Invasion of a dominant floral resource: effects on the floral community and pollination of native plants

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Abstract. Through competition for pollinators, invasive plants may suppress native flora. Community-level studies provide an integrative assessment of invasion impacts and insights into factors that influence the vulnerability of different native species. We investigated effects of the nonnative herb *Lythrum salicaria* on pollination of native species in 14 fens of the eastern United States. We compared visitors per flower for 122 native plant species in invaded and uninvaded fens and incorporated a landscape-scale experiment, removing *L. salicaria* flowers from three of the invaded fens. Total flower densities were more than three times higher in invaded than uninvaded or removal sites when *L. salicaria* was blooming. Despite an increase in number of visitors with number of flowers per area, visitors per native flower declined with increasing numbers of flowers. Therefore, *L. salicaria* invasion depressed visitation to native flowers. In removal sites, visitation to native flowers was similar to uninvaded sites, confirming the observational results and also suggesting that invasion had not generated a persistent build-up of visitor populations. To study species-level impacts, we examined effects of invasion on visitors per flower for the 36 plant species flowering in both invaded and uninvaded fens. On average, the effect of invasion represented about a 20% reduction in visits per flower. We measured the influence of plant traits on vulnerability to *L. salicaria* invasion using meta-analysis. Bilaterally symmetrical flowers experienced stronger impacts on visitation, and similarity in flower color to *L. salicaria* weakly intensified competition with the invader for visitors. Finally, we assessed the reproductive consequences of competition with the invader in a dominant flowering shrub, *Dasiphora fruticosa*. Despite the negative effect of invasion on pollinator visitation in this species, pollen limitation of seed production was not stronger in invaded than in uninvaded sites, suggesting little impact of competition for pollinators on its population demography. Negative effects on pollination of native plants by this copiously flowering invader appeared to be mediated by increases in total flower density that were not matched by increases in pollinator density. The strength of impact was modulated across native species by their floral traits and reproductive ecology.

Key words: alien plants; competition for pollinators; floral traits; flower density; indirect interactions; Lythrum salicaria; morphological similarity; nonnative plant; pollen limitation; pollinator visitation; purple loosestrife; trait-based analysis.

Introduction

Invasive, nonnative plants may compete for space and nutrients or may alter ecosystem structure or processes to the detriment of native plants (Levine et al. 2003, Ehrenfeld 2010, Skurski et al. 2014). Invasive plants can also compete with native plants for mobile resources, such as shared pollinators (Traveset and Richardson 2006, Bjerknes et al. 2007). Impacts of invasive plants on pollinator abundance, behavior, community structure, and composition all influence plant–pollinator interactions in invaded systems (Ghazoul 2004, Bjerknes et al. 2007, Goodell 2008, Moron et al. 2009, Palladini and Maron 2014), and invasion biology as a field has increased its focus on pollination more than any other ecological impact over the past decade (Skurski et al. 2014).

Understanding the effects of invasive plants on native plant–pollinator interactions is key to assessing invasion impacts on native plant reproduction and can illuminate how resilient the plant–pollinator interactions are to disturbances that may increase, rather than decrease floral abundance (e.g., Grabas and Laverty 1999, Chittka and Schurkens 2001, Ghazoul 2004, Moragues and Traveset 2005, Bjerknes et al. 2007, Bartomeus et al. 2008*b,* 2010, Chung et al. 2015). Two major goals of research on pollinator-mediated effects of invasion are (1) to determine whether, how often, and to what degree an invader has negative effects on native plant pollination overall and (2) to predict which plants are most at risk from competition from a particular invader. Illuminating the mechanisms of pollinator-mediated effects of invaders can provide predictive power to address both of these goals.

Plant invaders are often highly generalized in their interactions with pollinators (Richardson et al. 2000) and well-integrated into plant pollinator networks (Memmott

and Waser 2002, Bartomeus et al. 2008b, Vilà et al. 2009). Where abundant, invasive plants can dominate plant–pollinator interactions within invaded communities, sometimes altering them in ways that could change plant reproduction, relative abundance, or even the evolutionary trajectory of native plant–pollinator interactions (Ghazoul 2002, Vilà et al. 2009, Albrecht et al. 2014). While some invasive plants appear to have little influence on the pollination of native plants (Bartomeus et al. 2008b, 2010, Kaiser-Bunbury et al. 2011, Chung et al. 2015), a large number of studies have demonstrated negative impacts on pollinator visitation and reproduction of individual native plants (reviewed in Bjerknes et al. 2007, Goodell 2008, Morales and Traveset 2008, Skurski et al. 2014).

An invasive plant can negatively affect the pollination of native plants through a number of different mechanisms. First, the invader could depress the abundance of native flowers. Whether or not those native species co-flower with the invader, lower abundance could reduce the attractiveness of the floral display to pollinators, or reduce the population size or foraging efficiency of native pollinators that rely specifically on native plants (Rathcke 1983, Cox and Elmqvist 2000). Second, the invader could increase total flower number in the community. Competition for pollinators with native plants can occur if the invader increases floral abundance and the pollinator pool remains constant, reducing visitation rates on a per-flower basis (Essenberg 2012). Third, at the scale of individual foragers, pollinators may prefer the more abundant or rewarding invasive species, making it a disproportionately strong competitor for pollination (Traveset and Richardson 2006). However, if visitors continue to forage on native flowers, as well as the invasive flowers, they may deposit invasive plant pollen on native stigmas and disrupt pollen transfer dynamics, which may reduce seed production (Grabas and Laverty 1999, Brown et al. 2002, Da Silva and Sargent 2011; although see Bartomeus et al. 2008a). Finally, if native plant species vary in their susceptibility to plant–plant competition with the invader, the composition of native flowers may change. Average visitation to native plants will decline if less attractive species tend to persist in the presence of the invader.

On the other hand, invasive plants may facilitate the pollination of native species (Bjerknes et al. 2007, Bartomeus et al. 2008b, Muñoz and Cavieres 2008, McKinney and Goodell 2011, Ferrero et al. 2013). Highly attractive invasive plants can lure flower visitors to a patch and promote pollinator spillover to native flowers, improving visitation and reproduction of native species blooming in proximity to these magnet species (Laverty 1992, Lopezaraiza-Mikel et al. 2007, Molina-Montenegro et al. 2008, Bartomeus et al. 2010). In addition, greater floral resources could increase pollinator numbers at the site or landscape scale (Bjerknes et al. 2007, Goodell 2008, Tepedino et al. 2008), either by attracting visitors capable of long-distance flight or through the demographic response of pollinator populations limited by floral resources. Ultimately, the interplay between the invader's effect on pollinator demography and its effect on local-scale foraging choices will determine the overall visitation rates to native plants in invaded areas (Jakobsson et al. 2009). To distinguish increased pollinator numbers caused by a local demographic response from redistribution of pollinators among patches requires very large manipulations at the whole-site scale, a scale difficult to execute in pollination studies with invaders.

Most studies of the effects of invaders on pollination and reproduction of native plants consider particular pairs of native and invasive species (Skurski et al. 2014). Insofar as these studies set out to test for the impact of invasion on pollination, we expect that native–invasive pairs reflect a non-random choice of response species, those showing for example broad phenological overlap or high floral similarity with the invader (e.g., Brown et al. 2002). Thus, meta-analytical syntheses of these studies (e.g., Morales and Traveset 2009) might be best considered assessments of the *average maximum* effects of invaders, because they are unlikely to include plants that appear to be at low risk for competition or facilitation of pollinators (Moragues and Traveset 2005, Vilà et al. 2009, Gibson et al. 2013). In contrast, community-level studies may provide an improved assessment of the scale of impacts overall (Lopezaraiza-Mikel et al. 2007, Bartomeus et al. 2008b, 2010, Vilà et al. 2009). Community-wide studies of impact also provide an opportunity to study the factors that influence variation across different native species while also controlling for external variables such as habitat type, which vary among studies in meta-analytical approaches.

