

Indirect competition for pollinators is weak compared to direct resource competition: pollination and performance in the face of an invader

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Abstract Invasive plants have the potential to reduce native plant abundance through both direct and indirect interactions. Direct interactions, such as competition for soil resources, and indirect interactions, such as competition for shared pollinators, have been shown to influence native plant performance; however, we know much less about how these interactions influence native plant abundance in the field. While direct competitive interactions are often assumed to drive declines in native abundance, an evaluation of their influence relative to indirect mechanisms is needed to more fully understand invasive plant impacts. We quantified the direct effects of resource competition by the invasive perennial forb, *Euphorbia esula* (Euphorbiaceae), on the recruitment, subsequent performance, and ultimate adult abundance of the native annual, *Clarkia pulchella* (Onagraceae). We contrast these direct effects with those that indirectly resulted from competition for shared pollinators. Although *E. esula* dramatically reduced pollinator visitation to *C. pulchella*, plants were only weakly pollen-limited. Pollen supplementation increased the number of seeds per fruit from 41.28 to 46.38. Seed addition experiments revealed that the impacts of ameliorating pollen limitation only increased potential recruitment by 12.3 %. In contrast, seed addition

experiments that ameliorated direct competition with *E. esula* resulted in an increase in potential future recruitment of 574 %. Our results show that, while the indirect effects of competition for pollinators can influence plant abundance, its effects are dwarfed by the magnitude of direct effects of competition for resources.

Keywords *Clarkia pulchella* · Competition · *Euphorbia esula* · Exotic plants · Pollination

Introduction

Invasive plants often have well-documented negative impacts on native plant abundance (reviews by Levine et al. 2003; Vilá et al. 2011). These impacts are most commonly thought to derive from invasives outcompeting natives for resources such as nutrients or light (Melgoza et al. 1990; D'Antonio and Mahall 1991; Gorchov and Trisel 2003; Vilá and Weiner 2004; Combs et al. 2011); however, indirect interactions between invasives and natives, which can be mediated by soil microbes (Klironomos 2002; Stinson et al. 2006), herbivores (White et al. 2006; Meiners 2007; Orrock et al. 2008), or pollinators (Bjerknes et al. 2007; Morales and Traveset 2009) may also play a role. A key question concerns what the relative strength of direct versus indirect effects of invasives on natives might be. If native abundance is commonly reduced by direct resource competition with invasives, then management efforts to ameliorate this competition might be profitable (Alpert 2010; Blumenthal et al. 2010). Alternatively, if indirect effects are implicated in native decline, then the impact of invasives may be more far reaching, and insidious than currently appreciated. Thus, a consideration of the indirect effects of invasives on natives may be

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necessary in order to predict how native plants respond to invasion and restoration.

Evidence for direct competitive effects of invasives on natives comes in part from field studies that have manipulated exotic abundance around focal native plants and found negative effects on native plant performance (Levine et al. 2003; MacDougall and Turkington 2005; Biggerstaff and Beck 2007; Coleman and Levine 2007; Denoth and Myers 2007; Cipollini et al. 2008). Yet, whether these negative effects on native plant growth or reproduction are responsible for driving declines in native plant abundance has seldom been evaluated empirically (but see Williams and Crone 2006; Maron and Marler 2008). As such, there is a need for field experiments that evaluate the population-level consequences of competition between invasives and natives.

In addition to direct competition for abiotic resources, plants can also engage in indirect exploitative competition, in which the resources plants compete for are other species, such as shared pollinators (Rathcke 1983; Wooten 1994; Palmer et al. 2003; Bjerknes et al. 2007; Morales and Traveset 2009; Kaiser-Bunbury et al. 2011). Plant species that flower simultaneously often share pollinators (Bronstein 1994; Waser et al. 1996), which can reduce seed production if it results in either a reduction in pollinator visitation (Bjerknes et al. 2007; Morales and Traveset 2009) or an increase in deposition of heterospecific pollen grains on stigmas (reviewed in Morales and Traveset 2008). Pollinator sharing can also have positive outcomes (i.e., facilitation), whereby visitation rates are increased in the presence of another species due to enhanced attractiveness of the flowering patch (Moeller 2004; Ghazoul 2006) or when multiple flowering species jointly support larger populations of resident pollinators (Moeller 2004). However, in the case of pollinator sharing between exotic and native forbs, reduced visitation to natives is the most common outcome because exotics often have enhanced pollinator attractiveness relative to co-flowering native species (Brown et al. 2002; Moragues and Traveset 2005; Munoz and Cavieres 2008; Kandori et al. 2009; Morales and Traveset 2009). These competitive effects are exacerbated by the numerical dominance of invasives relative to natives (Bjerknes et al. 2007; Morales and Traveset 2009).

