

The presence of the invasive plant Solanum elaeagnifolium deters honeybees and increases pollen limitation in the native co-flowering species Glaucium flavum

T. Tscheulin & T. Petanidou

Biological Invasions

ISSN 1387-3547

Volume 15

Number 2

Biol Invasions (2013) 15:385-393

DOI 10.1007/s10530-012-0293-y



Your article is protected by copyright and all rights are held exclusively by Springer Science+Business Media B.V.. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your work, please use the accepted author's version for posting to your own website or your institution's repository. You may further deposit the accepted author's version on a funder's repository at a funder's request, provided it is not made publicly available until 12 months after publication.

The presence of the invasive plant *Solanum elaeagnifolium* deters honeybees and increases pollen limitation in the native co-flowering species *Glaucium flavum*

T. Tscheulin · T. Petanidou

Received: 30 September 2011 / Accepted: 23 July 2012 / Published online: 7 August 2012
© Springer Science+Business Media B.V. 2012

Abstract Invasive plants can impact biodiversity and ecosystem functioning by displacing native plants and crop species due to competition for space, nutrients, water and light. The presence of co-flowering invasives has also been shown to affect some native plants through the reduction in pollinator visitation or through the deposition of heterospecific pollen on the native's stigmas leading to stigma clogging. We examined the impact of the invasive plant *Solanum elaeagnifolium* Cavanilles (silver-leafed nightshade), native to South and Central America and South-western parts of North America, on the seed set of the native *Glaucium flavum* Crantz (yellow-horned poppy) on Lesvos Island, Greece. To do this we measured seed set and visitation rates to *G. flavum* before and after the placement of potted individuals of the invasive near the native plants. In addition, we hand-crossed *G. flavum* flowers with super-optimal amounts of conspecific pollen, bagged flowers to measure the rate of spontaneous selfing, and applied self-pollen to measure self-compatibility of *G. flavum*. The hand-selfing treatment resulted in very low seed set, which indicates that *G. flavum* is to a large degree self-incompatible and highlights the plant's need

for insect-mediated outcrossing. We show that the presence of the invasive significantly enhanced pollen limitation, although the overall visitation rates were not reduced and that this increase is due to a reduction in honeybee visitation in the presence of the invasive resulting in reduced pollination.

Keywords Pollination · Pollen limitation · Alien · Pollination services · Lesvos · Mediterranean

Introduction

Invasive plants have the potential to negatively impact biodiversity and ecosystem functioning (Pimentel et al. 2001; Traveset and Richardson 2006), because they compete with native plants and crop species for space, nutrients, water and light (Mack and D'Antonio 1998; Wardle et al. 1994; Weihe and Neely 1997). In few studies, the presence of a co-flowering invasive has also been shown to affect native plants through the disruption of pollination services (see Bjerknes et al. 2007 for a short review).

Plants competing for pollination services can suffer from an increase of heterospecific pollen deposition and/or a reduction in visitation rates, which can both lead to a decrease in seed set. In particular, invasives have been shown to affect pollinator–native plant interactions negatively by lowering visitation rates

T. Tscheulin (✉) · T. Petanidou
Laboratory of Biogeography and Ecology,
Department of Geography, University of the Aegean,
University Hill, 81100 Mytilene, Greece
e-mail: t.tscheulin@geo.aegean.gr

T. Petanidou
e-mail: t.petanidou@aegean.gr

(e.g. Brown et al. 2002; Chittka and Schürkens 2001; Larson et al. 2006; Moragues and Traveset 2005; Thijs et al. 2012; Totland et al. 2006) and seed set (e.g. Brown et al. 2002; Chittka and Schürkens 2001; Grabas and Laverty 1999; Thijs et al. 2012).

In contrast, there are also cases where invasives were shown to have a positive effect in terms of visitation (e.g. Grabas and Laverty 1999; Larson et al. 2006; Moragues and Traveset 2005) and seed set (e.g. Brown et al. 2002; Chittka and Schürkens 2001; Grabas and Laverty 1999), or no effect on visitation (e.g. Aigner 2004; Grabas and Laverty 1999; Larson et al. 2006; Moragues and Traveset 2005; Thijs et al. 2012) and seed set (e.g. Aigner 2004; Grabas and Laverty 1999; Moragues and Traveset 2005; Thijs et al. 2012; Totland et al. 2006).

The cases where invasives had a positive effect on the pollination of native plants were explained by arguing that they provide additional resources for pollinators, which could potentially lead to an overall increase in pollinator abundance, diversity, geographic range or even duration of their foraging season (Feldman et al. 2004; Memmott and Waser 2002; Tepedino et al. 2008).

