positive effect on pollinator abundance in the area we monitored bee abundance at the sites before and after the flowering period of *Lupinus*. This was accomplished by walking along a 200-m-long and 1-m-wide transect along the road verge, centred on the *Lotus* arrays, and counting all bumblebees, solitary bees and *Apis mellifera* in the transect. We repeated this on six different days at each site in both observation periods (before and after *Lupinus* flowering).

Flower visitors to *Lotus* were observed in 15-min-long censuses. In each observation period five censuses were made of each array at regular intervals. In total 1,047 flower visits were observed during the study. Flower visitors were categorized as bumblebees, solitary bees, *Apis mellifera*, butterflies or flies. Number of flowers and plants visited by each visitor arriving at the patch was noted, and only visitors touching the sexual organs of the flowers were recorded. After each census the number of flowers and plants with flowers were counted. Visit rate per plant was quantified by dividing the number of observed visits to plants by the number of observed plants, while visit rate per flower was quantified as the number of observed visits to flowers divided by the number of observed flowers. To estimate the amount of geitonogamy, i.e. the amount of pollen transferred within individual plants, we used the number of flowers visited by a pollinator on a plant before flying to the next plant. After the period of exposure the pots were returned to the experimental garden and were kept there until fruits were ripe and collected. Fruit set per inflorescence was estimated as the proportion of flowers producing fruits (number of fruits/number of flowers). Fruit length was measured to the closest millimetre. Seed predation on *Lotus* is common in the area and an exponential regression of seed number on fruit length from a study on plants from the same genetic stocks showed a high correlation between seed number and fruit length for non-predated fruits ($r^2 = 0.67$, $P < 0.05$, $n = 1{,}886$). We therefore estimated seed number per fruit by using the equation from the exponential regression, $y = 0.029x^{1.97}$, where $y$ = seed number and $x$ = fruit length. Mean seed number per fruit was calculated as the mean number of seeds in the fruits produced in an inflorescence. Seed number produced per flower was estimated as the product of fruit set and mean seed number per fruit.

Flower visitors to *Lupinus* were observed in 15-min census periods and categorized in the same way as above. We made six censuses per invaded site at regular intervals between 20 and 27 June. All observations during this study, on *Lotus*, *Lupinus* and in transects, were conducted between 0900 and 1800 hours on days with no rain and calm wind conditions, and care was taken to shift the hour of observation so that all sites were observed equally often in mornings and afternoons.

### Statistical analyses

Response variables were analysed with general linear mixed models with the following factors: $X = \mu$ + invasion status + exposure period + site (invasion status) + invasion status × exposure period + error.

The independent variables invasion status and exposure period were fixed factors and site a random factor. Analyses were conducted on site means. Total number of wild bees in transects, number of solitary bees in transects, number of bumblebees in transects, number of seeds produced per fruit, and number of seeds produced per flower were square root transformed. Fruit set, total visit rate per flower, bumblebee visit rate per flower and solitary bee visit rate per flower were arcsine transformed. Variances were homogeneous according to a Fligner-Killeen test of homogeneity of variances except for solitary bee visit rate per flower which did not show homogeneous variances despite transformation. Analyses were made in Statistica version 10 (StatSoft 2011) and R (R Development Core Team 2012).

## Results

The main pollinators observed on *Lotus* were bumblebees and solitary bees, which accounted for 43 and 57 % of the observed flower visits, respectively ($n = 969$). The main pollinators observed on *Lupinus* were bumblebees which performed 99 % of the observed flower visits ($n = 394$). Few *Apis mellifera* were observed, none on *Lotus* and only a few on *Lupinus* and in the walking transects, and these were not included in the analyses.

The seasonal change in the number of bumblebees quantified in transects differed between invaded and uninvaded sites, i.e. there was a significant interaction between invasion status and exposure period (Table 1). The number of bumblebees in invaded sites increased 3.9 times whereas it did not change in uninvaded sites [Tukey's honestly significant difference (HSD) $P = 0.0149$ and $P = 0.96$, respectively; Fig. 1a]. The number of solitary bees quantified in transects showed no significant difference between invaded and uninvaded sites in seasonal trend (Table 1) but the tendency was the same as observed for bumblebees (Fig. 1b).

