

# The showy invasive plant *Ranunculus ficaria* facilitates pollinator activity, pollen deposition, but not always seed production for two native spring ephemeral plants

Jeffery A. Masters · Sarah M. Emery

Received: 7 July 2014 / Accepted: 9 March 2015 / Published online: 15 March 2015  
© Springer International Publishing Switzerland 2015

**Abstract** Showy invasive plants can reduce pollinator visitation to native plants, resulting in a reduction of seed-set in insect-pollinated species. Seed set in native plants may also be reduced due to the presence of foreign pollen. Alternatively, additional floral resources provided by invasive plants may increase pollinator activity, and facilitate pollination of native species. *Ranunculus ficaria* is a perennial herb invading deciduous forests of the eastern United States. It produces many showy flowers that may influence pollinator activity in heavily invaded habitats. We compared pollinator visitation rates, stigma pollen loads, and seed production of two sympatrically flowering, entomophilous native species (*Claytonia virginica* and *Cardamine concatenata*) between habitats invaded by *R. ficaria* and uninvaded habitats. We found significantly higher pollinator activity (visits to plots) in invaded plots. We also found significantly higher per flower visitation rates to *C. virginica* in invaded plots. *Claytonia virginica* stigmas from invaded habitats had more conspecific pollen resulting in more seeds per capsule in invaded areas. There was more conspecific pollen on *C. concatenata* stigmas in

invaded compared to uninvaded habitats, but there were significantly more seeds per silique in uninvaded habitats. Our results indicated that this invasive species increases pollinator activity and conspecific pollen deposition on sympatrically flowering native ephemerals, but may have differential effects on native seed production. Management options should consider the facilitative effects of this species on pollination services, as well as the possible negative competitive effects.

**Keywords** Competition · Invasive species · Magnet effect · Pollination facilitation · *Ficaria verna*

## Introduction

Invasive species are known to alter native habitats, and pose threats to biodiversity (Pimentel et al. 2001). Consequently, determining the types of impacts of exotic species on native ecosystems is a major concern for conservation scientists and land managers. Invasive plant species usually impact native plants negatively through resource occlusion, acting as superior competitors for nutrients, water, space, and sunlight (Levine et al. 2003). Invasive plant species can also alter native plant populations by disrupting local pollination services (Bjerknes et al. 2007; Chittka and Schurkens 2001), for example by outcompeting native species for pollinators or through pollen occlusion (Brown et al.

**Electronic supplementary material** The online version of this article (doi:10.1007/s10530-015-0878-3) contains supplementary material, which is available to authorized users.

J. A. Masters (✉) · S. M. Emery  
Department of Biology, University of Louisville,  
Louisville, KY 40292, USA  
e-mail: jamast04@louisville.edu

2002; Chittka and Schurkens 2001; Morales and Traveset 2008). However, invasive plant impacts on pollinator services can also be a rare example of a positive consequence of invasion for native plant communities. Invasive species can act as “magnet species” (Molina-Montenegro et al. 2008), increasing visitation and seed set in native species. In other cases, invasive plants may increase pollinator activity without affecting native pollination systems; or invasion may have no effects on native pollination systems (Bartomeus et al. 2008, 2010). Currently, it is difficult to generalize or predict the effects of invasive plants on pollinator services, and managers must make decisions based on an incomplete understanding of both positive and negative consequences of plant invasion.

Many alien plants were introduced as ornamentals, and often have a strong scent and showy flowers, making them very attractive to pollinators. Native plants growing near these species may experience reduced pollinator visitation and pollen limitation due to relatively lower floral attractiveness (Brown et al. 2002). Invasive plants that are taxonomically similar to native species can also have a significant impact on pollination services because of similarities in flower morphologies (Memmott and Waser 2002). For example in Japan, pollinator visitation and seed set were reduced in the native dandelion *Taraxacum japonicum* when grown with the invasive congener *Taraxacum officinale*, probably because *T. officinale* produced more nectar (Kandori et al. 2009). Allogamous plants that rely on specific pollinators may be especially sensitive to invasive plant species, if that species is able to monopolize pollinators in the local habitat. However, reproductive success may be reduced even in generalist native plants, if the invasive plant population is dense enough (Dietzsch et al. 2011). For example, *T. officinale* has showy flowers and outcompeted the generalist species *Hypochaeris thrincioides* and *Perezia carthamoides* for pollinators when growing in high abundances in the central Chilean Andes populations (Munoz and Cavieres 2008).

