ORIGINAL PAPER

Presence of an invasive plant species alters pollinator visitation to a native

Vashti M. King · Risa D. Sargent

Abstract The degree to which pollinator-mediated interactions assist or impede plant invasions is currently poorly understood. Here we describe the findings of an experiment designed to investigate how pollinator-mediated interactions between invasive *Lythrum salicaria* (Purple loosestrife) and a closely related native North American species, *Decodon verticillatus* (Swamp loosestrife) are influenced by the stage of invasion (i.e., early or late). By comparing pollinator preference and constancy to plants in experimentally introduced arrays of *L. salicaria* and *D. verticillatus* in invaded and uninvaded communities, we were able to simulate the ecological implications of two different stages of *L. salicaria* invasion. Invasion status had no significant effect on pollinator visitation to *L. salicaria* and *D. verticillatus* when all pollinator taxa were considered together. However, when bumblebees, the dominant pollinator at all sites, were considered alone, we found a significant interaction between pollinator preference and the invasion status of the site, with *D. verticillatus* preferred at uninvaded sites only, and no preference exhibited at invaded sites. In addition, for all pollinator taxa, we found that interspecific pollinator movements were overrepresented at uninvaded sites and underrepresented at invaded sites, suggesting that heterospecific pollen deposition could be a significant impediment to pollinator-mediated reproduction for both species in the early stages of an invasion. We discuss the potential consequences of our findings to the establishment of animal-pollinated invasive plants and the persistence of native species in the face of invasion.

Keywords Pollination · Invasive species · Purple loosestrife · Pollinator constancy · Pollinator preference

Introduction

Animal pollinators play a key role in ecosystem function in most terrestrial plant communities. Indeed, pollinators are important mediators of inter- and intra-specific interactions among plants. Two recent reviews of the existing literature report that pollinator-mediated competition can impose fitness costs for natives in invaded communities (Bjerknes et al. 2007; Morales and Traveset 2009). Typically, studies have focused on how the presence, and in some cases density, of an invasive species can impact the quantity and/or quality of native plant species pollination, and consequently, their fitness (e.g., Brown and Mitchell 2001; Brown et al. 2002; Cariveau and Norton 2009;

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Dietzsch et al. 2011; Flanagan et al. 2009; Thijs et al.). Whether the presence of an invasive can affect pollinator fidelity and pollinator preference has rarely been studied directly.

If the presence of an invasive plant alters the interactions among native plants and their pollinators, fitness effects, including changes in pollinator visitation rates, compatible pollen transport and receipt, and, ultimately seed set, are predicted (Bjerknes et al. 2007; Ghazoul 2004). The direction and magnitude of the impact of pollinator-mediated interactions among native and invasive plants should depend heavily on the influence of the invasive on pollinator behavior. For example, if pollinators prefer an invasive to native plants and switch their foraging behavior, the resulting drop in pollinator attention may reduce the reproductive success of native plants in the vicinity (Burd 1994; Chittka and Schurkens 2001; Mitchell et al. 2009). On the other hand, the presence of a highly attractive invasive has occasionally been found to increase pollinator visitation rates to a community (e.g., Chittka and Schurkens 2001; Lopezaraiza-Mikel et al. 2007). The outcome of such interactions can be complex, and caution needs to be applied in their interpretation. For example (Lopezaraiza-Mikel et al. 2007) determined that although native plants in communities containing the invasive species *Impatiens glandulifera* had both higher pollinator densities and pollinator species richness, the overall impact on natives was likely negative because of the dominance of alien pollen in pollen loads. Similarly (E. Da Silva, unpublished data) reported higher seed set in the native *Decodon verticillatus* in the presence of the invasive *Lythrum salicaria*. However, it was unclear whether the increased seed set was due to an increase in geitonogamy (selfing) or outcrossing. Nevertheless, plant reproductive success can in some cases be enhanced by the presence of another species (Moeller 2004).