Conversely, some invasives have been shown to attract pollinators that were previously monopolized by the native species, which could lead to lower visitation rates to the natives, deposition of heterospecific pollen (Lopezaraiza-Mikel et al. 2007; Matsumoto et al. 2010) and subsequently to reduction in seed set (Jacobi et al. 2005; Larson et al. 2006).

Due to the inconstant foraging behaviour of many pollinators, especially generalists, which make up the vast majority of visitors to invasive plants, flowers may receive heterospecific pollen (Lopezaraiza-Mikel et al. 2007; Memmott and Waser 2002). As a direct result this can lower seed set in the natives even in the absence of pollinator limitation (Kasagi and Kudo 2005; Petanidou et al. 1995; Ruane and Donohue 2007). The reduction in seed set caused by the deposition of heterospecific pollen can be the result of several processes namely stigma clogging (Holland and Chamberlain 2007), stigma closing, pollen allelopathy, stylar clogging and stylar inhibition (see Brown and Mitchell 2001 and references therein). Heterospecific pollen deposition occurring between closely related species may lead to hybridization, a further threat to native flora (Brown and Mitchell 2001; Chapman et al. 2005; Kasagi and Kudo 2005). In

addition, heterospecific pollen deposition constitutes a loss of male gametes and therefore potentially reduces male fitness (McGuire and Armbruster 1991).

Here we examine the impact of the invasive plant *Solanum elaeagnifolium* Cavanilles (silver-leafed nightshade) on the visitation to and seed set of the native *G. flavum* Crantz (yellow-horned poppy). These species serve as an excellent system for study given that they co-occur in coastal habitats in the Mediterranean, have a prolonged period of overlapping flowering times, and share pollinators (Tscheulin et al. 2008, 2009). We hypothesize that the native *G. flavum* would receive fewer visits but would not necessarily produce fewer seeds in the presence of *S. elaeagnifolium* based on our previous work in this system (Tscheulin et al. 2009; Vila et al. 2009), which indicates that the presence of the invasive lowers visitation rates to the native but even high proportions of manually applied invasive pollen does not significantly reduce seed set in the native. In contrast to our previous work in this system where we used invaded and uninvaded stands of the native, we used potted individuals of the invasive to better control for confounding factors and we measured the seed set of *G. flavum* under natural conditions before and after the addition of the invasive.

Materials and methods

Study species

Both study species, *G. flavum* and *S. elaeagnifolium*, co-occur in coastal habitats in the Mediterranean, have a prolonged period of overlapping flowering times in summer, and share pollinators (Tscheulin et al. 2008, 2009).

Glaucium flavum is a perennial herb that typically occurs along the Mediterranean shores and the coasts of W. Europe in shingle or stable pebbles just above the beach (Thanos et al. 1989). Such pebble and shingle beaches and their perennial vegetation have been designated as special areas of conservation in Annex I of the EU Habitat Directive 92/43/EEC (EU 1992). The large yellow flowers of *G. flavum* have four silky petals, which drop on the same day of anthesis after which the stigma is no longer receptive and the long curved seed capsules develop). An average plant

produces above 400 seed capsules during a season (Thomas Tscheulin, personal observation).

Solanum elaeagnifolium is native to Central America and South-western parts of North America (Boyd et al. 1984; Brunel 2011). It is a known invasive in all countries of the Mediterranean Basin, Australia, Chile, Australia, India, New Zealand, Pakistan, Puerto Rico, South Africa, Taiwan and Zimbabwe (Bouhache and Tanji 1985; Boyd et al. 1984; Mekki 2007). In Greece *S. elaeagnifolium* is widespread especially on the mainland and locally very abundant (Boratynski et al. 1992; Economidou and Yannitsaros 1975; Petanidou et al. 2012; Tscheulin et al. 2008). *S. elaeagnifolium* is deep-rooted, which is the main reason why control with herbicides has shown only limited success (Baye et al. 2007; Eleftherohorinos et al. 1993). It lowers crop yield through competition, may lower the quality of hay taken from infested fields, and is toxic to livestock such as sheep, cattle and horses (Brunel 2011 and references therein). The flowers have poricidal anthers and are buzz-pollinated by bees (Buchmann and Cane 1989). Individual berries produce up to 150 seeds (Boyd and Murray 1982), which can add up to 5 million to 100 million seeds per acre (Cooley and Smith 1971). Seeds may be dispersed by animal faeces, water, machinery and agricultural produce and dried plants may also blow like tumbleweeds, spreading seed along the way (Boyd et al. 1984). *S. elaeagnifolium* can also spread by root fragments (Boyd and Murray 1982).

