

## Research Article

## The invasive aquatic plant *Ludwigia grandiflora* affects pollinator visitants to a native plant at high abundances

Iris Stiers\*, Kjell Coussement and Ludwig Triest

Plant Biology and Nature Management, Vrije Universiteit Brussel, Pleinlaan 2, BE-1050 Brussels, Belgium

E-mail: [istiers@vub.ac.be](mailto:istiers@vub.ac.be) (IS), [coussement.kjell@scarlet.be](mailto:coussement.kjell@scarlet.be) (KC), [ltriest@vub.ac.be](mailto:ltriest@vub.ac.be) (LT)

\*Corresponding author

Received: 19 December 2013 / Accepted: 30 March 2014 / Published online: 30 June 2014

Handling editor: Vadim Panov

### Abstract

The presence of an invasive species can either have a negative effect on pollination of natives by competing for pollinators or a positive effect since they may act as ‘magnet’ species facilitating pollinator visits to co-flowering species. We studied the plant-pollinator interactions for *Ludwigia grandiflora*, a highly invasive aquatic weed in Europe. First, a food web approach was used in one field site and our results showed an integration of *L. grandiflora* into the native plant-pollinator network with a dominance of *L. grandiflora* in terms of frequency of pollinator visits. Second, an experiment was designed to identify the pollinator guild of invasive *L. grandiflora* and native *Lythrum salicaria* and to measure interspecific pollinator switching. We also estimated the pollinator-mediated effect of high relative abundance of *L. grandiflora* (% cover of *L. grandiflora*) on *L. salicaria* plants. We monitored species composition, abundance and foraging behaviour of pollinators on *L. salicaria*. In addition, we assessed seed set per fruit of *L. salicaria*. Competition for pollinator services between invasive *L. grandiflora* and native *L. salicaria* seems minor as there was no evidence for decreased pollinator visitation or seed set of *L. salicaria*. On the contrary, more pollinators were recorded on *L. salicaria* plants when the cover of *L. grandiflora* was high compared to the control plants thereby indicating a facilitation effect, however this was not reflected in seed set. Despite the fact that *L. grandiflora* is well integrated in the native plant-pollinator network and highly attractive to pollinators, there was no evidence of negative impact of *L. grandiflora* on pollination of a native plant.

**Key words:** *Lythrum salicaria*, invasive alien species, plant-pollinator interactions, biodiversity impact, relative abundance, freshwater ecosystem

### Introduction

Pollination is one of the most important mechanisms contributing to biodiversity conservation and, like many ecosystem services, it can be influenced by alien invasive plants (Vilà et al. 2010). Previous studies have demonstrated that alien invasive plants can affect the interactions between native plants and pollinators (reviewed in Bjerknes et al. 2007). However, there is still no clear pattern on the effect of alien invasive species on pollinator services of native species. Reported positive (Lopezaraiza-Mikel et al. 2007; Bartomeus et al. 2008; Nielsen et al. 2008), neutral (Aigner 2004; Larson et al. 2006; Vanparys et al. 2011) or negative (Larson et al. 2006; Bartomeus et al. 2008; Thijs et al. 2012) results have depended on the native species considered, the year or the site.

Recent studies have included effects of density of invasive species to try and disentangle the impacts of showy invaders on floral visitation and/or reproductive output of natives (Muñoz and Cavieres 2008; Flanagan et al. 2010; McKinney 2010). The majority of these studies showed that the presence of an invasive species lowered the visitation rate and/or seed output of the native only at high abundance. A competition effect occurs when the native species suffers pollen limitation, i.e. inadequate pollen receipt that reduces plant reproductive success (Knight et al. 2005), as a result of pollinator sharing. A high degree of pollinator sharing can lead to interspecific pollen transfer when pollinators switch between flowers of different species during single foraging bouts or flights. This can lead to heterospecific pollen deposition (HPD) and/or conspecific pollen loss

(CPL) (Morales and Traveset 2008). Both processes can lead to reduced seed set (Jakobsson et al. 2008; Flanagan et al. 2009). HPD can affect seed set by different mechanisms such as stigma clogging, allelopathic inhibition of conspecific pollen or hybridization. Jakobsson et al. (2008) monitored HPD from invasive *Carpobrotus* spp. to natives and found a reduced seed production of the native *Helichrysum stoechas* probably due to stigma clogging.

