

Contrasting effects of plant invasion on pollination of two native species with similar morphologies

Shi-Guo Sun · Benjamin R. Montgomery ·
Bo Li

Received: 15 September 2012 / Accepted: 5 March 2013
© Springer Science+Business Media Dordrecht 2013

Abstract Invasive plants may decrease native plant density and disrupt interactions between native plants and their pollinators. We hypothesized that invasive *Solidago canadensis* (Asteraceae) competes for pollination services with two confamilial species, *Ixeris chinensis* and *Sonchus arvensis*. Breeding-system studies revealed that both native species are self-incompatible. In plots with all three species we found that *Solidago* received the highest visitation rates. To test the hypothesis of competition for pollination in the context of reduced native density, we established 3 plots for both native species with three *Solidago* densities (uninvaded, 50 and 75 % invaded) and corresponding

decreases in native density. We investigated the effects of varying densities of *Solidago* on honeybee visitation rates, number of successive visits within individual ramets, pollen-load composition on bees, and seed set. For both native species, increasing *Solidago* density and decreasing native density resulted in bees carrying higher ratios of *Solidago* pollen and in bees visiting fewer capitula prior to departing from a plant. However, for other aspects of pollination, the native species responded very differently to *Solidago*. With increasing *Solidago* and decreasing native density, *Ixeris* received fewer honeybee visits and produced fewer seeds, demonstrating competition for pollination, but *Sonchus* attracted more honeybee visits and showed a non-significant trend toward setting more seeds, suggesting facilitation. These opposing effects occurred despite similarities in the native species' floral morphology, suggesting that the effects of invasive plants are difficult to predict. In this case the different effects may relate to *Sonchus* being a taller plant with larger flowers.

Electronic supplementary material The online version of this article (doi:[10.1007/s10530-013-0440-0](https://doi.org/10.1007/s10530-013-0440-0)) contains supplementary material, which is available to authorized users.

S.-G. Sun
School of Life and Environmental Sciences, Shanghai
Normal University, Shanghai 200234, China

S.-G. Sun · B. Li (✉)
Coastal Ecosystems Research Station of Yangtze
River Estuary, Ministry of Education Key Laboratory
for Biodiversity Science and Ecological Engineering,
Institute of Biodiversity Sciences, Fudan University,
Shanghai 200433, China
e-mail: bool@fudan.edu.cn

B. R. Montgomery
Department of Natural Sciences and Engineering,
University of South Carolina Upstate, Spartanburg,
SC 29306, USA

Keywords Competition for pollination · *Ixeris chinensis* · Plant invasion · Plant-pollinator interactions · *Solidago canadensis* · *Sonchus arvensis*

Introduction

The most well-known competitive effects of invasive plants on natives involve direct competition for nutrients, light, space or water, resulting in adverse

impacts on native plant density and plant species diversity (Gordon 1998; Zavaleta et al. 2001; Sundaram and Hiremath 2012). However, many flowering plants also require pollinators for successful reproduction, and sufficient pollen acquisition is essential for the persistence of populations because it affects seed production and genetic variability (Burd 1994; Larson and Barrett 2000; Ashman et al. 2004; McKinney and Goodell 2010; Powell et al. 2011). Exotic species may disrupt interactions between plants and their pollinators by competing for pollinator services (Moragues and Traveset 2005; Bjerknes et al. 2007; Mitchell et al. 2009; Yang et al. 2011). For example, exotic plants may reduce pollinator services to natives by attracting pollinators away (Chittka and Schürkens 2001; Brown et al. 2002). Competition could also result from deleterious effects of heterospecific pollen receipt or pollen loss to heterospecific flowers by inconstant pollinators (Waser 1978; Bjerknes et al. 2007; Lopezaraiza-Mikel et al. 2007; Flanagan et al. 2009; Montgomery 2009a). Effects of competition for pollination may be particularly strong for populations at low density, as pollinators may opt to forage on more abundant species or may make more interspecific flights (Feinsinger et al. 1991; Kunin 1993).

Competitive effect of introduced species on pollination of natives is not a foregone conclusion (Bjerknes et al. 2007). Such effects do not occur when sufficient conspecific pollen is received and heterospecific pollen is acquired in small quantities or has limited effects (Montgomery 2009b, c). Indeed, pollinators may visit patches with competitors at higher rates if the competitors increase the available rewards (Lopezaraiza-Mikel et al. 2007; Bartomeus et al. 2008b). Consequently, a species may benefit from neighbors that attract pollinators from outside the plot or aid in persistence of pollinator populations (Rathcke 1983; Moeller 2004). Whether competition or facilitation occurs may depend on multiple factors including the size and density of interacting populations (Roy 1996; Moeller 2004; Ghazoul 2006), the relationship between floral density and visitation rate and whether heterospecific pollen receipt affects fecundity (Feldman et al. 2004). Facilitation is particularly likely when species with little rewards benefit from more rewarding neighbors (Lavery 1992), or when species offer complementary rewards (Ghazoul

2006). Finally, facilitation may occur if a species supports pollinator populations that benefit another species in subsequent seasons (Moeller 2004).

Plants reliant on pollinators to vector pollen may be more susceptible to competition for pollination than plants capable of autonomous pollination, and the effects may be especially strong for self-incompatible species, which require pollinators to transport pollen between individuals (Motten 1982; Kunin and Shmida 1997). Additionally reduced visit rates and loss of pollen to heterospecifics are expected to reduce fecundity only for plants that experience pollen limitation (Kwak and Jennersten 1991). Consequently, knowledge of a species' breeding system and degree of pollen limitation may inform predictions about whether or not it will experience competition for pollination.

Canada goldenrod (*Solidago canadensis*) was introduced as ornamental plant to China 1930s (Li and Xie 2002) and is spreading rapidly in east China (Dong et al. 2006b), and its clonal growth and large flowering displays render the plant a dominant member of the autumnal flowering community (Li and Xie 2002). Furthermore, elsewhere in its invasive range, *Solidago* invasion has resulted in decreased native plant richness and native plant cover (Moron et al. 2009; Skórka et al. 2010). In this study, we examined the impact of *S. canadensis* on components of pollination success of two native species, *Ixeris chinensis* and *Sonchus arvensis* under the assumption that these native species decrease in density following invasion (Dong et al. 2006b). Specifically, we compared pollinator services between uninvaded stands and adjacent invaded ones at two increasing invasion densities with correspondingly decreasing native densities. We addressed the following questions: (1) What are the breeding systems of the native species and does pollen augmentation increase their seed production? (2) Do the native species share pollinators with *S. canadensis*? If so, do they differ in attractiveness to insects? (3) Does *S. canadensis* show a competitive or facilitative effect on pollinator visitation rates, number of capitula visited per bout, and seed production to each species? We hypothesized that *Solidago* competes for pollinators with natives. Finally, (4) does increased *Solidago* density and decreased native density result in increased heterospecific pollen interference with a corresponding decrease in fecundity?

Methods

Study species and sites

Solidago canadensis (Asteraceae, hereafter ‘*Solidago*’), is an herbaceous perennial native to North America. It primarily grows in fields, roadsides and other early successional habitats in both its native and introduced range (Li and Xie 2002; Dong et al. 2006b). It spreads clonally, often forming large dense patches, and stems produce inflorescences of yellow flowers from late September through late November (Li and Xie 2002). It is self-incompatible, consequently reliant on outcrossing for fruit and seed set, and in its native range it is primarily pollinated by the introduced honeybee, *Apis mellifera* (Gross and Werner 1983).

