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ORIGINAL PAPER

Conspecific flowers of *Sinapis arvensis* are stronger competitors for pollinators than those of the invasive weed *Bunias orientalis*

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Abstract Biological invasions can affect the structure and function of ecosystems and threaten native plant species. Since most weeds rely on mutualistic relationships in their new environment, they may act as new competitors for pollinators. Pollinator competition is likely to be density dependent, but it is often difficult to disentangle competition caused by flower quality from effects caused by flower quantity. In order to test the effects of the presence and number of flowers of the invasive weed *Bunias orientalis* on the insect visitation rates in a native species (*Sinapis arvensis*), we performed two replacement experiments using plants with standardised flower numbers. The visitation rates in *S. arvensis* were significantly higher than in *B. orientalis* and the number of insect visits dropped significantly with increasing density of *S. arvensis* flowers. These results suggest that intraspecific competition among flowers of *S. arvensis* is stronger than the competitive effect of alien flowers. As flowers of *B. orientalis* do not seem to distract visitors from *S. arvensis*, it is unlikely that pollinator competition between these two plant species plays a crucial role. However, it cannot be excluded that mass blossom stands of *B. orientalis* may distract flower visitors from native species.

Keywords Competitive displacement · Facilitation · Flower visitors · Invasive plants · Pollination

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Introduction

Invasions of alien plant species can have severe consequences for native ecosystems, as they often lead to massive changes in the structure and function of indigenous biotic communities (Davis 2009; Lockwood et al. 2007; Mack et al. 2000; Williamson 1996). One major mechanism threatening native plant species is displacement by alien plants, which is usually explained by resource competition (Vilà et al. 2004). Typically, invasive plant species are able to colonise disturbed patches rapidly. Here they outcompete native plants by leaving not enough space, water, nutrients, or light for regrowth (Berger et al. 2008; Brown et al. 2002; Schenk 2006). Pre-emptive competition is, therefore, a major mechanism determining the invasion success of plants (Begon et al. 1996). However, after establishment exotic plant species also need to interact with other members of the native ecosystem. For example, a stronger resistance to herbivory can represent a key advantage of alien plant species (Harvey et al. 2010; Kühnle and Müller 2009). Furthermore, invasive plants often rely on mutualistic interactions with seed dispersers and pollinators and might disrupt such interactions in native communities (Harmon-Threatt et al. 2009; Richardson et al. 2000; Traveset and Richardson 2006; Vanparys et al. 2008).

Pollinators represent keystone species in many ecosystems as they are important for the reproduction of most plant species (Ebeling et al. 2008; Klein et al. 2007). The significance of pollinator competition between native and invasive species has only recently received increased attention and positive, negative or neutral effects of exotic plants on pollinator visitation rates have been reported (reviewed in Bjerknes et al. 2007). In some cases it has been shown that flowers of invasive plants are much more attractive than those of natives (Chittka and Schürkens 2001; Vanparys et al. 2008). This can lead to reduced reproductive success in the native competitors, if the native plants are pollen limited in their reproduction. On the other hand, introduced plant species might also contribute to a higher food diversity for pollinators leading to an increase in pollinator species richness or abundance (magnet effect, Thomson 1978).

Although many invasive plant species are known to produce large numbers of inflorescences (Nielsen et al. 2008), density effects have received little attention in pollination competition studies (Bjerknes et al. 2007; but see Kunin 1993; Molina-Montenegro et al. 2008). Density effects can also be masked by patterns caused by the attractiveness of single flowers, which can influence the performance of alien plants as competitors (Chittka and Schürkens 2001). A number of floral traits may affect flower attractiveness, including size, colour, odour, nectar quality, quantity and accessibility, phenology and others (Bianchi and Wäckers 2008). It is, therefore, crucial to distinguish quantity effects (i.e. the number of flowers) from quality effects (i.e. the floral traits of single flowers). Furthermore, most studies on pollinator competition suggest negative effects to dominate, although positive effects (e.g. pollinator attraction) have also been reported, which is important for an objective evaluation of invasion risks (Bjerknes et al. 2007).