Alternatively, prolifically flowering invasive species may provide facilitative effects for native species pollination (Moeller 2004). The additional floral resources provided by these invasive species can increase pollinator abundance and diversity as well as foraging range and duration (Feldman et al. 2004; Memmott and Waser 2002; Tepedino et al. 2008;

Tscheulin et al. 2009). Some invasive plant species that produce very attractive flowers may also act as “magnet species”, attracting more pollinators and increasing pollination in sympatric co-flowering native plants even for those species with lower floral attractiveness (Molina-Montenegro et al. 2008; Thomson 1978). If the flowers from different species in the community have the same relative attractiveness then adding more flowers of any species is expected to increase pollinator activity (Mitchell et al. 2009) suggesting that invasive species can act as magnet species even without superior floral attractants per individual flower.

Even if pollinator visitation rates increase in the presence of invasive plants, reproductive output in native plants may be reduced by heterospecific pollen deposition (Morales and Traveset 2008). Fertilization and seed production can be disrupted by heterospecific pollen through several mechanisms including stigma clogging, stylar clogging, and pollen allelopathy (Brown and Mitchell 2001; Holland and Chamberlain 2007; Tscheulin et al. 2009). Determining which specific mechanisms causes low seed set due to heterospecific pollen can be difficult, and usually the mechanism depends on the density of the heterospecific pollen (Murphy 2000). However, native stigmas do not have to be completely occluded from conspecific pollen to affect reproduction. For example, seed set in native *Decodon verticillatus* was reduced by 33.3 % when pollen from invasive *Lythrum salicaria* was added to stigma in a 1:1 mixture with conspecific pollen in a greenhouse study (Da Silva and Sargent 2011).

With these considerations, invasive species that present relatively large floral displays may be expected to influence pollinator activity and seed production. *Ranunculus ficaria* is an invasive species in riparian areas of temperate deciduous forests in the northeastern United States. A perennial native to Europe and western Asia, it was first reported in the United States in 1867, and was probably introduced as an ornamental due to its large yellow flowers (Axtell et al. 2010). This species emerges in fall, and forms thick mats of vegetation. It begins flowering in late winter, peaks by mid-spring, and often covers invaded areas with a collectively large floral display.

This study examines *R. ficaria* impacts on pollination services by comparing pollinator visitation rates, heterospecific pollen deposition, and seed production

in two native entomophilous co-flowering species in invaded and uninvaded habitats. This study addressed three main questions: (1) are pollinator visitation rates to native plants reduced in areas heavily invaded with *R. ficaria*? (2) if pollinators are shared, is there potential for *R. ficaria* pollen to clog stigmas in sympatric, co-flowering native species? (3) Is seed production reduced for native plants located in areas heavily invaded by *R. ficaria*?

## Materials and methods

### Study site

We conducted our study along Beargrass Creek (Middle Fork) in Cherokee Park (latitude 38.243301, longitude -85.698220) which is part of the Olmsted Parks in Louisville, Kentucky. The catchment in this area is urbanized and strongly channelized [ $\sim 33$  % impervious surface (Council 2005)], and the study sites are subject to flooding throughout the year. The dominant trees in these woodlands are *Acer saccharum*, *Fraxinus americana*, and *Celtis occidentalis*. The riparian corridor is heavily invaded with *R. ficaria*

(>90 % cover-Fig. 1), and very few native spring ephemerals are present. However, several invasive and weedy species shared the riparian corridor with *R. ficaria*. Violets (*Viola sororia*), dead nettle (*Lamium purpureum*), penny cress (*Thlaspi arvense*), dandelion (*Taraxacum officinale*), chickweed (*Stellaria media*), and invasive garlic mustard (*Alliaria petiolata*) were all in flower at the time of our study. There were also several native ephemerals in flower along the edges of the *R. ficaria* invasion, including spring beauty (*Claytonia virginica*), toothwort (*Cardamine concatenata*), sessile trillium (*Trillium sessile*), trout lily (*Erythronium americanum*), and Dutchman's breeches (*Dicentra cucullaria*). Nearby (<1 km away) uninvaded sites along the same stream were picked with approximately the same topography, canopy cover, and native flower density as the invaded sites. However, the intensity of seasonal flooding was much lower at the uninvaded sites, with some areas not flooding at all. Uninvaded sites were generally more xeric, and supported a slightly higher diversity of plants in flower during our study. The uninvaded areas were dominated by *C. virginica*, *C. concatenata*, and false anemone (*Enemion biternatum*). Sessile trillium, trout lily, and Dutchman's breeches were also in



**Fig. 1** Photo of study site showing riparian corridor with an extremely high cover of *R. ficaria* (visible as small light-colored blooms)

flower in uninvaded sites. The dominant trees at the uninvaded sites were oak (*Quercus* sp.), *A. saccharum*, and *F. americana*. The two most abundant native spring ephemerals that were co-flowering and sympatric with *R. ficaria* were spring beauty (*C. virginica*) and toothwort (*C. concatenata*). Both species require pollinator visitation for seed production under natural conditions (Schemske 1977; Spooner 1984).