Solidago’s capitula are individually small, 6–10 mm in diameter at our study site (mean \pm SE = 8.02 ± 0.14 , $N = 40$). However, *Solidago*’s capitula occur in simultaneously flowering aggregations that function similarly to individual capitula in our other two study species. For example, a medium-sized bee could walk among the florets of all capitula within an aggregation, just as it could among florets of a single capitulum in the other study species. Hence, we use the term ‘floral unit’ for an aggregation of capitula in *Solidago* and for each individual capitulum in our other study species (see Dicks et al. 2002). *Solidago* averaged $28.19 (\pm 2.26)$ floral units per ramet during our study. The number of capitula per floral unit for *Solidago* varied depending on phenological stages from several to forty (18.48 ± 0.48 , $N = 50$), resulting in a mean width of $1.98 (\pm 0.08)$ cm, and length of $6.78 (\pm 0.13)$ cm. A capitulum of *Solidago* contains a mixture of 9–15 pistillate ray (ligulate) flowers (12.23 ± 0.22 , $N = 50$) and approximately 7 perfect disc flowers (7.36 ± 0.05 , $N = 50$), resulting in an average of about 126 anther-bearing flowers per floral unit. The species ranges from 0.5 to 2.5 m tall, with an average height of $1.15 (\pm 0.04)$ m ($N = 30$), at the study site.

Ixeris chinensis (Thunb.) Nakai (Asteraceae, hereafter ‘*Ixeris*’) is a perennial herb that reproduces clonally and by seeds. The species occurs in northern, eastern and southern parts of China, and its primary habitat is forest understory or edges, as well as grasslands, roadsides and abandoned fields (Shi et al. 2011). *Ixeris* produces many yellow capitula (21.11 ± 0.82 , $N = 30$), consisting of only ray

flowers, with capitula containing 21–27 fertile ray flowers (24.35 ± 2.66 , $N = 40$) and ranging in size from 1.5 to 2 cm in diameter (1.67 ± 0.03 , $N = 40$). Flowering extends from late April to early November but peaks in September and October, overlapping with *Solidago*. At our study site, it reached a height of $0.18 (\pm 0.05)$ m ($N = 30$).

Sonchus arvensis L. (Asteraceae, hereafter ‘*Sonchus*’), is a perennial native to central Asia with its native range possibly extending across China, and it is an invader in North America (Lema and Messersmith 1990; Chu 1997). *Sonchus* is commonly found in cultivated areas, ditches, meadows, waste areas, sloughs, woods, and lawns (Chu 1997). The species predominantly reproduces sexually and to a lesser extent clonally from root sprouts. *Sonchus* flowers from July to October, but primarily in September and October, overlapping with *Solidago* (Chu 1997; Sun, personal observation). Capitula (flowering heads) consist of numerous bright yellow or orange-yellow five-lobed ray flowers (Chu 1997). *Sonchus* produces a similar number of capitula per ramet as *Ixeris* (20.75 ± 0.98 , $N = 30$), but larger capitula, each containing 80–250 fertile ray flower (152.09 ± 5.31 , $N = 40$) and ranging in size from 3.5 to 4 cm in diameter (3.78 ± 0.07 , $N = 38$). It reaches a height of $0.94 (\pm 0.02)$ m ($N = 30$) in our study populations. Both native species are commonly used in Chinese medicine and of social and economic importance (Tao 1999; Zhang et al. 2006).

Each ray flower of *Ixeris* and *Sonchus* or perfect flower of *Solidago* has five fused stamens and produces a mass of pollen but secretes little nectar (Chu 1997), and anther mass per flower does not differ significantly among these three species (Sun et al. unpublished data). Hence the number of anther-bearing flowers per floral unit can determine the level of available reward of three species. As described above, each floral unit of *Solidago* (mean of 126) or *Sonchus* (152) contains anther-bearing flowers several times higher than *Ixeris* (24), and thus the available reward.

We conducted our field surveys and experiments in a disturbed field associated with a plant nursery with a recent invasion of *Solidago*, located in Qianshao Farm (E 121.948742°, N 31.549608°), Chongming Island, Shanghai, China, during the flowering seasons of 2006–2007. *Solidago* normally grows densely and predominates in abundance in abandoned fields

(Li and Xie 2002). At our study site *Solidago* was interspersed with other species and grew less densely, probably due to frequent disturbance by humans. The site is about 10 ha, and both *Ixeris* and *Sonchus* were abundantly distributed among *Solidago* stands.

Breeding systems and pollinator limitation

In 2006, we investigated the breeding system and potential for autogamous pollination for both native species in uninvaded stands. Prior to anthesis, we randomly bagged flowering branches on 18 different individuals for each species with nylon nets to prevent insect visitation. Six enclosed inflorescences per species were left otherwise unmanipulated during flowering ('bagged'); six inflorescences per species were self-pollinated ('self-pollination'); and six inflorescences were outcrossed with pollen from multiple individuals at least 30 m away ('outcrossed'). Percent seed set was not variable in two of the three treatments (i.e. all individuals in two treatments set no viable seeds), so seed set was compared among treatments within species using the non-parametric Friedman rank-sum test.

To investigate pollen limitation for each native species, we left ten inflorescences exposed to pollinators without manipulation ('open'), and we performed supplementary hand pollinations on fifteen additional open inflorescences with pollen from multiple individuals at least 10 m away ('supplemental pollination'). Hand pollination was performed with soft brushes by slowly touching the surface of source capitula to collect pollen, then gently brushing the stigmas of target flowers. We repeated hand pollination for newly opened flowers each day over a week-long period (October 15–21, 2006). To assess seed set under the different conditions, we collected capitula 2 weeks later and counted seeds. Percent seed set was compared between treatments within species with a two-tailed *t* test.

Pollinator assemblage

In 2006, we selected two 6 m × 30 m survey plots, 300 m apart, containing all three species of study plants. In each plot, we established a central transect along the plot's long axis. Field work was conducted on sunny days with little wind and temperatures higher than 20 °C. To census pollinators, we slowly walked

each transect once, recording insects observed visiting capitula within 1 m of the transect and not more than 1 m ahead. We identified most visitors in the field, capturing unknown visitors for later identification. We only recorded visits for insects that contacted a flower's reproductive organs. We sampled each plot during either the morning (1,000 h) or afternoon (1,500 h), alternating the order of sampling on each occasion. We conducted field surveys on October 15–20, and a total of six samples were collected.

Before sampling the pollinator assemblage, we also measured the abundance of floral units, as defined above, of the focal three species for each transect. To accomplish this, five 2 m × 2 m quadrats per plot (ten in total) were randomly assigned along the transects. For each transect, we used χ^2 goodness-of-fit to test the differences between observed number of *Apis* visits observed to each species and the number expected based on the total number of visits observed across all species and the proportional abundance of floral units for each species.

Experimental arrays

In late autumn 2006–2007, we selected three plots per native species along one 500 m transect with a gradient of increasing *Solidago* density, and with the focal native species abundant. Each plot was 5 m × 5 m and assigned to one of three different treatments: one lacking *Solidago* (0 % *Solidago*), another one with equal numbers of floral units of *Solidago* and a native species (50 % *Solidago*), and the last one with a 3: 1 ratio of floral units of *Solidago* compared to the native species (75 % *Solidago*). Each plot was at least 100 m away from another and was manipulated to contain a final density of 300 floral units in total, including the native species and *Solidago*. Consequently the 0 % *Solidago* treatment plots contained 300 native capitula, the 50 % *Solidago* treatment plots contained 150 *Solidago* and 150 native floral units, and the 75 % *Solidago* plot included 225 *Solidago* and 75 native floral units. Thus, increasing *Solidago* ratio reflects two changes: an increase in *Solidago* density and a corresponding decrease in native density.