During the last decades, the Turkish cabbage *Bunias orientalis* (L.) has invaded large parts of Central and Western Europe (Dietz et al. 1999; Harvey et al. 2010; Kühnle and Müller 2009). It is believed to represent a threat to the native flora due to its high colonisation rates and abrupt development into dominant stands (Dietz and Ullmann 1997; Steinlein et al. 1996). Mass blossom stands up to 2,000 inflorescences/m^2 have been documented (Schürkens and Chittka 2001), suggesting that *B. orientalis* also represents a strong competitor for pollinators. In its new range, it is a weed of cultivation, occurring mainly at ruderal sites, such as roadside verges or rubble tips (Oberdorfer 1990). From these sites, it occasionally invades dry grasslands, particularly abandoned sites. *Sinapis arvensis* L. is an archeophyte that occurs in similar habitats as *B. orientalis*. As both species overlap in their flowering season (Harvey et al. 2010) and have similar floral traits and pollinator guilds, they represent ideal organisms for studies on pollinator competition. It remains unknown, whether single flowers of *B. orientalis* may distract flower visitors from those of *S. arvensis* or vice versa, and whether this relationship is density dependent. First, we wanted to test the hypothesis that the presence or density of the alien plant species reduces the number of insect visits in the native plant species. Second, we wanted to unravel whether changes in visitation rates are caused by reallocation of flower visitors (competition) or by attraction of further visitors (facilitation) on a small spatial scale. In the first experiment (density experiment), we altered the number of flowers of *B. orientalis* surrounding individuals of *S. arvensis*. This experiment allowed us to distinguish between interspecific competition (reduced visitation rates with increasing relative frequency of alien flowers) and intraspecific competition (reduced visitation rates with increasing relative frequency of native flowers). In a second experiment (competition experiment), we observed flower visitors in conspecific and heterospecific flower assemblages of both plant species in order to distinguish between competitive and facilitation effects. In both experiments, we noted the pollinator taxa separately in order to identify taxon-specific preferences.

Methods

Study objects

In order to test our hypothesis, we chose two Brassicaceae with yellow petals: the naturalised archeophyte *S. arvensis* Linnaeus 1753 and the invasive neophyte *B. orientalis* (Linnaeus 1753). The Turkish cabbage, *B. orientalis*, is indigenous to Asia and south-eastern Europe. During recent decades it expanded its range rapidly in large parts of Europe and North America (Birnbaum 2006; Harvey et al. 2010; Schürkens and Chittka 2001). Its inflorescence contains numerous little flowers (petals are 5–8-mm long), which are hermaphroditic and classified as fly- and beetle-pollinated, but Hymenoptera have also been frequently observed as flower visitors (Schürkens and Chittka 2001). The flowering season of *B. orientalis* lasts from May to July. The perennial or biennial plant species reaches up to 1.2 m height (Oberdorfer 1990). Native habitats of *B. orientalis* include woodland, sunny edges of forests, dappled shade and riverbanks (Clapham et al. 1962).

Wild mustard, *S. arvensis*, is an annual herbaceous weed, which occurs throughout most of the temperate regions of the world (Oberdorfer 1990). It is naturalised also in Central Europe but probably originates from the Mediterranean. The species occurs in croplands and other disturbed habitats, such as roadsides, meadows and ruderal sites (Oberdorfer 1990). The light yellow flowers are slightly larger than those of *B. orientalis* (petals are 7–12-mm long), but less numerous and less brightly coloured. Plants reach 20 to 80 cm in height. The flowering season lasts from May to July. Similar to *B. orientalis*, the flowers of *S. arvensis* are also classified as fly- and beetle-pollinated (Faegri and van der Pijl 1978).