In addition to a shift in preference, the introduction of an invasive species could precipitate a change in the fidelity of pollinator movements among conspecific natives (Brown et al. 2002). A decrease in pollinator fidelity (measured as the proportion of intraspecific pollinator movements) can result in reduced fitness through increased levels of interspecific pollen deposition, in addition to the loss of conspecific pollen deposition (Flanagan et al. 2009; Harder and Routley 2006). Either of these processes could have a detrimental effect on native plant population persistence.

Several hypotheses exist to explain the existence of pollinator fidelity or constancy—the tendency for pollinators to restrict their visits to only a few of the available floral species (Chittka et al. 1999). One frequently cited explanation is that constancy has evolved due to memory constraints that prevent a pollinator from efficiently handling more than one type of flower at a time, but a clear, straightforward explanation has not yet been proposed. The implications of constancy for the plant, however, are unambiguous - constancy reduces costly heterospecific pollen transfer (de Jager et al. 2011). The effect of a plant invasion on pollen movement patterns in a community should depend largely on the degree of constancy exhibited by the pollinator community. If, for example, pollinator constancy is uninfluenced by the new species, the impact on native plants should be minimal. On the other hand, and this is likely if the novel species is highly rewarding, an important pollinator that switches to a novel invader could devastate the reproductive success of any native plants that rely on it.

One interesting aspect of a successful plant invasion that is rarely captured by field studies is that a plant community is likely to change throughout the course of the invasion (Melbourne et al. 2007). Initially, the invasive species is likely to be present only in small numbers. If the invasive species is able to spread, its density increases. The impact of the invasive plant on pollinator-mediated interactions is likely to change over the course of the invasion for a variety of reasons, both ecological and evolutionary. At the early stages of invasion, the density of the invasive species is likely to be low, which could have important implications for its ability to attract pollinators (Agren 1996; Moeller 2004) and to find adequate mating opportunities (Eckert and Barrett 1992; Eckert et al. 1996). Moreover, the impact of the invasive on the native species in terms of competition for pollinators and other limited resources is likely to be negligible early on (Cappuccino 2004; Dietzsch et al. 2011). Over the course of a successful invasion, the density of the invasive is likely to increase, making it a more relevant ecological competitor. Finally, the surrounding community may impose selection on the invasive species (and vice versa), potentially altering the evolutionary trajectory of populations and species in the vicinity. Unfortunately, to our knowledge, no studies have examined pollinator dynamics at the early stages of an invasion, possibly because of the potential

for negative ecological effects. Yet, understanding the dynamics at an early stage of invasion is critical to our ability to predict whether the observation of an invasive at a low frequency is likely to proceed to a full scale invasion. The ability of a novel invasive to attract adequate attention from pollinators is likely to be an important piece of the puzzle.

Here, using a field array experiment, we explored the potential for ecological (especially density) impacts of pollinator-mediated interactions among the native plant *D. verticillatus* and the invasive *L. salicaria* at two different stages of invasion. Specifically, using observations of pollinator movements on an experimental array, we determined how preference and fidelity for both species depends on prior invasion of the community. We also examined the potential for differences in rewards (nectar) to influence pollinator visitation patterns to the two species. In this way, we were able to examine how the prior exposure of the pollinator community to an invasive species influences pollinator preference and pollinator fidelity to a native species.

Materials and methods

Study system

Lythrum salicaria (L., Lythraceae) is an herbaceous, perennial wetland plant first introduced to North America from Eurasia in the early 1800s (Thompson et al. 1987). Since its introduction, *L. salicaria* has spread throughout most of the United States and all of the Canadian provinces (Welk 2004). *L. salicaria* is largely self-incompatible (Colautti et al. 2010), meaning its sexual reproduction is limited by pollination. *L. salicaria* is able to reproduce clonally or asexually; however, sexual reproduction is likely important in the long term establishment of invasive populations (Dorken and Eckert 2001). The purple-pink flowers of *L. salicaria* are 1.3–2 cm wide, actinomorphic and tightly clustered on a long spike raceme at the top of an erect stem (Fig. 1a) (Neiring and Olmstead 1988).