#### Pollinator observations

To determine the effect of *R. ficaria* on pollinator activity, we conducted several observational studies over two seasons. In March 2012, we established 25 1 m by 1 m observation plots ranging from 0 to 281 open *R. ficaria* flowers  $\text{m}^{-2}$  to examine how local abundance of *R. ficaria* affected pollinator activity. Locations of the plots were preselected to be at least 2 m apart, and all contained at least 15 open flowers of any species (range 18–306). In 2012, we also followed 25 individual pollinators in the invaded sites.

In March 2013, we established 38 1 m by 1 m observation plots in invaded sites and 15 in uninvaded sites to evaluate effects of invasion at the landscape scale. In the uninvaded sites, densities of our target native species were relatively high, but patchy. To avoid oversampling these patches and to meet our minimum floral density requirements, we only sampled 15 plots in uninvaded sites. In 2013, all open flowers were identified and were counted for each species. The density of open *R. ficaria* flowers in invaded sites had a range of 1–222 per square meter.

In each year, we recorded all floral visitors to each plot over a 15 min observation period. We used 2012 and 2013 data to determine local scale (relative abundance) effects, and the 2013 data to determine landscape (overall pollinator activity) effects. If a pollinator left the observation plot and then returned, it was counted as a new pollinator. All pollinator observations were made between 11 am and 3 pm on mild ( $>16^\circ\text{C}$ , little wind), sunny/partly cloudy days. From the 2013 data, we examined visitation to only one of our native target species (*C. virginica*). While overall density of *C. concatenata* was high in our study area, local densities (patches) were small ( $<15$  open flowers), so no observation plots contained this species. As a result, we made no individual observations on *C. concatenata* flowers. Most data were log

$[\ln(x + 1)]$  or square root transformed to meet normality assumptions.

#### Landscape scale visitation rates

To get an estimate of pollinator activity on a landscape scale, we compared visitation rates (overall pollinator visits to plots over 15 min) between invaded and uninvaded areas using Student's *t* test on the 2013 data. These data required transformation  $[\ln(x + 1)]$  to meet test assumptions. We expected overall higher visitation rates to plots in invaded areas if *R. ficaria* is acting as a magnet species or otherwise increasing pollinator activity.

#### Local scale visitation rate

To examine local scale (plot level) effects of *R. ficaria* density on pollinator activity, we performed a linear regression between the relative abundance of *R. ficaria* and pollinator visitation rates over 15 min for all plots from the 2012 and 2013 observations. From these observations we determined if plots had differences in visitation rates due to the relative amount of *R. ficaria* flowers in the immediate vicinity. If *R. ficaria* is preferred or is a magnet species, the plot visitation rates were expected to rise with relative abundance of *R. ficaria*.

#### Claytonia virginica visitation rate

In 2013, *C. virginica* was the most abundant flower in all uninvaded plots but one, where the most abundant was *E. bitematum*. *Claytonia virginica* flower density in uninvaded plots had a range of 26–40 open flowers per square meter. *Claytonia virginica* flower density in invaded plots had a range of 0–122 open flowers per square meter. From the 2013 data, we determined visits to each *C. virginica* flower per 15 min in the plots that contained *C. virginica* (10 invaded and 14 uninvaded). For this test, data were square root transformed to meet normality assumptions. We also determined if pollinators preferred *R. ficaria* over other flowers by examining invaded plots where the abundance ratios of *R. ficaria* to *C. virginica* flowers were between 1:1 and 2:1 ( $n = 5$  plots). These ratios were chosen to represent an equal balance or a slight



advantage for *R. ficaria* in pollinator competition, and should give a good estimate of how well *C. virginica* can compete with *R. ficaria* for pollinators.

### Fidelity

In 2012, we estimated pollinator fidelity by following 27 individual pollinators in an invaded area across a park road from our established observation plots. The native plant density and species composition was the same as our observation plots, but the riparian corridor is this area was roughly twice as wide as the observation plot site resulting in an overall larger relative abundance of *R. ficaria* at the landscape level. This area also had less canopy cover. Pollinators were picked randomly as observers patrolled areas of sympatry at this study site. We followed each pollinator until the pollinator left the observer's sight (scared away or senescence of foraging in the immediate area). We recorded each flower species visited by each pollinator, and the time spent on each flower. We excluded pollinators that were on flowers <1 s. Because of the difference in sunlight between study areas and difficulties in positively identifying small bees in flight, the results of our fidelity study were not directly comparable to our plot observations. However, this study was intended to provide an estimate of general pollinator behavior in invaded areas.