While the impact of alien riparian and terrestrial plants mediated through pollinators has been studied, less attention has been paid to the introduced aquatic and semi-aquatic plants. Freshwater systems, however, are particularly vulnerable to the effects and rather complete domination of alien species as there is generally a lower native plant species diversity (Shea and Chesson 2002). Many amphibious aquatic plant invaders reproduce primarily from asexually rooting plant fragments. Many have flowers that would not be considered attractive or may not rely on insect pollinators, thus do not require pollinators. In such systems an alien aquatic invasive plant, possessing attractive flowers and present in high abundance, can act as a 'magnet' species attracting many pollinators that also visit native emergent species (Thomson 1978). However, the majority of alien aquatic plant species are termed as competitive species according to the definition of Grime (2001). They persist as 'good' invaders because of a combination of traits such as vegetative growth, rapid growth rate, a hydrophyte life form, high plasticity in growth response and a broad environmental tolerance (Thiébaud 2007; Thouvenot et al. 2013). Aquatic invasive plants can outcompete indigenous plants, change the nutrient cycling, degrade water quality and can have detrimental impacts on higher trophic levels, thereby affecting the entire aquatic ecosystem (Strayer 2010). Information is accumulating on how alien aquatic plant species compete directly with native species for resources such as space, light and nutrients (Strayer 2010) but information on the effect via indirect interactions, such as mediated by pollinators, is less known.

The invasive aquatic plant *Ludwigia grandiflora* (Michx.) Greuter and Burdet (Onagraceae) is an amphibious species, native to South America. *L. grandiflora* is widespread in the northern part of Belgium (Vanderhoeven 2013) and is known to usurp a large amount of space throughout the water column in the habitats it invades. The

species causes several economical and ecological problems. Its dense vegetation can block slow flowing waterways and thereby disturb recreational activities such as boating and fishing as well as affect drainage in lakes, ponds and ditches (Sheppard et al. 2006). In an earlier study we found that *L. grandiflora* negatively affected native plant species richness in temperate ponds (Stiers et al. 2011). In this study we use *L. grandiflora* as a model species to examine plant-pollinator interactions. Specifically, we address the following questions: 1) Is alien *L. grandiflora* integrated in the native plant-pollinator network? 2) What is the degree of pollinator overlap between invasive *L. grandiflora* and native *Lythrum salicaria*? 3) Does the high abundance of *L. grandiflora* influence pollinator visits and pollinator foraging behaviour on native *L. salicaria* and is this reflected in seed set? 4) Do pollinators move frequently between the two species?

## Materials and methods

### *Study species and sites*

The invasive alien *L. grandiflora* is an aquatic perennial herb that thrives in slow-flowing waterways, lakes, ponds and ditches (EPPO 2004). Because of its ability to produce both floating and emergent stems it is able to develop space monopolizing mats on both the open water and exposed mud. Reproduction is mainly by vegetative dispersal (Okada et al. 2009). *L. grandiflora* produces large and numerous yellow flowers (EPPO 2004), a trait that attracts a high number of pollinators (I. Stiers, personal observation and this study, Figure 1A). *L. grandiflora* is introduced in Belgium through the aquarium trade and is now recognized as a noxious weed in several European countries (DAISIE 2009).

*Lythrum salicaria* L. (Lythraceae) was used as a native target species to examine impact of *L. grandiflora* mediated through pollinators. This herbaceous perennial plant occurs in moist to wet ground along ditches, stream banks and ponds (Van Landuyt et al. 2006), and has the ability to reproduce prolifically by both seed and vegetative propagation. The plant produces showy, tristylous, magenta-coloured flowers (Pot 2003, Figure 1B) which are mainly visited by honeybees and bumblebees, but also other insects such as butterflies, syrphid flies and other Diptera contribute to pollination (Brown et al. 2002). *L. salicaria* was chosen as study plant because 1) the plant co-occurs with *L. grandiflora*, 2) it is visited by



**Figure 1.** Study species: flower of the invasive *L. grandiflora* with foraging *Apis mellifera* (A) and inflorescence of the native *L. salicaria* with foraging syrphid fly (B) (Photographs by I. Stiers, 2009).

a wide variety of insects, and 3) the peak flowering period overlaps with *L. grandiflora*. In addition, the floral morphology and colour is distinctly different from that of *L. grandiflora* ensuring that facilitation would not simply be due to an inability of pollinators to distinguish between species.

Four study sites (ponds) were selected in June 2009 in Flanders (northern Belgium) of which three were invaded by *L. grandiflora* (Table 1). One invaded site was used to build the visitation network (area 3, see 2.2.1) and two other sites, one no cover (control) site and one high cover site, were used to investigate the pollinator-mediated impact of *L. grandiflora* (area 1, see 2.2.2). The distance between the no cover and high cover sites was 100 m and the sites had comparable plant species diversity (Coussement 2010). One extra site with a low cover of *L. grandiflora* was selected (area 2) however as the distance between area 1 and area 2 was more than 100 km

(Table 1) we did not compare the results between area 1 and area 2 and only used it in a descriptive way. All sites were located in or close to nature reserves and were < 1 ha in size. The native vegetation of these sites was relatively poor in terms of insect-pollinated flowering plants (Table 1) and relative abundance of these individual plant species was always < 15 %.

