



Distance-dependent effects of invasive *Lupinus polyphyllus* on pollination and reproductive success of two native herbs

Anna Jakobsson^{a,*}, Benigno Padrón^b, Jon Ågren^a

^aPlant Ecology and Evolution, Department of Ecology and Genetics, EBC, Uppsala University, Norbyvägen 18 D, SE-752 36 Uppsala, Sweden

^bLa Erita 5, 38913, Frontera - El Hierro Santa Cruz de Tenerife, Canary Islands, Spain

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Abstract

A comprehensive understanding of the effects of invasive plants on native species requires identification of both the mechanisms of interaction and the spatial scale over which they act. Indirect interactions involving mobile organisms such as pollinators are likely to be scale-dependent, yet most studies examining effects of invasive species on pollination of native plants have considered effects across a single distance between interacting species. We examined the effects of the invasive herb *Lupinus polyphyllus* on pollination of two native herbs using multiple distances between the invasive and the natives. We recorded pollinator visitation and seed production in the native herbs *Lotus corniculatus* and *Lychnis viscaria* at 0, 5 m or 200 m away from *L. polyphyllus*. To reduce the influence of confounding factors, we used experimentally established populations of the invasive and potted individuals of the natives. In the immediate vicinity to *L. polyphyllus*, visitation to *L. corniculatus* was higher than 200 m away, and seed production per flower was higher than 5 m and 200 m away. In *L. viscaria*, bumblebee visitation was higher adjacent to *L. polyphyllus* than 5 m and 200 m away, but total pollinator visitation and reproductive success did not vary with distance. The results indicate that *L. polyphyllus* facilitates pollination of the native plants, and that this occurs at a very local spatial scale as effects dropped off already at a distance of 5 m. Presence of *L. polyphyllus* could benefit both pollinators and pollination of native herbs, and these positive effects should be considered along with likely negative effects due to resource competition. Moreover, the results illustrate the necessity to consider scale-dependent effects when assessing the impact of invasive flowering plants on native pollination interactions.

Zusammenfassung

Ein umfassendes Verständnis der Einflüsse invasiver Pflanzen auf einheimische Arten erfordert die Bestimmung des Mechanismus der Interaktion sowie der räumlichen Skala, auf der diese agieren. Indirekte Interaktionen, an denen mobile Organismen, z.B. Bestäuber, beteiligt sind, sind wahrscheinlich skalenabhängig, aber die meisten Studien, die Einflüsse von invasiven Arten auf die Bestäubung von einheimischen Pflanzen untersuchten, betrachteten Einflüsse für nur eine Entfernung zwischen den interagierenden Arten. Wir untersuchten die Einflüsse der invasiven Staude *Lupinus polyphyllus* auf die Bestäubung von zwei einheimischen Krautpflanzen (*Lotus corniculatus* und *Lychnis viscaria*). Wir erfassten Bestäuberbesuche und Samenproduktion an den einheimischen Pflanzen in 0 m, 5 m und 200 m Entfernung zu *L. polyphyllus*-Beständen. Um den Einfluss von Störfaktoren zu reduzieren, nutzten wir experimentell begründete Populationen der invasiven Art und getopfte Individuen

*Corresponding author. Tel.: +46 705442980; fax: +46 18 55 34 19.
E-mail address: anna.jakobsson@ebc.uu.se (A. Jakobsson).