Study sites and experimental setup

We conducted all observations and flower treatments in three natural *G. flavum* populations on Lesvos island, in 2008. The sites were located in Skala Vasilikon (39°08'54.98"N, 26°14'59.27"E), in Mytilene (39°06'46.54"N, 26°33'39.89"E) and in Chroussos beach, southwest of Mesotopos (39°06'27.32"N, 25°57'52.89"E), hereafter called Chroussos. The populations are a minimum of 5 km away from the closest population of *S. elaeagnifolium*, a distance which we consider beyond the maximum foraging range of bees visiting *S. elaeagnifolium* (Gathmann and Tscharnke 2002; Greenleaf et al. 2007; Tscheulin et al. 2011). The sites are a minimum distance of 20 km from each other. During all rounds and in all sites, the study plants were the single most

abundant and dense flower source in the respective study areas.

In each site, we randomly chose and marked 50 *G. flavum* plants, apart from Chroussos where we marked all available 43 plants. In total we visited the sites three times (May/June, July and August) during the main flowering period of both plant species apart from the Skala Vasilikon site, in which the *G. flavum* plants failed to produce adequate numbers of flowers in rounds 2 and 3. In each round and site we conducted 4 days of flower observations and flower treatments, on day 1, in the absence of the invasive and the remaining days in the presence of the invasive. On day 2 of each round, before 9.00, 50 (43 in Chroussos) *S. elaeagnifolium* pots were placed next to individual *G. flavum* plants, so that each marked native plant had a maximum distance of 0.5 m from an invasive plant, and so that there were equal numbers of marked native plants and invasive plants (Table 1). Care was taken that the plant heights within each pair were similar. On day 4 after the end of the main pollinator activity, the plant pots were removed from the sites.

All *S. elaeagnifolium* plants were grown in black plastic flower pots (diameter 220 mm, height 250 mm) in standard greenhouse medium under identical conditions of light, temperature and fertilization. Plants were grown from seeds collected on the island and were in full flowering at the time of the experiment.

Pollination treatments

All *G. flavum* flowers for the hand-crossing, hand-selfing and spontaneous selfing treatment on the chosen experimental plants were covered with tulle bags before anthesis unless stated otherwise. The bags were removed for the treatment on the day of anthesis and immediately replaced after treatment except for

Table 1 Schedule of experimental activities carried out in each site and round, in the morning (AM) and afternoon (PM)

Activity	Day 1 Invasive absent	Day 2 Invasive present	Day 3 Invasive present	Day 4 Invasive present
Setting up pots (9.00)		X		
Removal of pots (16.00)				X
AM observation <i>Glaucium</i>	X			X
PM observation <i>Glaucium</i>	X		X	
AM observation <i>Solanum</i>				X
PM observation <i>Solanum</i>			X	
Open pollination	X			X
Hand-crossing		X		
Spontaneous selfing		X		
Hand-selfing		X		
Stigma collection	X			X

the spontaneous selfing treatment, in which the flowers remained covered throughout anthesis. For hand-pollinations we used the anthers of dehiscent flowers, which we daubed onto the receiving stigmas and thus applied the grains directly on the stigmas until they were visibly covered with pollen assuming that the transfer occurred with equal facility in each replicate and treatment. The number of pollen applied to each flower by far exceeded the expected number of ovules. We applied the spontaneous selfing and hand-selfing treatment once to one flower on each experimental plant in round 1 in the Mytilene population (totaling 50 flowers per treatment) and the hand-crossing treatment once to one flower on each experimental plant in all rounds and sites (totaling 329 flowers per treatment). In the spontaneous selfing treatment flowers were left untreated but covered with tulle bags, which were removed after the flowers had senesced. All pollen-donor flowers were first day, virgin flowers that had been covered with tulle bags before anthesis to prevent contact with flower visitors. The flowers for the hand-crossing treatment were taken from *G. flavum* plants at a distance of at least 10 m. The flowers for the hand-selfing treatment were taken from the same *G. flavum* plants as the pollen receiving flower. All tulle bags were removed after the flowers had senesced.

In addition, we marked one flower per experimental plant that was left untreated and uncovered to test for open pollination (free seed set) before (day 1) and after (day 3 & 4) the addition of the invasive plant (totaling 329 marked flowers in each group).

When mature all seed capsules were harvested and the seeds counted.

Pollen loads on stigmas

We examined stigmas of native flowers on mixed stands to assess the presence of *S. elaeagnifolium* pollen on them. To do this we collected 30 stigmas from *G. flavum* flowers each round before (on day 1) and after (on day 3) the addition of the potted invasive plants. The stigmas were collected, when the main pollinator activity was over (after 16.00), and inserted into small vials with alcohol (70 %) to fix pollen grains settled on stigmas. In the laboratory, stigmas were extracted and placed in distilled water, and the proportions of *G. flavum* and *S. elaeagnifolium* pollen grains were counted under a dissecting microscope.