The implications of reduced pollinator visits resulting from competition for shared pollinators on native seed set has been less well studied, but, when examined, effects are usually negative (reviewed by Morales and Traveset 2009). However, while previous studies are useful in indicating whether indirect competition is occurring, they do not typically reveal whether reductions in native seed set affect native plant abundance. Linkages between seed production and recruitment need not be strong as they are often decoupled by compensatory density dependent factors such

as seedling survival. Such factors may limit the extent to which changes in fecundity translate to changes at the population level (Ashman et al. 2004; Price et al. 2008; Feldman and Morris 2011; Horvitz et al. 2011).

While indirect interactions between native and invasive plants via shared pollinators have been the focus of much attention over the last decade (reviews by Bjerknes et al. 2007; Morales and Traveset 2008, 2009), these interactions do not occur in isolation. Rather, competition for pollinators and competition for other resources occur simultaneously and are fundamentally linked (Campbell and Halama 1993). First, competition for resources could limit the extent to which changes in reproduction due to pollen receipt influence plant abundance by decreasing recruitment, survival, or flowering. Second, seed production is influenced by both pollen receipt and resource availability (Haig and Westoby 1988; Campbell and Halama 1993; Burd 1994; Ashman et al. 2004; Burkle and Irwin 2008). Seed production may be limited by pollen receipt when the supply of pollen grains is inadequate (i.e., pollen limitation) or the quantity and quality of pollen may be more than adequate, but seed production may be limited by resources (i.e., resource limitation). Moreover, there need not be a dichotomy between resource and pollen limitation. For example, pollination and resource levels may affect different components of female fitness such as seed production and flower number, or resource levels may influence floral attractiveness with possible implications for pollination (Zimmerman 1983; Zimmerman and Pyke 1988; Campbell and Halama 1993; Munoz et al. 2005; Burkle and Irwin 2008). Most studies of pollen limitation of natives in invaded sites have compared seed production for plants growing near and at variable distances from competitors (but see Chittka and Schürkens 2001; Brown et al. 2002; Cariveau and Norton 2009; Bartomeus et al. 2010; Flanagan et al. 2010). However, plants growing near competitors engage not only in competition for pollinators but also competition for resources. Attributing reductions in seed production to reduced visitation requires the assumption that seed production is solely limited by pollen receipt. However, plants growing near the competitor may produce fewer seeds due to resource constraints resulting from resource competition.

Here, we ask how the invasive forb, *Euphorbia esula*, indirectly and directly influences the abundance of the annual native forb, *Clarkia pulchella*. We examined pollinator visitation and the degree to which *C. pulchella* seed production is limited by pollen receipt in invaded and native-dominated communities. We also examined the direct effects of competition by *E. esula* on *C. pulchella* recruitment and performance. We then used these data to evaluate both indirect and direct impacts of an invasive forb on native plant abundance.

Materials and methods

Study design

We selected 15 grassland sites in western Montana. Seven sites were heavily invaded by *E. esula* (Euphorbiaceae) and eight were dominated by native forbs. *E. esula* is a Eurasian perennial that invades grasslands throughout the northern Great Plains and Rocky Mountains. It spreads clonally via rhizomes and often occurs at high densities within invaded sites. It produces abundant inflorescences of reduced female and male flowers (cyathia) beginning in late May and continuing for several weeks. Copious nectar is produced by glands at the base of each inflorescence and is attractive to a variety of pollinators, including native bees, honeybees (*Apis mellifera*), and flies. Native sites were characterized by abundant cover of the perennial bunchgrasses *Festuca idahoensis* and *Festuca scabrella*. Abundant forbs included *Balsamorhiza sagittata* (Asteraceae), *Achillea millefolium* (Asteraceae), and *Lupinus sericeus* (Fabaceae). At all sites, there were low numbers of other exotic species that co-flower with *C. pulchella*. We performed different experiments and observations across the 15 sites (Online Resource 1).

C. pulchella is a native annual, distributed from British Columbia south through northern California and east through South Dakota. *C. pulchella* is self-compatible, though protandry and herkogamy promote outcrossing (Lewis 1953). Individuals produce 1–15 flowers in mid-summer that are primarily pollinated by solitary bees. Capsules are formed in late July and early August. Seeds germinate rapidly when exposed to moisture and proper temperatures in the field, thus the seed bank likely contributes little to population dynamics (Lewis 1953; Newman and Pilson 1997).