Studies to date incorporating multiple response species show substantial variation in the impact of invasion among species (Moragues and Traveset 2005, Vilà et al. 2009, Gibson et al. 2013). The ability to forecast which native plants will experience competition or facilitation for pollinators would help predict the impact of invasive species and aid management for species of conservation concern. Phenotypically similar species experience greater interspecific competition (May and MacArthur 1972, May 1974), including for pollinators (e.g., Waser 1983). Native plants with traits that predispose them to share pollinators with invasive species may suffer greater impacts of invasion (Bjerknes et al. 2007, Morales and Traveset 2009, Gibson et al. 2012, Carvalheiro et al. 2014). Similarity of floral traits, such as flower color, flower morphology, or inflorescence architecture, may reduce discrimination by foragers and increase the intensity of competition between plant species (Waser 1986, Chittka et al. 1999, Bjerknes et al. 2007). Less abundant species are also expected to be more vulnerable to competition for pollinators (Rathcke 1983), and small-statured species simply might be obscured by the large plants (Seifan et al. 2014). We used meta-analysis of our community-wide data set to explore whether such plant traits contribute to variation in vulnerability among species.

Changes in pollinator visitation will influence plant reproduction and demography if native seed production is limited by pollen receipt or quality (Ashman et al. 2004). The estimation of pollen limitation, then, provides a context for interpreting invasion impacts on pollinator communities and visitation rates. A recent review of studies published between 2001 and 2013 found that nearly all invasion studies that detected reduced pollinator visitation in native plants also found reduced seed set (Skurski et al. 2014). The implication is that pollen limitation of native species is stronger in invaded populations. Several studies of pollen limitation in the presence and absence of an invader support this notion (Muñoz and Cavieres 2008, McKinney and Goodell 2010, Tscheulin and Petanidou 2013).

In this study, we integrate three approaches to assess the impact of an invasive plant on plant–pollinator interactions: a community-wide comparison of visitation to native flowers including an experimental invader removal, a meta-analytic approach investigating variation in impact among individual species, and an evaluation of the reproductive consequences in one representative species. We assess the impact of the invasive herb *Lythrum salicaria* in calcareous fens, a plant community of conservation interest (Kiviat et al. 2010). We investigate the mechanisms by which *L. salicaria* affects pollinator visitation to native flowers of all flowering plant species. Specifically, we ask (1) Do native plants in invaded sites have higher or lower visitation per flower than those in uninvaded sites? (2) By what mechanisms might the invader be influencing visitation to native plants? Specifically, is the impact of invasion associated with changes in flower density, increases in numbers of pollinators either proportional or disproportional to the number of flowers, or changes in plant composition? (3) Do whole-site removals of invasive flowers increase or decrease visitation to native flowers? (4) Which native plant traits are associated with strong negative impacts of invasion on pollination? And finally (5) Does impact on visitation translate into greater pollen limitation across populations of a dominant, widespread native plant? Our three-tiered approach seeks to compare multiple measures of impact, illuminate mechanisms, and provide a context for evaluating and comparing past studies.

Methods

Lythrum salicaria was introduced into North America from Eurasia in the 1800s and has proliferated in wetlands, lake margins, and ditches throughout northeastern North America. Its tendency to form dense stands suggests negative impacts on native flora and fauna (Thompson et al. 1987, Weihe and Neeley 1997). *Lythrum salicaria*'s showy, resource-rich flowers attract a variety of bee and butterfly pollinators (Grabas and Laverty 1999). By transforming the floral resource availability within a community from sparse and variable to stable and prolific, the copious flowers of *L. salicaria* could positively

affect pollinator populations (Goodell 2008). On the other hand, *L. salicaria's* tall stature and dense vegetative growth could shield shorter native plants from pollinators or create shade that discourages pollinator foraging, as observed in other invasive plants (McKinney and Goodell 2010, Seifan et al. 2014). *Lythrum salicaria* appears to change pollinator behavior, reducing fidelity of visitors to native flowers in mixed experimental arrays compared to monospecific arrays (Brown et al. 2002, Flanagan et al. 2009), although this inconstancy may be transient if it primarily reflects the novelty of the interaction (King and Sargent 2012). Inconstancy of visitors in the presence of *L. salicaria* can increase heterospecific pollen transfer to native stigmas (Brown and Mitchell 2001, Brown et al. 2002) and cause pollen losses during intervening visits to the invader (Flanagan et al. 2009), both reducing seed production. The conclusions from these array studies are intriguing and somewhat contradictory. They suggest that *L. salicaria* may operate as a "magnet species," and the net impact of this invader through pollinator behavior could be positive or negative, depending on context. The nature of *L. salicaria* impacts for any particular habitat, therefore, is a question best addressed at a large scale and in natural populations.

Calcareous fens are small, spatially discrete ecosystems formed where ground water seeps up through mineral-rich soils largely composed of limestone (Motzkin 1994). Their unique abiotic conditions, including seasonally waterlogged, calcium-rich soils with high pH, harbor an unusual suite of calciphilic plants, including some rare plant and animal species (Tiner 1998, Kiviat et al. 2010). We selected 14 fens in northwestern New Jersey, USA based on the presence of native fen plant species that could be compared across sites. Fens were separated by at least 5 km (Fig. 1) and varied in size from 0.5 to 2.5 ha. We used the entire fen for nine small fens, and a representative subset of the fen (~2.0 ha) for five larger fens. Fens were dominated by sedges (*Carex* spp.), widely spaced shrubs, and herbaceous plants, and were nested within a broader landscape composed of forests, small farms, and low-density residential properties. Seven of the fens were invaded by nonnative *L. salicaria*. This study was designed to compare floral resources between invaded and uninvaded sites, not to quantify the impact of invasion on native plant communities at the landscape scale. Because *L. salicaria* flowering was suppressed by a biological control agent in one fen, we omitted this site from all comparisons except pre-bloom periods and peak bloom 2002, when *L. salicaria* flowered again.

In year two of the study, we removed *L. salicaria* flowers from three of the invaded sites, selected at random from the six sites where it flowered consistently. In June, before flowering began, we selectively trimmed the aboveground stalks of the *L. salicaria* plants with hedge shears to approximately 10 cm; in very dense patches, we used a gas-powered trimmer fitted with a brush blade. Other plant species in the removal sites were left intact. Each week we returned to the removal sites to trim new shoots before
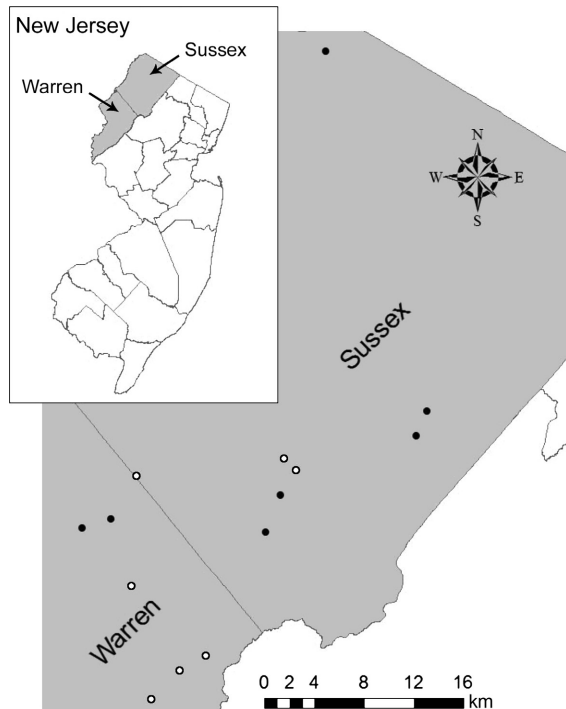
Fig. 1.   Field site locations with invaded (black circles) and uninvaded (white circles). Inset shows New Jersey state map with county boundaries (NJOIT-OGIS 2010).

they flowered. Removals covered the entire site, and in one site in which the sample area included a subset of the fen, a buffer area that extended 50 m beyond the sample area (mean removal area = 6,783 m^2, SD = 2,795 m^2).