der einheimischen Arten. In unmittelbarer Nachbarschaft zu *L. polyphyllus* waren die Besuchsraten an *L. corniculatus* höher als in 200 m Entfernung, und die Samenproduktion je Blüte war höher als in 5 m und 200 m Entfernung. Bei *L. viscaria* war der Besuch durch Hummeln unmittelbar neben *L. polyphyllus* höher als in 5 m oder 200 m Entfernung, aber der Besuch durch Bestäuber insgesamt und der reproduktive Erfolg variierten nicht mit der Distanz. Die Ergebnisse zeigen, dass *L. polyphyllus* die Bestäubung von einheimischen Pflanzen begünstigt und dass dies nur in der nächsten Nachbarschaft geschieht, denn die Effekte verschwanden schon bei einer Entfernung von 5 m. Das Vorhandensein von *L. polyphyllus* könnte sowohl dem Bestäuber wie der Bestäubung einheimischer Krautpflanzen zugutekommen, und diese positiven Effekte sollten zusammen mit den wahrscheinlichen negativen Effekten, die sich aus der Konkurrenz um Ressourcen ergeben, beachtet werden. Darüber hinaus zeigen die Ergebnisse die Notwendigkeit, skalenabhängige Effekte in Betracht zu ziehen, wenn der Einfluss von invasiven Blütenpflanzen auf einheimische Bestäubungsinteraktionen beurteilt werden soll.

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Introduction

Impact of invasive species on native ecosystems and communities is of worldwide concern and has caused large losses in terms of both biological and economical values (e.g. Pimentel, Lach, Zuniga, & Morrison 2000; Pysek et al. 2012). Invasive species may influence natives through competition for space and resources, but also by affecting the intensity of interactions with mutualists and antagonists (Traveset & Richardson 2006). They may reduce pollination success in native plants through competition for pollinators (e.g. Chittka & Schürkens 2001; Brown, Randall, Graham 2002; Thijs, Brys, Verboven, & Hermy 2012) or interspecific pollen transfer that causes stigma clogging (e.g. Grabas & Lavery 1999; Brown & Mitchell 2001; Jakobsson, Padrón, & Traveset 2008). Invasives can also facilitate native pollination. They may act as “magnet species” and attract pollinators which also visit natives (Lopezaraiza-Mikel, Hayes, Whalley, & Memmott 2007), or they may offer abundant flower resources and thereby increase pollinator populations and visits to natives flowering later in the season (Jakobsson & Padrón 2013). However, meta-analyses indicate that negative effects on native pollination predominate (Bjerknes, Totland, Hegland, & Nielsen 2007; Morales & Traveset 2009). Proper understanding and prediction of the effects of invasive plants on native pollination is of particular interest in the perspective of general declines in pollinator abundance (Kearns, Inouye, & Waser 1998).

Because of the foraging behaviour and mobility of flower visitors, indirect plant–plant interactions through effects on pollinators are likely to be scale-dependent. Pollinators tend to optimize foraging efforts by visiting patches with many resources (Rathcke 1983; Bennett, Gensler, & Cahill 2014) or more diverse resources (Ghazoul 2006). This results in groups of plants competing for pollinators, where groups with more resources may attract more pollinators. Thus, even if natives growing next to an attractive invasive receive fewer visits than those growing at a small or intermediate distance, they may still receive more visits than natives far away. Such

nonlinear effects of distance to attractive invasive species are a neglected aspect of pollination interactions between invasive and native plants (Jakobsson, Padrón, & Traveset 2009). Most studies examining effects of invasive species on pollination of native plants have considered effects across a single distance between interacting species (short, 3–20 m, Brown et al. 2002; Moragues & Traveset 2005; Totland, Nielsen, Bjerknes, & Ohlson 2006; Kandori, Hirao, Matsunaga, & Kurosaki 2009 or longer, 200–5000 m, Lopezaraiza-Mikel et al. 2007; Bartomeus, Vilá, & Steffan-Dewenter 2010; King & Sargent 2012; Thijs et al. 2012; but see Nielsen, Heimes, & Kollmann 2008, Cariveau & Norton 2009).

Most assessments of the effects of invasive species on native pollination success are correlational and do not control for variation in other factors potentially influencing pollination success, which can be problematic. For example, many invasive plants are introduced for ornamental purposes (Lambdon et al. 2008) and have dispersed from gardens, and vicinity to gardens can affect pollination because they host both flower resources and suitable nest sites for wild-bees (Goulson, Hughes, Derwent, & Stout 2002; Cussans et al. 2010). Experimentally created invasive populations would much reduce such confounding effects, but have to our knowledge not been used in studies examining effects over distances larger than 15 m. We examined pollinator visitation and seed production in two native plants at three distances (0, 5 and 200 m) from transplanted populations of the invasive herb *Lupinus polyphyllus*. We asked the following questions: Does the invasive species compete for or facilitate pollinator visits to the natives? If so, how do the directions and magnitudes of effects relate to distance to the invasive?