### *Experimental design and statistical analysis*

#### Construction of a visitation network

As a first step, given the lack of information on pollinator guild of *L. grandiflora* and the sharing with native species, a food web approach (Memmot 1999) was used in one site with a high relative abundance of *L. grandiflora* (75–100 % cover of *L. grandiflora*). A permanent transect of nine 4 m<sup>2</sup> quadrats was placed near the shore to include both *L. grandiflora* and the adjacent native community. Once a week from mid July to mid August 2009 each quadrat was observed during 5 min. and each plant-pollinator interaction was recorded. Plants were identified using standard taxonomic keys to species level, insects to family and order and included Apidae (*Apis mellifera*, *Bombus* spp.), other Hymenoptera, Syrphidae, other Diptera and Coleoptera. Flower abundance was measured in blossom units, i.e. defined as the floral unit that a medium-sized bee has to fly, rather than walk, between (Dicks et al. 2002). The data were used to draw a quantitative plant visitation web using software [bipartite package (Dormann et al. 2008)] written in R (R Development Core Team 2008).

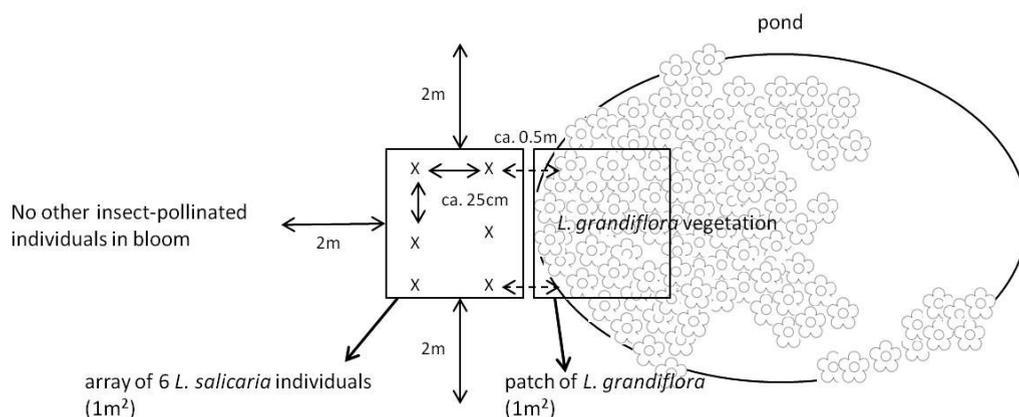
#### Pollinator observations

To determine impact of *L. grandiflora* on pollinator service in native plants, two sites were used (area 1): one control pond (no cover of *L. grandiflora*) and one pond with a high relative abundance of *L. grandiflora* (50–75 % cover of *L. grandiflora*). In addition, one extra site (area 2) with a low cover of *L. grandiflora* (1–5 %) was used to record pollinator observations.

The experiment was carried out when both focal plant species were at peak flowering period (mid July – mid August 2009). For this part of the study, seedlings of *L. salicaria* were collected in the field and grown separately in 10 L pots filled with potting soil and placed in plastic buckets filled with water in a garden site (51°00'37"N; 5°05'46"E). Upon flowering six potted *L. salicaria* plants were planted in an array (1 m<sup>2</sup>,

**Table 1.** Characteristics of the four study sites.

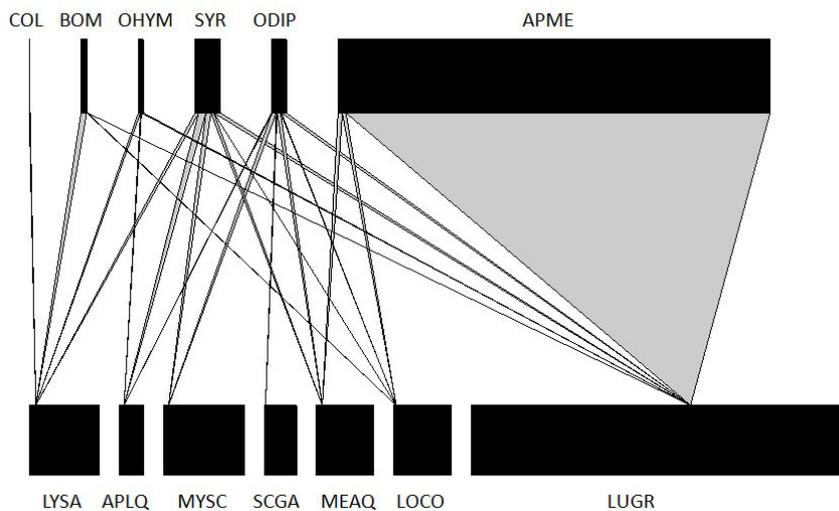
| Site   | Experiment         | Location                                       | Cover <i>L. grandiflora</i> (%) | Dominant insect-pollinated flowering plant species present at site              |
|--------|--------------------|--|---------------------------------|---|
| Area 1 | No cover site      | Antwerp (Belgium)<br>N: 51°11', E: 5°12'       | /                               | <i>L. salicaria</i> , <i>Eupatorium cannabinum</i> , <i>Lysimachia vulgaris</i> |
| Area 1 | High cover site    | Antwerp (Belgium)<br>N: 51°11', E: 5°12'       | 50–75                           | <i>L. salicaria</i> , <i>L. vulgaris</i>  |
| Area 2 | Low cover site     | East-Flanders (Belgium)<br>N: 51°03', E: 4°05' | 1–5                             | <i>L. salicaria</i> , <i>E. cannabinum</i> , <i>Nymphaea sp.</i>                |
| Area 3 | Visitation network | Limburg (Belgium)<br>N: 50°57', E: 5°08'       | 75–100                          | <i>L. salicaria</i> , <i>Myosotis scorpioides</i>                               |