We removed extra capitula of *Solidago* and native plants using scissors and left stems and leaves intact. Floral units were measured as described above. Besides the three focal species, there were five

simultaneously flowering species, *Humulus scandens*, *Taraxacum* spp., *Pharbitis purpurea*, *Erigeron annuus* and *Conyza canadensis* with floral abundance up to twenty units per plot, and flowers of these species were removed throughout the study. To keep the immediate vicinity similar to study plots, we reduced the density of extra inflorescences of exotic and native species from neighboring patches within 25 m of each plot to approximately match the treatment. We removed flowers throughout the study to maintain the assigned densities.

Our previous survey revealed that *A. mellifera* was the primary pollinator for all three species either in pollinator abundance (also see Results of pollinator assemblage) or in pollination efficiency in terms of pollen transfer during one single visit (Sun 2008). Hence we conducted our observations only to honeybees. We observed honeybee activity during 30 min observation periods in the competition plots on sunny days over a 16 day period from October 10 to 25, between 1,000 and 1,500, an interval that accounted for about 70 % of daily visits (Sun, unpublished data). Honeybees were observed for 20 h per treatment each year (40 observation periods per treatment), for a total of 120 h across all species across both flowering seasons (240 observation periods in total). We recorded the number of honeybee visits to individual ramets, and the number of consecutive capitula visited prior to departure. We defined visitation rate as the number of visits by honeybee per floral unit per 30 min census. One month later, by which time flowering had ceased and seeds had developed, we harvested fruits and counted seed number for the terminal capitulum for 20 randomly selected ramets per treatment for both native species. The terminal capitulum develops first and is largest in both species, so consistent sampling of this position eliminated variation attributable to the effects of sequence or position.

For both native species, we then determined whether visitation patterns and seed set varied among the treatments with different *Solidago* ratios. We analyzed effects of *Solidago* ratio on honeybee visitation rates for each of native species, for *Solidago* itself, and for visitation rates per floral unit irrespective of focal species. Additionally, we analyzed the number of consecutive capitula visited prior to departure for both native species. Analyses were performed separately for each measure, using mixed-effects

ANOVA, with fixed effects of native species in the plot (*Ixeris* or *Sonchus*), *Solidago* ratio (absent, low, high), and a random effect of year. Analysis of visitation rates to *Solidago* excluded uninvaded plots. Initial analyses detected significant interactions between effects of species and *Solidago* ratio for visitation rates and successive visits for both native species and for visitation rates irrespective of focal species (see “Results”), so we subsequently analyzed treatments including *Ixeris* and those including *Sonchus* separately for these measures. The model for these subsequent analyses included a fixed effect of *Solidago* density, a random effect of year and an interaction between these terms. For variables with a significant interaction between year and density, we reanalyzed results from each year separately.

We additionally analyzed seed set of both native species using the same approach. A significant interaction between native species and *Solidago* ratio occurred, so subsequent analyses were performed separately for each native species. To improve normality of residuals and homogeneity of variance, seed set was logarithm transformed prior to analysis. For all tests, Tukey’s test was used to determine which *Solidago* density levels differed when analyses detected a significant effect of *Solidago* ratio. Tukey’s test was performed in the analysis including both years’ data if there was no significant interaction between *Solidago* ratio and year, but performed separately for each year when the interaction was significant. We performed analyses in MiniTab 15.

Pollen load analysis

In order to evaluate the fidelity of honeybees to focal plants, we analyzed pollen loads from visiting honeybees. In 2006 (October 12–22), a total of 263 bees (*Apis mellifera*) were captured from both target native species (119 and 144 individuals for *Ixeris* and *Sonchus*, respectively) in the established experimental plots varying in invasion density. To avoid pollen contamination among specimens, honeybees were caught individually and placed in clean vials with cotton and a few drops of ethyl acetate. To sample pollen, we gently brushed each bee’s ventral surface, the region that contacts stigmas in Compositae (Bartomeus et al. 2008a) with a small cube of glycerine jelly containing basic fuchsin stain (Kearns and Inouye 1993). We avoided sampling their corbicula loads as

the pollen is unlikely to be available for pollination. After the pollen being sampled, the jelly was placed on a microscope slide, melted and covered with a cover slip for later analysis in the laboratory. We identified and counted 100 pollen grains per sample using a microscope at $\times 400$ magnification. Pollen identification was based on a reference collection of the native and exotic species in experimental plots. We grouped the identified pollen grains into three categories: conspecific (pollen from the plant species on which the honeybee was caught; i.e., *Ixeris* or *Sonchus*), *Solidago* pollen, and other heterospecific pollens. For each species, we performed one-way ANOVA followed by Tukey's test to examine the effect of *Solidago* ratio on conspecific pollen receipt.

Results

Breeding system and pollinator limitation

For both native species, seed production occurred in outcross-pollinated treatment but no viable seed production occurred in either the bagged or self-pollination treatment, indicating self-incompatibility and absence of apomixis. We harvested a few smaller seeds (c. 1/3 normal size) from bagged or self-pollinated *Sonchus* flowers, but these seeds failed to germinate when placed in appropriate conditions. Seed set significantly differed among treatments for *Sonchus* (Friedman $\chi^2 = 12$, $df = 2$, $P = 0.002$),

with seed set of $0.73 (\pm 0.03)$ in outcross-pollinated flowers, and for *Ixeris* (Friedman $\chi^2 = 12$, $df = 2$, $P = 0.002$), with seed set of $0.70 (\pm 0.03)$ in outcross-pollinated flowers. In the pollen supplementation experiment, seed set was significantly higher for hand-pollinated than open control flowers for both *Sonchus* (0.72 ± 0.01 vs. 0.47 ± 0.02 ; $t_{23} = 13.77$, $P < 0.0001$) and *Ixeris* (0.72 ± 0.01 vs. 0.52 ± 0.01 ; $t_{23} = 11.76$, $P < 0.0001$).

Pollinator assemblage

The main insect families that visited the three study species were Apidae, Pierididae, Syrphidae, Muscidae and Vespidae. *Apis mellifera* was the most abundant pollinator to all three species and accounted for over 70 % of all observed pollinators (Table 1). Since its introduction into China from Europe in 1898, *A. mellifera* has naturalized in many parts of China and is considered to be a primary pollinator for a wide range of local plants (Chen 1993). The mean numbers of floral units per quadrat for *Solidago*, *Ixeris* and *Sonchus*, respectively, were 59.2, 19.2 and 27.8 on the first transect and 81.0, 29.8 and 36.2 on the second transect. The corresponding expected numbers of honeybee visits to each species are given in Table 1 under the assumption that floral units were equally attractive to bees. For both transects there was a significant difference between expected and observed values (transect 1: $\chi^2 = 22.29$, $df = 2$, $N = 164$, $P < 0.001$; transect 2: $\chi^2 = 20.23$, $df = 2$, $N = 209$,

Table 1 Number of visits from different insect groups observed on floral units of the native plants *Ixeris chinensis* and *Sonchus arvensis*, and the invasive plant *Solidago canadensis* along two transects with all three plant species present

Insect species	Family	Transect 1				Transect 2			
		N	<i>Solidago</i>	<i>Ixeris</i>	<i>Sonchus</i>	N	<i>Solidago</i>	<i>Ixeris</i>	<i>Sonchus</i>
<i>Apis mellifera</i>	Apidae	164	121 (91.4)	13 (29.7)	30 (42.9)	209	146 (115.2)	22 (42.4)	41 (51.5)
<i>Polistes chinensis</i>	Vespidae	23	14	3	6	25	20	2	3
<i>Syrphidia</i> sp.	Syrphidae	20	15	3	2	16	7	5	4
Unidentified flies	Muscidae	9	6	3	–	16	11	3	2
<i>Pieris canidia</i>	Pierididae	14	9	1	4	9	3	4	2
<i>Coccinella</i> sp.	Coccinellidae	5	5	–	–	11	11	–	–
<i>Vespa affomos</i>	Vespidae	1	–	1	–	3	–	3	–
<i>Macroglossum</i> sp.	Sphingidae	3	3	–	–	–	–	–	–

The numbers in parentheses represent the expected number of visits by honeybees (*Apis*) to each species if visitation rates were proportional to floral abundance

$P < 0.001$), with more visits than expected to *Solidago*, slightly fewer visits than expected to *Sonchus* and substantially fewer visits to *Ixeris*.