Decodon verticillatus (L. Elliot, Lythraceae) is a perennial, wetland plant, native to North America (Dickinson et al. 2004). Unlike *L. salicaria*, *D. verticillatus* is self-compatible, although populations in the region of our experiment are known to suffer from high inbreeding depression, making selfing costly (Eckert and Barrett 1994). *D. verticillatus* is also capable of reproducing clonally (Eckert 2002). The dark pink flowers of *D. verticillatus* are 1.3 cm long, actinomorphic and clustered in dense axillary cymes near the end of arching stems (Fig. 1b) (E. Da Silva, unpublished data; Neiring and Olmstead 1988).

The two species co-occur, co-flower, and share pollinators (E. Da Silva, unpublished data) during late July and early August in the wetlands of Lake Opinicon near the Queen's University Biological Station, Leeds and Grenville County, ON (44.567°N
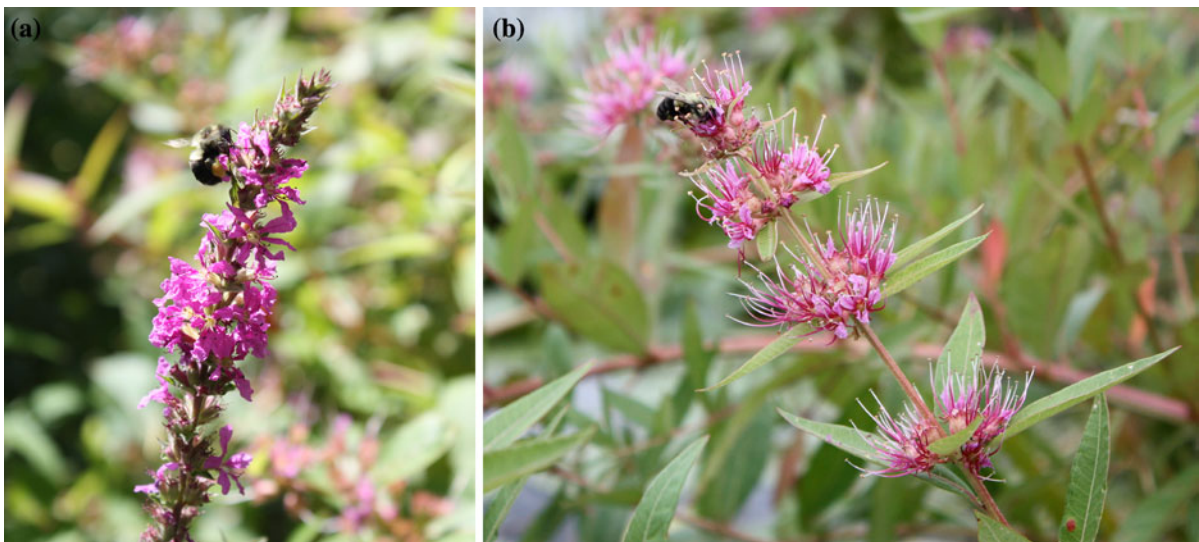

Fig. 1 **a** *Bombus* sp. foraging on inflorescence of *L. salicaria*. **b** *Bombus* sp. foraging on inflorescence of *D. verticillatus*

76.324°W), where this study was conducted. Four experimental sites (i.e., two invaded and two uninvaded populations of *D. verticillatus*) were identified on the basis of their relatively similar *D. verticillatus* population size (all sites), *L. salicaria* population size (invaded sites only, Table 1), and native plant community composition. Sites were a minimum of 200 m apart and in most cases more. Sites also had to be within reasonable distance from the Biological Station in order to facilitate daily transport to the site by canoe.

Pollinator foraging patterns

Decodon verticillatus and *L. salicaria* were the dominant flowering plants at the invaded sites. The two species were found at similar densities at these sites (Table 1). At uninvaded sites, *D. verticillatus* was the dominant flowering plant and *L. salicaria* was absent.