Flower visitation

In each census we recorded the total number of flowers and the number of flower visits per insect visitor on each plant. Each flower visitor was classified as either honeybee, buzz-pollinator or other pollinator. This grouping was chosen as buzzing (sonicating) bees are more likely to be able to extract pollen from the poricidal *S. elaeagnifolium* flowers and therefore have a higher potential to impact on *G. flavum* seed set through the deposition of invasive pollen. The 'buzz-pollinators' belonged to *Bombus terrestris*, *Xylocopa violacea*, *Xylocopa iris*, *Pseudapis* spp. and *Amegilla* spp.; the 'other pollinators' belonged to non-buzzing Halictidae; other non-identified, non-buzzing bees; Syrphidae; and bee beetles (Trichiinae). Observations were carried out in the morning and afternoon for 3 min on each plant and time, and took place between 9.00 and 12.00 (morning observations) and 12.00 and 15.00 (afternoon observations) on sunny and calm days.

Each round we recorded flower visitation to *G. flavum* before (on day 1, in the morning and afternoon) and a minimum of 24 h after (on day 3 morning and day 4 afternoon) the introduction of *S. elaeagnifolium* (Table 1). We also recorded flower visitation to *S. elaeagnifolium* (on day 3 morning and day 4 afternoon).

Statistical analysis

We carried out separate Mann–Whitney U tests to compare seed set per fruit in the treatments hand-selfing, spontaneous selfing and the open-pollinated control in the Mytilene population, round 1, using SPSS, version 15.0 (SPSS 2006). Bonferroni corrections were applied.

Visits to flowers and flower number per plant were averaged over morning and afternoon observations, and pooled over round. Likewise seed set data per site were pooled over round. We calculated the pollen limitation experienced in the three populations of *G. flavum* for every round and treatment as follows:

$$\text{Pollen limitation} = 1 - \frac{\text{Free seed set}}{\text{Hand cross seed set}}$$

and Δ pollen limitation (Δpl) as a measurement of change of pollen limitation in presence of *S. elaeagnifolium* for every round as follows:

$$\Delta pl = \left(1 - \frac{\text{Free seed set}_{\text{invasive absent}}}{\text{Hand - cross seed set}}\right) - \left(1 - \frac{\text{Free seed set}_{\text{invasive present}}}{\text{Hand - cross seed set}}\right)$$

The predictor variables were treatment (presence or absence of the invasive), round and the differences between the *G. flavum* visitation rates per hour and flower ((visitation rates in the absence of the invasive) – (visitation rates in the presence of the invasive)) by the three main pollinator groups: Δ honeybee visitation rate per hour and flower, Δ buzz-pollinator visitation rate per hour and flower, and Δ other pollinator visitation rate per hour and flower. Two models were constructed using the response variables pollen limitation and Δ pollen limitation, which fulfilled the requirements of normality and homoscedasticity. Only models based on predictor variables that were not significantly correlated were constructed. We applied linear mixed effects models fitted by maximum likelihood using the “nlme function” in R, version 2.8 (R Development Core Team 2008). Within the mixed models the factor site was specified as random effect and round (essentially a time effect) as a fixed effect to account for the repeated measures. A nested design was applied with round being nested in site. For every response variable we constructed maximal models containing all predictor variables and their interactions. We then simplified the models using a stepwise backward elimination of the terms.

Throughout the manuscript all error bars are SE.

Results

Pollination treatments

Due to the ongoing growth of the plants some seed capsules could not be found and did not enter the analysis. In total, we collected 262 and 235 seed capsules in the free seed set (open pollination) treatment in absence and presence of the invasive, respectively, and 240, 36 and 44 seed capsules in the hand-crossing, hand-selfing and spontaneous selfing treatment, respectively. The seeds in all seed capsules were counted. Flowers produced significantly fewer seeds in the selfing treatments compared to the hand-

crossing treatment, which indicates that *G. flavum* is to a large degree self-incompatible (Fig. 1).

Pollen limitation, which exists even in the absence of the invasive, was significantly affected by the treatment (Fig. 2; Table 2). This shows that the presence of the invasive further enhances pollen limitation and therefore has a strong negative effect on seed production. The effects of round were not significant.

Pollen loads on stigmas

The *G. flavum* stigmas collected in the presence of *S. elaeagnifolium* had very low (below 1 % in every sample) invasive pollen on them (data not presented). In the light of the results of Tscheulin et al. (2009) that showed that the manual deposition of even high proportions of the invasive's pollen did not affect seed set, the invasive pollen counts were deemed to be too low to significantly impact seed set and are therefore not considered further here.