The seasonal change in total visit rate per plant differed between invaded and uninvaded sites (Table 1). Total visit rate per plant increased 2.1 times in invaded sites, whereas it decreased 4.4 times in uninvaded sites (Tukey HSD $P = 0.027$ and $P = 0.017$, respectively; Fig. 2a). When visit rate per plant was analysed separately for bumblebees no significant effects were found (Table 1; Fig. 2b), whereas the seasonal change in solitary bee visit rate per plant differed between invaded and uninvaded areas (Table 1). Solitary bee visit rate increased 4.4 times in invaded areas whereas there was no significant change in uninvaded sites (Tukey HSD $P = 0.014$ and $P = 0.49$, respectively; Fig. 2c). The seasonal change in total visit rate per flower also differed between invaded and uninvaded sites (Table 1). Total visit rate per flower did not change in invaded sites, whereas it decreased 16 times in uninvaded sites (Tukey HSD $P = 0.99$ and $P = 0.02$, respectively). Bumblebee visit rate per flower was only affected by time and was 12 times lower in the second exposure period (Table 1; Fig. 2e). Solitary bee visit rate per flower was not significantly affected by any variables (Table 1; Fig. 2f), and we note that this variable did not exhibit homogeneous variances despite transformation. The number of flowers visited by a pollinator on a plant before flying to the next plant was not affected by any variable (Table 1); each pollinator visited an average of 2.05 flowers per plant before flying to the next plant.

Fruit set, seeds produced per fruit and seeds produced per flower were only affected by the main factors exposure period and invasion status (Table 2). Fruit set was 2.1 times lower in the second exposure period and 1.4 times higher in uninvaded compared to invaded sites (Fig. 3a). Seeds produced per fruit were 1.6 times lower in the second exposure period (Fig. 3b). Seeds produced per flower (the product of fruit set and seed produced per fruit) was 1.3 times lower in the second exposure period and 1.5 times higher in uninvaded compared to invaded sites (Fig. 3c). The number of flowers per plant did not differ between invaded and uninvaded sites but was higher in the second exposure period (Table 2; mean number of flowers per plant before–121, after–661).

**Table 1** The result from ANOVAs of effects of presence of the invasive flowering herb *Lupinus polyphyllus* and exposure period (before vs. after flowering of *Lupinus polyphyllus*)