**Figure 2.** Schematic overview of the experimental design to record the pollinator observations on *L. grandiflora* and *L. salicaria*.

ca. 25 cm between every plant) next to each pond on the shore. The array was placed at least 2 m away from any conspecific or heterospecific insect-pollinated individual in bloom to avoid potentially confounding effects of plant density and interspecific interactions (Figure 2). The experimental design ensured equal numbers of the three morphs for *L. salicaria*.

Insect observations for *L. grandiflora* were performed on a random monospecific patch (1 m<sup>2</sup>), less than 1 m away from the *L. salicaria* array, as individual plants were not distinguishable. For *L. salicaria* two randomly selected plants in each array were observed each period. We defined a visiting insect as a potential pollinator when it touched the sexual parts of the flowers. Ten minute periods of pollinator observations were performed from 9.30 am till 5.30 pm during 4 dry and sunny days for each site and species to record maximum pollinator activity (N = 6 observation periods per day, per species and per site). We recorded type of pollinator and number of arriving pollinators. Each pollinator was

identified ‘on the wing’ and classified to family and order as previously defined. In the low and high cover sites individual pollinators visiting *L. salicaria* and *L. grandiflora* were classified into three switching modes: a) a conspecific species, b) a heterospecific native species, and c) an unknown pollen source. For pollinators visiting *L. salicaria*, a fourth category was added d) switching to *L. grandiflora*. In addition, a total of 85 pollinators were individually censused on *L. salicaria* for foraging behaviour by recording number of flowers visited and time spent per flower (N = 6 observation periods per day, per species and per site). Each pollinator approaching a flower was considered a new individual and was thus recorded as a separate visit. Visitation rate to *L. salicaria* was defined as the total number of pollinators divided by the number of flowers on the two observed individuals. We harvested 30 fruits of *L. salicaria* per site (5 from each individual) upon ripening in late September and determined seed set per fruit (viable seeds/viable seeds + aborted seeds). Seeds per fruit were



**Figure 3.** Quantitative visitation web showing plant-pollinator interactions in area 3. Plants (bottom) and insects (top) are represented by a rectangle, links represent plant-pollinator interactions. The width of the rectangles reflects the relative abundance at the field site and the size of the interactions represents the visitation frequency. Abbreviations used: COL = Coleoptera, BOM = *Bombus* spp., OHYM = other Hymenoptera, SYR = Syrphidae, ODIP = other Diptera, APME = *Apis mellifera*, LYSA = *Lythrum salicaria*, APLQ = *Alisma plantago-aquatica*, MYSC = *Myosotis scorpioides*, SCGA = *Scutellaria galericulata*, MEAQ = *Mentha aquatica*, LOCO = *Lotus corniculatus*, LUGR = *Ludwigia grandiflora*.