Flower visitation and pollen limitation

Glaucium flavum and *S. elaeagnifolium* plants were observed for a total of 60 (including observations before and after the addition of the invasive) and 30 h, respectively. A total of 9,072 *G. flavum* flowers (4,501

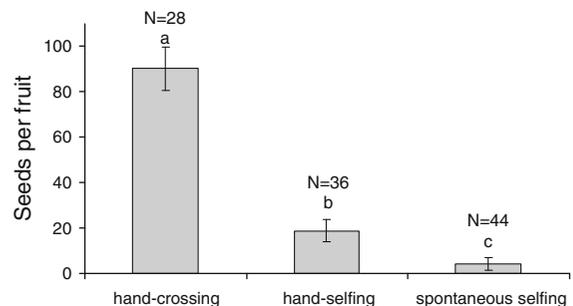


Fig. 1 *Glaucium flavum* seed set in three different pollination treatments in the Mytilene population, round 1. Different letters above the bars indicate significant difference between the treatments. Also given is the sample size N (# of capsules)

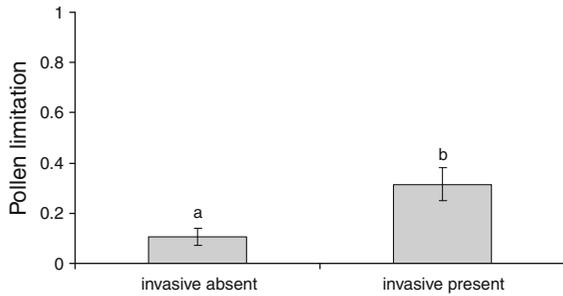


Fig. 2 *Glaucium flavum* pollen limitation in absence and presence of *S. elaeagnifolium*. Different letters above the bars indicate significant differences between the treatments. The values are based on the seed counts of 262 and 235 seed capsules produced in the absence and presence of the invasive, respectively. All counts were averaged over round before the statistical comparison of the treatments

Table 2 Results of mixed effects models using a nested design with round (fixed factor) nested in site (random factor)

	Pollen limitation		Δ Pollen limitation	
	df	F, P	df	F, P
Treatment	1, 6	9.52, 0.022		
Round		n.s.		
Δ Honeybee visitation			1, 3	243.75, 0.0006
Δ Buzzer visitation				n.s.
Δ Small pollinator visitation				n.s.

For every response variable we constructed maximal models containing all predictor variables and their interactions. We then simplified the models using a stepwise backward elimination of the terms. The variables in the top row are response variables, the variables in the first column are predictor variables

before and 4,571 after the addition of the invasive) and 4,679 *S. elaeagnifolium* flowers were observed of which the former received 1,662 (774 before and 888 after the addition of the invasive) and the latter 154 pollinator visits (Fig. 3; Table 3). Thus, *G. flavum* overall flower visitation rate increased slightly in the presence of the invasive due to the increase in buzz-pollinator visits. At the same time the flower visitation rates of honeybees and other pollinators decreased in the presence of the invasive. Although not recorded separately, very rarely insects (mainly *B. terrestris*) were seen visiting both *G. flavum* and

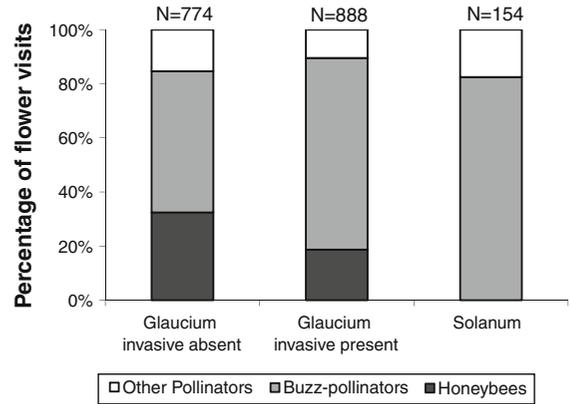


Fig. 3 Percentages of visits to *G. flavum* in absence and presence of the invasive and to the invasive itself performed by different pollinator groups for all sites and rounds combined

S. elaeagnifolium flowers in the same bout (Tscheulin, personal observation).

Δ pollen limitation was significantly negatively affected by Δ honeybee visitation (Table 2), showing that the increase in pollen limitation when the invasive is present is driven by a decline in honeybee visits.

Discussion

Pollination treatments

Spontaneous selfing, achieved by excluding pollinators before and during anthesis, resulted in very low seed set. This result is in accord with Eisikowitch (1979), who showed that spontaneous selfing in several populations of *G. flavum* in Israel occurred only rarely, in 1.8 % of flowers. The low seed set in the hand-selfing treatment indicates that *G. flavum* is to a large degree self-incompatible, which highlights the plant's need for insect-mediated outcrossing and enhances the potentially negative pollination-related effects from invasive species (Tscheulin et al. 2009).