Flowers and flower visitors were quantified in each fen three times during the growing season for two years. The three sample periods coincided with the period before the *L. salicaria* bloom (late May/early June), early bloom period (July) and peak bloom (August). Each site was visited once during each bloom period. Random sample points were selected from a permanent 5-m grid that we laid out over the entire site. Sampling of flowers and visitors was done concurrently to minimize damage to the fen vegetation by trampling. At each point, an observer noted all flowering species within a 2 m radius plot and recorded all flower visitors during a 4-min observation period, noting flower species and the insect type to the lowest taxonomic level possible (genus for bees, family, or order for other insects). Representative samples were collected, identified in the lab, and saved as voucher specimens. Observations, rather than collections, were made because of the difficulty obtaining consistent netting yields from the heterogeneous vegetation. All observations were conducted in fair weather with temperatures at least 18°C and little or no wind. Following the observation, we counted or estimated the number of flowers of each species in the plot. Flower numbers were expressed in "floral units," defined as a unit between which a bee would fly rather than crawl (Dicks et al. 2002). The

number of plots sampled varied among sites and periods (40.0 ± 11.06 [mean ± SD]), with fewer plots sampled in smaller sites to avoid resampling the same location twice. New random points were selected for each period.

Community-level analyses

To assess the influence of invasion on characteristics of the floral resources across the season, we used a mixed effects model with the mean total flower density, native flower density, and native flower richness as dependent variables. Parameters for this and subsequent mixed models were estimated using restricted maximum likelihood. The invasion status, sample period, and the interaction between them were fixed effects; year and site nested within invasion status were random effects in the models. For analyses of total flower density, removal sites were omitted. For analysis of native flower density and richness, removal sites were classified as "invaded." Because flower sampling intensity varied with site size, we rarefied the flower richness data to the lowest number of plots sampled per site ($n = 20$). We used a resampling procedure to generate 1,000 estimates of flower richness and calculated the mean richness for each site–sample–year combination. We expected that *L. salicaria* invasion would increase flower density during its bloom period in invaded relative to uninvaded sites because of its characteristically large floral displays per plant. During the pre-bloom period, invaded sites would have similar or lower flower density than uninvaded sites depending on whether *L. salicaria* replaced native plants that bloom early in the season. Thus total flower density should show a significant invasion status by sample period interaction term. Where interaction terms were significant, the effect of invasion was explored for each sample period separately. The total and native flower densities were natural log transformed and richness was square root transformed to meet the assumptions of the analyses. These and all other general linear models were conducted in JMP Pro 11.0.0 (SAS Institute 2013) and SAS 9.4 (SAS Institute 2002–2012).

To test whether flower visitor abundance at the site scale was positively associated with total flower abundance, we used general linear models with the total visitors per area sampled as the dependent variable. We analyzed the 2001 visitor data with a mixed model with site as a random effect and total flowers per area sampled, invasion status, sample period, and all interactions as fixed effects. We analyzed 2002 visitor data by sample period because we included the removal treatment during the early and peak bloom periods. We used general linear least squares models with total flowers per area sampled, invasion status, and their interaction as fixed effects.

To examine whether native plants suffered competition for flower visitors in invaded sites and whether that competition was alleviated by *L. salicaria* removals, we calculated visitors per flower as the number of visitors observed on a plant species in a plot divided by the total number of flowers of that species in a plot. Then measures

were combined over plots for each species to obtain average visitors per flower for each site and sample. Species means were averaged to obtain a measure of visitors per native flower for each site. Visitors per native flower (log-transformed) in 2001 were analyzed with general linear mixed model analysis of variance with the invasion status, sample period, the density of native flowers and their interactions as fixed independent factors and site a random factor. The 2002 visitation data were analyzed by sample period to accommodate the removal treatment using general linear least squares models with invasion status (invaded, uninvaded and removal), native flower density, and their interaction as fixed independent factors.

Flowering community composition

A reduction in number of visitors to flowers in invaded sites could reflect a change in plant composition toward less attractive native species. We addressed this in two ways, measuring the effect of invasion at the species level (see *Species-level analysis*) and comparing the composition of flowers in invaded and uninvaded sites using Permutational Multivariate Analysis of Variance (per-MANOVA). This analysis used flower density as the variate and a Bray-Curtis distance matrix. We used the adonis function in the R vegan library, with 999 permutations (R Core Team 2015). We compared invaded to uninvaded communities for the entire 2001 data set, then again excluding *L. salicaria*, in each of the three sample periods (pre-bloom, early bloom, and peak bloom).

Species-level analyses

To quantify the effect of *L. salicaria* invasion at the species level, we compared visitation between invaded and uninvaded sites for each plant species that flowered in both types of sites ($n = 36$). We used the effect size measure log response ratio ($\ln R$), the natural log of the ratio of mean responses for experimental (invaded) divided by control (uninvaded), where $\ln R < 0$ indicates a negative effect of invasion on visitors per flower, and $\ln R > 0$ indicates a positive effect of invasion on visitation. The parameter $\ln R$ is commonly used in meta-analysis of ecological data for positive measures that have a natural zero point; it is appropriate here because visitation rates can differ by orders of magnitude among species, making difference-based metrics difficult to compare. We also used effect sizes to explore the influence of floral trait similarity in determining the effect of invasion on visitation.

We calculated effect size and associated variance using steps detailed in Appendix S1. Effect sizes were weighted by the inverse of the variance. Species with the largest weighted effect sizes had the largest proportional difference in visitors per flower between invaded and uninvaded and the smallest variance. We fitted weighted effect sizes to a normal distribution and tested the goodness of fit with a Shapiro-Wilks test in JMP v. 11 (SAS Institute 2013). We calculated the cumulative effect size of invasion across all species with a random effects model, which allows for variation in effect size among studies (here, species) using MetaWin software (Rosenberg et al. 2007, Mengersen et al. 2013). Confidence intervals were calculated using a bootstrap randomization procedure (999 iterations) and were bias corrected. Significant effect sizes had 95% CI that did not overlap zero.

To test whether similarity of floral traits, plant density, or plant height were associated with impacts of *L. salicaria* invasion on visitation, we collected information from field observations and the literature on plant traits likely to influence pollinator visitation: flower color, flower symmetry, and inflorescence architecture. Floral traits were classified by their similarity to *L. salicaria* flowers (Morales and Traveset 2009). Pink, purple, and red flowers were categorized as "similar," while white and yellow flowers were "dissimilar." Radial symmetry was classified as similar to *L. salicaria* and bilateral as dissimilar. For inflorescence architecture, plants with spikes were classified as similar to *L. salicaria*, other architectures as dissimilar. We expected that less common species would be more vulnerable to competition for pollinators with the invader, and that short plants may be less apparent to pollinators in the presence of *L. salicaria*, which commonly grows to 1.5 m in height. We calculated plant stature for each species as maximum height of flowers, measured in the field and averaged across plots and sites. For information on traits, we supplemented field observations with web resources, including the USDA PLANTS database , the Connecticut Botanical Society, Missouri Botanical Garden Plant Finder, the New England Wildflower Society, Robert W. Freckmann Herbarium Plants of Wisconsin (all *available online*).[4, 5, 6, 7, 8]

We performed heterogeneity tests to determine whether effect sizes differed significantly between similar and dissimilar floral trait categories. We examined the probability value P_{rand} for the $Q_{between}$ statistic, which indicates the amount of variation in effect sizes attributable to differences among categories. Resampling tests used 9999 iterations and randomized plants to categories. We designated significant results at $\alpha < 0.10$, considering small sample sizes and the conservative weighting scheme. We generated bootstrapped, bias-corrected 95% CI for cumulative mean effect sizes for each category. We performed continuous analyses with plant stature and plant density as predictors of variation in effect size. We report the Q statistic and P values for the regression model, the residual, and the total (sum of model and residual). The percent variance explained by the model is the ratio of the (Q_{model}/Q_{total}) × 100 (Rosenberg 2013).