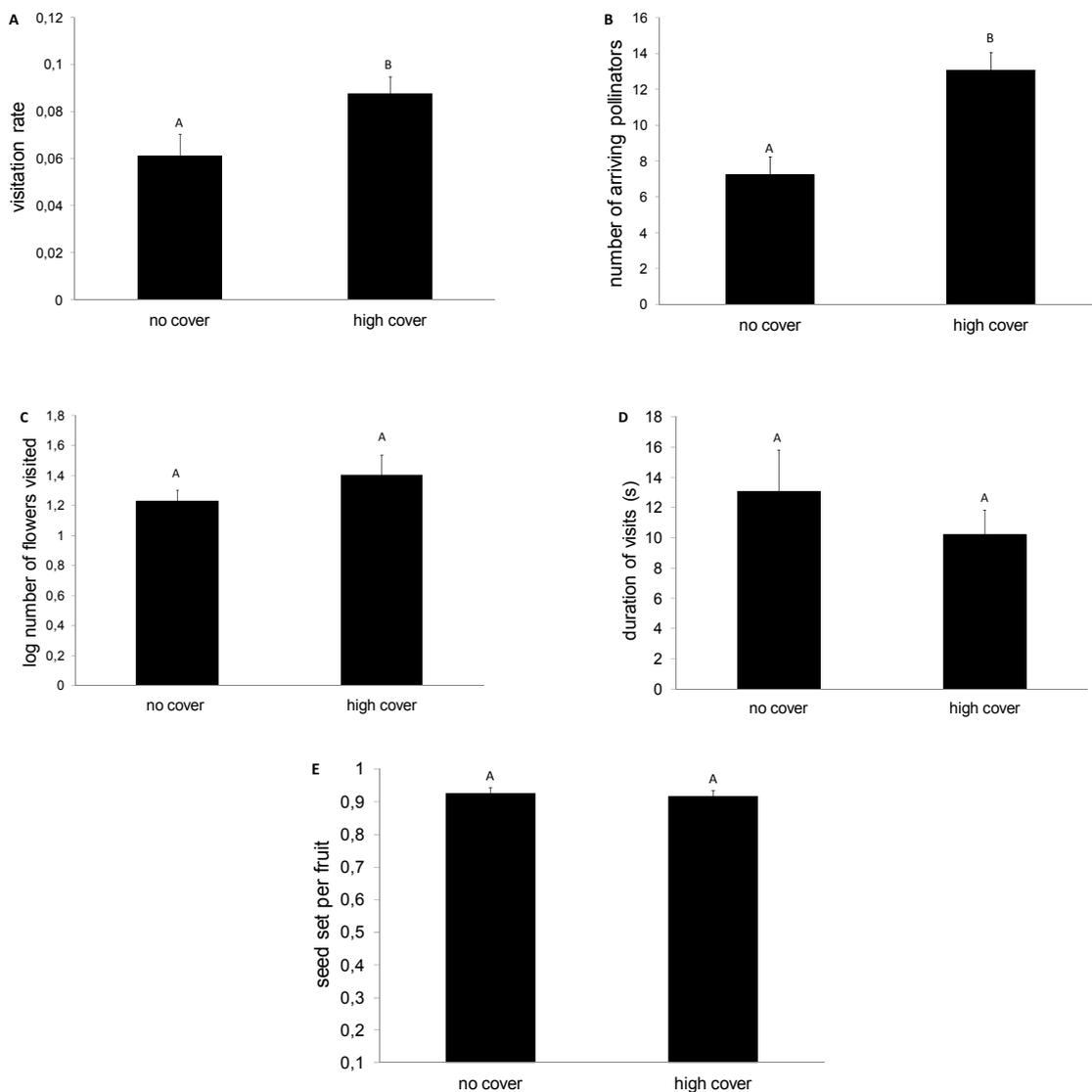
**Table 2.** Composition of visitors, number of individuals of each taxon observed (N), and percentage (%) of total visits that each pollinator taxon made to native *L. salicaria* and invasive *L. grandiflora* in the two different areas. Data are summed over the study period.

|                       | Area 1              |     |                     |     |                       |     | Area 2              |     |                       |     |
|-----------------------|---------------------|-----|---------------------|-----|-----------------------|-----|---------------------|-----|-----------------------|-----|
|                       | No cover            |     | High cover          |     |                       |     | Low cover           |     |                       |     |
|                       | <i>L. salicaria</i> |     | <i>L. salicaria</i> |     | <i>L. grandiflora</i> |     | <i>L. salicaria</i> |     | <i>L. grandiflora</i> |     |
|                       | N                   | %   | N                   | %   | N                     | %   | N                   | %   | N                     | %   |
| <i>Apis mellifera</i> | -                   | -   | -                   | -   | 336                   | 73  | 112                 | 48  | 84                    | 43  |
| Syrphidae             | 25                  | 29  | 65                  | 42  | 51                    | 11  | 60                  | 26  | 66                    | 34  |
| Other Diptera         | 3                   | 3   | 5                   | 3   | 43                    | 9   | 7                   | 3   | 36                    | 18  |
| <i>Bombus</i> spp.    | 34                  | 39  | 57                  | 37  | 17                    | 4   | 9                   | 4   | -                     | -   |
| Other Hymenoptera     | 1                   | 1   | 10                  | 7   | 14                    | 3   | 41                  | 18  | 9                     | 5   |
| Lepidoptera           | 24                  | 28  | 16                  | 10  | -                     | -   | -                   | -   | -                     | -   |
| Coleoptera            | -                   | -   | 2                   | 1   | -                     | -   | 3                   | 1   | -                     | -   |
| Total                 | 87                  | 100 | 155                 | 100 | 461                   | 100 | 230                 | 100 | 195                   | 100 |

averaged for all fruits from the same individual to provide one mean seeds per fruit value for each individual. Proportional similarity (PS, range 0–1) of the pollinator categories was calculated to measure the pollinator overlap between *L. grandiflora* and *L. salicaria* in the low cover and high cover sites.