Flower visitation and pollen limitation

The presence of the invasive significantly enhanced pollen limitation in *G. flavum*, which resulted in a pronounced decrease in seed set in open-pollinated flowers in relation to hand-crossed flowers. This increase in pollen limitation was driven by a reduction in honeybee visitation in the presence of *S.*

Table 3 Total number of visits and visitation rates (visits per hour and flower) by the three pollinator groups to *G. flavum* in the absence and presence of the invasive *S. elaeagnifolium* and to the invasive itself

	Total number of visits		<i>Solanum</i>	Flower visitation rate ^{-h}		<i>Solanum</i>
	<i>Glaucium</i>			<i>Glaucium</i>		
	Invasive absent	Invasive present		Invasive absent	Invasive present	
Honeybees	251	166	0	0.56	0.36	0
Buzz-pollinators	404	629	127	0.88	1.39	0.27
Other Pollinators	119	93	27	0.26	0.10	0.06
Total	774	888	154	1.70	1.85	0.33

elaegnifolium. None of the other pollinator groups significantly influenced pollen limitation. We have previously shown that the presence of *S. elaeagnifolium* can cause an overall decrease in flower visitation to *G. flavum* by pollinators including honeybees where both plant species co-occur (Tscheulin et al. 2009). In contrast to the present study, however, Tscheulin et al. (2009) found a decrease in buzz-pollinator visitation in invaded habitats. As the two plant species in this study were not in competition for any resource other than pollinators we are confident that there were no non-pollination related effects on seed set. Several other studies have found a negative impact of invasive plants on the visitation of native plants (Bartomeus et al. 2008; Brown et al. 2002; Chittka and Schürkens 2001). Conversely, Aigner (2004) observed no significant difference in visitation to the native whether or not two invasives were present, and Bartomeus et al. (2008) and Lopezaraiza-Mikel et al. (2007) showed that invaded plots had significantly higher flower visitation.

The increase in pollen limitation when the invasive was present could also stem from seed set lowering processes associated with the deposition of heterospecific pollen such as stigma clogging (Holland and Chamberlain 2007), stigma closing, pollen allelopathy, stylar clogging and stylar inhibition (see Brown and Mitchell 2001 and references therein). As shown, however, in our previous work, these processes do not seem to have any major effects on *G. flavum* at even high levels of invasive pollen deposition (Tscheulin et al. 2009). This in combination with the results from the stigma pollen counts therefore rules out any major impact of heterospecific pollen deposition in the present study and suggests that solely the decrease of honeybee visits lead to the increase in pollen limitation when the invasive was present. Likewise

Jakobsson et al. (2008) have found that invasive *Carpobrotus* spp. pollen had very little effect on the seed set of the native community because of the low frequency of pollen transfer.

Given that experimental flowers were hand-crossed every round prior to the placement of the potted individuals it could also be argued that resource limitation could have caused the decrease in seed production of *G. flavum*. However, in the light of the large number of flowers and seed caspules *G. flavum* produces naturally during a flowering season we consider any possible effect negligible.

Honeybees are known to show a high degree of flower constancy (Chittka et al. 1999 and references therein), which is one reason why they are often employed for the pollination of crops. As honeybees were never recorded on *S. elaeagnifolium*, which is probably due to the flowers' lack of nectar glands and the presence of poricidal anthers it cannot be argued, however, that the invasive draws honeybees away from *G. flavum*. Chittka et al. (2009) have pointed out that there is a speed-accuracy trade-off in foraging pollinators that have to distinguish between profitable and less profitable flowers. The presence of the invasive may therefore increase the amount of time spent on decision-making in mixed stands, which might in turn render the visitation of *G. flavum* flowers less profitable leading to a decrease in visitation rates and ultimately a decrease in *G. flavum* seed set. This is also supported by Spaethe et al. (2006), who show that bees incur a cost when distinguishing between target and non-target flowers. When this cost passes a threshold it could in turn potentially lead to bees avoiding a mixed patch altogether (Chittka, personal communication).

This study emphasizes the importance of honeybees for the pollination of *G. flavum* given that seed set

decreased significantly with the decrease of honeybee visits despite the overall increase in pollinator visits seen after the addition of *S. elaeagnifolium*. The presence of *S. elaeagnifolium* in natural populations of *G. flavum* therefore has the potential to indirectly impact on the reproduction of this native plant, which can be expected to ultimately have negative effects on the demography of the plant.

Acknowledgments This research project was financed by the E.U.-European Social Fund (80 %), and the Greek Ministry of Development-GSRT (20 %). Financial support was also received from the Helmholtz Centre for Environmental Research (UFZ).