Density experiment

The experiment was performed on 30 May and 04 and 06 June 2008, each between 1100 and 1300 hours at a forest edge with an adjacent meadow at the Petrisberg in Trier, Germany (49°45′21″ N, 6°39′54″ E), where both plant species do not occur naturally. This site was chosen in order to avoid confounding effects of local adaptation of the pollinators. The study plants were collected from nearby allotopic populations of both species (*S. arvensis*: 49°44′55″ N, 6°40′36″ E; *B. orientalis*: 49°43′51″ N, 6°41′47″ E). All plants had open flowers and were standardised to similar heights (20 cm) and an equal number of flowers (15 flowers per plant). For each plant we arranged the cut inflorescence in a brown glass bottle filled with water. Three of these bottles were placed on top of a dark bucket (in a distance of 20 cm). We used brown bottles and dark buckets to obtain a natural height and avoid attraction of insects to both buckets and bottles. We then observed one inflorescence of *S. arvensis* for 2 h (observed plant). Three treatments were compared: (1) a control treatment with three native plants, (2) a treatment with two natives and one invasive plant and (3) a treatment with one native and two invasive plants (Fig. 1). If two or three plants of *S. arvensis* were present (treatments 1 and 2), the observed plant was randomly chosen. Fifteen buckets were placed linearly at the forest edge with a distance of 10 m between two buckets. Flowers of other plant species were virtually absent at this site (except for some single flowers of *Rubus fruticosus* aggr.). At each day, treatments were randomly assigned to the buckets by drawing lots and fresh plants were used. The experiment was performed by 30 observers (two per replicate), who were instructed before the experiment was started in order to adjust the data quality. Uniform clothing (blue trousers, black shirts) was used to avoid attraction of flower visitors. During the observation time, each insect visit at the observed plant was noted including the taxon (Diptera, Hymenoptera, Coleoptera and others) and the duration of the visit. Originally, we distinguished more taxa, but these were combined later as the number of records was too low (see "Results" section). Identification to species level was not conducted, as this would have required the removal of insects and a disturbance of the experiment. We also recorded weather conditions and temperature. However, as these are strongly affected by the date (and date comprises the full weather complexity), we decided to include only "date" in the models. Due to the high number of observers, we were able to perform 15 simultaneous observations per day (i.e. five replicates of each treatment). This allowed us to better control for weather variation. Altogether, we performed 15 replicates of each treatment.

Competition experiment

This experiment was performed on 09 June 2010 between 1100 and 1300 hours and between 1400 and 1600 hours at the same location as given above. The experimental design was similar to the density experiment, but only two bottles (i.e. inflorescences) with 15 flowers each were placed on the buckets (distance between bottles, 20 cm). Both inflorescences were observed. For each species, we performed a conspecific treatment (two conspecific inflorescences), in which we observed the flower visits of both inflorescences (which we noted separately). Furthermore, we performed a heterospecific treatment, in which we used one inflorescence per species. Ten replicates of each treatment were performed, five of which were conducted simultaneously (one run from 1100 to 1300 hours and one run from 1400 to 1600 hours). The experiment was performed by three observers, who rotationally recorded the flower visits at each replicate for 5 min. The experiment lasted 2 h, so that each replicate was revisited every 25 min and a total of 25 observation minutes for each replicate was noted. Since visits of Coleoptera often last longer than 25 min, all beetles were removed from the inflorescences to avoid pseudoreplication. As the number of visits and not the number of individuals was recorded, this was not important for the other taxa. In this experiment, we did not note the duration of the flower visit (as the results concerning durations were not significant, see below).

Data analysis

For the density experiment, we used generalised linear models (GLM, family Poisson) to analyse the effect of the treatment (control, one invasive plant and two invasive plants) and date on the number of insect visits. If necessary, the models were adjusted for overdispersion (Crawley 2007). The Poisson distribution was more suitable for this analysis as there was a great number of zero values in the

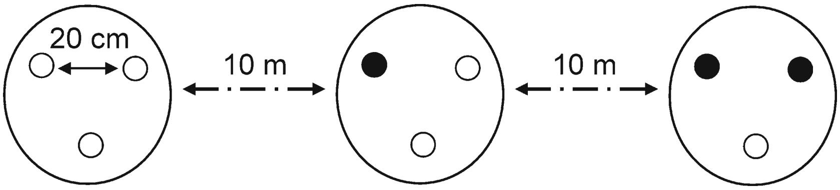

Fig. 1 Experimental design of the density experiment: on each bucket (*large circle*) three bottles (*small circles*) with one inflorescence each (consisting of 15 flowers either of *S. arvensis*: *open circles* or *B. orientalis*: *closed circles*) were placed. Flower visitation rates were noted for 2 h at one inflorescence of *S. arvensis*. Three factor levels were chosen: **a** Three *S. arvensis*; **b** two *S. arvensis*+one *B. orientalis*; **c** one *S. arvensis*+two *B. orientalis*

count data. As a second response variable, we chose the duration of the visits. We used two-factorial ANOVAs in order to analyse effects on the visit durations. If necessary, we applied Box–Cox transformation using Venables and Ripley's MASS library for R (Venables and Ripley 2002), which reveals the optimal power transformation (λ) to fit the data to meet the model assumptions.