Materials and methods

Study species

Lupinus polyphyllus Lindl. (Fabaceae) is of North American origin, it is spreading in Europe (Kowarik 2003) and a

common invader in the study region in south-western Sweden especially in road-verges. The native target species *Lotus corniculatus* L. (Fabaceae) and *Lychnis viscaria* (Caryophyllaceae) share pollinator species (bumblebees and solitary bees (Pettersson, Cederberg, & Nilsson 2004), flowering period (approximately end of May until end of June), and habitat (road verges and semi-natural grasslands) with *L. polyphyllus*. Both *L. polyphyllus* and *L. corniculatus* have closed zygomorphic flowers (blue and yellow, respectively), that needs to be opened by the pollinator in order to access pollen and/or nectar. *L. viscaria* has open actinomorphic magenta-coloured flowers.

The native species were raised from a common seed source (seeds of Swedish origin, acquired from the company Praten-sis AB, Lönashult) to control for possible genetic effects on seed production. Plants were grown individually in 1.45 dm³ pots filled with commercial soil mix (Weibulls Kronmull, yrkes- och plantjord). The degree of self-incompatibility in the *L. corniculatus* and *L. viscaria* populations used had been determined in previous studies. Seed production in *L. corniculatus* was totally dependent on cross-pollination (Jakobsson & Padrón 2013) and seed production in *L. viscaria* was much reduced if not cross-pollinated (Jakobsson & Ågren 2014).

Experimental design

The field experiment was performed in south-western Sweden (58°22'N; 11°30'E) in 2010 (*L. corniculatus*) and 2011 (*L. viscaria*). We identified eight 200 m long transects along road verges with no *L. polyphyllus* within 200 m. Transects were situated within an area of 6 km² and minimum distance between transects was 300 m. One end of each transect was randomly assigned to be invaded by *L. polyphyllus*. In May 2010, 30 *L. polyphyllus* individuals were transplanted with an interplant distance of 0.3–0.4 m to each of the sites. Transplanted individuals produced at least two, often more inflorescences. Each experimental population was further increased by 15 vases with three *L. polyphyllus* inflorescences in each vase. These inflorescences stayed fresh for at least 5 days, and were changed every 5th day. The rate of pollinator visitation to *L. polyphyllus* inflorescences in vases was not different from that to inflorescences on transplanted plants ($p > 0.05$, $F = 0.50_{1,84}$, $n = 43$).

In each transect, we established arrays with potted individuals at different distance from the invasive. Arrays consisted of 8 plants arranged in two rows for *L. corniculatus* and 9 plants arranged in three rows for *L. viscaria*, both with an interplant distance of 10 cm. One array was placed in immediate vicinity to *L. polyphyllus*, one 5 m away from *L. polyphyllus*, and one 200 m away from *L. polyphyllus* (at the other end of the road-verge transect). Finally, one array was placed 5 m from the array at the 200 m distance to produce an arrangement of arrays analogous to the 0 and 5 m arrays with consideration to pollen donors

and collective flower display of the study species, but pollinator visits and seed production was not scored in this array.