[4] http://plants.usda.gov

[5] http://www.ct-botanical-society.org

[6] http://www.missouribotanicalgarden.org

[7] http://gobotany.newenglandwild.org

[8] http://wisplants.uwsp.edu

Impacts on reproductive ecology of a dominant native species

To link the impact of invasion on pollinator visitation to plant reproduction, we focused on a dominant, widespread native species. We compared visitation and pollen limitation of reproductive output of *Dasiphora fruticosa* between invaded and uninvaded fens because it was the only species that occurred in all sites and samples. *Dasiphora fruticosa* produces abundant, perfect flowers that offer nectar at the base of a shallow corolla. Upon pollination, the flowers mature into multiple single-seeded achenes. This species was visited by all major groups of flower visitors and ranked close to the top in visitor richness. We investigated the degree to which *D. fruticosa* depends on pollinators for seed production by contrasting the number of seeds per flower between bagged flowers and unmanipulated (open pollinated) flowers. We also compared the success of self-pollinated and outcross-pollinated flowers on the same plants (*n* = 15 plants in each of four sites; see Appendix S2 for details).

We measured pollen limitation of reproduction in four sites in 2001 and eight sites in 2002 using 15 pairs of plants per site. For each pair of plants, we randomly assigned one as experimental and the other as an unmanipulated control. On each experimental plant, we used two pairs of buds (one pair opening in July and one pair in August). Supplemental and open pollination treatments were randomly assigned to a bud within each pair. Treatment flowers received pollen from two to three plants within 10 m of the focal plant every 2 d until senescence (usually twice per flower). We similarly marked two pairs of buds on the 15 control plants and allowed them to be open pollinated. We collected the achenes of all marked flowers on both treatment and control plants when the calyxes dried and counted the number of seeds produced per flower.

To determine whether invasion by *L. salicaria* increased pollen limitation in *D. fruticosa,* we compared the difference in seed production between supplemental and open pollinated treatments between invaded and uninvaded sites (removal sites omitted) using general linear mixed models with the MIXED procedure in SAS v. 9.4 (SAS 2002–2012). Invasion status was a fixed effect, and year, site nested within invasion status. To test for the effect of *L. salicaria* removal on pollen limitation, we repeated the above analysis for just the 2002 data to compare pollen limitation between invaded, uninvaded, and removal sites.

Results

Impact on flower abundance and visitation at the community level

Lythrum salicaria was the dominant invasive flowering plant and comprised approximately 53% of flowers surveyed in invaded sites during the early and peak bloom sample periods. Invasion by *L. salicaria* increased total flower density during the early and peak bloom periods by factors of 3.6 and 3.0, respectively, and had a marginally significant negative effect on the total flower density during the pre-bloom period (Fig. 2; Appendix S3). Of the 152 species surveyed (Appendix S4), 30 were nonnative. Nonnatives other than *L. salicaria*, were rarely abundant, comprising only about 3% of the flowers in fens (0.6% in invaded fens, 9% in uninvaded fens).

Invasion by *L. salicaria* had measurable effects on the density and composition of native flowers, but different effects were apparent during different periods of the season. Native flower density was significantly lower in invaded than uninvaded sites during the pre-bloom period, but not significantly different during the early and late bloom periods (Fig. 2; Appendix S3). Native flower richness ranged from 1 to 35 species per site for a given sample period (1–21.7 for rarefied richness data), and increased over the season. Flower species richness did not differ significantly between invaded and uninvaded fens during the *L. salicaria* bloom periods, but was significantly lower in invaded sites in the pre-bloom period (Appendix S3). The composition of the flowering community differed significantly between invaded and uninvaded sites when *L. salicaria* abundance was included, as expected (pseudo-$F_{1,12}$ = 4.4, R^2 = 0.27, *P* = 0.002 for early bloom, pseudo-$F_{1,12}$ = 2.3, R^2 = 0.16, *P* = 0.016 for peak bloom). In contrast, when the invader's own abundance was excluded from the analysis, the composition of the flowering community did not differ across treatments either in the pre-bloom period (pseudo-$F_{1,12}$ = 0.99, R^2 = 0.08, *P* = 0.46) or the peak bloom period (pseudo-$F_{1,12}$ = 1.2, R^2 = 0.09, *P* = 0.28); however, flower composition did differ significantly in the early bloom period (pseudo-$F_{1,12}$ = 1.9, R^2 = 0.14, *P* = 0.014).

We observed a total of 3,952 insect visitors to native flowers. Observations of 911 visits to *L. salicaria* by one observer able to identify bees on the wing (K. Goodell) revealed that bumble bees (*Bombus* spp.) and honey bees (*Apis mellifera*) comprised 71% of all visitors to *L. salicaria* flowers (Appendix S5). Visitors to *L. salicaria* overlapped broadly with those to native flowers; we recorded no insect genera (family or order for non-bee taxa) on native plants that were not also recorded on *L. salicaria*.

Visitors per native flower declined with increasing density of native flowers across all sample periods in both years, indicating greater competition for visitors as native flower density increased (Fig. 3; Appendix S6). In addition to the effects of native flower density, invasion was associated with fewer visitors per flower during peak bloom, suggesting the most intense competition for visitors when invasive flower density was highest (Fig. 3; Appendix S6). Analysis of the visitation data using total flower density instead of native flower density revealed that the additional effect of invasion on visitors per native flower was not significant (Appendix S7), suggesting that the effect of invasion could be accounted for by the increase in overall
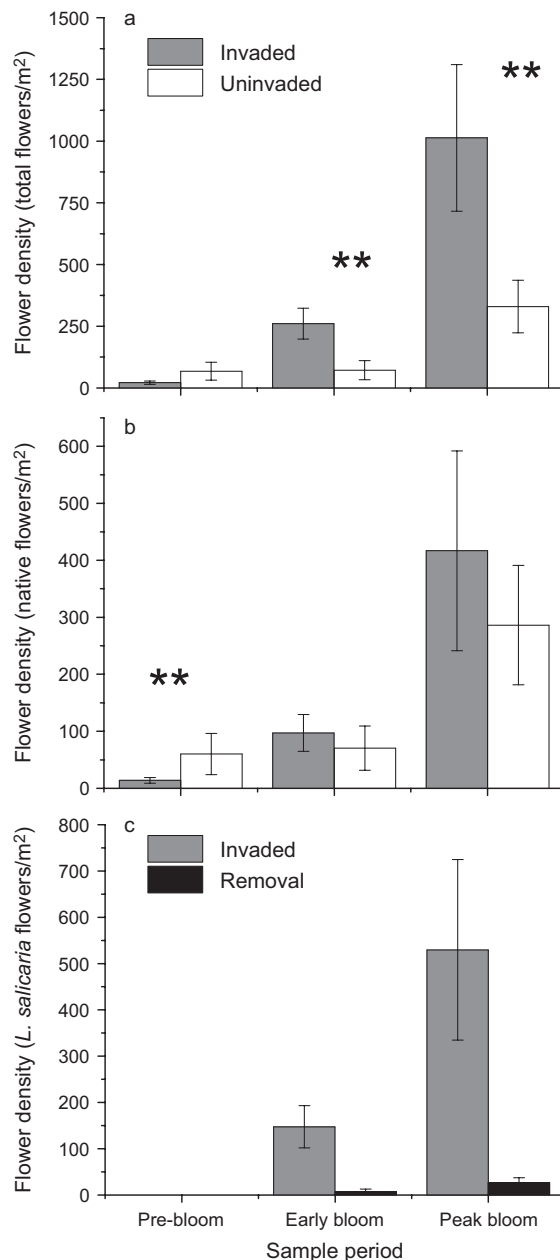
Fig. 2. The density (mean ± SE) of (a) all flowers, (b) native flowers, and (c) *Lythrum salicaria* flowers in fen sites that were invaded or uninvaded by *L. salicaria*. We sampled seven invaded sites and seven uninvaded sites at three times: in May–June before *L. salicaria* bloomed (pre-bloom), in July at the outset of *L. salicaria* bloom (early bloom), and in August when *L. salicaria* was in full flower (peak bloom) over two years. Because we applied *L. salicaria* removal treatments to three invaded sites, these sites were excluded from averages of all flowers and *L. salicaria* flowers. Means and standard errors were calculated across all site–sample–year combinations for each treatment. Two asterisks ** indicate significant differences between invaded and uninvaded sites at $P < 0.01$.

flower density, regardless of the identity of the flowers. Total number of visitors observed per area increased with the total number of flowers per area regardless of invasion

status, sample period, or their interaction (Appendix S8). The site-wide manual removal treatment in 2002 reduced *L. salicaria* flowering density by 81% in the early bloom period and 91% in the peak bloom period (Fig. 2). The number of visitors per native flower in removal sites was closest to that in uninvaded sites, although in post-hoc tests it did not differ significantly from either invaded or uninvaded (Fig. 3; Appendix S6).