For the competition experiment, we performed three-factorial ANOVAs using species (*S. arvensis*, *B. orientalis*), treatment (conspecific, heterospecific) and run (a.m., p.m.) as explanatory variables and number of flower visits as response variable. We stepwise simplified the models using the "step" function in R. All statistical analyses were conducted in R 2.10.0 (R Development Core Team 2010).

Results

Density experiment: number of flower visitors

A total of 757 flower visits was recorded, including 444 Diptera, 201 Coleoptera, 85 Hymenoptera and 27 other taxa. The total number of flower visitors observed within 2 h was significantly lower in the control treatment (one standardised *S. arvensis* together with two more standardised plants of *S. arvensis*) than when flowers of *B. orientalis* were present (GLM, $z=-3.76$, $P<0.001$; Fig. 2a). The date of observation also influenced our results. On the second day (04 June), the number of visits was higher than on the other days (GLM, $z=-2.00$, $P=0.045$). We also detected a

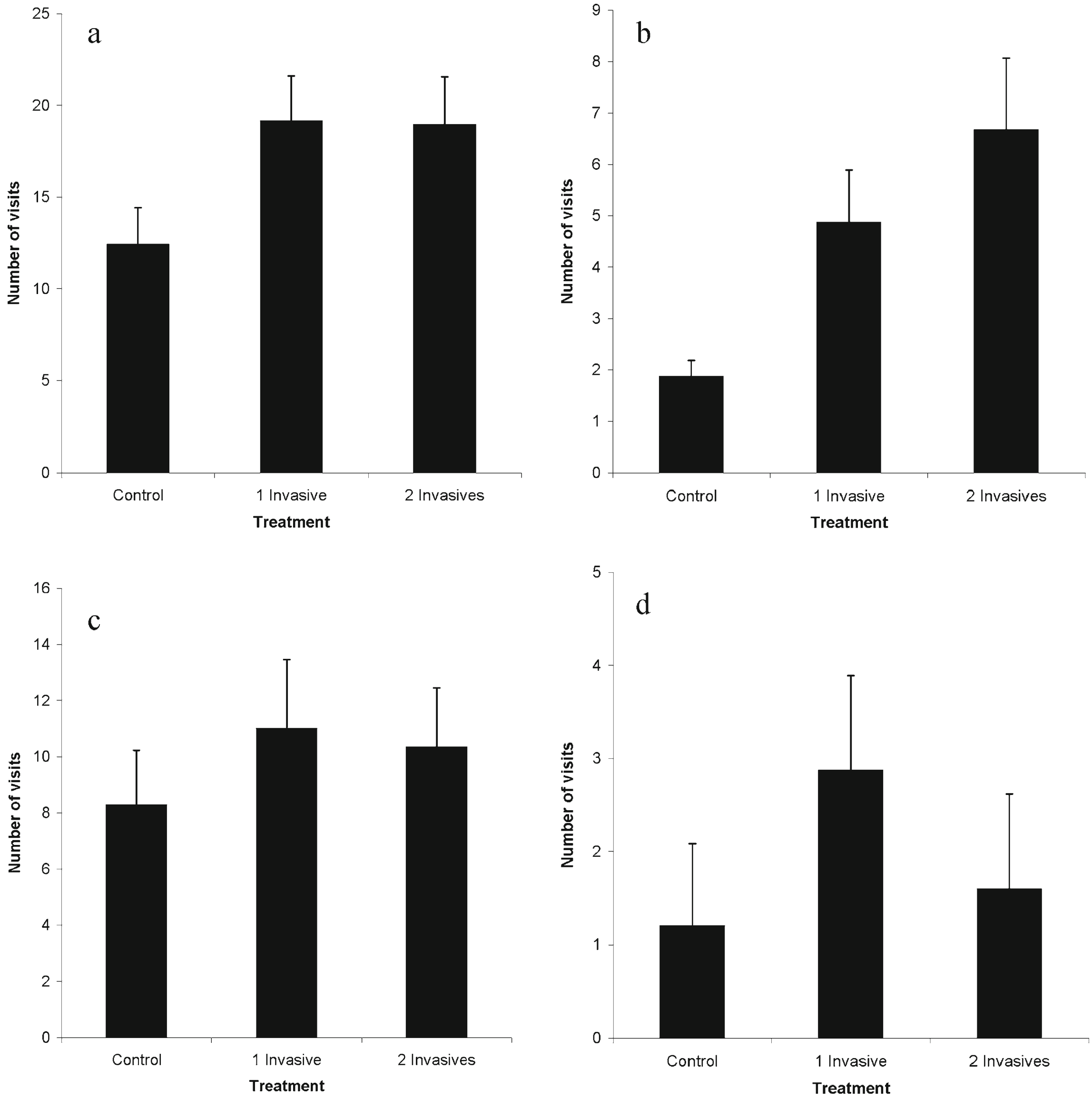

Fig. 2 Mean number of visits at 15 flowers of a native plant (*S. arvensis*) within 2 h with presence of two conspecific competitors (*control*), one conspecific and one heterospecific (*B. orientalis*) competitor (*1 invasive*) and two alien competitors (*2 invasives*); **a** total number of flower visits; **b** Coleoptera visits; **c** Diptera visits; **d** Hymenoptera visits. *Error bars* are standard errors ($n=15$)

significant interaction between treatment and day (GLM, $z=-1.97$, $P=0.049$) with the number of visits differing significantly among the treatments on 30 May and 06 June, but not on 04 June.

The number of Coleoptera visits was significantly higher when two invasive plants were present than in the treatment with only one invasive plant (GLM, $z=-2.01$, $P=0.044$) and also higher than in the control (GLM, $z=-2.76$, $P=0.006$; Fig. 2b). Furthermore, the number of visits was lower on the first than on the third day (GLM, $z=3.34$, $P<0.001$). A significant interaction between date and treatment was also detected: on the second day (04 June), the number of Coleoptera visits in the treatment with one invasive plant was greater than in the treatment with two invasive plants.