Indirect effects: pollinator visitation and pollen limitation

To determine how *E. esula* invasion influenced pollinator visitation to *C. pulchella*, we grew individuals from seed to flowering in pots and observed pollinator visitation to *C. pulchella* at six invaded sites and five native sites in 2010. To eliminate the influence of background variation in *C. pulchella* abundance on visitation, we used only sites that lacked naturally occurring *C. pulchella* populations. At each site, we placed three arrays 10 m apart from each other. Each array contained three potted plants which were placed 0.5 m apart. During site visits, we observed each array for 15 min. Our goal was to visit each site on four separate days; however, this was not possible at all sites due to inclement weather during the period when *C. pulchella* was in bloom. As a result, one native and one

invaded site were observed on 3 days, and one native and one invaded site were observed twice. All observations took place between 22 and 29 June 2010, between 0900 and 1500 hours. We observed arrays only on rain-free days when temperatures were greater than 14 °C. Observers sat 1 m from the array and recorded all pollinator visits to *C. pulchella* flowers and the number of open flowers on each plant. Visits were counted only if the insect made contact with reproductive parts of the flower. To estimate pollinator activity at the sites, we hand-netted solitary bees, which were the only observed visitors to *C. pulchella*, within 30 m of the array for 45 min following one randomly chosen observation period.

We examined the extent to which *C. pulchella* reproduction was limited by pollen-receipt (i.e., pollen limitation) in 2011 at three native sites and three invaded sites. Pollen limitation is generally assessed by comparing seed production under ambient pollen loads to seed production under experimentally supplemented pollen loads. We used naturally occurring *C. pulchella* at one invaded and all three native sites. At two invaded sites, we used plants that recruited from seeds that were experimentally added to plots in fall 2010 (see below). At the three native and three invaded sites, we haphazardly selected plants and randomly assigned half to receive supplemental pollen. On these, we marked one receptive flower and supplemented pollen to the stigma, and on the remaining plants we marked a single flower but did not add pollen. At all three native sites and the one invaded site, we selected 60 plants, while at two invaded sites with low *C. pulchella* abundance, we were only able to select 28 and 21 plants, respectively. At each site, we collected supplemental pollen from dehisced anthers of plants at least 5 m from recipient plants. We collected marked fruits prior to dehiscence in late July, and counted the number of filled seeds. Within a plant, supplementing pollen to a single flower did not affect subsequent flower production (J.D. Palladini, unpublished data) and progressive hand-pollination of all flowers in a congeneric species did not influence flower production (Moeller 2004), suggesting that our estimates of pollen limitation may be minimally biased by resource reallocation. However, it remains possible that *C. pulchella* plants reallocated resources to supplemented flowers, in which case our design will tend to overestimate the magnitude of pollen limitation (Knight et al. 2006).

Direct effects: recruitment and performance

We examined the direct competitive effects of *E. esula* on *C. pulchella* recruitment, performance and ultimate abundance by adding seeds to subplots embedded within 1-m-radius circular plots that either had *E. esula* experimentally removed from them or were left intact. We placed

20 plots at randomly selected locations within two heavily invaded sites lacking natural *C. pulchella* populations. Ten of these plots were randomly assigned to receive the *E. esula* removal treatment, while the other half remained non-manipulated controls. Pre-treatment density of *E. esula* stems did not differ between experimental and control plots ($F = 2.213$, $P = 0.143$), or between sites ($F = 2.056$, $P < 0.157$). We removed *E. esula* from treatment plots in spring 2010 when *E. esula* was just beginning to appear above ground. Because *E. esula* establishes dense underground rhizomes, manual removal would have greatly disturbed the soils, thus we used chemical means of removal. We applied 1.8 % glyphosphate (Roundup RTU®) to the tips of *E. esula* stems within a 1.0-m-radius circular plot while avoiding damage to other plant species present, and removed dead *E. esula* stems from the site.

In each plot, we established three evenly spaced 15 cm × 15 cm subplots separated by at least 15 cm. In fall 2010, we added 10, 50, or 100 *C. pulchella* seeds to a randomly selected subplot. These seed density levels were designed to encompass densities lower than, approximately equal to, and greater than observed seed production in invaded sites. We purchased seeds from a local native seed supplier (who grew his plants from seeds collected at a source population that was approximately 20 km from our study sites). In spring and summer 2011, we recorded the number of recruits that survived to flower in each subplot. In addition, we measured plant height (at peak plant size) to the nearest cm and counted the total number of flowers produced per plant. For comparison, we also counted the number of flowers produced on plants in one additional *C. pulchella* population that naturally occurred with *E. esula*, and at three native sites.