| Response variable | Source of variation | *df* | MS | *F* | *P* |
|---|---|---|---|---|---|
| Sqrt no. of bumblebees in transects | Site (Invasion) | 6 | 0.19 | 3.24 | 0.089 |
| | Invasion | 1 | 0.42 | 2.23 | 0.19 |
| | Exposure period | 1 | 0.73 | 13.37 | 0.011 |
| | Invasion × exposure period | 1 | 0.51 | 8.77 | 0.025 |
| | Error | 6 | 0.06 | | |
| Sqrt no. of solitary bees in transects | Site (Invasion) | 6 | 0.05 | 0.64 | 0.7 |
| | Invasion | 1 | 0.13 | 0.05 | 0.15 |
| | Exposure period | 1 | 0.50 | 6.57 | 0.043 |
| | Invasion × exposure period | 1 | 0.13 | 1.64 | 0.25 |
| | Error | 6 | | | |
| Total visit rate per plant | Site (Invasion) | 6 | 0.18 | 10.66 | 0.006 |
| | Invasion | 1 | 0.16 | 0.87 | 0.38 |
| | Exposure period | 1 | 0.01 | 0.09 | 0.77 |
| | Invasion × exposure period | 1 | 0.61 | 35.51 | 0.001 |
| | Error | 6 | 0.02 | | |
| Bumblebee visit rate per plant | Site (Invasion) | 6 | 0.04 | 1.87 | 0.23 |
| | Invasion | 1 | 0.01 | 0.18 | 0.69 |
| | Exposure period | 1 | 0.13 | 5.81 | 0.053 |
| | Invasion × exposure period | 1 | 0.01 | 0.33 | 0.58 |
| | Error | 6 | 0.02 | | |
| Solitary bee visit rate per plant | Site (Invasion) | 6 | 0.07 | 2.2 | 0.18 |
| | Invasion | 1 | 0.24 | 3.36 | 0.12 |
| | Exposure period | 1 | 0.10 | 3.11 | 0.13 |
| | Invasion × exposure period | 1 | 0.48 | 15.16 | 0.008 |
| | Error | 6 | 0.03 | | |
| Arcsine total visit rate per flower | Site (Invasion) | 6 | 0.01 | 2.3 | 0.17 |
| | Invasion | 1 | 0.01 | 0.18 | 0.68 |
| | Exposure period | 1 | 0.08 | 15.8 | 0.01 |
| | Invasion × exposure period | 1 | 0.07 | 13.2 | 0.01 |
| | Error | 6 | 0.01 | | |
| Arcsine bumblebee visit rate per flower | Site (Invasion) | 6 | 0.01 | 1.08 | 0.46 |
| | Invasion | 1 | 0.02 | 1.94 | 0.21 |
| | Exposure period | 1 | 0.08 | 7.2 | 0.034 |
| | Invasion × exposure period | 1 | 0.01 | 0.83 | 0.4 |
| | Error | 6 | 0.01 | | |
| Arcsine solitary bee visit rate per flower | Site (Invasion) | 6 | 0.01 | 1.34 | 0.366 |
| | Invasion | 1 | 0.01 | 0.63 | 0.459 |
| | Exposure period | 1 | 0.01 | 0.42 | 0.54 |
| | Invasion × exposure period | 1 | 0.01 | 4.69 | 0.073 |
| | Error | 6 | 0.01 | | |
| No. of flowers visited on a plant before flying to the next | Site (Invasion) | 6 | 2.49 | 0.67 | 0.68 |
| | Invasion | 1 | 3.44 | 1.34 | 0.28 |
| | Exposure period | 1 | 1.58 | 0.43 | 0.54 |
| | Invasion × exposure period | 1 | 0.05 | 0.01 | 0.92 |
| | Error | 6 | 3.7 | | |

Various measures of pollinator visitation rates. See text for details as to how each response variable was measured. All visit rates are estimated per 15 min

*Sqrt* Square root

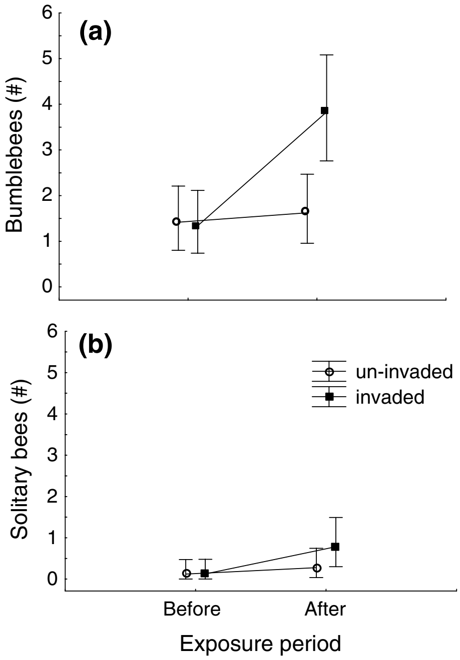

**Fig. 1** Effects of exposure period (before vs. after flowering of *Lupinus polyphyllus)* and invasion status (uninvaded vs. invaded by *L. polyphyllus*) on **a** number of bumblebees observed in 200-m walking transects, and **b** number of solitary bees observed in 200-m walking transects. Analyses were preformed on square root-transformed data and figures depict back-transformed results. Values are mean ±0.95 confidence intervals ($n = 4$)