Similar to the overall pattern, Diptera (the most abundant group) visited the control treatment significantly less often than the two treatments with exotic plants (GLM, $z=-3.72$, $P<0.001$; Fig. 2c). Again, the number of visits varied significantly among the observation days. The number visits on the third day (06 June) was significantly smaller than on the first (GLM, $z=-3.43$, $P<0.001$) and second day (GLM, $z=-4.71$, $P<0.001$). Furthermore, we detected a significant interaction between treatment and day. The number of visits in the treatment with two invasive plants was significantly reduced at the second day (04 June; GLM, $z=4.04$, $P<0.001$).

Among Hymenoptera, the number of visits in the treatment with one invasive plant was significantly higher than in the other two treatments (GLM, $z=3.02$, $P=0.003$; Fig. 2d). On the second day, the number of visits was significantly greater than at day 1 and day 3 (GLM, $z=2.69$, $P=0.007$). Again, we found a significant interaction between treatment and day. At the second day, the pattern of visits was reversed, with the lowest number of visits in the treatment with one invasive plant (GLM, $z=-4.04$, $P<0.001$). Other flower visitors were observed rarely (3.5%) and showed no significant differences in the number of visits per treatment or per day.

Density experiment: duration of flower visits

No significant effect of the treatment on the duration of flower visits was found for any insect taxon, but we uncovered a significant difference in the duration of visits among days for the total number of flower visitors (ANOVA, log-transformed data, $F_{2,\ 36}=8.31$, $P=0.001$). On the first day, the mean duration was 204.97 (±45.45) s, on the second 524.32 (±144.33) s and on the third 777.25 (±200.68). However, this was mainly caused by the increasing number of beetle visits during the observation period (day 1, 41 visits; day 2, 76 visits; day 3, 84 visits). Beetles stayed on average for 1,756.77 s, while Diptera stayed only for 101.05 s and Hymenoptera for 46.1 s.

Competition experiment

A total of 185 flower visits was recorded, including 56 Coleoptera, 40 Diptera, 24 Hymenoptera and 65 other taxa (mainly ants). The total number of flower visitors was significantly lower in *B. orientalis* than in *S. arvensis* (ANOVA, $F_{1,\ 56}=5.71$, $P=0.02$). There was also a significant interaction between treatment and species (ANOVA, $F_{1,\ 56}=9.05$, $P=0.003$): in *B. orientalis* the number of visits was higher in the conspecific than in the heterospecific treatment, while the opposite was true for *S. arvensis* (Fig. 3). In the conspecific treatments, the mean number of flower visits was nearly identical. No significant effect was detected for the run (a.m. or p.m.).