To investigate whether the species composition of the surrounding plant community (i.e., community context) influences pollinator foraging patterns, permanent experimental arrays, consisting of 16 florist water tubes (Afloral.com, Jamestown, New York) were established at each site (Fig. 2). The florist tubes

Table 1 Mean flowering density of *Decodon verticillatus* and *Lythrum salicaria* within a 2 m radius of array sites

Site	*D.v.* density	*L.s.* density
CM[a]	108.3 (3)[b]	97.3 (3)
NES	128 (2)	98.5 (2)
DBB	192 (2)	0 (2)
LI	183 (2)	0 (2)

[a] Site abbreviations are: *CM* Cow Marsh, *NES* North East Sanctuary, *DBB* Deadlock Bay B, *LI* Little Island

[b] Numbers in brackets indicate the number of survey dates upon which average flowering densities are based
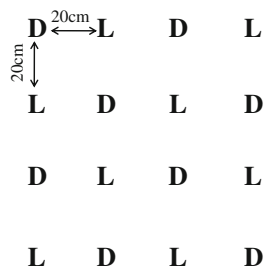

Fig. 2 Experimental array design. Letters represent the two study species: D, *D. verticillatus* and L, *L. salicaria*

were fastened to garden stakes spaced 20 cm apart. At invaded sites, the array was placed within an area where *D. verticillatus* and *L. salicaria* plants were densely interspersed, and in many cases each other's nearest neighbour. Because plant distribution in these sites is somewhat clumped, we were able to place the arrays in naturally occurring gaps and plant removal for the placement of arrays was therefore not necessary. At uninvaded sites, the array was placed within a natural gap of *D. verticillatus* plants.

An experimental array consisted of 16 cut inflorescences, 8 *D. verticillatus* and 8 *L. salicaria*, arranged in a checkerboard pattern in the permanently arranged florist tubes (Fig. 2). Inflorescences came from a single, large source community containing both *D. verticillatus* and *L. salicaria*. This community was also a study site; however, where the cuttings were collected from and where the array was established were well over 100 m apart. Inflorescences for the arrays were selected based on the relative size of the floral display, rather than the number of open flowers, as *L. salicaria* naturally has more open flowers than *D. verticillatus* and we wanted to include natural differences in the two species that could influence visitation patterns. *L. salicaria* and *D. verticillatus* inflorescences used in the arrays had floral displays 6–16 cm in length, with *D. verticillatus* inflorescences having 3–18 open flowers (mean = 9.19 ± 0.72 SE) and *L. salicaria* inflorescences having 11–41 open flowers (mean = 22.38 ± 1.59 SE).

Pollinator activity was observed in experimental arrays during the peak of the flowering period, which occurred between late July and early August in 2010. Each day two different sites were sampled, one in the morning and one in the afternoon, providing a two-day sampling cycle. For each cycle, to account for weather and time-of-day variation, we randomized the site order. Inflorescences were collected twice a day, once in the morning for the first site visited, and then again around noon for the second site. Two 30-min observation periods were conducted each time a site was visited, during which two researchers watched the array and pollinator activity on the array was recorded using voice recorders. For each pollinator observed visiting the array, its taxonomic identity and visitation sequence were recorded. Pollinators were identified 'on the wing' as belonging to one of six functional groups: *Bombus* spp., *Apis mellifera*, solitary bees, wasps, syrphid flies, or butterflies (Eckert 2002). The

record of the visitation sequence included the sequence of species visited while the pollinator was foraging within the array, as well as the number of individual flowers visited on each inflorescence. A pollinator was considered to have visited an inflorescence or flower when it approached an inflorescence, probed a flower, and made contact with the stigma and/or anthers of the flower. All array observation periods occurred during peak pollinator activity, between 0900 and 1600 h (Eckert 2002), on days without precipitation and that were not overly windy. The study was designed so that array observations were replicated at each of the four sites 10 times throughout the course of the experimental period, for a total of 40 periods of observation.

Nectar rewards

Nectar volume was collected in order to investigate differences in floral rewards between the two species. Following standard techniques, pollinator exclosure bags (sleeves made of bridal veil) were placed on flowering ramets for 48 h prior to nectar collection. Pollinator exclosure bags were placed on ramets that contained open flowers and buds and were at least 2 m away from another bagged ramet [to ensure they were taken from across several genets (Dorken and Eckert 2001)].