References

- Aigner PA (2004) Ecological and genetic effects on demographic processes: pollination, clonality and seed production in *Dithyrea maritima*. *Biol Conserv* 116:27–34
- Bartomeus I, Vilà M, Santamaría L (2008) Contrasting effects of invasive plants in plant-pollinator networks. *Oecologia* 155:761–770
- Baye Y, Ameur A, Bouhaches M et al (2007) Strategy for the chemical control of *Solanum elaeagnifolium* Cav. in Morocco. *EPPO Bull* 37:145–152
- Bjerknes AL, Totland Ø, Hegland SJ et al (2007) Do alien plant invasions really affect pollination success in native plant species? *Biol Conserv* 138:1–12
- Boratynski A, Browicz K, Zielinski J (1992) Chorology of trees and shrubs in Greece. Polish Academy of Sciences, Sorus, Poznan/Kornik
- Bouhache M, Tanji A (1985) Assessment of the stock of *Solanum elaeagnifolium* Cav. Yellow Nightshade seeds in the soil of the Tadla (Morocco). *Weed Res* 25:11–14
- Boyd JW, Murray DS (1982) Growth and development of Silverleaf Nightshade (*Solanum elaeagnifolium*). *Weed Sci* 30:238–243
- Boyd JW, Murray DS, Tylr RJ (1984) Silverleaf Nightshade, *Solanum elaeagnifolium*, origin, distribution, and relation to man. *Econ Bot* 38:210–217
- Brown BJ, Mitchell RJ (2001) Competition for pollination: effects of pollen of an invasive plant on seed set of a native congener. *Oecologia* 129:43–49
- Brown BJ, Mitchell RJ, Graham SA (2002) Competition for pollination between an invasive species (Purple Loosestrife) and a native congener. *Ecology* 83:2328–2336
- Brunel S (2011) Pest risk analysis for *Solanum elaeagnifolium* and international management measures proposed. *EPPO Bulletin* 41:232–242
- Buchmann SL, Cane JH (1989) Bees assess pollen returns while sonicating *Solanum* flowers. *Oecologia* 81:289–294
- Chapman MA, Forbes DG, Abbott RJ (2005) Pollen competition among two species of *Senecio* (Asteraceae) that form a hybrid zone on Mt. Etna, Sicily. *Am J Bot* 92:730–735
- Chittka L, Schürkens S (2001) Metrology: successful invasion of a floral market. *Nature* 411:653
- Chittka L, Thomson JD, Waser NM (1999) Flower constancy, insect psychology, and plant evolution. *Naturwissenschaften* 86:361–377
- Chittka L, Skorupski P, Raine NE (2009) Speed-accuracy tradeoffs in animal decision making. *Trends Ecol Evol* 24:400–407
- Cooley AW, Smith DT (1971) Silverleaf Nightshade (White-weed) establishment from seed and clipped seedlings. Progress Report of Texas A&M University, Texas Agricultural Experiment Station PR-3198
- Economidou E, Yannitsaros A (1975) Recherches sur la flore adventice de Grèce, V, Distribution et écologie de *Solanum elaeagnifolium* Cav. *Revue de Biologie et d'Ecologie Méditerranéenne* 2:29–44
- Eiskowitch D (1979) Horned poppy, *Glaucium flavum*. In Israel: notes on its pollination and distribution. *Isr J Bot* 28:87–94
- Eleftherohorinos IG, Bell CE, Kotoula-Syka E (1993) Silverleaf Nightshade (*Solanum elaeagnifolium*) control with foliar herbicides. *Weed Technol* 7:808–811
- EU (1992) Council Directive on the conservation of natural habitats and of wild fauna and flora 92/43/EEC, OJ L 206. <http://eur-lex.europa.eu/LexUriServ/site/en/consleg/1992/L/01992L0043-20070101-en.pdf>. Accessed 30 Sept 2011
- Feldman TS, Morris WF, Wilson WG (2004) When can two plant species facilitate each other's pollination? *Oikos* 105:197–207
- Gathmann A, Tschamtk T (2002) Foraging ranges of solitary bees. *J Anim Ecol* 71:757–764
- Grabas GP, Lavery TM (1999) The effect of purple loosestrife (*Lythrum salicaria* L.; Lythraceae) on the pollination and reproductive success of sympatric co-flowering wetland plants. *Ecoscience* 6:230–242
- Greenleaf SS, Williams NM, Winfree R et al (2007) Bee foraging ranges and their relationship to body size. *Oecologia* 153:589–596
- Holland JN, Chamberlain SA (2007) Ecological and evolutionary mechanisms for low seed:ovule ratios: need for a pluralistic approach? *Ecology* 88:706–715
- Jacobi CM, Ramalho M, Silva M (2005) Pollination biology of the exotic rattleweed *Crotalaria retusa* L. (Fabaceae) in NE Brazil. *Biotropica* 37:357–363
- Jakobsson A, Padron B, Traveset A (2008) Pollen transfer from invasive *Carpobrotus* spp. to natives—a study of pollinator behaviour and reproduction success. *Biol Conserv* 141:136–145
- Kasagi T, Kudo G (2005) Interspecific pollinator movements and heterospecific incompatibility: comparisons between *Phyllodoce caerulea* and *Phyllodoce aleutica* along snowmelt gradients. *Evol Ecol Res* 7:73–87
- Larson DL, Royer RA, Royer MR (2006) Insect visitation and pollen deposition in an invaded prairie plant community. *Biol Conserv* 130:148–159
- Lopezaraiza-Mikel ME, Hayes RB, Whalley MR et al (2007) The impact of an alien plant on a native plant-pollinator network: an experimental approach. *Ecol Lett* 10:539–550
- Mack RN, D'Antonio CM (1998) Impacts of biological invasions on disturbance regimes. *Trends Ecol Evol* 13:195–198
- Matsumoto T, Takakura KI, Nishida T (2010) Alien pollen grains interfere with the reproductive success of native congener. *Biol Invasions* 12:1617–1626