The influence of high abundance of *L. grandiflora* on pollinator visitation (visitation rate and number of arriving pollinators) and foraging behaviour (duration of visits and number of flowers visited) on *L. salicaria* plants was analysed using repeated measures ANOVA (general linear

models procedure) with observation day as the unit of replication and site as categorical predictor (Sokal and Rohlf 2003). Number of flowers visited was log transformed to satisfy assumptions of normality, homogeneity of variances, and sphericity. A Wilcoxon matched paired test was used to test if pollinators moved more often to a conspecific species than to a heterospecific species within a site. The mean seed set per fruit per plant for *L. salicaria* between the no cover and high cover sites was analysed using a t-test. All analyses were performed using STATISTICA v8 (Statsoft, inc, Tulsa, OK, USA).



**Figure 4.** Mean  $\pm$  SE of A) flower visitation rate, B) number of arriving pollinators (per 10 min), C) number of flowers visited (per 10 min), D) duration of visits (s) and E) seed set per fruit on native *L. salicaria* in area 1. Different letters indicate significant differences.

## Results

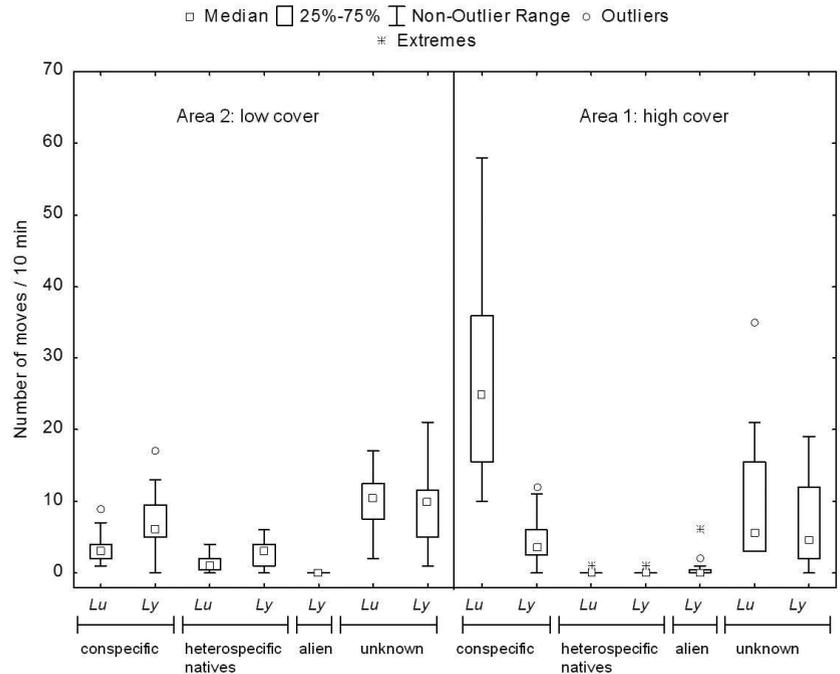
### *The visitation network*

A total of 1992 interactions were recorded among seven species of flowering plants (*Ludwigia grandiflora*, *Lythrum salicaria*, *Alisma plantago-aquatica*, *Myosotis scorpioides*, *Scutellaria galericulata*, *Mentha aquatica* and *Lotus corniculatus*) and six categories of pollinators (Figure 3). All plant and insect species are native

to the area. Ninety-one percent of the interactions were with *L. grandiflora*. *L. grandiflora* was linked to all insect categories except Coleoptera. The most frequent visitor of *L. grandiflora* was *Apis mellifera* (97 %).

### *Pollinator guild*

A total of respectively 656 and 472 insects were recorded on *L. grandiflora* and *L. salicaria*. *L. grandiflora* was visited by different pollinator



**Figure 5.** Box plots for number of moves to conspecific, heterospecific and alien species (*L. grandiflora*) and moves to unknown for *L. salicaria* (*Ly*) and *L. grandiflora* (*Lu*). A solid line separates area 1 and area 2.

taxa with *Apis mellifera* as the most frequent pollinator in both sites (43 % and 73 % of all visits, Table 2). Likewise, *L. salicaria* was also visited by a variety of different pollinator taxa, with the most frequent taxa being *Bombus* spp. (39 %) in the control site, *Apis mellifera* (48 %) in the low cover site, and Syrphidae (42 %) in the high cover site (Table 2). Two pollinator taxa, Lepidoptera and Coleoptera, were only recorded on *L. salicaria*.