## Discussion

Our study aimed to investigate if presence of the invasive plant *Lupinus polyphyllus* has a positive effect on wild bee population sizes and thereby increases visitation and seed production in the bee-pollinated *Lotus corniculatus*. Bumblebees, which were observed to visit *Lupinus* frequently, increased almost four times in number in invaded areas during the study period, whereas no change in number of bumblebees was detected in uninvaded areas. This suggests that pollen and nectar are limiting resources for bumblebees in the study area during the study period and that *Lupinus* adds to these resource levels. Thus the result supports the first part of the hypothesis. Total visit rate per plant in the native species *Lotus corniculatus* also increased over the season in invaded areas and was around two times higher in invaded areas after the flowering of *Lupinus,* whereas it was four times lower in uninvaded sites after the flowering of *Lupinus*. The increase in visit rate per plant in invaded areas was driven by visits of solitary bees, whereas decline in visit rate per plant in uninvaded sites was driven by declines in both bumblebee and solitary bee visitation.

Although solitary bees are reported to frequently visit *Lupinus* (Pettersson et al. 2004), few visits were observed in our study and we can therefore not directly link the increase in solitary bee visitation to *Lotus* in invaded sites to the food resources supplied by *Lupinus*. An explanation could be that flower resources that would have been otherwise utilized by bumblebees became available to solitary bees during the period when bumblebees visit *Lupinus*, and thereby solitary bee population sizes increase. There was, however, only a non-significant tendency for solitary bee population sizes to increase more over the season in invaded areas according to the results from the walking transects, and an alternative explanation for the increased visitation rates to *Lotus* in invaded areas could be that in the second exposure period the numerous bumblebees in invaded areas displaced solitary bees from their most preferred food source, and that solitary bees in these areas therefore switched to their next-preferred food source which was *Lotus*. To examine the mechanisms behind the increased visitation to *Lotus* in invaded areas additional studies of bee foraging on *Lupinus* and other food sources in the area should be performed. No corresponding increase in reproductive success was found in invaded areas, as estimated seed production per flower, fruit set and seed number per fruit were overall lower in the second exposure period. Thus the second part of the hypothesis is only partly supported, as pollinator visits to the native did increase in invaded areas but the mechanism for this is unknown, and no facilitation of reproductive success was found.

Total visit rate per flower remained unaltered in invaded sites and decreased in uninvaded sites during the study period. The discrepancy between response in visit rate per flower and visit rate per plant (where visit rates increased in invaded sites and decreased in uninvaded) is most likely caused by the fact that the number of flowers in the arrays was much higher in the second exposure period whereas the number of plants was constant over the two periods. When the increase in pollinator abundance does not exceed the increase in number of flowers, then visit rate per flower decreases or remains the same. The increase in pollinator visits in invaded areas was just high enough to keep visit rate per flower at levels equal to the first exposure period. Both visit rate per plant and visit rate per flower are important variables to consider. Visit rate per plant could be more likely to indicate information about the amount of cross-pollen received by a plant, if the first visited flower on the plant gets the lion's share of cross-pollen and the rest of the flowers receive mostly self-pollen. This would be especially important in our study species since it is self-incompatible and thus cannot be fertilized by pollen transferred among its own flowers. Visit rate per flower is on the other hand also an important variable since it is directly connected to the flower unit which is also the unit of seed production.

Reproductive success was overall lower in the second compared to the first exposure period. The higher number of flowers per plant in the second exposure period could