For each species, at each site, nectar samples were collected from flowers on 5-9 ramets. For each ramet, nectar samples were taken from 5 different flowers. To control for differences in nectar production as a function of floral age, nectar samples were only collected from flowers with recently dehisced anthers. Nectar was extracted from flowers using 5 and 10 µL microcapillary tubes (Kearns and Inouye 1993). Nectar volume per flower was calculated by measuring the height of the nectar within a microcapillary tube, dividing this value by the total height of the tube, then multiplying the quotient by the volume of the tube.

Statistical tests

In order to analyze the effect of community context on pollinator preference we used a mixed-effects ANCOVA. The response variable in this model was pollinator visitation rate (number of visits/inflorescence/h). Factors included were community context (invaded or uninvaded) and plant species visited

(*D. verticillatus* or *L. salicaria*) as fixed effects, site (Cow Island Marsh, North East Sanctuary, Dead Lock Bay B or Little Island) nested within context and observation period nested within site and context as a random effects, and the interaction between context and visited plant species. Pollinator taxa was not included as a factor in the analysis, as only two pollinator taxa were observed at all four sites—*Bombus* spp. and Syrphid flies. Instead, we ran the model with all pollinator taxa data pooled, and then again with only *Bombus* spp. data. *Bombus* was the dominant functional group and one of only two types observed across all four sites.

In order to examine the effect of community context on pollinator constancy we used two-way contingency tables with Pearson χ^2 test statistics. The variables included were movement type (*D. verticillatus* to *D. verticillatus*, *L. salicaria* to *L. salicaria*, *D. verticillatus* to *L. salicaria* or *L. salicaria* to *D. verticillatus*) and community context (invaded or uninvaded). Again, we conducted the analysis with all pollinator taxa data pooled, and then again with only *Bombus* spp. data. Before pooling data from sites within contexts, we tested for differences between sites.

Finally, nectar volume data was analyzed using a mixed-effects ANOVA. The dependent variable was the average flower nectar volume per ramet (square-root transformed) and the factors included were plant species (*D. verticillatus* and *L. salicaria*) as a fixed-effect and site (Cow Island Marsh, North East Sanctuary, Dead Lock Bay B and Little Island) as a random effect.

Nectar volume was square-root transformed to meet the assumption of normality (Quinn and Keough 2002). All other response variable fit the assumptions of normality and homoscedasticity without transformation. All analyses were preformed using JMP-version 8.0.2 statistical package (JMP 2009).

Results

Pollinator community

The taxonomic composition of pollinators foraging within the experimental arrays varied across sites and contexts. *Bombus* was the most common pollinator at all four sites, with the proportion of all visits ranging from 65 to 97%. Syrphid flies were also present at all four sites, but were far less common; the proportion of

visits ranged from 1 to 6%. Wasps were present at all sites except Dead Lock Bay B, and solitary bees were observed at all sites apart from Cow Island Marsh. The invasive European honeybee, *Apis mellifera,* was observed at invaded sites, accounting for 8% and 27% of pollinator visits at Cow Island Marsh and North East Sanctuary, respectively. Butterflies were only observed at uninvaded sites. In order to account for a possible confound between community context and pollinator taxa, we analyzed the data for *Bombus* separately from the other pollinator taxa, as this pollinator type was present at high frequencies at all sites.

Pollinator foraging patterns

Pollinator preference

Overall, visitation to *D. verticillatus* was significantly higher than to *L. salicaria* (Table 2; Fig. 3a). When visits by all pollinator taxa were pooled, recipient plant preference did not vary significantly across contexts (Table 2; Fig. 3a). However, when we considered only visits by *Bombus* spp., visitation to *D. verticillatus* was significantly higher than to *L. salicaria* at uninvaded sites but not at invaded sites (Table 2; Fig. 3b), indicating that site invasion status

Table 2 ANCOVA on inflorescence visitation rate for (a) all pollinator taxa and (b) *Bombus* spp.