Experimental arrays

The initial analysis including effects of *Solidago* ratio on both native species detected a significant interaction between species and *Solidago* ratio for visitation rates to floral units of the native species ($F_{2,473} = 87.99$, $P < 0.001$) and floral units in the plot including both a native species and *Solidago* ($F_{2,473} = 46.68$, $P = 0.021$), successive visits ($F_{2,473} = 6.71$, $P = 0.001$), and seed set ($F_{2,233} = 152.23$, $P < 0.001$), indicating that the effect of *Solidago* differed between the native species. However, the visitation rate to *Solidago* itself was not affected by any variable or interaction, no matter which native species was included in the plot (all $P > 0.10$; analysis omitted). Visitation rates to *Solidago* across all treatments and years averaged 0.343 (± 0.003) visits per floral unit per 30 min census.

For *Ixeris*, there were negative effects of *Solidago* on honeybee visitation rates per capitulum, successive visits within individual ramets, and seed set, with significant decreases in visitation rates for each increase in *Solidago* ratio for all three variables (Supplementary Material; Fig. 1a–c). ANOVA revealed a significant interaction between year and *Solidago* ratio for both the number of successive visits and seed set; however, for both response variables in both years, the effect of *Solidago* was to decrease reproductive success. Visitation rates per floral unit irrespective of focal species, in plots with *Ixeris* did not differ with *Solidago* ratio (Appendix 1 in ESM; Fig. 1d).

In contrast, the effect of *Solidago* on *Sonchus* depended on the variable being analyzed. Increasing *Solidago* ratio significantly increased visitation rates (Appendix 1 in ESM; Fig. 1e). The number of successive visits significantly decreased with *Solidago* ratio (Fig. 1f). Seed set was not significantly affected, but tended to increase with increasing *Solidago* ratio (Fig. 1g). There was a significant interaction between year and *Solidago* ratio for the number of successive visits, attributable to a stronger negative effect of *Solidago* in 2006 than in 2007. For plots with *Sonchus*, visitation rates per floral unit irrespective of focal species increased with increasing *Solidago* ratio and were higher in 2006 than in 2007 (Appendix 1 in ESM; Fig. 1h).

Pollen load analysis

A total of 26,300 pollen grains were identified from pollen loads carried by the collected honeybees, and all pollen loads included a mixture of all three pollen sources. As the *Solidago* ratio increased, conspecific pollen counts decreased significantly for pollen from honeybees collected on *Ixeris* ($F_{2,116} = 50.84$, $P < 0.001$, Table 2). Conversely, the number of *Solidago* pollen grains increased significantly with the *Solidago* ratio ($F_{2,116} = 54.60$, $P < 0.001$). The same pattern occurred in pollen collected from honeybees on *Sonchus*: conspecific pollen counts significantly decreased ($F_{2,141} = 52.64$, $P < 0.001$) and invasive pollen counts significantly increased ($F_{2,141} = 46.19$, $P < 0.05$; Table 2) with increasing *Solidago* ratio.

Discussion

Our results demonstrate that there were contrasting effects of *Solidago* invasion coupled with decreasing native density on two native plant species, despite apparent similarities in the native species' reproductive biology. All three species shared honeybees as the primary pollinator, and *Solidago* received significantly more visits than the other species. There was some evidence of competitive effects of *Solidago* on both native species, as pollen from *Solidago* was found on all honeybees visiting both native species, with a significantly decreased proportion of conspecific pollen and significantly increased proportion of *Solidago* pollen in plots with higher densities of *Solidago*. Moreover for both native species, the number of successive visits within an individual ramet was reduced sharply with increasing *Solidago* ratio. However, *Ixeris* received fewer honeybee visits and produced fewer seeds with increasing *Solidago* ratio, suggesting competition for pollination. In contrast, *Sonchus* attracted more honeybee visits and showed a trend toward setting more seeds with increasing *Solidago* ratio, suggesting facilitation.

Several studies on pollinator-mediated interactions between invasive plants and native plants have found results ranging from competition to facilitation (reviewed in Bjerknes et al. 2007). For example, some studies have detected competitive effects of invaders on seed set (Flanagan et al. 2010) or visitation rates