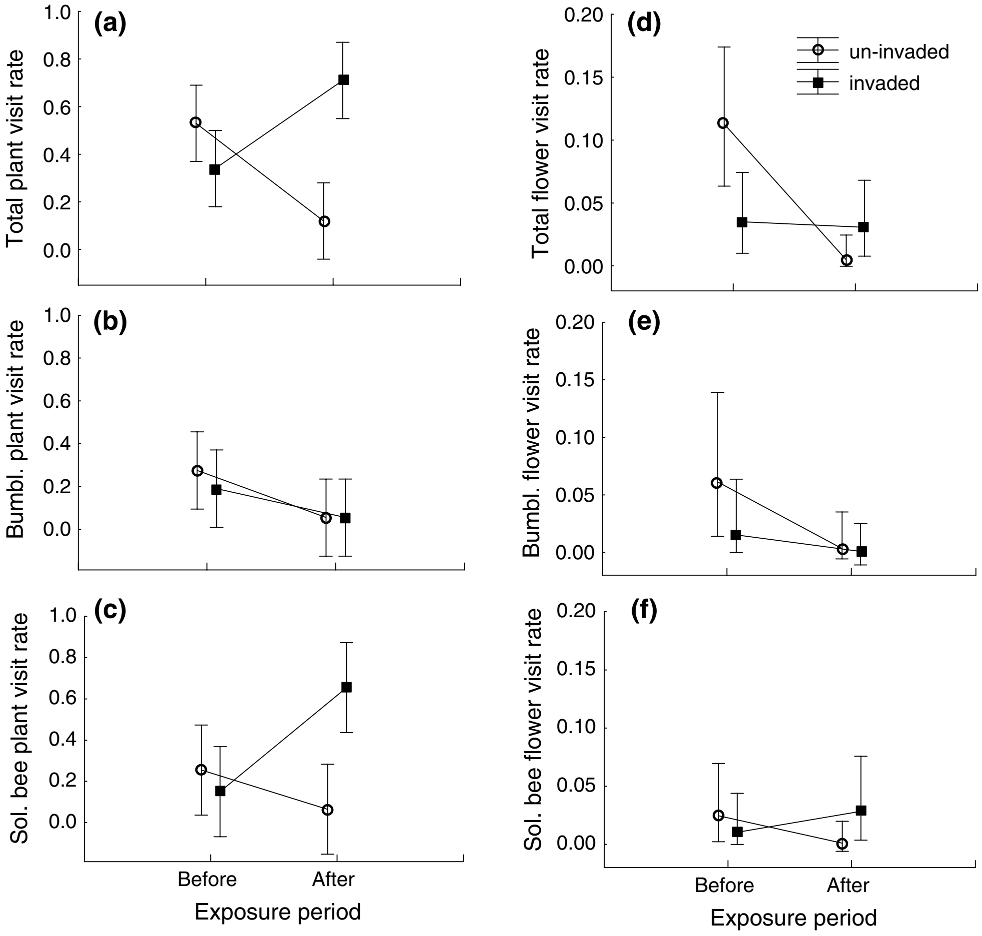

**Fig. 2** Effects of exposure period (before vs. after flowering of *Lupinus polyphyllus*) and invasion status (uninvaded vs. invaded by *Lupinus polyphyllus*) on pollinator visit rates in *Lotus corniculatus*: **a** total visit rate per plant (both solitary bees and bumblebees), **b** bumblebee visit rate per plant, **c** solitary bee visit rate per plant, **d** total visit rate per flower, **e** bumblebee visit rate per flower, **f** solitary bee visit rate per flower. Visit rates denote number of visits per 15 min. Analyses on total visit rate per flower, bumblebee visit rate per flower, and solitary bee visit rate per flower were performed on arcsine-transformed data and figures depict back-transformed results. Values are means ±0.95 confidence intervals ($n = 4$)

increase the amount of geitonogamy (self-pollen transferred between flowers on the same individual), and thereby reduce seed production. However, the number of flowers a pollinator visited on a plant before flying to the next plant was not higher in the second than in the first exposure period, indicating that the lower seed production in the second exposure period was not due to an increased frequency of geitonogamy. Reproductive success measured as fruit set and number of seeds produced per flower were also higher in uninvaded compared to invaded sites. Visual inspection of the graphs shows that this difference is driven by differences between invaded and uninvaded areas in the first exposure period. Our experiment was designed to investigate the difference in seasonal change within invaded and uninvaded areas, not to directly compare invaded and uninvaded areas which would require a higher replicate number. Thus, we cannot tell if the initial difference in reproductive success in invaded and uninvaded areas depends on chance events or on negative carryover effects from *Lupinus* over years.