Estimation of pollinator visits and seed production

The experimental arrays of *L. corniculatus* were exposed to pollinators from 9th to 29th June, 2010, while *L. viscaria* arrays were exposed to pollinators from 7th to 20th June, 2011. Pollinator visits were monitored in sunny or partly cloudy weather during ten-minute censuses. Pollinators were identified to the following groups: beetles, butterflies, flies, hoverflies, bumblebees, solitary bees, and honey bees. In total, we conducted 144 censuses of *L. corniculatus* arrays ($n = 6$ per array) and 192 censuses of *L. viscaria* arrays ($n = 8$ per array). We noted the number of inflorescences (*L. corniculatus*) or flowers (*L. viscaria*) visited by each pollinator arriving at the array. Only visitors contacting the sexual parts of the flower were considered as pollinators. After each census, the number of open inflorescences/flowers in the array was counted. Inflorescence/flower visitation rate was calculated by dividing the number of observed visits to inflorescences/flowers by the total number of observed inflorescences/flowers. When the native target plants had ceased flowering they were brought back to the experimental garden where fruits were allowed to mature. To confirm that *L. polyphyllus* shared pollinators with the native species, we observed pollinator visits to *L. polyphyllus* in ten-minute censuses evenly distributed among the experimentally invaded sites (2010, total $n = 31$; 2011, total $n = 32$).

In *L. corniculatus*, four to six inflorescences per plant were marked (32–48 inflorescences per array) and the number of flowers in each inflorescence were recorded. Number of fruits and the length of each fruit were determined in the lab. Seed predation in *L. corniculatus* is common in the area and we therefore estimated seed number per fruit using an exponential regression of seed number on fruit length for undamaged fruits produced by *L. corniculatus* plants of the same genetic stock, $y = 0.029x^{1.97}$, where y is number of seeds and x is fruit length ($r^2 = 0.67$, $p < 0.05$, $n = 1886$). For each inflorescence, fruit set was calculated as the number of fruits divided by the number of flowers, and number of seeds produced per flower was estimated as the product of fruit set and mean seed number per fruit.

In *L. viscaria*, six fruits per individual were collected (54 fruits per array). *L. viscaria* flowers are open for only two to four days, and we therefore collected three early matured fruits and three later matured fruits to cover the whole experimental period. In *L. viscaria*, all flowers produced a fruit, and number of seeds per fruit therefore equals number of seeds per flower. Number of seeds per fruit was determined for four fruits per individual using the image analysis software imageJ (<http://rsbweb.nih.gov/ij/index.html>). There was some seed predation, and fruits with signs of seed

predation were replaced by undamaged fruits from the same collection date.

Statistical analysis

The effects of distance to *L. polyphyllus* on site means were analyzed with general linear mixed models with transect as a random factor and distance to *L. polyphyllus* as a fixed factor. The response variables investigated were visit rate per inflorescence, fruit set, number of seeds produced per fruit, and number of seeds produced per flower in *L. corniculatus*, and visit rate per flower and number of seeds produced per flower in *L. viscaria*. Fruit set was arcsine transformed prior to analysis and all response variables showed homogeneous variances according to the Cochran C test. Analyses were made in Statistica version 10 (StatSoft, Inc. 2011).

Results

Bumblebees were the most common pollinators of all three species. In 2010, bumblebees accounted for 99% of visits to flowers of the invasive *L. polyphyllus* ($n = 1137$), and for 58% of visits to inflorescences of *L. corniculatus* ($n = 1159$). In 2011, they accounted for 96% of visits to *L. polyphyllus* flowers ($n = 1749$), and for 46% of flower visits to *Lychnis viscaria* ($n = 2000$). Bumblebees were identified to species in some censuses, and these data indicate that the most common bumblebee on all three species was *Bombus terrestris*, and that some visits of *B. lapidarius* and *B. humilis* occurred to all species. Other important pollinators were solitary bees in *L. corniculatus* (21% of observed flower visits), and solitary bees and hoverflies in *L. viscaria* (12% and 24% of observed flower visits, respectively). *L. polyphyllus* was occasionally visited by solitary bees, honeybees and hoverflies.

Total visit rate per inflorescence in *L. corniculatus* was negatively related to distance from *L. polyphyllus* (Table 1). It was significantly higher adjacent to the *L. polyphyllus* patch (0 m) than 200 m away, and intermediate 5 m from the *L. polyphyllus* patch (Fig. 1A). Separate analysis of bumblebee visits to *L. corniculatus* showed a marginally significant effect of distance on bumblebee visit rate per inflorescence (Table 1), which followed the same pattern as total visit rate (Fig. 1B). For visitation of solitary bees there were no effect of distance to *L. polyphyllus* (Table 1). Fruit set of *L. corniculatus* was not related to distance from *L. polyphyllus*, but both number of seeds per fruit and number of seeds produced per flower (i.e. the product of fruit set and seed per fruit) were higher adjacent to *L. polyphyllus* than 5 m and 200 m away (Table 1, Fig. 2).