Impact on visitation at the species level

At the species level, the average effect of the invader was significantly negative. The mean effect size of invasion on the number of visitors per flower to the 36 native plant species present in invaded and uninvaded sites was negative with CI that did not overlap 0 (average effect size = −1.65, 95% CI −2.83 to −0.32), indicating that we observed significantly fewer visitors on these native plants in invaded than uninvaded sites. Flower symmetry was related to the effect of invasion on native flower visitation; bilateral flowers (dissimilar from *L. salicaria*) had a significantly lower effect size than radially symmetrical flowers (Fig. 4, Table 1). Similarity of flower color was marginally significantly associated with effect of invasion, with pink/purple flowers (similar to *L. salicaria*) tending to have lower response ratios than flowers of other colors (Fig. 4, Table 1). Similarity of inflorescence structure did not significantly influence effect size. Continuous meta-analysis showed that neither flower density nor stature was related to the effect of *L. salicaria* invasion on individual species (Table 2); in other words, the data did not support our prediction that rare species and short species would be more vulnerable.

Impact on reproduction in a dominant native plant

Dasiphora fruticosa experienced a reduction in visitation with invasion that was close to the median of the distribution for native plant species ($\ln R = -0.69$; var = 0.019, see Appendix S9), and this reduction was significant during the peak bloom (data not shown). Pollination greatly enhanced seed production, and outcrossing resulted in more than twice as many seeds over self-pollination (Appendix S2). But despite reduced number of visitors per flower in invaded sites, *D. fruticosa* plants were not significantly more pollen limited in invaded than in uninvaded sites (Fig. 5, invaded vs. uninvaded [all years], $F_{1,6} = 0.02$, $P = 0.88$). Removal treatments in 2002 also did not significantly affect pollen limitation of *D. fruticosa* (invaded vs. uninvaded vs. removal, $F_{2,5} = 3.02$, $P = 0.14$).

DISCUSSION

To assess the impact of an invasive plant on plant–pollinator interactions, we integrated three approaches: a community-wide comparison that included observations and experimental removals, a meta-analytic approach to
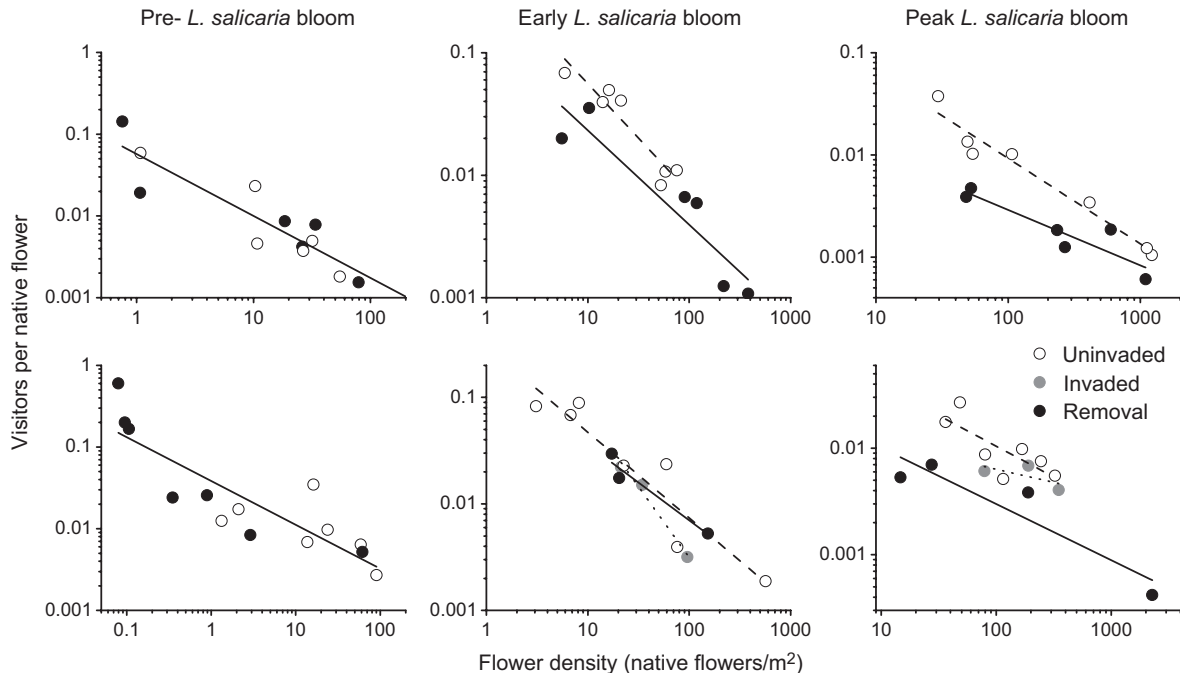
Fig. 3. Visitors per native flower as a function of the native flower density shown for each sample period in 2001 (top panels) and 2002 (bottom panels). Points show site averages. Linear fits show significant density dependence of visitation for uninvaded sites. Fits for pre-bloom periods include both invaded and uninvaded sites.

investigate variation in response among native species, and a study examining effects on reproduction in a widespread, dominant species. This integration allowed us to compare multiple measures of impact, illuminate mechanisms, and provide a context for comparing past studies. At the community level, we found a significant negative effect of invasion on visitation to native plants, measured as a reduction in the number of pollinator visitors per flower. This negative impact was corroborated by a modest, but significant, average effect across species in the meta-analysis and a significant negative effect on visitation, but not pollen limitation, in a common and widespread native species.

Impacts on flowers visitation at the community level

While *L. salicaria* was blooming, native plants received fewer flower visitors in invaded than uninvaded fen communities. This effect was not apparent during the pre-bloom period, suggesting that the flowers of the invader, and not underlying differences between the invaded and uninvaded sites, explain the reduced visitation to native flowers.

The presence of an invasive plant could affect pollination of native plants through a number of different mechanisms. First, the invader could depress the abundance of native flowers. While this study was not specifically designed to quantify impact on plant populations, *L. salicaria* invaded sites did have reduced native flower abundance, but only significantly during the pre-bloom

period, when there would not be direct competition between native and *L. salicaria* flowers. Reduced native flower abundance could diminish the attractiveness of the floral display to pollinators, or reduce the population size or foraging efficiency of native pollinators that rely on
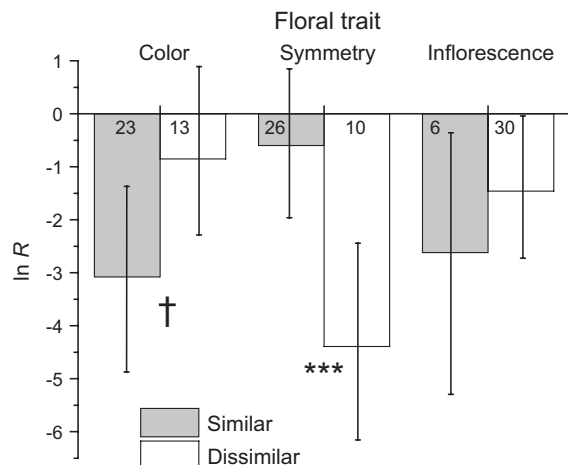

Fig. 4. Mean effect sizes of *Lythrum salicaria* invasion on visitors per flower to native plants with similar (shaded columns) or dissimilar (white columns) floral traits to *L. salicaria* expressed as log response ratios (ln R). Categories in which the 95% CI of the effect size overlap 0 show no significant effect of invasion for that group. Sample sizes, shown on columns, are the number of plant species. Statistical comparisons are between similar and dissimilar categories for each plant trait; †$P < 0.10$, ***$P \leq 0.01$.

TABLE 1. Summary of results of categorical meta-analyses showing the contribution of similarity to *Lythrum salicaria* in three floral traits to the effect of *L. salicaria* invasion on floral visitation to 36 native species.