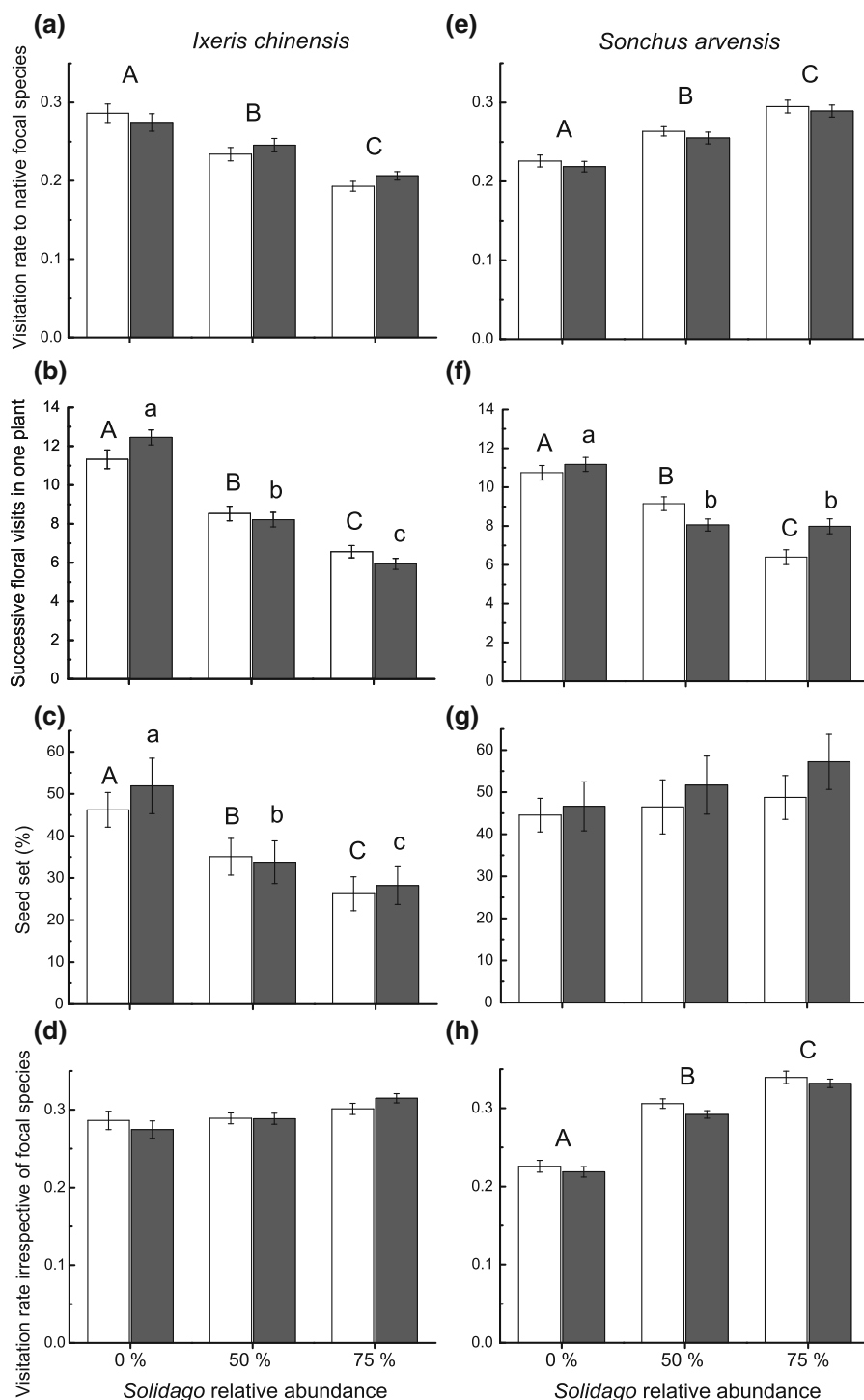


Fig. 1 Visitation rate (the number of visits by honeybees per floral unit per 30 min census) to native focal species (**a**, **e**), successive visits within individual ramets (**b**, **f**), seed set (**c**, **g**) and visitation rate irrespective of focal species (**d**, **h**) for plots with *I. chinensis* and *S. arvensis* in pure stands or in stands with

Solidago floral units comprising 50–75 % of the flower display in 2006 (open bars) and 2007 (filled bars). Standard error bars are shown. Different letters above pairs of bars/single bars indicate significant differences at $P < 0.05$ level (Tukey's multi-comparison test). Seed set was logarithm transformed prior to analysis

Table 2 Mean (\pm SE) number of conspecific, heterospecific (excluding *Solidago*) and *Solidago* pollen grains from samples of 100 pollen grains from pollen loads of honeybees (*Apis**mellifera*) in plots with the one native species (*Ixeris* or *Sonchus*) present either in pure stands or in stands with *Solidago* comprising 50–75 % of floral units

Composition	<i>Ixeris chinensis</i>				<i>Sonchus arvensis</i>			
	N	Conspecific	Heterospecific	<i>Solidago</i>	N	Conspecific	Heterospecific	<i>Solidago</i>
Pure	43	64.16 \pm 2.09 ^a	12.86 \pm 0.96	23.14 \pm 1.83 ^a	58	69.10 \pm 1.43 ^a	8.37 \pm 0.69	22.55 \pm 1.28 ^a
50 % <i>Solidago</i>	39	49.24 \pm 1.87 ^b	13.79 \pm 1.18	36.97 \pm 1.83 ^b	45	52.87 \pm 2.28 ^b	10.78 \pm 1.26	36.87 \pm 2.09 ^b
75 % <i>Solidago</i>	37	38.63 \pm 1.70 ^c	13.71 \pm 1.11	47.66 \pm 1.55 ^c	41	43.07 \pm 2.09 ^c	10.66 \pm 0.88	46.34 \pm 2.25 ^c

Different letters indicate significant differences at $P < 0.05$ level within a column (Tukey's multi-comparison test); letters in bold are significantly different at $P < 0.001$

and seed set of native species (Chittka and Schürkens 2001; Brown et al. 2002; Kandori et al. 2009). Other studies have detected competitive effects on visit rates but not seed set (Totland et al. 2006; Bartomeus et al. 2010) or facilitative (magnet species) effects on visit rates (Lopezaraiza-Mikel et al. 2007; McKinney and Goodell 2011). Similarly, Moragues and Traveset (2005) found that an invasive plant had a competitive effect on visitation on some species but a facilitative effect on others. Bartomeus et al. (2008b) found contrasting effects of two invasive species, with one competing for visits and one facilitating visits to native flowers. Finally, another study did not detect evidence of effects of exotic invasions on either pollinator visits or fruit set (Kaiser-Bunbury et al. 2011).

Given this disparity of effects, there has been interest in determining what traits or conditions influence interactions for pollination. Flower attractiveness, similarity in floral morphology, and degree of generalization of the pollination system all play a role (Bjerknes et al. 2007), with increased similarity in flower size and other traits resulting in increased pollinator sharing between invasive and native plants (Gibson et al. 2012). A meta-analysis of individual studies revealed that invasive plants are more likely to reduce than facilitate native plant pollination, with stronger competitive effects occurring when floral symmetry and color are similar (Morales and Traveset 2009). Memmott and Waser (2002) also found that exotic plants with a taxonomic affinity to natives most successfully invaded plant–pollinator networks, presumably as a result of similarity in floral traits.

Solidago, like many exotic plants introduced as ornamentals, has a sweet scent, large quantities of pollen grains and showy large inflorescences, features that increase its attractiveness (Weber 1997; Chittka and Schürkens 2001; Li and Xie 2002). Hence it is an

important nectar source plant in late autumn (Dong et al. 2006a). Elsewhere in its introduced range, *Solidago* facilitated the pollination of a native species with different floral traits, an outcome attributed to resource complementarity (Ghazoul 2006). In this study, all three species are Composites, actinomorphic and produce yellow capitula. Nevertheless, exotic *Solidago* exhibited different effects on two native species, possible reasons for which we discuss below.

Introduced plants with attractive flowers may facilitate visitation by attracting pollinators from elsewhere, but may compete on a local scale by attracting visitors away from other species (Morales and Traveset 2009). Consequently, neighboring species with attractive flowers are more likely to experience facilitation than those with less attractive flowers. The pollinator-assemblage study demonstrates that *Ixeris* is less attractive to pollinators than *Sonchus*, and in experimental arrays increasing *Solidago* ratio resulted in increased visits to natives and increased visitation rates per floral unit irrespective of focal species in plots with *Sonchus* but not *Ixeris*. *Sonchus* may be more attractive than *Ixeris* for multiple reasons. First, *Sonchus* has larger capitula than does *Ixeris*, and normally, larger flowers are more attractive to pollinators (Benitez-Vieyra et al. 2006; Albert et al. 2008; Andersson 2008; Sletvold et al. 2010). Moragues and Traveset (2005) similarly found that an invasive plant, *Carpobrotus*, had a facilitative effect on *Cistus salviifolius* which had flowers nearly as large, but a competitive or neutral effect on *Cistus monspeliensis*, which had smaller flowers (Page 2012). Moreover, *Solidago*'s floral units are more similar in size to capitula of *Sonchus* than *Ixeris*, potentially allowing *Sonchus* to benefit more from pollinators initially attracted into plots by *Solidago*. Additionally, *Sonchus* offers a larger pollen reward

than does *Ixeris*, and reward size influences attractiveness (Lopezaraiza-Mikel et al. 2007). Finally, *Sonchus* is nearly as tall as *Solidago*, but *Ixeris* is substantially shorter. Taller flowers are often more attractive to pollinators (Lortie and Aarssen 1999; Carromero and Hamrick 2005; Tor ng et al. 2006).

Both native species are self-incompatible and pollen limited in their seed production, making them vulnerable to decrease in seed production with decreasing quantity or quality of pollinator services. Thus, it is not surprising that decreased pollinator visitation rates to *Ixeris* resulted in decreased seed production. Self-incompatibility could render both species susceptible to pollen interference from geitonogamous pollination. Consequently, the finding for both native species that successive visits decreased with increasing *Solidago* ratio suggests that these conditions may have decreased geitonogamy and increased outcrossing. However, increased *Solidago* ratio may also have increased heterospecific pollen transfer and conspecific pollen loss, as pollinators were found to carry more heterospecific pollen and less conspecific pollen in plots with more *Solidago*. It is likely that for *Sonchus* harmful effects of heterospecific pollen receipt and pollen loss nearly counteracted the benefit of increased visitation rates, such that seed set only increased marginally significantly in plots with higher proportion of *Solidago*. The composition of loads on pollinators may differ from the composition of pollen on stigmas (Larson et al. 2006; Bartomeus et al. 2008a), so our data are suggestive but not definitive about the occurrence of heterospecific pollen transfer and pollen loss.