Several studies have investigated how native pollinators respond to invasive flowering plants, by comparing pollinator abundance and richness in invaded and uninvaded areas. Lopezaraiza-Mikel et al. (2007) found higher abundance and species richness of pollinators in invaded areas, Williams et al. (2011) and Nienhuis et al. (2009) found no difference in pollinator abundance between areas, and Moron et al. (2009) found lower abundance and diversity of bees, butterflies and hoverflies in invaded areas. All four studies were performed during the flowering of the invasive, and effects on pollinator populations can therefore not be separated from the magnet species effect, i.e. the invasive attracting pollinators from the surroundings. However, attraction and utilization of the invasive by

**Table 2** Effects of the invasive flowering herb *Lupinus polyphyllus* and exposure period (before vs. after flowering of *Lupinus polyphyllus*) on different measures of reproductive success in *Lotus corniculatus*

| Response variable | Source of variation | *df* | MS | *F* | *P* |
|---|---|---|---|---|---|
| Arcsine fruit set | Site (Invasion) | 6 | 0.01 | 0.71 | 0.065 |
| | Invasion | 1 | 0.09 | 6.7 | 0.038 |
| | Exposure period | 1 | 0.32 | 23.18 | 0.003 |
| | Invasion × exposure period | 1 | 0.04 | 1.55 | 0.26 |
| | Error | 6 | 0.03 | | |
| Sqrt seeds per fruit | Site (Invasion) | 6 | 0.11 | 1.36 | 0.358 |
| | Invasion | 1 | 0.45 | 4.18 | 0.087 |
| | Exposure period | 1 | 1.71 | 21.7 | 0.003 |
| | Invasion × exposure period | 1 | 0.01 | 0.02 | 0.887 |
| | Error | 6 | 0.08 | | |
| Sqrt seeds per flower | Site (Invasion) | 6 | 0.11 | 0.78 | 0.62 |
| | Invasion | 1 | 0.68 | 6.23 | 0.047 |
| | Exposure period | 1 | 3.94 | 27.84 | 0.002 |
| | Invasion × exposure period | 1 | 0.12 | 0.14 | 0.396 |
| | Error | 6 | | | |
| Number of flowers per plant | Site (Invasion) | 6 | 70.45 | 1.55 | 0.3 |
| | Invasion | 1 | 82.38 | 1.17 | 0.32 |
| | Exposure period | 1 | 11694 | 257.28 | 0.001 |
| | Invasion × exposure period | 1 | 156.28 | 3.44 | 0.11 |
| | Error | 6 | 45.45 | | |

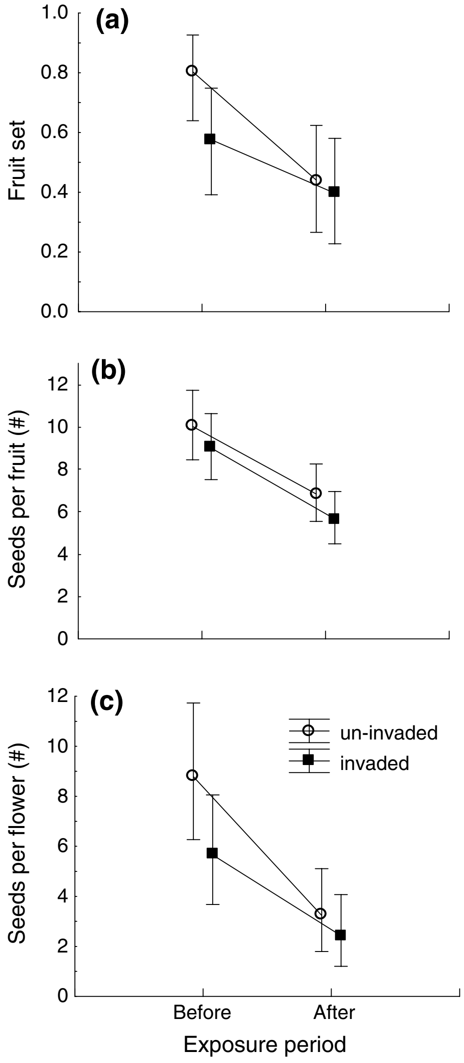

**Fig. 3** Effects of exposure period (before vs. after flowering of *Lupinus polyphyllus*) and invasion status (uninvaded vs. invaded by *Lupinus polyphyllus*) on seed production in *Lotus corniculatus*: **a** fruit set, **b** seed number produced per fruit, **c** seed number produced per flower (the product between fruit set and seed number produced per fruit). The analysis on fruit set was performed on arcsine-transformed data and analyses of seed production per fruit and per flower were performed on square root-transformed data. Figures depict back-transformed results. Values are means ±0.95 confidence intervals ($n = 4$)

native pollinators is the first step to alter population carrying capacity. Other studies documenting pollinators using nectar and pollen from invasive species have suggested that invasive species may increase the carrying capacity for pollinator populations (Tepedino et al. 2008; Nienhuis et al. 2009).