Trait	$Q_{between}$	P_{rand}
Color	2.05	**0.10**
Symmetry	7.25	**0.007**
Inflorescence	0.32	0.51

Notes: Heterogeneity statistics ($Q_{between}$) and probabilities generated from randomization tests (P_{rand}) are presented. Boldface type indicates significance at $\alpha \leq 0.10$.

native plants (Bjerknes et al. 2007). Per-capita visitation to native flowers, however, declined, rather than increased with native flower density, meaning that reduction in the number of native flowers would be mitigated by an increase in visitors per flower. (One caveat is that if individual bees respond to higher flower density by visiting more flowers per plant, our metric of visitors per flower rather than visits per flower may have overestimated the negative relationship between flowers and visits from the plant perspective.) In addition, pollinators that specialize on native flowers were rare; all pollinator genera observed also visited *L. salicaria*. Similar to other studies, we found the invader highly connected within the plant pollinator network (Memmott and Waser 2002, Bartomeus et al. 2008b, 2010, Albrecht et al. 2014). Therefore, impacts on visitation are likely to be mediated through the abundance of all flowers, including the invader, rather than the abundance of native flowers alone.

This second mechanism, that the invader can increase total flower abundance in the community, appears to be the most important factor in the *L. salicaria* system. We saw more than a threefold increase in total flower number in invaded sites during peak *L. salicaria* bloom. This increase in floral display at the site scale, however, did not facilitate visitation to native plants despite positive effects of flowers on visitor numbers per area. Bartomeus et al. (2010) similarly found that increased floral density in patches invaded by *Impatiens glandulifera* failed to

TABLE 2. Summary of results and variance explained by weighted regressions to determine the effects of continuous variables on the effect size of *Lythrum salicaria* invasion on floral visitation to 36 native species.

Predictor and source	Q	df	P
Height†			
Regression	1.682	1	0.19
Residual	26.86	34	0.80
Total	28.55	35	0.77
Density‡			
Regression	0.004	1	0.94
Residual	24.54	34	0.88
Total	24.54	35	0.91

† Model explains 6% of variance.
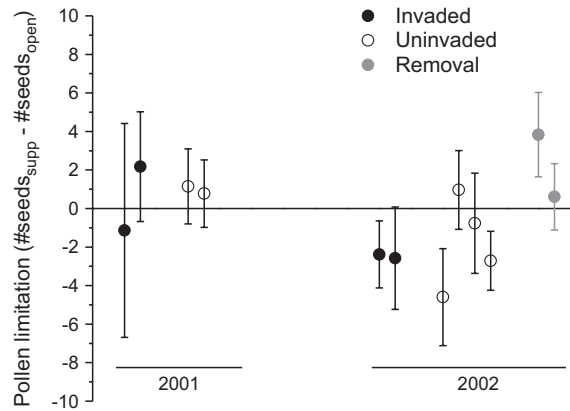‡ Model explains 0.01% of variance.

FIG. 5. Pollen limitation of seed production per flower in *Dasiphora fruticosa* expressed as mean differences between the number of supplemental minus the number of open-pollinated seeds produced per flower averaged across plants within sites. Black circles, invaded sites; open circles, uninvaded sites; gray circles, removal sites. Error bars represent ± SE. Lines under symbols indicate that treatments were not significantly different in either year.

increase visitation to native plants. In the calcareous fens, visitors per native flower showed a negative response to total flower number, and so visitation rates to native plants decreased. In addition to simply adding flowers, a third mechanism of *L. salicaria* impact would be a non-additive competitive effect; if *L. salicaria* is an exceptionally strong competitor for pollinators, then it would have a disproportionate effect on the relationship between visitation and flower number. We did not find strong evidence at the whole-community level that visitation declined disproportionately in the presence of the invader (i.e., there was no significant response in visitation to the interaction between total flower number and invasion). The strength of the impact of *L. salicaria* varied among native species (see *Impacts on visitation at the species level*); however, at the community scale, invasion of *L. salicaria* affected pollinator visitation primarily by exacerbating competition through increased flower abundance.

Competition for pollinators at the level of individual flowers could be reduced in the invaded plant community if pollinator populations could respond demographically to the large influx of flowers (Ye et al. 2014). This mechanism is difficult to address and is sensitive to scale, because some pollinators are highly mobile. Studies conducted within the foraging ranges of pollinators often show a redistribution of visitors between flower patches of different qualities (e.g., Grabas and Laverty 1999, Lopezaraiza-Mikel et al. 2007, Bartomeus et al. 2008b, 2010, Muñoz and Cavieres 2008, McKinney and Goodell 2010, 2011). Our invaded and uninvaded sites were separated by at least 5 km, greater than the normal foraging ranges of most pollinator species. Thus, we can test two predictions with our community-level, site-scale comparisons: first, if populations of visitors were inflated in

invaded sites, visitor numbers per flower would be inflated in the pre-bloom period (they were not). Second, in sites where *L. salicaria* flowers were experimentally removed, visitor numbers would be temporarily inflated compared to uninvaded sites (they were not). The saturation of pollinators relative to flowers suggests that factors other than current floral resources limit pollinator abundances, such as nesting habitat, vulnerability to predators, parasites, or disease, or phenological or spatial mismatches between resource availability and need (Carvell et al. 2008, Westphal et al. 2009, Williams et al. 2010, 2012, Roulston and Goodell 2011, Jha and Kremen 2013). Fens provide poor quality nesting habitat for fossorial bees, which may limit their ability to exploit enriched resource availability following invasion. Pollinator responses to resource distributions are likely to be species-specific (Essenberg 2013) and we are investigating elsewhere how invasion alters the composition of visitors, which could have repercussions for plant reproduction not considered here.

Finally, if native plant species vary in their susceptibility to invasion, the resulting change in composition of native flowers could affect pollinators. For example, loss of species that pollinators rely on early in the season could drive pollinator deficits later (Rathcke 1983), and average visitation to native plants would decline if less attractive species tended to persist in the presence of the invader. We did observe a significant change in overall community composition of native flowers in the early bloom period, but not the pre-bloom or peak bloom periods. To decouple the direct impact on visitation from the indirect effect through plant composition, we turn to species-specific analyses.

Impacts on visitation at the species level

Our species-level analysis also showed that *L. salicaria* invasion reduced visitation to native plants. For the 36 species found in both invaded and uninvaded sites, the response of pollinator visitation to *L. salicaria* invasion resulted in a modest, but significantly negative, average effect size, consistent with our conclusion from the community-level analyses. Together, these two analytical approaches show that *L. salicaria* depressed visitation to native plants at both a species level and a community level, refuting the idea that turnover in plant species alone explains community-level differences in pollinator visitation following invasion. Our results corroborate those from a meta-analysis by Morales and Traveset (2009), despite using markedly different approaches. Morales and Traveset summarized impacts of invasions in many habitats from numerous studies that included responses of a single species; we summarized impacts across all native species within natural populations of a single habitat. Thus, our approach assesses the overall impact of an abundantly flowering invasive plant on native plant pollination holding habitat type constant but still encompassing substantial variation across native species.

Variation among species in their susceptibility to competition for visitors with *L. salicaria* might be related to plant traits. For example, two syntheses found that phylogenetic relatedness, used as a proxy for floral similarity, was positively related to the impact of invasive plants on native plant pollination (Morales and Traveset 2009, Carvalheiro et al. 2014). In our study, it was not possible to evaluate the effect of phylogenetic relatedness in the fen species because few plants were closely related to *L. salicaria*. Gibson et al. (2012) found that native and invasive plant species of similar flower color tend to share flower visitors, which may explain meta-analysis results that similarity in floral color and symmetry intensify competition for visitors (Morales and Traveset 2009). Native fen species with flower colors similar to *L. salicaria* also competed more intensely. In contrast, dissimilar symmetry was associated with stronger impacts of the invader, possibly driven by its underlying correlation with other traits that influence competition. For example, in our study sites, the common bilateral flowers *Impatiens capensis*, *Scutellaria epilobiifolia*, *Sagittaria latifolia*, and *Mimulus ringens* were among the most nectar rich, surpassed only by *L. salicaria* (K. Goodell, *unpublished data*). It seems likely that *L. salicaria* competed strongly with these natives for pollinators attracted to large nectar rewards. Furthermore, we expected, but did not find, that in the presence of *L. salicaria* pollinators would be particularly likely to overlook less abundant species, as well as shorter species. Comparisons of visitation done at smaller scales that control for relative flower density may be more likely to detect effects of height and density (e.g., Flanagan et al. 2010, Iler and Goodell 2014, Seifan et al. 2014).