### Stigma analysis

In March 2013, we collected 15 stigmas each from *C. concatenata* and *C. virginica* in invaded sites and 15 stigmas each from uninvaded sites. We collected stigmas after 3 pm on mild (>16 °C), sunny/partly cloudy days. Stigmas were collected with forceps and dissecting scissors and each was placed in a vial with 70 % ethanol for transport back to the lab. For pollen identification and counting, we treated stigmas with aniline blue to stain pollen grains (Kearns and Inouye 1993). The numbers of pollen grains on each of the native species' stigmas were counted in 3 categories: *R. ficaria* pollen, conspecific pollen, and other heterospecific pollen. Larger depositions of heterospecific pollen were expected to increase the likelihood of stigma clogging (Tscheulin and Petanidou 2013). Student's *t* tests were used to compare pollen loads in invaded and uninvaded sites after data transformation [ $\ln(x + 1)$ ].

### Seed set

To compare the average number of seeds per flower for the two native species in invaded and uninvaded areas, we returned to the field sites 2 weeks after our pollinator observations and stigma collection in 2013 to collect mature fruit. We collected one silique each from 50 randomly chosen *C. concatenata* plants in both invaded and uninvaded sites. Each *C. concatenata* ovary has 10–14 ovules and develops into a single silique (Spooner 1984). We also collected 50 mature capsules each from randomly chosen *C. virginica* plants in both invaded and uninvaded sites. Each *C. virginica* flower contains six ovules and develops into a single capsule (Schemske 1977). We estimated reproductive output by determining the average number of seeds produced per fruit for each species. Student's *t* tests were used to compare average seed per fruit in invaded to uninvaded sites.

## Results

### Pollinator observations

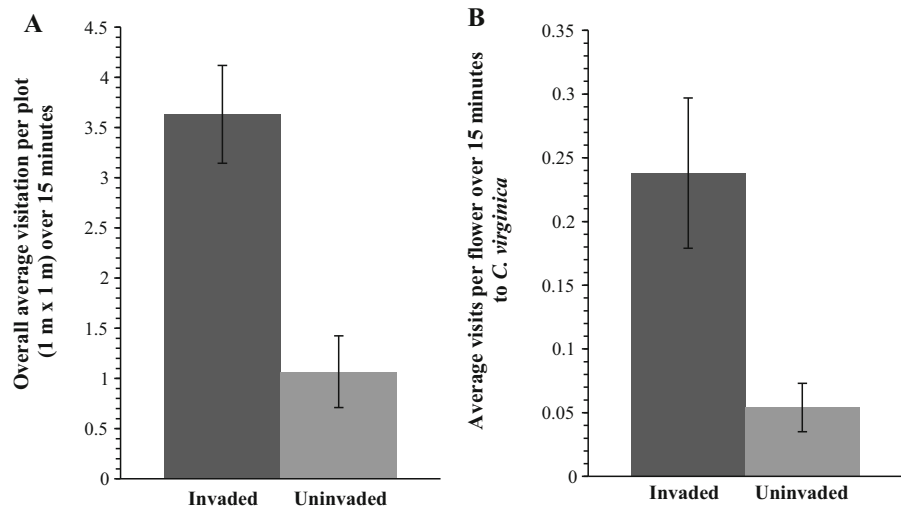
#### Landscape and local scale visitation rates

We found significantly higher (240.4 %) overall visitation rates (pollinator visits to each plot per 15 min) in invaded plots compared to uninvaded plots in 2013 ( $t = 4.267$ ,  $df = 51$ ,  $P < 0.001$ ; Fig. 2a). However, regression analysis showed no effect of the relative abundance of *R. ficaria* flowers on pollinator activity (visitation rates to plots) in 2012 ( $R^2 = 0.020$ ,  $F_{1,23} = 0.469$ ,  $P = 0.500$ ; Online resource 1) or 2013 ( $R^2 = 0.010$ ,  $F_{1,51} = 0.503$ ,  $P = 0.481$ ; Online resource 1). Total flower abundance of all species did not significantly affect pollinator activity in either year at the plot level (2012:  $R^2 = 0.009$ ,  $F_{1,23} = 0.203$ ,  $P = 0.657$ ; 2013:  $R^2 = 0.002$ ,  $F_{1,51} = 0.103$ ,  $P = 0.750$ ; data not shown).

#### Claytonia virginica visitation rates

We found significantly higher (342.3 %) per flower visitation rates to *C. virginica* flowers in invaded plots ( $t = 2.657$ ,  $df = 22$ ,  $P = 0.014$ ; Fig. 2b). Pollinators also preferred *C. virginica* over *R. ficaria* in mixed plots. In plots where the abundance ratio of *R. ficaria*

**Fig. 2** **a** Overall average visitation rates per plot over 15 min in invaded and uninvaded sites and **b** average visitation rates to *Claytonia virginica* per flower over 15 min—2013. Error bars represent  $\pm 1$  SE



flowers to *C. virginica* flowers was between 1:1 to 2:1, 78 % of pollinators visited *C. virginica* ( $n = 33$  pollinators).