Total pollinator visit rate per flower to *L. viscaria* was not affected by distance from *L. polyphyllus* (Table 1). However, bumblebee visit rate per flower was significantly higher adjacent to *L. polyphyllus* than 5 m and 200 m away (Table 1, Fig. 3A). Visit rate of hoverflies, the second most

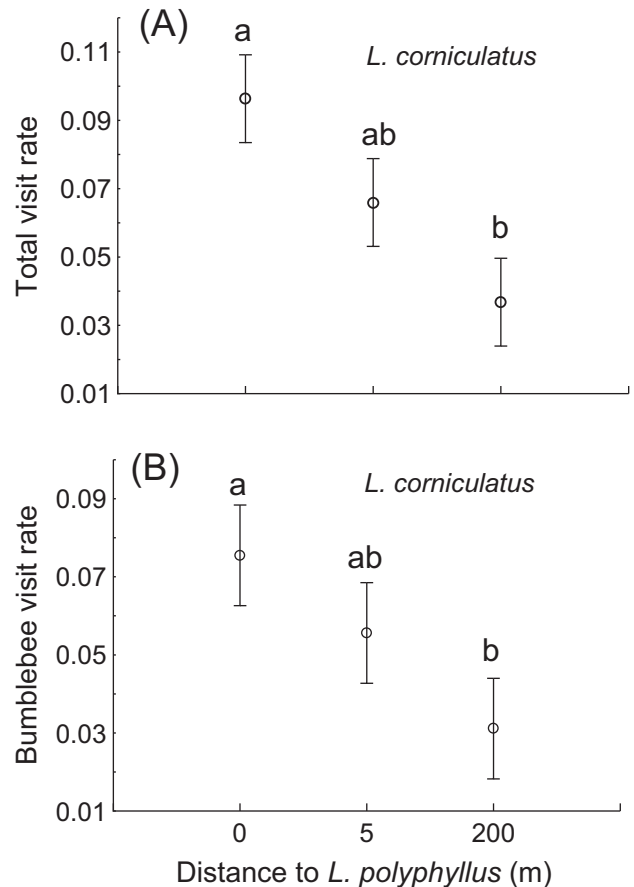


Fig. 1. Effects of distance to the invasive plant *Lupinus polyphyllus* on (A) total pollinator visit rate and (B) bumblebee visit rate in the native plant *Lotus corniculatus*. Visit rate denotes number of pollinator visits per inflorescence per 10 min. Vertical bars denote standard errors around least-square means. Different letters above bars indicate significant difference according to Tukey HSD test ($p < 0.05$) in (A), and $p = 0.069$ in (B).

important category of pollinator, was not affected by distance to *L. polyphyllus* (Table 1). Visit rate of solitary bees, which performed 12% of visits, were higher adjacent to *L. polyphyllus* compared to 200 m away (Table 1, Fig. 3B). Fruit and seed production of *Lychnis* were not related to distance from *L. polyphyllus* (Table 1).

Discussion

Mechanisms of facilitation

In the present study, pollination of two native plants was facilitated in the immediate vicinity of the invasive herb *L. polyphyllus*. Pollinator visitation and seed production per flower of *L. corniculatus* were higher adjacent to the *L. polyphyllus* patch than 200 m away. In *L. viscaria*, total pollinator visitation and reproductive success was not affected by *L. polyphyllus*, but bumblebee visitation was higher adjacent

Table 1. Effects of distance from experimentally created populations of the invasive plant *Lupinus polyphyllus* (0, 5 and 200 m) on pollinator visitation and seed production in the native plants *Lotus corniculatus* and *Lychnis viscaria* analyzed with general linear mixed models.