- McGuire A, Armbruster S (1991) An experimental test for reproductive interactions between two sequentially blooming *Saxifraga* species (Saxifragaceae). *Am J Bot* 78:214–219
- Mekki M (2007) Biology, distribution and impacts of Silverleaf Nightshade (*Solanum elaeagnifolium* Cav.). EPPO Bull 37:114–118
- Memmott J, Waser NM (2002) Integration of alien plants into a native flower-pollinator visitation web. *Proc R Soc Lond B* 269:2395–2399
- 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
- Petanidou T, Den Nijs JCM, Oostermeijer JGB (1995) Pollination ecology and constraints on seeds et of the rare perennial *Gentiana cruciata* L. in The Netherlands. *Acta Bot Neerlandica* 44:55–74
- Petanidou T, Godfree RC, Song DS et al (2012) Self-compatibility and plant invasiveness: comparing species in native and invasive ranges. *Perspect Plant Ecol Evol Syst* 14:3–12
- Pimentel D, McNair S, Janecka J et al (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. *Agric Ecosyst Environ* 84:1–20
- R Development Core Team (2008) R: A language and environment for statistical computing, 2.8 edn. The R Foundation for Statistical Computing, Vienna
- Ruane LG, Donohue K (2007) Environmental effects on pollen-pistil compatibility between *Phlox cuspidata* and *P. drummondii* (Polemoniaceae): implications for hybridization dynamics. *Am J Bot* 94:219–227
- Spaethe J, Tautz J, Chittka L (2006) Do honeybees detect colour targets using serial or parallel visual search? *J Exp Biol* 209:987–993
- SPSS (2006) Version 15.0 for Windows. LEAD Technologies, SPSS Inc. All rights reserved, Chicago
- Tepedino VJ, Bradley BA, Griswold TL (2008) Might flowers of invasive plants increase native bee carrying capacity? Intimations from Capitol Reef National Park, Utah. *Nat Areas J* 28:44–50
- Thanos CA, Georghiou K, Skarou F (1989) *Glaucium flavum* seed germination - an ecophysiological approach. *Ann Bot* 63:121–130
- Thijs KW, Brys R, Verboven HAF et al (2012) The influence of an invasive plant species on the pollination success and reproductive output of three riparian plant species. *Biol Invasions* 14:355–365
- Totland Ø, Nielsen A, Bjerknes AL et al (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
- Traveset A, Richardson DM (2006) Biological invasions as disruptors of plant reproductive mutualisms. *Trends Ecol Evol* 21:208–216
- Tscheulin T, Petanidou T, Zografou C et al (2008) Invading the Mediterranean: study of *Solanum elaeagnifolium*, a successful invasive plant from C. America. Earth Conference. University of the Aegean, Mytilene
- Tscheulin T, Petanidou T, Potts SG et al (2009) The impact of *Solanum elaeagnifolium*, an invasive plant in the Mediterranean, on the flower visitation and seed set of the native co-flowering species *Glaucium flavum*. *Plant Ecol* 205: 77–85
- Tscheulin T, Neokosmidis L, Petanidou T et al (2011) Influence of landscape context on the abundance and diversity of bees in Mediterranean olive groves. *Bull Entomol Res* 101:557–564
- Vila M, Bartomeus I, Dietzsch AC et al (2009) Invasive plant integration into native plant-pollinator networks across Europe. *Proc Roy Soc B Biol Sci* 276:3887–3893
- Wardle DA, Nicholson KS, Ahmed M et al (1994) Interference effects of the invasive plant *Carduus nutans* L. against the nitrogen fixation ability of *Trifolium repens* L. *Plant Soil* 163:287–297
- Weihe PE, Neely RK (1997) The effects of shading on competition between Purple Loosestrife and Broadleaved Cattail. *Aquat Bot* 59:127–138