Source of variation	df	SS	F	p
(a) All taxa visitation				
Recipient plant	1	6.86646	14.0783	0.0006*
Context	1	9.8438	6.9077	0.1194
Site (context)	2	2.8501	0.5143	0.6023
Observation period (site, context)	36	99.7521	5.6812	<0.0001*
Context × recipient plant	1	0.71489	1.4657	0.2335
(b) *Bombus* spp. visitation				
Recipient plant	1	1.7813	4.7935	0.0348*
Context	1	14.3969	7.6734	0.1094
Site (context)	2	3.75244	0.7373	0.4855
Observation period (site, context)	36	91.6139	6.8482	<0.0001*
Context × recipient plant	1	1.59966	4.3047	0.0448*

* Statistical significance at the 0.05 level

impacted the preference for *D. verticillatus* by *Bombus*, one of the community's dominant pollinators.

Pollinator constancy

There were no significant differences in movement patterns for sites with the same context (invaded all taxa $\chi^2 = 2.067$, $df = 3$, $p = 0.5587$; uninvaded all taxa $\chi^2 = 0.599$, $df = 3$, $p = 0.8968$; invaded *Bombus* spp. $\chi^2 = 1.658$, $df = 3$, $p = 0.6464$; uninvaded *Bombus* spp. $\chi^2 = 2.434$, $df = 3$, $p = 0.4874$); therefore the data for each context was pooled.

The frequency of movement type was strongly dependent on community context (Tables 3, 4). Specifically, intraspecific movements (D–D, L–L) were underrepresented at uninvaded sites and overrepresented at invaded sites, while interspecific movements (D–L, L–D) were overrepresented at uninvaded sites and underrepresented at invaded sites.

Using only the *Bombus* data, we found that movement type was again not independent of context ($\chi^2 = 37.042$, $df = 3$, $p < 0.0001$; Table 4). Overall, as with the pooled data, interspecific movements were overrepresented at uninvaded sites and underrepresented at invaded sites. However, in contrast to the pooled pollinator data, *D. verticillatus* to *D. verticillatus* movements were overrepresented at uninvaded sites and underrepresented at invaded sites (Table 4).

Floral rewards

Average nectar volume was significantly higher in *D. verticillatus* (least squares mean = 3.5314 μL ± 0.0114 SE) than *L. salicaria* flowers (least squares mean = 0.5235 μL ± 0.0402, $p < 0.001$; Fig. 4).

Discussion

Our results demonstrate that the quantity (pollinator preference) and the quality (pollinator constancy) of pollinator visitation to *D. verticillatus* and *L. salicaria* varies according to the presence of *L. salicaria* invasion at a site. Specifically, the dominant pollinator (*Bombus* spp.) preferred the native plant species, *D. verticillatus* to the invasive plant species, *L. salicaria*, at sites where *L. salicaria* was not present prior to the introduction of the experimental array (i.e., uninvaded sites). No preference was evident at sites

Fig. 3 Least-squares mean $\pm$ 1 SE of pollinator visitation rate to *D. verticillatus* and *L. salicaria* inflorescences within experimental array at uninvaded (n = 20) and invaded (n = 20) sites for **a** all taxa and **b** *Bombus* spp.
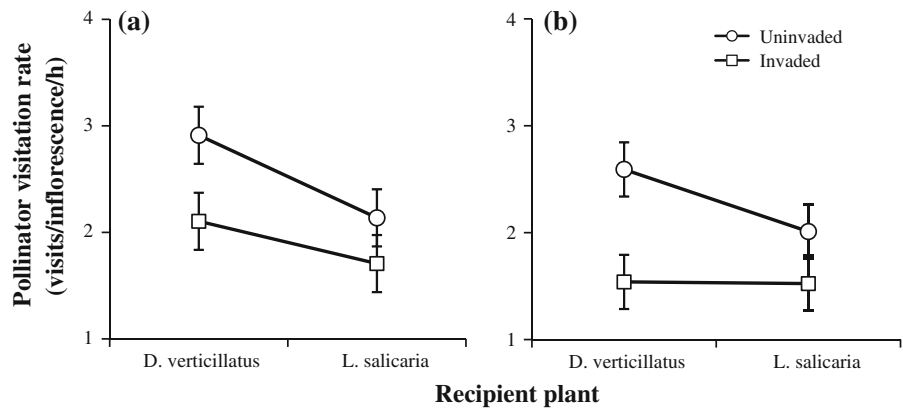
Table 3 Frequency of observed pollinator movements in uninvaded and invaded contexts for all pollinator taxa