Response variable	Source of variation	df	MS	F	P
<i>Lotus corniculatus</i>					
Total visit rate per inflorescence	Transect	7	0.003	2.08	0.115
	Distance	2	0.007	5.30	0.018
	Error	14	0.001		
Bumblebee visit rate per inflorescence	Transect	7	0.004	2.73	0.052
	Distance	2	0.004	2.98	0.084
	Error	14	0.001		
Solitary bee visit rate per inflorescence	Transect	7	0.00005	1.57	0.225
	Distance	2	0.000002	0.07	0.932
	Error	14	0.00003		
Arcsine fruit set	Transect	7	0.03	3.16	0.032
	Distance	2	0.01	1.18	0.337
	Error	14	0.01		
Seeds per fruit	Transect	7	7.1	5.33	0.004
	Distance	2	8.1	6.04	0.013
	Error	14	1.3		
Seeds per flower	Transect	7	10.8	5.23	0.004
	Distance	2	11.1	5.36	0.018
	Error	14	2.1		
<i>Lychnis viscaria</i>					
Total visit rate per flower	Transect	7	0.003	1.67	0.197
	Distance	2	0.002	0.77	0.482
	Error	14	0.002		
Bumblebee visit rate per flower	Transect	7	0.001	2.11	0.111
	Distance	2	0.003	6.25	0.012
	Error	14	0.001		
Hoverfly visit rate per flower	Transect	7	0.0008	0.80	0.598
	Distance	2	0.0003	0.35	0.712
	Error	14	0.001		
Solitary bee visit rate per flower	Transect	7	0.0002	6.24	0.002
	Distance	2	0.0008	3.86	0.046
	Error	14	0.00002		
Seeds per flower	Transect	7	281	3.52	0.022
	Distance	2	73	0.91	0.426
	Error	14	80		

to the *L. polyphyllus* patch than 5 m and 200 m away, and solitary bee visitation was higher adjacent to *L. polyphyllus* than 200 m away. The term “magnet species” was first used by Thomson (1978) who found that a species of hawkweed (*Hieracium*) received fewer pollinator visits in monospecific stands compared to when intermingled with another hawkweed species, and facilitation of pollination rates in nectarless or less attractive species by more attractive “magnet species” has been documented in several studies (e.g. Nilsson 1983; Johnson, Craig, Nilsson, & Ågren 2003). However, the native species in our study produce both nectar and pollen (Jones & Turkington 1986), and are rather attractive food plants for pollinators in the area (personal observation). Still, both species received more pollinator visits in the vicinity of the invasive species. *L. polyphyllus* produces only pollen (Haynes & Mesler 1984), but in large amounts. Pollen is crucial for the development of bumblebee larvae, and

L. polyphyllus is sometimes grown as a food resource for bees (e.g. Sheffield 2008). Pollinators have been shown to collect only nectar from some species producing both pollen and nectar and choosing other species for pollen collection (Ghazoul 2006). Thus the mechanism behind the observed facilitation could be that *L. polyphyllus* attracts pollinators that prefer its pollen and also visit the native flowers, or that there are more resources or more diverse resources (both nectar and the preferred pollen) in the site with both the invasive and the native. Moreover, *L. polyphyllus* with its showy inflorescences on tall shoots presents a visible cue attracting pollinators from a distance (e.g. Lihoreau et al. 2012).

Facilitation vs. competition

Several factors may influence whether an attractive invasive plant sharing pollinators with co-flowering native species