Impacts on reproduction in a dominant native plant

We measured the reproductive consequences of reduced visitation with a focal study on a dominant, widespread native species, *D. fruticosa*, a copiously flowering shrub. On average, *D. fruticosa* experienced lower pollinator visitation in invaded than uninvaded sites, with an effect size that placed it in the middle of the distribution of native species in terms of the sensitivity of its visitation rates to invasion. However, we did not detect higher pollen limitation in invaded sites relative to uninvaded sites in either year. A link between reduced visitation and seed production in the presence of invaders has been shown in most recent studies (reviewed in Skurski et al. 2014), but not all (Totland et al. 2006). We expected that *D. fruticosa* might be vulnerable to pollen limitation based on its breeding system; we found that seed production in this species was greatly increased by pollination, and in particular outcross pollination. Therefore, high levels of autogamy cannot explain the lack of response of pollen limitation to invasion. Instead, the long-lived flowers of *D. fruticosa*, which allow multiple opportunities for pollination, may have buffered its reproduction. We conclude that this dominant flowering

plant is resilient to competition for pollinators and expect little demographic effect from the reduced visitation observed in this study. Stable presence of this long-flowering plant, in turn, may help maintain the integrity of plant–pollinator interactions in invaded sites. On the other hand, native species with more extreme effect sizes may experience increased pollen limitation and are key targets for follow-up studies.

Conclusions

Taken together, our results provide an important confirmation of the conclusion of previous syntheses of single-species studies, that invasive plants have negative impacts on pollinator visitation across a broad range of co-occurring native plants. They also provide insights into mechanisms of impact. *Lythrum salicaria* dramatically increased floral resources in the community, and pollinator populations did not increase proportionally, driving down per-flower visitation. The range of flower types, plant sizes and flower densities shown by species negatively affected in our study suggests only limited importance of floral traits in determining impact in this system. However, traits that buffer plants against pollen limitation may play an important role in maintaining plant reproduction when experiencing competition from invasive species.

Literature Cited

Albrecht, M., B. Padron, I. Bartomeus, and A. Traveset. 2014. Consequences of plant invasions on compartmentalization and species' roles in plant–pollinator networks. Proceedings of the Royal Society B 281:2014077.

Ashman, T. L., et al. 2004. Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. Ecology 85:2408–2421.

Bartomeus, I., J. Bosch, and M. Vilà. 2008a. High invasive pollen transfer, yet low deposition on native stigmas in a *Carphbrotus*-invaded community. Annals of Botany 102: 417–424.

Bartomeus, I., M. Vilà, and L. Santamaria. 2008b. Contrasting effects of invasive plants in plant–pollinator networks. Oecologia 55:761–770.

Bartomeus, I., M. Vilà, and I. Steffan-Dewenter. 2010. Combined effects of *Impatiens glandulifera* invasion and landscape structure on native plant pollination. Journal of Ecology 98:440–450.

Bjerknes, A. L., O. Totland, S. J. Hegland, and A. Nielsen. 2007. Do alien plant invasions really affect pollination success in native plant species? Biological Conservation 138: 1–12.

Brown, B. J., and R. J. Mitchell. 2001. Competition for pollination: effects of pollen of an invasive plant on seed set of a native congener. Oecologia 129:43–49.

Brown, B. J., R. J. Mitchell, and S. A. Graham. 2002. Competition for pollination between an invasive species (purple loosestrife) and a native congener. Ecology 83:2328–2336.

Carvalheiro, L. G., et al. 2014. The potential for indirect effects between co-flowering plants via shared pollinators depends on resource abundance, accessibility and relatedness. Ecology Letters 17:1389–1399.

Carvell, C., P. Rothery, R. F. Pywell, and M. S. Heard. 2008. Effects of resource availability and social parasite invasion on field colonies of *Bombus terrestris*. Ecological Entomology 33:321–327.

Chittka, L., and S. Schurkens. 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.

Chittka, L., J. D. Thomson, and N. M. Waser. 1999. Flower constancy, insect psychology, and plant evolution. Naturwissenschaften 86:361–377.

Chung, Y. A., L. A. Burkle, and T. M. Knight. 2015. Minimal effects of an invasive flowering shrub on the pollinator community of native forbs. PLoS ONE 9:e109088.

Cox, P. A., and T. Elmqvist. 2000. Pollinator extinction in the Pacific Islands. Conservation Biology 14:1237–1239.

Da Silva, E. M., and R. D. Sargent. 2011. The effect of invasive *Lythrum salicaria* pollen deposition on seed set in the native species *Decodon verticillatus*. Botany 89:141–146.

Dicks, L. V., S. A. Corbet, and R. F. Pywell. 2002. Compartmentalization in plant–insect flower visitor webs. Journal of Animal Ecology 71:32–43.

Ehrenfeld, J. G. 2010. Ecosystem consequences of biological invasions. Annual Review of Ecology Evolution and Systematics 41:59–80.

Essenberg, C. J. 2012. Explaining variation in the effect of floral density on pollinator visitation. American Naturalist 180: 153–166.

Essenberg, C. J. 2013. Scale-dependent shifts in the species composition of flower visitors with changing floral density. Oecologia 171:187–196.

Ferrero, V., S. Castro, J. Costa, P. Acuna, and J. Loureiro. 2013. Effect of invader removal: pollinators stay but some native plants miss their new friend. Biological Invasions 15:2347–2358.

Flanagan, R. J., R. D. Mitchell, D. Knutowski, and J. D. Karron. 2009. Interspecific pollinator movements reduce pollen deposition and seed production in *Mimulus ringens* (Phrymaceae). American Journal of Botany 96:809–815.

Flanagan, R. J., R. D. Mitchell, and J. D. Karron. 2010. Increased relative abundance of an invasive competitor for pollination, *Lythrum salicaria*, reduces seed number in *Mimulus ringens*. Oecologia 164:445–454.

Ghazoul, J. 2002. Flowers at the front line of invasion? Ecological Entomology 27:638–640.

Ghazoul, J. 2004. Alien abduction: disruption of native plant–pollinator interactions by invasive species. Biotropica 36: 156–164.

Gibson, M. R., D. M. Richardson, and A. Pauw. 2012. Can floral traits predict an invasive plant's impact on native plant–pollinator communities? Journal of Ecology 100:1216–1223.

Gibson, M. R., A. Pauw, and D. M. Richardson. 2013. Decreased insect visitation to a native species caused by an invasive tree in the Cape Floristic Region. Biological Conservation 157:196–203.

Goodell, K. 2008. Invasive exotic plant-bee interactions. Pages 166–183 *in* R. R. James and T. L. Pitts-Singer, editors. Bee

pollination in agroecosystems. Oxford University Press, Oxford, UK.

Grabas, G. P., and T. M. Laverty. 1999. The effect of purple loosestrife (*Lythrum salicaria* L., Lythraceae) on the pollination and reproductive success of sympatric co-flowering wetland plants. Ecoscience 6:230–242.

Iler, A. M., and K. Goodell. 2014. Relative floral density of an invasive plant affects pollinator foraging behaviour on a native plant. Journal of Pollination Ecology 13:174–183.

Jakobsson, A., B. Padrón, and A. Traveset. 2009. Competition for pollinators between invasive and native plants: effects of spatial scale of investigation. Ecoscience 16:138–141.

Jha, S., and C. Kremen. 2013. Resource diversity and landscape-level homogeneity drive native bee foraging. Proceedings of the National Academy of Sciences USA 110:555–558.

Kaiser-Bunbury, C. N., T. Valentin, J. Mougal, D. Matatiken, and J. Ghazoul. 2011. The tolerance of island plant–pollinator networks to alien plants. Journal of Ecology 99:202–231.