There are, however, several reasons why the effect of invasive plants on pollinator population sizes may vary among systems. Pollinators might not be able to exploit the new resource, if they are unable to handle the flowers (Corbet et al. 2001). When pollinators do exploit the resource it might be unrelated to population development because of temporal mismatch. If the new resource fills a gap when food sources are scarce it may increase pollinator population size, but if it becomes available during a period with a non-limiting supply of nectar and pollen it would not make a difference. Moreover, abundance of flower resources after the flowering of the invasive species may be of importance. For example even though bumblebee colonies initially produced more workers in areas with mass flowering oil-seed rape, this did not translate into higher recruitment rates of colonies since the many workers could not compensate for the shortage of food resources that followed later in the season (Westphal et al. 2009). Our study was restricted to a rather short period after the flowering of the invasive *Lupinus* and additional studies are needed to determine how long the positive effect on bumblebee abundance lasts. What is a valuable food source for some pollinator species might not be of value to other species. Some studies indicate that mainly generalist bee taxa feed on invasive plants (Lopezaraiza-Mikel et al. 2007; Tepedino et al. 2008; Padrón et al. 2009), and if these are favoured they might out-compete more specialized bee species that are not able to exploit the new resource. Our study focused on flower visitors known to visit the invasive plant, and the invasive may, by direct competition for abiotic factors such as space, light and nutrients, replace native flowering plants that would otherwise support other pollinator populations. Ramula and Pihlaja (2012) found lower plant species richness in *Lupinus*-invaded sites than in uninvaded sites, and Valtonen et al. (2006) observed lower abundances of butterflies in road verges invaded by *Lupinus* compared to uninvaded road verges. Future studies should therefore examine effects on pollinator groups not visiting the invasive species to assess effects on a larger part of the pollinator community.

Maintenance of pollination services is of crucial importance for the conservation of biodiversity, and the aim of this study was to improve our understanding of pollination interactions in invaded habitats. Studies of pollinator-sharing among plant species and the resulting competition or facilitation have a long tradition in ecology (for a review see Mitchell et al. 2009), but the proposed dominance of negative interactions and the need for information that can serve as a basis for decisions concerning eradication of invasive plant species justify a special focus on pollination interactions among invasive and native plants. *Lupinus* is a common invader in the study region, and subjected to eradication in some areas. There is concern that flower resources in small grassland fragments, as for example road verges, can be too small to sustain viable pollinator populations (Öckinger and Smith 2007), and it has been suggested that the decline of bee abundance in agricultural landscapes is partly caused by the loss of food sources (e.g. Steffan-Dewenter and Tscharntke 1999; Kremen et al. 2002). The results from the present study therefore suggest that the removal of invasive species that increase food abundance for pollinators should be carefully assessed in landscapes with deprived floral resources. This is also supported by pollination network models where removal of well-established invasive plants negatively affected the persistence of pollinator interactions (Valdovinos et al. 2009). The total effect of an invasive species on native plant pollination is complex and difficult to predict. However, the results of the present study point to the possibility of facilitation by invasive plant species mediated through positive effects on pollinator population sizes. Because this possibility has been largely ignored in previous studies of invasive/native pollination interactions, the dominance of negative interactions suggested by meta-analyses (Bjerknes et al. 2007; Morales and Traveset 2009) may be biased.

**Acknowledgments** We are grateful for many constructive comments on the text from professor J. Ågren and two anonymous reviewers. We also thank P. Börjesson for statistical advice. The study was financed by grants to A. Jakobsson from the foundation Oscar and Lilli Lamms Minne and the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning. The experiments comply with the current laws of Sweden in which the experiments were performed.

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