The density of interacting species can affect the nature and magnitude of their interactions for pollination (Moeller 2004; Ghazoul 2006; Bjerknes et al. 2007; Mu oz and Cavieres 2008; Dietzsch et al. 2011), with increased effects of competition for pollination for species at decreasing low densities (Kunin 1993). For example, Mu oz and Cavieres (2008) demonstrated that the effect of the invader *Taraxacum officinale* (Compositae) on two co-familial species shifted with increasing invader density from neutral to competitive for one and facilitative to competitive for the other. In this study, we observed that the effect of *Solidago* on visitation rates, whether competitive or facilitative, increased at higher invader density, with a similar trend for seed set.

In our competition plots, we kept the total floral units in experimental plots constant; consequently,

increased *Solidago* density resulted in decreased native density. We could alternatively have kept native flower density constant while varying *Solidago* density, an approach that would more precisely detect the effect of invasion density on pollination of native species (e.g., Mu oz and Cavieres 2008; Flanagan et al. 2010). However, our approach reflects the fact that *Solidago* negatively affects native populations (Moron et al. 2009; Sk rka et al. 2010), and this approach has also been used previously (e.g., Ghazoul 2006; Dietzsch et al. 2011). Our design thus does not strictly separate intraspecific density effects from those of *Solidago*; however, the design was identical for each native species, such that the results are directly comparable. Moreover, the finding of increased pollination success for *Sonchus* with increased *Solidago* density is more consistent with a facilitative effect of *Solidago* than with decreased conspecific density increasing pollination success.

The experimental arrays were replicated across years but with only one plot per treatment within each year. The lack of spatial replication limits our ability to generalize the effects from this study. Pollinator communities and plant-pollinator interactions may change during the flowering season (reviewed in Bjerknes et al. 2007; Burkle and Alarc n 2011), sometimes resulting in a change in magnitude or direction of interactions (McKinney and Goodell 2011), so our results are not necessarily representative of interactions throughout the flowering season. Honeybees, the dominant pollinator during our study, become active in spring and, given the relatively mild climate of the field site, maintain their activity through the flowering seasons of all three species. Consequently, it is likely that they remain dominant throughout the three species' flowering, though it is possible that they switch their foraging preferences during this time (Gross and Werner 1983).

Ixeris and *Sonchus*, despite their similarities, responded differently in visitation to increasing *Solidago* ratio. As *Solidago* continues its spread in Chinese temperate and sub-tropical areas, there is potential for it to exert effects on a broader range of native species. However, this research indicates that the effects of *Solidago*'s invasion on the pollination of native species may be quite variable. *Solidago* exerts a strong competitive effect on vegetative growth of other species (Walck et al. 1999) and reduces species richness in its native (Meiners et al. 2001) and

introduced range (Moron et al. 2009; Skórka et al. 2010). Consequently, future work should ideally investigate whether *Solidago* has an overall detrimental effect on other species, when interactions for pollination and other resources are both taken into account.

Acknowledgments We thank Li Guo, Long Tang and Meng Lu for assistance in the field and in the lab; Lvshen Plant Nursery for providing the study site; and Dr. Hong Liu and two anonymous reviewers for their insightful comments on the earlier versions of this paper, which greatly improved its quality. This work was financially supported by National Basic Research Program of China (Grant No. 2013CB430404), Leading Academic Discipline Project of Shanghai Municipal Education Commission (J50401), National Natural Sciences Foundation of China (Grant Nos. 30600036, 30930019 and 30910362).

References

- Albert MJ, Iriondo JM, Escudero A, Torres E (2008) Dissecting components of flowering pattern: size effects on female fitness. *Bot J Linn Soc* 156:227–236. doi:[10.1111/j.1095-8339.2007.00735.x](https://doi.org/10.1111/j.1095-8339.2007.00735.x)
- Andersson S (2008) Pollinator and nonpollinator selection on ray morphology in *Leucanthemum vulgare* (Oxeye daisy, Asteraceae). *Am J Bot* 95:1072–1078. doi:[10.3732/ajb.0800087](https://doi.org/10.3732/ajb.0800087)
- Ashman TL, Knight TM, Steets JA, Amarasekare P, Burd M, Campbell DR, Dudash MR, Johnston MO, Mazer SJ, Mitchell RJ, Morgan MT, Wilson WG (2004) Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. *Ecology* 85:2408–2421. doi:[10.1890/03-8024](https://doi.org/10.1890/03-8024)
- Bartomeus I, Bosch J, Vila M (2008a) High invasive pollen transfer, yet low deposition on native stigmas in a *Carpobrotus*-invaded community. *Ann Bot* 102:417–424. doi:[10.1093/aob/mcn109](https://doi.org/10.1093/aob/mcn109)
- Bartomeus I, Vila M, Santamaria L (2008b) Contrasting effects of invasive plants in plant-pollinator networks. *Oecologia* 155:761–770. doi:[10.1007/s00442-007-0946-1](https://doi.org/10.1007/s00442-007-0946-1)
- Bartomeus I, Vila M, Steffan-Dewenter I (2010) Combined effects of *Impatiens glandulifera* invasion and landscape structure on native plant pollination. *J Ecol* 98:440–450. doi:[10.1111/j.1365-2745.2009.01629.x](https://doi.org/10.1111/j.1365-2745.2009.01629.x)
- Benítez-Vieyra S, Medina AM, Glinos E, Cocucci AA (2006) Pollinator-mediated selection on floral traits and size of floral display in *Cyclopogon elatus*, a sweat bee-pollinated orchid. *Func Ecol* 20:948–957. doi:[10.1111/j.1365-2435.2006.01179.x](https://doi.org/10.1111/j.1365-2435.2006.01179.x)
- Bjerknes AL, Totland Ø, Hegland SJ, Nielsen A (2007) Do alien plant invasions really affect pollination success in native plant species? *Biol Conserv* 138:1–12. doi:[10.1016/j.biocon.2007.04.015](https://doi.org/10.1016/j.biocon.2007.04.015)
- Brown BJ, Mitchell RJ, Graham SA (2002) Competition for pollination between an invasive species (purple loosestrife) and a native congener. *Ecology* 83:2328–2336. doi:[10.2307/3072063](https://doi.org/10.2307/3072063)
- Burd M (1994) Bateman's principle and plant reproduction, the role of pollen limitation in fruit and seed set. *Bot Rev* 60:83–139. doi:[10.1007/BF02856594](https://doi.org/10.1007/BF02856594)
- Burkle LA, Alarcón R (2011) The future of plant–pollinator diversity: understanding interaction networks across time, space, and global change. *Am J Bot* 98:528–538. doi:[10.3732/ajb.1000391](https://doi.org/10.3732/ajb.1000391)
- Carronero W, Hamrick JL (2005) Determinants of local abundance and range size in forest vascular plants. *Int J Plant Sci* 166:979–983. doi:[10.1086/449315](https://doi.org/10.1086/449315)
- Chen YC (1993) Apiculture in China. China Agriculture Press, Beijing
- Chittka L, Schürkens S (2001) Successful invasion of a floral market—an exotic Asian plant has moved in on Europe's river-banks by bribing pollinators. *Nature* 411:653. doi:[10.1038/35079676](https://doi.org/10.1038/35079676)
- Chu S (1997) Flora of China: Compositae, vol 80. Science Publisher, Beijing
- Dicks LV, Corbet SA, Pywell RF (2002) Compartmentalization in plant-insect flower visitor webs. *J Anim Ecol* 71:32–43. doi:[10.1046/j.0021-8790.2001.00572.x](https://doi.org/10.1046/j.0021-8790.2001.00572.x)
- Dietzsch AC, Stanley DA, Stout JC (2011) Relative abundance of an invasive alien plant affects native pollination processes. *Oecologia* 167:469–479. doi:[10.1007/s00442-011-1987-z](https://doi.org/10.1007/s00442-011-1987-z)
- Dong M, Lu BR, Zhang HB, Chen JK, Li B (2006a) Role of sexual reproduction in the spread of an invasive clonal plant *Solidago canadensis* revealed using intersimple sequence repeat markers. *Plant Spec Biol* 21:13–18. doi:[10.1111/j.1442-1984.2006.00146.x](https://doi.org/10.1111/j.1442-1984.2006.00146.x)
- Dong M, Lu JZ, Zhang WJ, Chen JK, Li B (2006b) Canada goldenrod (*Solidago canadensis*): an invasive alien weed rapidly spreading in China. *Acta Phytotaxon Sin* 44:72–85. doi:[10.1360/aps050068](https://doi.org/10.1360/aps050068)
- Feinsinger PH, Tiebout MI, Young BE (1991) Do tropical bird-pollinated plants exhibit density-dependent interactions? field experiments. *Ecology* 72:1953–1963. doi:[10.2307/1941550](https://doi.org/10.2307/1941550)
- Feldman TS, Morris WF, Wilson WG (2004) When can two plant species facilitate each other's pollination? *Oikos* 105:197–207. doi:[10.1111/j.0030-1299.2004.12845.x](https://doi.org/10.1111/j.0030-1299.2004.12845.x)
- Flanagan RJ, Mitchell RJ, Knutowski D, Karron JD (2009) Interspecific pollinator movements reduce pollen deposition and seed production in *Mimulus ringens* (Phrymaceae). *Am J Bot* 96:809–815. doi:[10.3732/ajb.0800317](https://doi.org/10.3732/ajb.0800317)
- Flanagan RJ, Mitchell RJ, Karron JD (2010) Increased relative abundance of an invasive competitor for pollination, *Lythrum salicaria*, reduces seed number in *Mimulus ringens*. *Oecologia* 164:445–454. doi:[10.1007/s00442-010-1693-2](https://doi.org/10.1007/s00442-010-1693-2)
- Ghazoul J (2006) Floral diversity and the facilitation of pollination. *J Ecol* 94:295–304. doi:[10.1111/j.1365-2745.2006.01098.x](https://doi.org/10.1111/j.1365-2745.2006.01098.x)
- Gibson MR, Richardson DM, Pauw A (2012) Can floral traits predict an invasive plant's impact on native plant–pollinator communities? *J Ecol* 100:1216–1223. doi:[10.1111/j.1365-2745.2012.02004.x](https://doi.org/10.1111/j.1365-2745.2012.02004.x)
- Gordon DR (1998) Effects of invasive, non-indigenous plant species on ecosystem processes, lessons from Florida. *Ecol Appl* 8:975–989. doi:[10.2307/2640955](https://doi.org/10.2307/2640955)