The presence of *L. grandiflora* increased pollinator densities during the study period. When *L. grandiflora* was present in high abundance, seven times as many insects visited the patches. A high cover of *L. grandiflora* decreased the visitation of Lepidoptera and increased the visitation of Syrphidae (Table 2). The degree of pollinator sharing between *L. grandiflora* and *L. salicaria*, expressed using PS, was 0.81 in the low cover site and 0.21 in the high cover site.

#### Pollinator-mediated impact of *L. grandiflora*

The high abundance of *L. grandiflora* had a significant impact on the visitation rate (rm ANOVA:  $F_{1,10} = 5.521$ ,  $P = 0.033$ ; Figure 4A) and number of arriving pollinators on *L. salicaria* (rm ANOVA:  $F_{1,10} = 15.806$ ,  $P = 0.016$ ; Figure 4B). More pollinators arrived and visited *L.*

*salicaria* when the abundance of *L. grandiflora* was high. In contrast to pollinator visitation the foraging behaviour (number of visited flowers and duration of visits) on *L. salicaria* flowers was not significantly different between the no cover and high cover sites (Figures 4C, 4D). There were no significant interactions between site and day. Seed set per fruit per plant for *L. salicaria* was not significantly influenced by the high abundance of *L. grandiflora* (Figure 4E).

#### Pollinator movement

In area 1 and 2 and for both species the switching pollinators were always moving more often to a conspecific species than to a heterospecific species ( $P < 0.05$  for all combinations, Figure 5). Only 4.2 % of the pollinators moved from *L. grandiflora* to other species. In the low cover site Syrphidae (43 %) and *Apis mellifera* (37.5 %) were the dominant switching pollinators to move from *L. grandiflora* to other native plants, but not to *L. salicaria*. In the high cover site we seldom observed pollinators to switch from invasive *L. grandiflora* to native plants (Figure 5). Only in the high cover site were pollinators observed leaving *L. salicaria* for the invasive species and the most frequent switching pollinators were Syrphidae (77.8 %).

## Discussion

In this study we investigated the plant-pollinator interactions for the aquatic invasive plant *L. grandiflora*. We found that showy, invasive *L. grandiflora* shared pollinators with at least six native emergent species, was visited by a variety of insects, and caused facilitation of pollinator visitation to *L. salicaria*. Insect visitors of native plants are often generalists (Waser et al. 1996) and they readily include alien species in their diets (Lopezaraiza-Mikel et al. 2007; Bartomeus et al. 2008; Vilà et al. 2009). *L. grandiflora* is no exception in this. *L. grandiflora* was integrated in the native plant-pollinator network and showed dominance in terms of frequency of visits, but only by *Apis mellifera*.

*L. grandiflora* definitely was highly attractive to pollinators. In all areas, in spite of possible differences in the pollinator community, there was an overwhelming abundance of pollinators and especially of honeybees. Publications on *L. elegans* (Gimenes 2002) and *L. peploides* ssp. *glabrescens* (Estes and Thorp 1974) showed that both flowers and visiting insects of this genus were generalists, and Gimenes (2002) reported *A. mellifera* as a frequent visitor.

We can conclude that in area 1 *L. grandiflora* was visited by diverse pollinators and received high proportions of visits, but did not attract pollinators away from *L. salicaria* even when the invasive species was abundant in the immediate vicinity to the native plants. On the contrary, the presence of *L. grandiflora* positively influenced the pollinator visitation (total visitation over the study period, mean visitation rate and mean number of arriving pollinators) to *L. salicaria*. With *L. grandiflora* present in high abundance, *L. salicaria* received in total 1.8 times more pollinators. Westphal et al. (2003) showed that mass-flowering plants can increase pollinator densities. Visitation rate and mean number of pollinators for *L. salicaria* was higher in the high cover site compared to the no cover site, while duration of visits and number of flowers visited was unaffected. These results are consistent with Ghazoul (2006) in showing that facilitation of pollinator visitation can occur between species that have distinct floral morphologies. In this case, it seems that *L. grandiflora* increased the floral display in a community and attracted pollinators to the area which than also visited the native *L. salicaria*. However, this positive effect was not reflected in the seed set of *L. salicaria*.

There are several cases of invasive plant facilitation of pollinator visitation to native plants in the literature with no effect on seed set (Moragues and Traveset 2005; Nielsen et al. 2008; McKinney 2010). If pollen transport networks are dominated by alien *L. grandiflora* pollen, then any potential increase in seed set of *L. salicaria* due to increased visitation is counteracted (Lopezaraiza-Mikel et al. 2007). Moreover, according to Totland et al. (2006) seed set may be more robust than pollinator visitation to alien invasion. In addition, neutral effects of invasive plants on native plant reproductive success may also occur when seed output is not pollen-limited. However, this is a link that has been rarely investigated in studies of native-invasive plant interactions (but see Muñoz and Cavieres 2008; McKinney and Goodell 2010).