King, V. M., and R. D. Sargent. 2012. Presence of an invasive plant species alters pollinator visitation to a native. Biological Invasions 14:1809–1818.

Kiviat, E., G. Mihocko, G. Stevens, P. M. Groffman, and D. Van Hoewyk. 2010. Vegetation, soils, and land use in calcareous fens of eastern New York and adjacent Connecticut. Rhodora 112:335–354.

Laverty, T. M. 1992. Plant interactions for pollinator visits: a test of the magnet species effect. Oecologia 89:502–508.

Levine, J. M., M. Vilà, C. M. D'Antonio, J. S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society B 270:775–781.

Lopezaraiza-Mikel, M. E., R. B. Hayes, M. R. Whalley, and J. Memmott. 2007. The impact of an alien plant on a native plant–pollinator network: an experimental approach. Ecology Letters 10:539–550.

May, R. M. 1974. On the theory of niche overlap. Theoretical Population Biology 5:297–332.

May, R. M., and R. H. MacArthur. 1972. Niche overlap as a function of environmental variability. Proceedings of the Royal Society B 69:1109–1113.

McKinney, A. M., and K. Goodell. 2010. Shading by invasive shrub reduces seed production and pollinator services in a native herb. Biological Invasions 12:2751–2763.

McKinney, A. M., and K. Goodell. 2011. Plant–pollinator interactions between an invasive and native plant vary between sites with different flowering phenology. Plant Ecology 212:1025–1035.

Memmott, J., and N. M. Waser. 2002. Integration of alien plants into a native flower–pollinator visitation web. Proceedings of the Royal Society B 269:2395–2399.

Mengersen, K., C. H. Schmid, M. D. Jennions, and J. Gurevitch. 2013. Statistical models and approaches to inference. Pages 89–107 *in* J. Koricheva, J. Gurevitch, and K. Mengersen, editors. Handbook of meta-analysis in ecology and evolution. Princeton University Press, Princeton, New Jersey, USA.

Molina-Montenegro, M. A., E. I. Badano, and L. A. Cavieres. 2008. Positive interactions among plant species for pollinator service: assessing the "magnet species" concept with invasive species. Oikos 117:1833–1839.

Moragues, E., and A. Traveset. 2005. Effect of *Carpobrotus* spp. on the pollination success of native plant species of the Balearic Islands. Biological Conservation 122:611–619.

Morales, C. L., and A. Traveset. 2008. Interspecific pollen transfer: magnitude, prevalence and consequences for plant fitness. Critical Reviews in Plant Sciences 27:221–238.

Morales, C., and A. Traveset. 2009. A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. Ecology Letters 12:716–728.

Moron, D., M. Lenda, P. Skorka, H. Szentgyoergyi, J. Settele, and M. Woyciechowski. 2009. Wild pollinator communities are negatively affected by invasion of alien goldenrods in grassland landscapes. Biological Conservation 142:1322–1332.

Motzkin, G. 1994. Calcareous fens of western New England and adjacent New York State. Rhodora 96:44–68.

Muñoz, A. A., and L. A. Cavieres. 2008. The presence of a showy invasive plant disrupts pollinator service and reproductive output in native alpine species only at high densities. Journal of Ecology 96:459–467.

NJOIT-OGIS. 2010. State of New Jersey, New Jersey State Plane NAD83. Office of geographic information systems. New Jersey Office of Information Technology, Trenton, New Jersey, USA.

Palladini, J. D., and J. L. Maron. 2014. Reproduction and survival of a solitary bee along native and exotic floral resource gradients. Oecologia 176:789–798.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Rathcke, B. 1983. Competition and facilitation among plants for pollination. Pages 305–331 *in* L. Real, editor. Pollination biology. Academic Press, New York, New York, USA.

Richardson, D. M., N. Allsop, C. M. D'Antonio, S. J. Milton, and M. Rejmánek. 2000. Plant invasions—the role of mutualisms. Biological Reviews 75:65–93.

Rosenberg, M. S. 2013. Moment and least-squares based approaches to meta-analytic inference. Pages 108–124 *in* J. Koricheva, J. Gurevitch, and K. Mengersen, editors. Handbook of meta-analysis in ecology and evolution. Princeton University Press, Princeton, New Jersey, USA.

Rosenberg, M. S., D. C. Adams, and J. Gurevitch. 2007. MetaWin statistical software for meta-analysis. Sinauer Associates, Sunderland, Massachusetts, USA. www.metawinsoft.com

Roulston, T. H., and K. Goodell. 2011. The role of resources and risks in regulating wild bee populations. Annual Review of Entomology 56:293–312.

SAS Institute. 2002–2012. The SAS system for windows. SAS Institute, Cary, North Carolina, USA.

SAS Institute. 2013. JMP V. 11.0. SAS Institute., Cary, North Carolina, USA.

Seifan, M., E. M. Hoch, S. Hanoteaux, and K. Tielboerger. 2014. The outcome of shared pollination services is affected by the density and spatial pattern of an attractive neighbour. Journal of Ecology 102:953–962.

Skurski, T. C., L. J. Rew, and B. D. Maxwell. 2014. Mechanisms underlying nonindigenous plant impacts: a review of recent experimental research. Invasive Plant Science and Management 7:432–444.

Tepedino, V. J., B. A. Bradley, and T. L. Griswold. 2008. Might flowers of invasive plants increase native bee carrying capacity? Intimations from Capitol Reef National Park, Utah. Natural Areas Journal 28:44–50.

Thompson, D. Q., R. L. Stuckey, and E. B. Thompson. 1987. Spread, impact and control of purple loosestrife (*Lythrum salicaria*) in North American wetlands. Research Report No. 2. 1–65. United States Department of the Interior, Fish and Wildlife Service, Washington, D.C., USA.

Tiner, R. W. 1998. In search of swampland—a wetland sourcebook and field guide. Rutgers University Press, New Brunswick, New Jersey, USA.

Totland, O., A. Nielsen, A. L. Bjerknes, and M. Ohlson. 2006. Effects of an exotic plant and habitat disturbance on pollinator visitation and reproduction in a boreal forest herb. American Journal of Botany 93:868–873.

Traveset, A., and D. M. Richardson. 2006. Biological invasions as disruptors of plant reproductive mutualisms. Trends in Ecology & Evolution 21:208–216.

Tscheulin, T., and T. Petanidou. 2013. The presence of the invasive plant *Solanum elaeagnifolium* deters honeybees and increases pollen limitation in the native co-flowering species *Glaucium flavum*. Biological Invasions 15:385–393.

Vilà, M., I. Bartomeus, A. C. Dietzsch, T. Petanidou, I. Steffan-Dewenter, J. C. Stout, and T. Tscheulin. 2009. Invasive plant integration into native plant–pollinator networks across Europe. Proceedings of the Royal Society B 276:3887–3893.

Waser, N. M. 1983. Competition for pollination and floral character differences among sympatric plant species: a review of the evidence. Pages 227–293 *in* C. G. Jones and R. J. Little, editors. Handbook of Experimental Pollination Biology. Academic Press, New York, New York, USA.

Waser, N. M. 1986. Flower constancy: definition, cause and measurement. American Naturalist 127:593–603.

Weihe, P. E., and R. K. Neeley. 1997. The effects of shading on competition between purple loosestrife and broad-leaved cattail. Aquatic Botany 59:127–138.

Westphal, C., I. Steffan-Dewenter, and T. Tscharntke. 2009. Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. Journal of Applied Ecology 46:187–193.

Williams, N. M., E. E. Crone, T. H. Roulston, R. L. Minckley, L. Packer, and S. G. Potts. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. Biological Conservation 143:2280–2291.

Williams, N. M., J. Regetz, and C. Kremen. 2012. Landscape-scale resources promote colony growth but not reproductive performance of bumble bees. Ecology 95: 1049–1058.

Ye, Z.-M., W.-K. Dai, X.-F. Jin, R. W. Gituru, Q.-F. Wang, and C.-F. Yang. 2014. Competition and facilitation among plants for pollination: Can pollinator abundance shift the plant–plant interactions? Plant Ecology 215:3–13.