Analysing each taxon separately revealed a similar pattern for Diptera: the number of flower visitors was higher in *S. arvensis* than in *B. orientalis* (ANOVA, $F_{1,\ 56}=7.30$, $P=0.009$). In the conspecific treatments, the number of flower visits by Diptera was similar for both species. The number of visits observed in *B. orientalis* decreased in the heterospecific treatment, while the opposite was observed in *S. arvensis* (ANOVA, $F_{1,\ 56}=10.72$, $P=0.002$). All other taxa showed no significant patterns.

Discussion

Our results show that *S. arvensis* is a stronger competitor for pollinators than *B. orientalis*. Although the number of flower visitors remained constant among the treatments of our competition experiment, the allocation to the inflorescences varied. When *B. orientalis* was placed near a conspecific

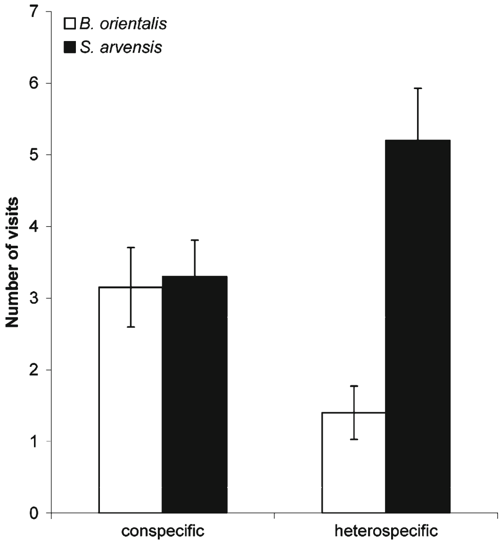

Fig. 3 Mean number of flower visitor observations at 15 flowers of *S. arvensis* and *B. orientalis* in conspecific treatments (two conspecific inflorescences) and heterospecific treatments (one inflorescence of each plant species). *Error bars* are standard errors ($n=15$)

individual, the number of visits was nearly identical to *S. arvensis*, suggesting that the number of potential pollinators is rather constant for each patch. However, when both species were placed together, the number of flower visitors (particularly Diptera) decreased strongly in *B. orientalis* for the benefit of *S. arvensis*. These results are in contrast to those of Harmon-Threatt et al. (2009), who showed that flower visitation rates of native and invasive congeneric plant species are rather similar. The density experiment showed that the number of visits in *S. arvensis* decreased with greater density of conspecific flowers, while it increased if flowers of *B. orientalis* were present. These data suggest that intraspecific competition among flowers of *S. arvensis* is substantially greater than interspecific competition with the exotic species. Daily variation in the treatment effects was rather low. Only on the second day of our experiment, we found some deviations from the general pattern. It was not in the scope of our experiment to analyse temporal variation in competition. However, this might be an interesting question for future studies. It is also evident that the greater number of visits was not caused by shorter visits, as no effect of the treatment on the duration of the visits was detected.

A second aim of our study was to test density effects in competition for potential pollinators. Such density effects were mainly found in Coleoptera, the visitation rates of which increased with higher densities of *B. orientalis*, suggesting that the competitive ability of *B. orientalis* flowers is rather low. Three factors might confound these results: first, there was some variation in density effects among days (probably caused by weather conditions). On the second day, *S. arvensis* had more visiting Coleoptera when one invasive plant was present than with two invasive plants. Nevertheless, the number of Coleoptera was still lower when it was surrounded by native plants only. Second, autogamy is believed to be an important cause of the success of invasive plant species (Harmon-Threatt et al. 2009). Although both species are self-fertile (Clapham et al. 1962), no information on the amount of selfing is available (Dietz et al. 1999). Third, *B. orientalis* typically has a greater number of flowers per plant than *S. arvensis* (Schürkens and Chittka 2001), but we standardised the plants to 15 flowers as our main interest was the competitive potential of single flowers and not of the whole plant. The effect of the alien plant species might thus be stronger under natural conditions. Indeed, floral display has been proposed to play a major role for attractiveness of other invasive plants (Brown and Mitchell 2001; Vanparys et al. 2008). However, in contrast to the invasive weed *Impatiens glandulifera* (Chittka and Schürkens 2001), the flowers of *B. orientalis* do not seem to represent stronger attractors for insects than those of the native species. This might be caused by the slightly different flower morphologies of both species (Morales and Traveset 2009). Flowers of *B. orientalis* are smaller and darker yellow than those of *S. arvensis*. Furthermore, it cannot be ruled out that olfactoric traits or the amount of nectar differs. Our experimental design did not allow to disentangle the effects of such floral differences. Hence, the reason for the stronger attraction of insects by *S. arvensis* remains unknown.