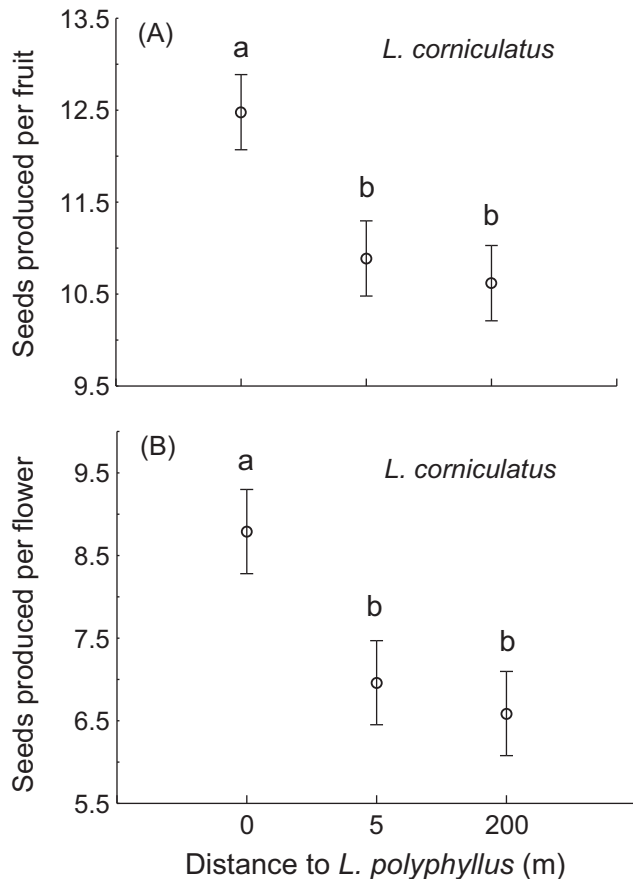


Fig. 2. Effects of distance to the invasive plant *Lupinus polyphyllus* on (A) number of seeds per fruit and (B) number of seeds produced per flower in the native plant *Lotus corniculatus*. Vertical bars denote standard errors around least-square means. Different letters above bars indicate significant difference according to Tukey HSD test ($p < 0.05$).

will facilitate or compete for pollinator visits. First, this can be related to the resources offered by the plants to flower visitors. In our study the natives produced nectar whereas the invasive only produced pollen, and this could increase the likelihood of facilitation because pollinators need to visit the natives for nectar collection. Second, the relative abundance of the invasive is likely to affect the direction and strength of interactions. Negative effects of invasive species on the pollination of native plants often increase with the abundance of the invasive (e.g. Muñoz & Cavieres 2008; Dietzsch, Stanley, & Stout 2011). The size of the experimentally created populations in this study (45 individuals) was within the range of many naturalized populations in the area (personal observation), but *L. polyphyllus* occasionally also occur in very large populations (>1000 individuals) and this could alter the strength and/or the direction of the interaction. The strength of the effect of the invasive on the focal native species could potentially be affected by the composition of the surrounding plant community, and specifically by the natural occurrence of the focal species. In the road verges used for the present experiment,