### Fidelity

The primary pollinators visiting plants in both invaded and uninvaded areas in both years were syrphid flies and small bees. We observed very little pollinator sharing. In the 2012 fidelity study, only one syrphid fly of the 27 pollinators followed was observed visiting both *C. virginica* and *R. ficaria*. The other 26 pollinators were loyal to single plant species during observations, including 5 pollinators observed on *C. concatenata*, 18 only on *R. ficaria*, and two others observed only on *C. virginica* (Online resource 2).

### Stigma analysis and seed set

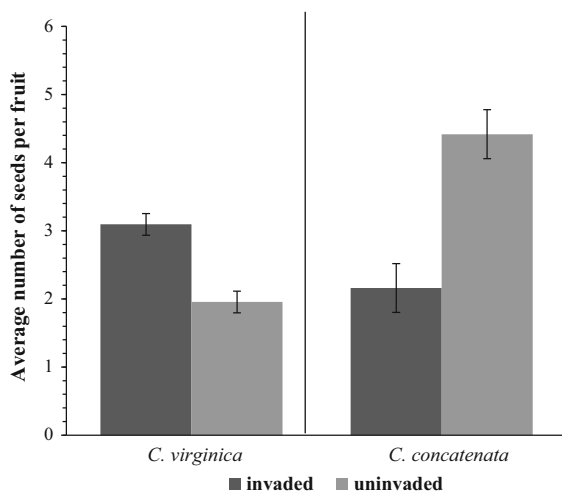
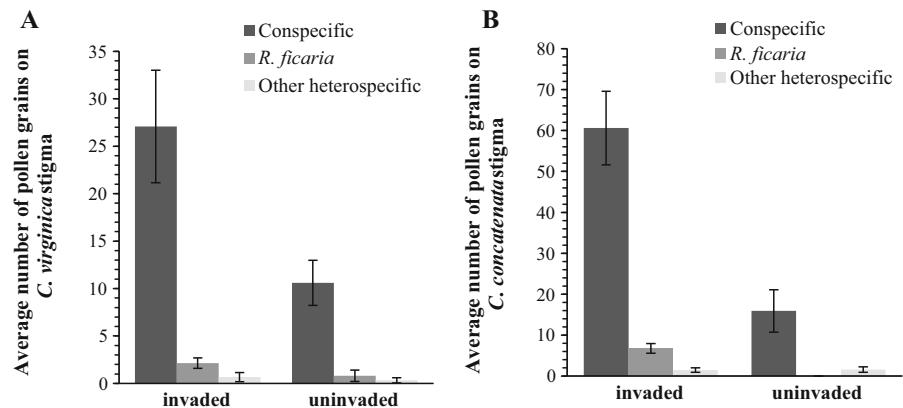
Individual *Claytonia virginica* stigmas from invaded habitats had on average 155.3 % more conspecific pollen ( $t = 2.680$ ,  $df = 28$ ,  $P < 0.012$ ) than in uninvaded areas resulting in 58.3 % more seeds per capsule in invaded areas ( $t = 5.054$ ,  $df = 102$ ,  $P < 0.001$ ) (Figs. 3a, 4). In invaded sites, 51.56 % of *C. virginica* ovaries matured to seed versus 32.5 % in uninvaded sites (Fig. 4). There was an average of 280.3 % more conspecific pollen ( $t = 5.269$ ,  $df = 28$ ,  $P < 0.001$ ) on individual *C. concatenata* stigmas in invaded compared to uninvaded habitats, but there were 104.6 % more seeds per silique ( $t = -4.456$ ,

$df = 100$ ,  $P < 0.001$ ) in uninvaded habitats (Figs. 3b, 4). In invaded sites, 15.42 % of *C. concatenata* ovaries matured to seed versus 31.56 % in uninvaded sites (estimated 14 ovules per fruit) (Fig. 4). There was very little *R. ficaria* pollen on stigmas from both species in invaded areas (mean = 2.13 grains per stigma for *C. virginica*, mean = 6.80 grains per stigma for *C. concatenata*, Fig. 3). There were also small amounts of *R. ficaria* pollen detected on *C. virginica* stigmas in uninvaded areas but it was significantly less than pollen on stigmas in invaded areas ( $t = 2.233$ ,  $df = 28$ ,  $P = 0.034$ ) (Fig. 3a). There was no *R. ficaria* pollen detected on *C. concatenata* stigmas from uninvaded areas (Fig. 3b).