Invasive plant species are often believed to decrease pollination rates in native species, although the number of studies that have reported increased visitation rates is even slightly higher than the number of studies that found negative effects (reviewed in Bjerknes et al. 2007). Of course, any effect on visitation rates does not necessarily imply a consequence for the reproductive success, but a recent study shows that both correlate (Kandori et al. 2009). Studies on the effects of invasive plant species on the reproduction of native plant species are scarce (but see e.g. Brown et al. 2002; McKinney and Goodell 2011; McKinney and Goodell 2010; Muñoz and Cavieres 2008) and most of them have documented neutral or negative effects (Bjerknes et al. 2007; Morales and Traveset 2009). As we did not measure the reproduction of *S. arvensis*, we cannot draw any final conclusions concerning this point.

It has been suggested that a presence of heterospecific plant species might offer greater opportunities for flower visitors and might, therefore, increase the number of visits of plants in the vicinity (magnet effect, Ghazoul 2006; Laverty 1992; Thomson 1978). In our example the visitation rates remained constant among the assemblages. Hence, no evidence for facilitation was found. Furthermore, two different dimensions of positive effects have to be distinguished: (1) small-range/short-term attraction of insects at a specific site and (2) long-term changes in pollinator communities (Moron et al. 2009). Our results clearly falsify the first hypothesis, but long-term changes are more difficult to assess. However, the experiments were performed at a site without natural occurrence of either species and each observation period lasted only for 2 h. Hence, a long-term adaptation or conditioning of the pollinator community can be ruled out as an explanation for the data.

Based on our data, it seems unlikely that competition for pollinators by *B. orientalis* reduces the fitness of *S. arvensis*. In fact, the invasion of *B. orientalis* seems to be driven by other processes than pollinator competition. Dietz and Ullmann (1998) showed that this species profits from high disturbance, suggesting that pre-emptive competition is more important than pollinator competition. Furthermore, it has been shown that leaf extracts of *B. orientalis* inhibit seed germination of other plants (Dietz et al. 1996) and that the exotic species seems to be less sensitive to leaf herbivory (studied in one herbivore) than the related crop *Sinapis alba* (Kühnle and Müller 2009). Altogether, these data imply that the competitive ability during germination and growth of the plants is more important than that of the flowers. Its resistance to mowing and grazing is much stronger than in many native plant species (Dietz and Ullmann 1998; Woitke 2001). On the other hand, it also remains unknown whether and to what extent the invasion of *B. orientalis* affects biodiversity. It has recently been argued that the invasiveness of species does not correlate with the impact on native communities (Ricciardi and Cohen 2007), but it is also evident that in mass stands of *B. orientalis* other plant species are often missing.

In our study, the majority of flower visitors in *S. arvensis* were Diptera and Coleoptera (mainly *Byturus tomentosus* and *Byturus ochraceus*), which fits very well into the pollination classification scheme (Faegri and van der Pijl 1978). Schürkens and Chittka (2001) observed that *B. orientalis* is mainly visited by Hymenoptera. It is unlikely that different pollination niches of both plant species explain our results as we found no significant differences among species when only the conspecific treatments (of the competition experiment) were considered. It is more probable that the unusual insect community observed by Schürkens and Chittka (2001) was influenced by the location of their study (a botanical garden), where bee species are common due to the diverse vegetation (including many Asteraceae). Our site probably better reflects the natural conditions, and the observed flower visitors seem to reflect the flower morphologies of both species very well.

Conclusions and outlook

Our results show that intraspecific competition among native plants can be stronger than interspecific competition with an exotic species. Thus, a stronger competitive ability of flowers is not a general trait of invasive plant species. *S. arvensis* (and possibly other native plant species) do not seem to be threatened by pollinator competition with *B. orientalis*, but this might be different in mass blossom stands of the latter species. The effect of such mass blossom stands should be studied in the future. Furthermore, the effects of differential flower visitation rates on pollination and reproductive success remain unknown. It would also be useful to study the effects of autogamy and the effectiveness of each pollinator (or of each pollinator guild). Finally, pollinator competition among these species also needs to be studied under natural conditions, i.e. at localities, where both species co-occur naturally.

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