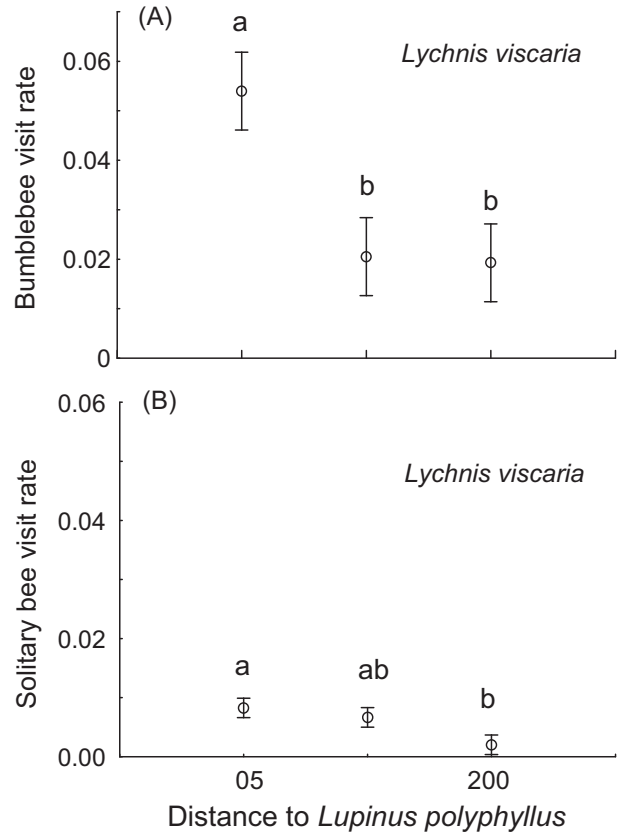


Fig. 3. Effect of distance to the invasive plant *Lupinus polyphyllus* on (A) bumblebee visit rate and (B) solitary bee visitation rate in the native plant *Lychnis viscaria*. Visit rate denotes number of pollinator visits per flower per 10 min. Vertical bars denote standard errors around least-square means. Different letters above bars indicate significant difference according to Tukey HSD test ($p < 0.05$).

L. viscaria was absent and *L. corniculatus* occurred only sparsely. The latter sparse occurrences are unlikely to have influenced the results through effects on pollinator attraction or availability of compatible pollen donors.

Distance-dependent effects

The examination of effects across different spatial scales is important when investigating biotic interactions because distances over which facilitation/competition effects operate are typically not known a priori, and both the strength and direction of effects may change with distance (Cariveau & Norton 2009). In this study facilitation was very local and dropped off already 5 m away from the experimental *L. polyphyllus* patch. Similarly, in a study of the magnet species effect between two invasive species, seed production in the target species was higher at a distance of up to 0.2 m compared to a distance of 3 m (Molina-Montenegro, Badano, & Cavieres 2008). Such effects over very short distances demonstrate that small-scale distribution of potential food plants influence the

foraging pattern of pollinators, and the mechanisms behind this deserves further attention.

We did not detect any nonlinear effects of distance to invasive on native pollination success. In contrast, Cariveau and Norton (2009) found that visitation in the native *Monarda fistulosa* was higher 0 and 15 m from the invasive *Carduus nutans* than at a 1 and 5 m distance. Instead our findings are similar to the observation that visitation and seed production in the native *Mimulus guttatus* decrease with distance to the invasive *Heracleum mantegazzianum* (Nielsen et al., 2008). However, nonlinearity may have occurred at distances between 5 and 200 m away from the invasive.

Effects on population growth rates

The increased reproductive success found in *L. corniculatus* adjacent to *L. polyphyllus* does not necessarily translate into effects on population growth rate. Positive effects on seed production of natives may be overridden by negative effects on other fitness components. Presence of *L. polyphyllus* has been shown to be negatively related to native plant species richness in various habitats, suggesting negative overall effects on population growth rate in several species (Ramula & Kati Pihlaja 2012). As *L. polyphyllus* at times occurs in large, dense populations it has the potential to reduce the performance of natives through competition for space and resources. To determine whether the positive effect of *L. polyphyllus* on seed production in *L. corniculatus* is likely to translate into a positive effect on population growth will require demographic studies.

Conclusions and implications

Meta-analyses suggest that invasive plants often affect the pollination success of native species negatively (Bjerknes et al. 2007; Morales & Traveset 2009). However, in this study we found facilitation of pollination in two co-flowering native species in the vicinity of the invasive *L. polyphyllus*. Moreover, another study conducted in the same area found the invasive to increase bumblebee abundance and pollinator visits to a native flowering after the invasive in the season (Jakobsson & Padrón 2013). There is a concern that flower resources in small grassland fragments, as for example road verges, can be too small to sustain viable pollinator populations (Öckinger & Smith 2007), and it has been suggested that the decline of bee abundance in agricultural landscapes is partly caused by loss of food sources (e.g. Steffan-Dewenter & Tschamtké 1999; Kremen, Williams, & Thorp 2002). Our studies suggest that *L. polyphyllus* may benefit some pollinators and pollination of native herbs in a situation when pollinators are declining. However, effects on other pollinator and plant species in the grassland habitat remain unknown, and positive effects should be considered along with likely negative impact due to resource competition. Our results also illustrate the necessity to consider scale-dependent effects

when assessing the impact of invasive flowering plants on native pollination interactions.

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