Context	Movement type			
	D–D	L–L	D–L	L–D
Uninvaded	262	160	341	345
	279	**207**	**309**	**314**
Invaded	205	186	176	181
	188	**139**	**208**	**212**

Expected values are shown in bold type font. D represents *D. verticillatus* and L represents *L. salicaria*. $\chi^2 = 44.0$, $df = 3$, $p < 0.001$

Table 4 Frequency of observed *Bombus* spp. movements in uninvaded and invaded contexts

Context	Movement type			
	D–D	L–L	D–L	L–D
Uninvaded	232	155	321	325
	223	**202**	**302**	**306**
Invaded	123	167	160	162
	132	**120**	**179**	**181**

Expected numbers are displayed in bold type font. D represents *D. verticillatus* and L represents *L. salicaria*. $\chi^2 = 37.0$, $df = 3$, $p < 0.001$

Fig. 4 Least-squares mean $\pm$ 1 standard error of flower nectar volume averaged by ramet for *D. verticillatus* (n = 27) and *L. salicaria* (n = 10)

where *L. salicaria* was already established in the community (invaded sites), suggesting that pollinator preference is context-dependent in this system. Moreover, for all pollinators, intraspecific movements were underrepresented at uninvaded sites and overrepresented at invaded sites, while interspecific movements we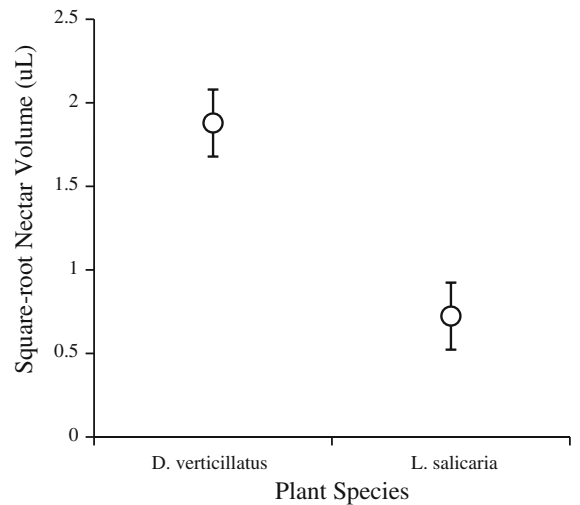re overrepresented at uninvaded sites and underrepresented at invaded sites. We hypothesize that the preference for *D. verticillatus* at uninvaded sites could be due to its higher nectar volume. Preference by *Bombus* is also known to be influenced by the frequency of a particular morph in the array (Epperson and Clegg 1987; Smithson and Macnair 1996). Although our arrays were constant across the experiment, the background community was not, and therefore frequency-dependent foraging patterns could play a role in explaining our results. In the following sections we discuss the potential consequences of our findings to both *L. salicaria* and *D. verticillatus* fitness and persistence.

In contrast to previous studies (e.g.Brown et al. 2002; Levin 1970; Yang et al. 2011), we found no

evidence that the species with the larger, showier floral display, *L. salicaria,* was preferred by pollinators and could hence detract pollinators from the native. On the contrary, our results suggest that pollinators in most cases preferred the less showy native, *D. verticillatus*, likely due to higher levels of nectar production per flower (Heinrich and Raven 1972), and possibly due to the influence of frequency dependence on pollinator foraging patterns (Epperson and Clegg 1987; Smithson and Macnair 1996).