### Discussion

Invasive species that contribute additional floral resources to a community can increase overall pollinator abundance, diversity, and activity resulting in more conspecific pollen deposition and higher reproductive output by native plants (Feldman et al. 2004; Memmott and Waser 2002; Tepedino et al. 2008; Tscheulin et al. 2009). Overall higher pollinator visitation rates in our invaded plots and more conspecific pollen deposition on sympatric native species indicated that *R. ficaria* has a positive effect on pollinator activity in our study system. However, this corresponded to an increase in seed set for only one of the two native species examined.

**Fig. 3** Average number of pollen grains per stigma for **a** *Claytonia virginica* and **b** *Cardamine concatenata* in invaded and uninvaded sites. Error bars represent  $\pm 1$  SE



**Fig. 4** Average number of seeds per fruit for **a** *Claytonia virginica* and **b** *Cardamine concatenata* in invaded and uninvaded sites. Error bars represent  $\pm 1$  SE

The relative density of invasive plants and flowers often determines the invasive species' impacts on pollinator behavior and on native plant reproduction (Dietzsch et al. 2011; Munoz and Cavieres 2008). In our study, overall pollinator visits were higher in invaded areas, but the relative abundance of *R. ficaria* within invaded sites had no effect on local-scale visitation rates, and pollinators showed no preference for *R. ficaria*, suggesting that simple presence of the invasive plant may be a more important influence on pollinator activity than relative abundance in this system. In the fidelity study, more pollinators were observed on *R. ficaria* than native ephemerals (Online resource 2). This was likely due to a higher relative abundance of *R. ficaria* at the fidelity study site and observer bias rather

than a preference for *R. ficaria* in this study. While we did not directly observe pollinator visits to *C. concatenata*, pollen deposition data indicated that visits were higher in invaded areas for this species as well. It appears that *R. ficaria* is a strong magnet species for pollinators in this system on a landscape scale.

The low amounts of *R. ficaria* pollen and the large amounts of conspecific pollen found on both native species suggest that reduced fitness due to heterospecific pollination was low or non-existent. Our fidelity observations also indicated that pollinators foraged on only one plant species at a time, reducing the probability of heterospecific pollen deposition. The small amount of *R. ficaria* pollen found on native stigmas in both invaded and uninvaded plots may be due to some pollinator overlap between invaded and uninvaded sites. Our uninvaded sites were only about 1 km from invaded sites, while some pollinator flight distances can range up to 6 km (Pasquet et al. 2008).

*Claytonia virginica* and *C. concatenata* are both entomophilous, so observing seed set in these species gives a good indication of the fitness impacts of *R. ficaria* due to mechanisms associated with pollinators. *Claytonia virginica* had significantly higher seed set per fruit as expected from higher visitation rates and conspecific pollen deposition in the invaded sites. However, seed set per fruit in *C. concatenata* was lower despite higher conspecific pollen deposition in invaded sites. *C. concatenata* had no heterospecific pollen deposition in uninvaded sites, while *C. virginica* had small amounts of *R. ficaria* pollen in both invaded and uninvaded sites. The simple presence of *R. ficaria* pollen on *C. concatenata* stigmas in invaded sites may have interfered with seed production due to

pollen allelopathy (El-Ayeb et al. 2009; Gaur et al. 2007). However, pollen allelopathy has never been reported in the Ranunculaceae. Most pollen allelopathy has been reported in the families Poaceae, Asteraceae, and Brassicaceae (Matsumoto et al. 2010; Murphy 2001; Murphy et al. 2009a, b). It is still unclear exactly why seed set was reduced in *C. concatenata* but not in *C. virginica* and further work is needed to tease apart possible mechanisms.

Many management protocols call for the removal of invasive species as the first step in restoration, however it is important for managers to consider both positive and negative effects of invasive species on native plant communities before making management decisions. For example, invasive *Oxalis pes-caprae* in the Mediterranean basin has some facilitative effects on native pollination, and removal of this species decreased pollinator efficiency and reproductive output in native plants (Ferrero et al. 2013). Competition for other resources such as light or nutrients may override any benefits of invasives on pollinator services, though. In particular, while this study shows that *R. ficaria* has either positive or neutral effects on pollinator services, some of our previous work (Masters and Emery, in press), has shown that *R. ficaria* can also directly compete with native plants for light and space, reducing native biodiversity. In other cases, reduced biodiversity and low occurrence of native species are due to anthropogenic disturbance, and presence of the invasive species is just a symptom of a degraded ecosystem. Restoration of native plant communities will only occur after the disturbance regime is adjusted (MacDougall and Turkington 2005). For example, the invaded sites in our study are highly disturbed by frequent flooding and urban run-off, and no native ephemerals occur directly in the riparian area with *R. ficaria*. Disturbance from urban flooding may be the main driver of low diversity in our study system, and counter to conventional wisdom, removal of the invasive species may further damage ecosystem services or inhibit restoration, especially for native plants dependent on insect pollinators. Our results indicate that invasive plants can have both competitive and facilitative effects, and so a better understanding of whole community responses to invasion is needed to make sound management decisions.