Recent experiments on density-effect impacts found that the presence of an invasive species lowered the visitation rate and/or seed output of the native only at high abundance (Muñoz and Cavieres 2008; Flanagan et al. 2010; McKinney 2010). The lack of negative impact of the high abundance of *L. grandiflora* on *L. salicaria* in our case can be explained by several reasons. Other factors such as flower attractiveness and pollinator behaviour influence pollinator-mediated impacts (Potts et al. 2003; Stang et al. 2006). First, the high potential of *L. salicaria* in attracting pollinators on its own can explain the observed lack of competition. *L. salicaria* is a very rewarding plant attracting numerous insects. The species produces large and showy flowers and is a prolific nectar producer (Levin 1970). Furthermore, in its invasive range (North-America) *L. salicaria* is able to dominate plant-pollinator interactions (Brown et al. 2002; Flanagan et al. 2010; 2011). Secondly, pollinator overlap was limited (PS = 0.21) and we rarely observed interspecific movements between the species. This reduces the possibility of high HPD which can affect reproductive success.

In spite of possible differences in the pollinator community across area 1 and 2, the frequency of pollinator switching was low in both areas. Pollinators from both species moved more often to conspecific than to heterospecific individuals, although the degree of pollinator overlap was rather high in area 2 (PS = 0.81). This is evidence for high pollinator fidelity. This was especially the case in the high cover site for the pollinator *A. mellifera*, which was the main pollinator of *L. grandiflora*, but never visited *L. salicaria* even if the distance was less than 1 m between the plants. High pollinator visitation and

pollinator constancy is expected in dense populations (Kunin 1997; Mustajarvi et al. 2001). In the high cover site *L. grandiflora* reached very high densities compared to *L. salicaria*. We could observe the same pattern in the visitation network: there was a high cover of *L. grandiflora* with *A. mellifera* as the dominant pollinator that never visited the native *L. salicaria*. The social bee *A. mellifera* shows a high level of flower constancy, is attracted to mass flowering stands (Goulson 1994; Butz Huryn 1997; Williams and Tepedino 2003), and therefore foraging on the dense stands of *L. grandiflora* might be extremely rewarding. In general, a high cover can increase the attractiveness and visitation frequency of a species (Kunin 1997). Results of the few studies that focused on interspecific pollinator movements are not uniform. Movements from alien to native species can be either rare (Jakobsson et al. 2008; Yang et al. 2011) or common (Brown et al. 2002; Flanagan et al. 2011) however, if there is a greater morphological similarity pollinator constancy is often lower (Chittka et al. 1999). Some syrphid flies were leaving *L. salicaria* for *L. grandiflora*, but only at the high cover site, which might indicate a certain attractiveness of the high abundance of *L. grandiflora*.

Although we do not have evidence for any negative impact of *L. grandiflora* on pollinator services in native *L. salicaria*, care has to be taken to extrapolate this effect to other native species. Moragues and Traveset (2005) showed in their study that the impact of invasive *Carpobrotus* spp. was native species-specific. Likewise, Thijs et al. (2012) found a competitive effect between invasive *Impatiens glandulifera* and *L. salicaria*, but not between the invasive species and *Alisma plantago-aquatica* or *Oenothera biennis*. Other native species may respond different to the presence of *L. grandiflora* depending on the overlap of pollinator community and quantity and quality of forage resources. Extended resources offered by this mass-flowering generalist alien species and the prevalence of generalist pollinators in natural communities may induce changes in pollinator services to other native plants with consequences for their reproductive success.

Our results suggest that *L. grandiflora* shares pollinators with different native emergent aquatic species, attracts mainly honeybees and can alter pollinator visitation to native *L. salicaria*. We acknowledge the fact that this type of study would benefit from more than one field season as we are aware that number of pollinators and

pollinator community show a temporal and spatial variability. The results of Larson et al. (2006), Vanparys et al. (2008) and Flanagan et al. (2010), showing differences in visitation and/or in composition of pollinators between years and/or sites, emphasize the importance of studying plant-pollinator interactions in multiple years and across multiple sites. Although our study only represents a snapshot, it indicates the importance of the abundance of invasive plants in influencing interactions for pollinators between co-flowering plants.

## Acknowledgements

The authors thank M. Vanderlinden and R. Stiers for their logistic assistance, Natuurpunt for providing localities and Dr. K. Quisthoudt for her assistance with the software R. We thank I. McMillan for English correction and three anonymous reviewers for helpful comments on a previous version of the paper. This research is part of the project 'ALIEN IMPACT' financed by the Belgian Science Policy, contract number SD/BD/01A and by the Vrije Universiteit Brussel (BAS 42).

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