In spite of differences in the pollinator community across experimental sites, constancy was consistently higher at invaded sites where both species had previously established in the community (and where pollinators were familiar with *L. salicaria* and *D. verticillatus*) than at uninvaded sites where only *D. verticillatus* was present before the introduction of the experimental array. This result contradicts the results of previous studies that have examined the effect of community context on pollinator constancy. In their observations of pollinators foraging on experimental arrays containing three species of *Castilleja* (Hersch and Roy 2007) found that pollinator constancy was lower when the surrounding context contained all three species than when any of the three species was the sole plant in the surrounding community. (Wilson and Stine 1996) measured floral constancy by 'interviewing' wild individuals of *Bombus vagans* foraging in monotypic and mixed flowering communities of *Trifolium pratense*, *T. repens*, *Viccia cracca*, and *Prunella vulgaris*. When presented with the choice between two plant species, pollinators were found to be more constant when foraging in monotypic populations versus communities where they were exposed to multiple species. According to (Wilson and Stine 1996), our results are consistent with a classical explanation of constancy, where constancy is an adaptive behavior that minimizes handling time of flowers and optimizes foraging return. Applying this explanation to our system, we propose that pollinators foraging in mixed communities of *L. salicaria* and *D. verticillatus* have previously encountered and evaluated both of these species and have decided to specialize on one or the other, leading to our observation of more constancy in the uninvaded communities. In contrast, pollinators foraging in communities where only *D. verticillatus* is present have not encountered both species and and are not therefore specializing on a particular species. While there are

many proposed mechanisms for why constancy occurs, a single simple explanation has yet to be proposed (Chittka et al. 1999). Whatever the mechanism, patterns of constancy have important ecological and evolutionary consequences.

Our results suggest that a relatively lower rate of pollinator visitation is unlikely to impede the invasion of *L. salicaria* in sites where it is establishing. Although lower levels of pollinator constancy at uninvaded sites may negatively impact the fitness of both *D. verticillatus* and *L. salicaria*, our results suggest that it is likely that the effects on *D. verticillatus* fitness would be minimal, at least in the early stages of invasion. Reduced constancy in a newly colonized community could be far more detrimental for *L. salicaria*, as there are far fewer individuals and interspecific pollen transfer would be more common. Then again, perhaps as a result of relaxed constancy, individuals of *L. salicaria* are able to achieve high pollination quantity during colonization and successfully establish in *D. verticillatus* dominated communities. A recent study demonstrated that pollination by a mixture of *L. salicaria* and *D. verticillatus* pollen can reduce total seed set by as much as 1/3 in *D. verticillatus* (Da Silva and Sargent 2011; Yang et al. 2011). Whether the reciprocal is true has not been studied, however, evidence from other systems indicates that a negative impact of heterospecific pollen transfer is likely (Arceo-Gomez and Ashman in press).

One caveat of our study is that invaded sites may have had other distinguishing characteristics that could have played a role in our findings. For example, there were differences in the pollinator community among sites. To control for this possibility, we performed our analyses on the pooled pollinator data, but also on the data from the dominant pollinator across sites (*Bombus*) alone. Nevertheless, we acknowledge that site differences besides invasion status could have influenced our findings. Future studies could control for site differences by artificially creating invaded and uninvaded sites (e.g., through species removal or addition). It may also be desirable to examine a gradient of invasiveness in order to investigate whether our findings hold over the course of an invasion of a community by *L. salicaria*. The creation of artificially invaded populations with a gradient of *L. salicaria* population sizes could be used to accomplish this goal.

Our study sheds light on how pollinator-mediated interactions between invasive and native plant species could change over the course of an invasion. In the absence of measures of fruit set, seed set or recruitment data we can only speculate that the observed pollinator foraging patterns will have consequences for seed set and population persistence. Future research should focus on quantifying the effects of changing pollinator foraging patterns on native and invasive seed fitness in different stages of invasion. In light of rapidly changing species distributions, investigating the role of competition for pollination on alien plant invasions is an important research avenue.

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