**Acknowledgments** The authors would like to thank Carl Cloyed, Cherise Montgomery, Tommy Ross, and Ryan King for help in the field and Joseph Clagg for pollen counting.

## References

- Axtell AE, DiTommaso A, Post AR (2010) Lesser celandine (*Ranunculus ficaria*): a threat to woodland habitats in the Northern United States and Southern Canada. *Invasive Plant Sci Manag* 3:190–196. doi:10.1614/ipsm-d-09-00044.1
- Bartomeus I, Vila M, Santamaria L (2008) Contrasting effects of invasive plants in plant-pollinator networks. *Oecologia* 155:761–770. doi:10.1007/s00442-007-0946-1
- Bartomeus I, Vila M, Steffan-Dewenter I (2010) Combined effects of *Impatiens glandulifera* invasion and landscape structure on native plant pollination. *J Ecol* 98:440–450. doi:10.1111/j.1365-2745.2009.01629.x
- Bjerknes AL, Totland O, Hegland SJ, Nielsen A (2007) Do alien plant invasions really affect pollination success in native plant species? *Biol Conserv* 138:1–12. doi:10.1016/j.biocon.2007.04.015
- Brown BJ, Mitchell RJ (2001) Competition for pollination: effects of pollen of an invasive plant on seed set of a native congener. *Oecologia* 129:43–49
- Brown BJ, Mitchell RJ, Graham SA (2002) Competition for pollination between an invasive species (purple loosestrife) and a native congener. *Ecology* 83:2328–2336
- Chittka L, Schurkens S (2001) Successful invasion of a floral market—an exotic Asian plant has moved in on Europe's river-banks by bribing pollinators. *Nature* 411:653
- Council BCW (2005) Beargrass creek watershed: state of the streams. Louisville and Jefferson County Metropolitan Sewer District
- Da Silva EM, Sargent RD (2011) The effect of invasive *Lythrum salicaria* pollen deposition on seed set in the native species *Decodon verticillatus*. *Botany Botanique* 89:141–146. doi:10.1139/b11-001
- Dietzsch AC, Stanley DA, Stout JC (2011) Relative abundance of an invasive alien plant affects native pollination processes. *Oecologia* 167:469–479. doi:10.1007/s00442-011-1987-z
- El-Ayeb A, Omezzine F, Haouala R (2009) Status of pollen allelopathy research. *Allelopathy J* 23:71–83
- Feldman TS, Morris WF, Wilson WG (2004) When can two plant species facilitate each other's pollination? *Oikos* 105:197–207
- Ferrero V, Castro S, Costa J, Acuna P, Navarro L, Loureiro J (2013) Effect of invader removal: pollinators stay but some native plants miss their new friend. *Biol Invasions* 15:2347–2358. doi:10.1007/s10530-013-0457-4
- Gaur S, Rana A, Chauhan SVS (2007) Pollen allelopathy: past achievements and future approach. *Allelopathy J* 20: 115–126
- Holland JN, Chamberlain SA (2007) Ecological and evolutionary mechanisms for low seed: ovule ratios: need for a pluralistic approach? *Ecology* 88:706–715
- Kandori I, Hirao T, Matsunaga S, Kurosaki T (2009) An invasive dandelion unilaterally reduces the reproduction of a native congener through competition for pollination. *Oecologia (Berlin)* 159:559–569. doi:10.1007/s00442-008-1250-4
- Kearns CA, Inouye DW (eds) (1993) Techniques for pollination biologists. University Press of Colorado, Niwoi