- Gross RS, Werner PA (1983) Relationships among flowering phenology, insect visitors, and seed-set of individuals—experimental studies on 4 co-occurring species of goldenrod (*Solidago*, Compositae). *Ecol Monogr* 53:95–117. doi:[10.2307/1942589](https://doi.org/10.2307/1942589)
- Kaiser-Bunbury CN, Valentin T, Mougil J, Matatiken D, Ghazoul J (2011) The tolerance of island plant-pollinator networks to alien plants. *J Ecol* 99:202–213. doi:[10.1111/j.1365-2745.2010.01732.x](https://doi.org/10.1111/j.1365-2745.2010.01732.x)
- Kandori I, Hirao T, Matsunaga S, Kurosaki T (2009) An invasive dandelion unilaterally reduces the reproduction of a native congener through competition for pollination. *Oecologia* 159:559–569. doi:[10.1007/s00442-008-1250-4](https://doi.org/10.1007/s00442-008-1250-4)
- Kearns CA, Inouye DW (1993) Techniques for pollination biologist. University Press of Colorado, Colorado
- Kunin WE (1993) Sex and the single mustard: population density and pollinator behavior effects on seed-set. *Ecology* 74:2145–2160. doi:[10.2307/1940859](https://doi.org/10.2307/1940859)
- Kunin WE, Shmida A (1997) Plant reproductive traits as a function of local, regional, and global abundance. *Conserv Biol* 11:183–192. doi:[10.1046/j.1523-1739.1997.95469.x](https://doi.org/10.1046/j.1523-1739.1997.95469.x)
- Kwak MM, Jennersten O (1991) Bumblebee visitation and seed set in *Melampyrum pratense* and *Viscaria vulgaris*—heterospecific pollen and pollen limitation. *Oecologia* 86:99–104. doi:[10.1007/BF00317395](https://doi.org/10.1007/BF00317395)
- Larson BMH, Barrett SCH (2000) A comparative analysis of pollen limitation in flowering plants. *Biol J Linn Soc* 69:503–520. doi:[10.1111/j.1095-8312.2000.tb01221.x](https://doi.org/10.1111/j.1095-8312.2000.tb01221.x)
- Larson DL, Royer RA, Royer MR (2006) Insect visitation and pollen deposition in an invaded prairie plant community. *Biol Conserv* 130:148–159. doi:[10.1016/j.biocon.2005.12.009](https://doi.org/10.1016/j.biocon.2005.12.009)
- Lavery TM (1992) Plant interactions for pollinator visits—a test of the magnet species effect. *Oecologia* 89:502–508
- Lema WK, Messersmith CG (1990) The biology of Canadian weeds. 94. *Sonchus arvensis* L. *Can J Plant Sci* 70:509–532
- Li ZY, Xie Y (2002) Invasive alien species in China. China Forestry Publishing House, Beijing
- Lopezaraiza-Mikel ME, Hayes RB, Whalley MR, Memmott J (2007) The impact of an alien plant on a native plant-pollinator network: an experimental approach. *Ecol Lett* 10:539–550. doi:[10.1111/j.1461-0248.2007.01055.x](https://doi.org/10.1111/j.1461-0248.2007.01055.x)
- Lortie CJ, Aarssen LW (1999) The advantage of being tall: higher flowers receive more pollen in *Verbascum thapsus* L. (Scrophulariaceae). *Ecoscience* 6:68–71
- McKinney AM, Goodell K (2010) Shading by invasive shrub reduces seed production and pollinator services in a native herb. *Biol Invasions* 12:2751–2763. doi:[10.1007/s10530-009-9680-4](https://doi.org/10.1007/s10530-009-9680-4)
- McKinney AM, Goodell K (2011) Plant-pollinator interactions between an invasive and native plant vary between sites with different flowering phenology. *Plant Ecol* 212:1025–1035. doi:[10.1007/s11258-010-9882-y](https://doi.org/10.1007/s11258-010-9882-y)
- Meiners SJ, Pickett STA, Cadenasso ML (2001) Effects of plant invasions on the species richness of abandoned agricultural land. *Ecography* 24:633–644
- Memmott J, Waser NM (2002) Integration of alien plants into a native flower-pollinator visitation web. *Proc R Soc Lond B* 269:2395–2399. doi:[10.1098/rspb.2002.2174](https://doi.org/10.1098/rspb.2002.2174)
- Mitchell RJ, Flanagan RJ, Brown BJ, Waser NM, Karron JD (2009) New frontiers in competition for pollination. *Ann Bot* 103:1403–1413. doi:[10.1093/aob/mcp062](https://doi.org/10.1093/aob/mcp062)
- Moeller DA (2004) Facilitative interactions among plants via shared pollinators. *Ecology* 85:3289–3301. doi:[10.1890/03-0810](https://doi.org/10.1890/03-0810)
- Montgomery BR (2009a) Do pollen carryover and pollinator constancy mitigate effects of competition for pollination? *Oikos* 118:1084–1092. doi:[10.1111/j.1600-0706.2009.17064.x](https://doi.org/10.1111/j.1600-0706.2009.17064.x)
- Montgomery BR (2009b) Effect of introduced *Euphorbia esula* on the pollination of *Viola pedatifida*. *Botany-Botanique* 87:283–292. doi:[10.1139/b08-139](https://doi.org/10.1139/b08-139)
- Montgomery BR (2009c) Pollination of *Sisyrinchium campestre* (Iridaceae) in prairies invaded by the introduced pant *Euphorbia esula* (Euphorbiaceae). *Am Midl Nat* 162:239–252. doi:[10.1674/0003-0031-162.2.239](https://doi.org/10.1674/0003-0031-162.2.239)
- Moragues E, Traveset A (2005) Effect of *Carpobrotus* spp. on the pollination success of native plant species of the Balearic Islands. *Biol Conserv* 122:611–619. doi:[10.1016/j.biocon.2004.09.015](https://doi.org/10.1016/j.biocon.2004.09.015)
- Morales CL, Traveset A (2009) A meta-analysis of impacts of alien versus native plants on pollinator visitation and reproductive success of co-flowering native plants. *Ecol Lett* 12:716–728. doi:[10.1111/j.1461-0248.2009.01319.x](https://doi.org/10.1111/j.1461-0248.2009.01319.x)
- Moron D, Lenda M, Skorka P, Szentgyorgyi H, Settele J, Woyciechowski M (2009) Wild pollinator communities are negatively affected by invasion of alien goldenrods in grassland landscapes. *Biol Conserv* 142:1322–1332. doi:[10.1016/j.biocon.2008.12.036](https://doi.org/10.1016/j.biocon.2008.12.036)
- Motten AF (1982) Autogamy and competition for pollinators in *Hepatica americana* (Ranunculaceae). *Am J Bot* 69:1296–1305. doi:[10.2307/2442754](https://doi.org/10.2307/2442754)
- Muñoz AA, Cavieres LA (2008) The presence of a showy invasive plant disrupts pollinator service and reproductive output in native alpine species only at high densities. *J Ecol* 96:459–467. doi:[10.1111/j.1365-2745.2008.01361.x](https://doi.org/10.1111/j.1365-2745.2008.01361.x)
- Page RG (2012) The *Cistus* and *Halimium* website. <http://www.cistuspage.org.uk/>. Accessed 1 Jan 2012
- Powell KI, Krakos KN, Knight TM (2011) Comparing the reproductive success and pollination biology of an invasive plant to its rare and common native congeners: a case study in the genus *Cirsium* (Asteraceae). *Biol Invasions* 13:905–917. doi:[10.1007/s10530-010-9878-5](https://doi.org/10.1007/s10530-010-9878-5)
- Rathcke B (ed) (1983) Competition and facilitation among plants for pollination. Pollination biology. Academic Press, Orlando
- Roy BA (1996) A plant pathogen influences pollinator behavior and may influence reproduction of nonhosts. *Ecology* 77:2445–2457. doi:[10.2307/2265745](https://doi.org/10.2307/2265745)
- Shi Z, Chen YL, Chen YS, Lin YR, Liu SW, Ge XJ, Gao TG, et al. (2011) Asteraceae (Compositae). In: Wu ZY, Raven PH, Hong DY (ed) Flora of China vol 20–21. http://www.efloras.org/florataxon.aspx?flora_id=2&taxon_id=10074 Accessed 1 Feb 2012. Science Press, Beijing; Missouri Botanical Garden Press, St. Louis
- Skórka P, Lenda M, Tryjanowski P (2010) Invasive alien goldenrods negatively affect grassland bird communities in Eastern Europe. *Biol Conserv* 143:856–861. doi:[10.1016/j.biocon.2009.12.030](https://doi.org/10.1016/j.biocon.2009.12.030)
- Sletvold N, Grindeland JM, Agren J (2010) Pollinator-mediated selection on floral display, spur length and flowering phenology in the deceptive orchid *Dactylorhiza lapponica*.