Analysis

All analyses were run with the statistical software R 2.13.2 (R Development Core Team 2011). Gaussian mixed effects models were fitted with the function `lme` (library: `nlme`; Pinheiro et al. 2011) and Poisson mixed effect models were fitted with the function `lmer` (library: `lme4`; Bates et al. 2011).

We examined whether the number of pollinator visits per flower differed between invaded and native sites using a generalized linear mixed effects model (GLMM, Gaussian family/identity link), with observation date nested in array, and array nested in site. We used a Mann–Whitney U test to examine possible differences in bee activity between invaded and native sites. To determine whether the supplemental pollen treatment increased seed production and whether invasion influenced the magnitude of pollen limitation, we used GLMM (Gaussian family/

identity link) with treatment, invasion status, and the interaction between the two as fixed effects, and site as a random effect.

We used GLMM (Poisson family/log link) to determine the extent to which increasing seed density increased *C. pulchella* recruitment, and whether the presence of *E. esula* influenced this pattern. *E. esula* removal was a whole-plot factor and seed density was a subplot factor in a split-plot design. Seed density was included as a categorical variable rather than a continuous variable due to the small number of seed densities used. We included seed density, treatment (*E. esula*-removal vs. control), and density × treatment as fixed effects, and plot in treatment in site as a random effect. We determined whether *C. pulchella* height was influenced by the *E. esula* removal treatment by using GLMM (Gaussian family/identity link), with treatment as a fixed effect and plot nested in site as a random effect. A similar model was used to examine differences in flower number among *E. esula* removal and control treatments, as well as native sites. Testing fixed effects was done with Wald tests. Finally, we used GLMM (Gaussian family/identity link) to examine whether *C. pulchella* height and flower number were related to *C. pulchella* density, with the number of recruits in each subplot as a fixed factor and plot in site as a random factor.

We then used these data to evaluate the influence of indirect and direct effects of *E. esula* on *C. pulchella* abundance. Where treatment effects were significant, we used treatment means to simulate amelioration of pollen limitation (i.e., indirect effects) and direct competitive effects in combination and alone to determine how the number of predicted recruits is influenced by *E. esula*. We also compared these to the expected number of recruits in native sites using observed flower number and ambient seed production in native sites. Because seed additions were not performed in native sites, we used the observed recruitment estimated from seed additions in invaded sites. Because our calculations begin with a single plant, the number of recruits expected is equivalent to the population growth rate.

Results

Indirect effects: pollinator visitation and pollen limitation

C. pulchella growing with *E. esula* received 90 % fewer pollinator visits ($\bar{x} = 0.07$ visits per flower in a 15-min period) compared to plants growing in native-dominated sites ($\bar{x} = 0.72$ visits per flower; $F_{1,9} = 6.54$, $P = 0.0001$; Fig. 1a), despite the fact that there was no difference in bee activity between *E. esula* invaded and native sites ($Z = 16.0$, $n = 10$, $P = 0.547$).