- Levine JM, Vila M, D'Antonio CM, Dukes JS, Grigulis K, Lavelle S (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proc R Soc B Biol Sci* 270:775–781. doi:[10.1098/rspb.2003.2327](https://doi.org/10.1098/rspb.2003.2327)
- MacDougall AS, Turkington R (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86:42–55. doi:[10.1890/04-0669](https://doi.org/10.1890/04-0669)
- Matsumoto T, Takakura K-I, Nishida T (2010) Alien pollen grains interfere with the reproductive success of native congener. *Biol Invasions* 12:1617–1626. doi:[10.1007/s10530-009-9574-5](https://doi.org/10.1007/s10530-009-9574-5)
- Memmott J, Waser NM (2002) Integration of alien plants into a native flower-pollinator visitation web. *Proc R Soc Lond Ser B Biol Sci* 269:2395–2399. doi:[10.1098/rspb.2002.2174](https://doi.org/10.1098/rspb.2002.2174)
- Mitchell RJ, Flanagan RJ, Brown BJ, Waser NM, Karron JD (2009) New frontiers in competition for pollination. *Ann Bot* 103:1403–1413. doi:[10.1093/aob/mcp062](https://doi.org/10.1093/aob/mcp062)
- Moeller DA (2004) Facilitative interactions among plants via shared pollinators. *Ecology* 85:3289–3301. doi:[10.1890/03-0810](https://doi.org/10.1890/03-0810)
- Molina-Montenegro MA, Badano EI, Cavieres LA (2008) Positive interactions among plant species for pollinator service: assessing the ‘magnet species’ concept with invasive species. *Oikos* 117:1833–1839. doi:[10.1111/j.0030-1299.2008.16896.x](https://doi.org/10.1111/j.0030-1299.2008.16896.x)
- Morales CL, Traveset A (2008) Interspecific pollen transfer: magnitude, prevalence and consequences for plant fitness. *Crit Rev Plant Sci* 27:221–238. doi:[10.1080/07352680802205631](https://doi.org/10.1080/07352680802205631)
- Munoz AA, Cavieres LA (2008) The presence of a showy invasive plant disrupts pollinator service and reproductive output in native alpine species only at high densities. *J Ecol* 96:459–467. doi:[10.1111/j.1365-2745.2008.01361.x](https://doi.org/10.1111/j.1365-2745.2008.01361.x)
- Murphy SD (2000) Field testing for pollen allelopathy—a review. *J Chem Ecol* 26:2155–2172. doi:[10.1023/a:1005572516948](https://doi.org/10.1023/a:1005572516948)
- Murphy SD (2001) The role of pollen allelopathy in weed ecology. *Weed Technol* 15:867–872. doi:[10.1614/0890-037x\(2001\)015\[0867:tropai\]2.0.co;2](https://doi.org/10.1614/0890-037x(2001)015[0867:tropai]2.0.co;2)
- Murphy SD, Flegel S, Smedes J, Finney N, Zhang B, Walton K, Henstra S (2009a) Identification of pollen allelochemical in *Hieracium x dutillyanum* Lepage and its ecological impacts on *Conyza canadensis* (L.) Cron. and *Sonchus arvensis* L. dominated community in southern Ontario. *Can Allelopathy J* 23:85–94
- Murphy SD, Sherr I, Bullock C (2009b) Allelopathic pollen in Canadian invasive species: *Alliaria petiolata* and *Hesperis matronalis*. *Allelopathy J* 23:63–70
- Pasquet RS et al (2008) Long-distance pollen flow assessment through evaluation of pollinator foraging range suggests transgene escape distances. *Proc Natl Acad Sci USA* 105:13456–13461. doi:[10.1073/pnas.0806040105](https://doi.org/10.1073/pnas.0806040105)
- Pimentel D et al (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. *Agric Ecosyst Environ* 84:1–20. doi:[10.1016/s0167-8809\(00\)00178-x](https://doi.org/10.1016/s0167-8809(00)00178-x)
- Schemske DW (1977) Flowering phenology and seed set in *Claytonia virginica* (Portulacaceae). *Bull Torrey Bot Club* 104:254–263. doi:[10.2307/2484307](https://doi.org/10.2307/2484307)
- Spooner DM (1984) Reproductive features of *Dentaria laciniata* and *D. diphylla* (Cruciferae) and the implications in the taxonomy of the Eastern North-American *Dentaria* complex. *Am J Bot* 71:999–1005. doi:[10.2307/2443670](https://doi.org/10.2307/2443670)
- Tepedino V, Bradley B, Griswold T (2008) Might flowers of invasive plants increase native bee carrying capacity? Intimations from Capitol Reef National Park, Utah. *Nat Areas J* 28:44–50. doi:[10.3375/0885-8608\(2008\)28\[44:mfoipj\]2.0.co;2](https://doi.org/10.3375/0885-8608(2008)28[44:mfoipj]2.0.co;2)
- Thomson JD (1978) Effects of stand composition on insect visitation in 2-species mixtures of *Hieracium*. *Am Midl Nat* 100:431–440. doi:[10.2307/2424843](https://doi.org/10.2307/2424843)
- Tscheulin T, Petanidou T (2013) The presence of the invasive plant *Solanum elaeagnifolium* deters honeybees and increases pollen limitation in the native co-flowering species *Glaucium flavum*. *Biol Invasions* 15:385–393. doi:[10.1007/s10530-012-0293-y](https://doi.org/10.1007/s10530-012-0293-y)
- Tscheulin T, Petanidou T, Potts SG, Settele J (2009) The impact of *Solanum elaeagnifolium*, an invasive plant in the Mediterranean, on the flower visitation and seed set of the native co-flowering species *Glaucium flavum*. *Plant Ecol* 205:77–85. doi:[10.1007/s11258-009-9599-y](https://doi.org/10.1007/s11258-009-9599-y)