- New Phytol 188:385–392. doi:[10.1111/j.1469-8137.2010.03296.x](https://doi.org/10.1111/j.1469-8137.2010.03296.x)
- Sun SG (2008) Reproductive strategy and adaptation of an invasive plant *Solidago canadensis* in China. Fudan University, Dissertation
- Sundaram B, Hiremath AJ (2012) *Lantana camara* invasion in a heterogeneous landscape: patterns of spread and correlation with changes in native vegetation. Biol Invasions 14:1127–1141. doi:[10.1007/s10530-011-0144-2](https://doi.org/10.1007/s10530-011-0144-2)
- Tao HJ (1999) Divine Farmer's Materia Medica: A Translation of the Shen Nong Ben Cao Jing (trans: Yang SZ). Blue Poppy Press, Boulder
- Toräng P, Ehrlén J, Ågren J (2006) Facilitation in an insect-pollinated herb with a floral display dimorphism. Ecology 87:2113–2117. doi:[10.1890/0012-9658\(2006\)87\[2113:FIAIHW\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2113:FIAIHW]2.0.CO;2)
- Totland O, Nielsen A, Bjerknes AL, Ohlson M (2006) Effects of an exotic plant and habitat disturbance on pollinator visitation and reproduction in a boreal forest herb. Am J Bot 93:868–873. doi:[10.3732/ajb.93.6.868](https://doi.org/10.3732/ajb.93.6.868)
- Walck JL, Baskin JM, Baskin CC (1999) Relative competitive abilities and growth characteristics of a narrowly endemic and a geographically widespread *Solidago* species (Asteraceae). Am J Bot 86:820–828. doi:[10.2307/2656703](https://doi.org/10.2307/2656703)
- Waser NM (1978) Interspecific pollen transfer and competition between co-occurring plant species. Oecologia 36:223–236. doi:[10.1007/bf00349811](https://doi.org/10.1007/bf00349811)
- Weber E (1997) Morphological variation of the introduced perennial *Solidago canadensis* L sensu lato (Asteraceae) in Europe. Bot J Linn Soc 123:197–210. doi:[10.1111/j.1095-8339.1997.tb01413.x](https://doi.org/10.1111/j.1095-8339.1997.tb01413.x)
- Yang SA, Ferrari MJ, Shea K (2011) Pollinator behavior mediates negative interactions between two congeneric invasive plant species. Am Nat 177:110–118. doi:[10.1086/657433](https://doi.org/10.1086/657433)
- Zavaleta ES, Hobbs RJ, Mooney HA (2001) Viewing invasive species removal in a whole-ecosystem context. Trends Ecol Evol 16:454–459. doi:[10.1016/s0169-5347\(01\)02194-2](https://doi.org/10.1016/s0169-5347(01)02194-2)
- Zhang S et al (2006) Bioactive guaianolides from *Siyekucui* (*Ixeris chinensis*). J Nat Prod 69:1425–1428. doi:[10.1016/S1875-5364\(09\)60008-X](https://doi.org/10.1016/S1875-5364(09)60008-X)