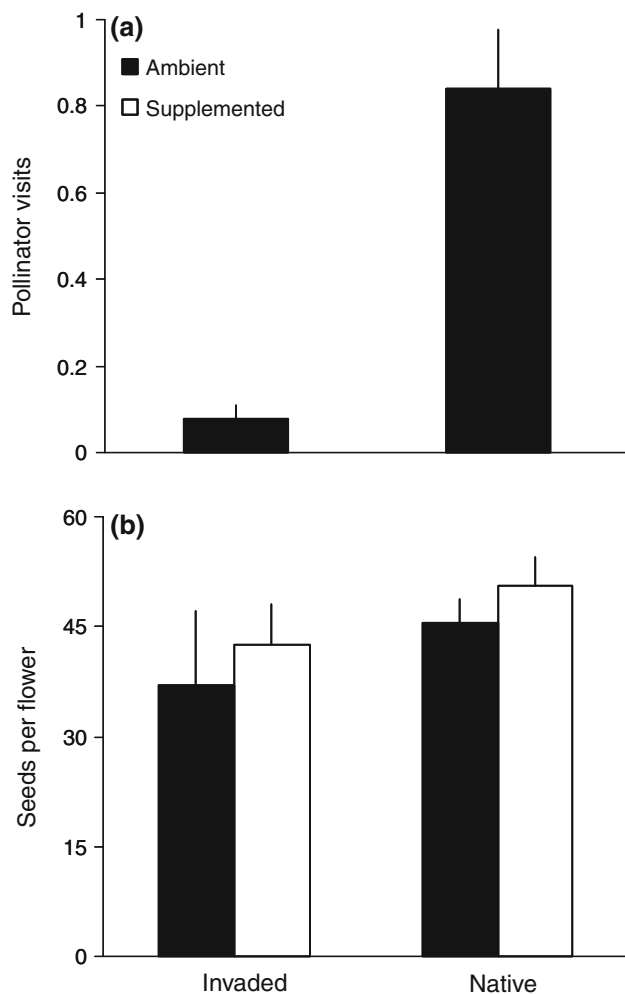


Fig. 1 Influence of invasion by *E. esula* on **a** mean number of pollinator visits per *C. pulchella* flower over a 15-min observation period and **b** seeds produced in invaded and native sites given ambient and supplemental pollen receipt. *Solid bars* are mean seed production under ambient conditions; *open bars* are seed production when pollen is supplemental. *Vertical lines* +1SEM

Flowers receiving experimentally supplemented pollen produced more seeds than those receiving ambient pollen ($F_{1,274} = 4.15$, $P = 0.042$; Fig. 1b). However, plants were not more pollen-limited in invaded than uninvaded sites (treatment \times invasion status: $F_{1,273} = 0.05$, $P = 0.816$), and across sites, supplemental pollen increased seed production by only 10.6%. Pollen limitation tended to be more variable at invaded sites than at native sites; one invaded population was strongly pollen-limited while the other two invaded populations showed little or no evidence of pollen limitation. In contrast, at native sites the increase in seed production with supplemental pollen was consistent among sites. There was no overall difference in the number of seeds produced per flower between invaded and native sites ($F_{1,4} = 0.98$, $P = 0.376$).

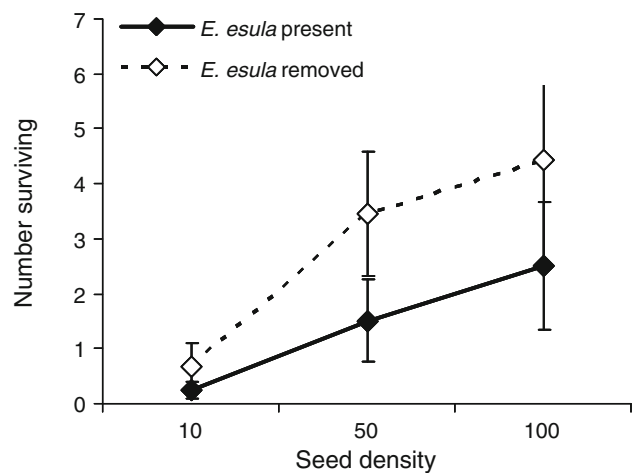


Fig. 2 Number of *C. pulchella* plants (mean \pm SE) surviving to flower as a function of seed density in plots with *E. esula* removed or present

Direct effects: recruitment and performance

Our *E. esula* removal treatment was effective in reducing the number of *E. esula* stems in treatment plots compared to control plots ($t_{10} = -4.71$, $P < 0.001$). The number of *C. pulchella* plants recruiting and surviving to flower across treatments increased from 10 to 50 seeds added ($z = -3.68$, $N = 51$, $P < 0.001$), and differences in recruitment between 50 and 100 seed subplots were non-significant ($z = 1.06$, $N = 51$, $P = 0.287$). Removal of *E. esula* increased recruitment across seed densities ($z = -2.54$, $N = 51$, $P = 0.011$, Fig. 2) but there was no significant seed density \times removal treatment interaction. The mean recruitment rate across seed densities in *E. esula* removal treatments was 0.026% compared to 0.053% in control plots.

E. esula strongly affected the performance of *C. pulchella* target plants (Fig. 3). Individuals in *E. esula*-removal plots averaged 12.9 cm in height, compared to 7.5 cm in plots containing *E. esula* ($F_{1,11} = 24.96$, $P < 0.001$). Flower production also differed among treatments ($F_{2,15} = 10.75$, $P = 0.001$). Flowering was greater in *E. esula* removal plots compared to control plots (3.8 and 1.1 flowers per plant, respectively, $t_{15} = -4.2$, $P < 0.001$), and was greater still in native sites (4.82 flowers per plant, $t_{15} = 3.19$, $P = 0.006$). There was no evidence of density-dependent reductions in *C. pulchella* performance. Neither height ($F_{1,101} = 0.33$, $P = 0.562$) nor flower number ($F_{1,101} = 1.74$, $P = 0.190$) were related to the number of *C. pulchella* plants in each subplot.

Comparison of direct and indirect effects

Using treatment means to simulate amelioration of pollen limitation (i.e., indirect effects) in invaded sites only

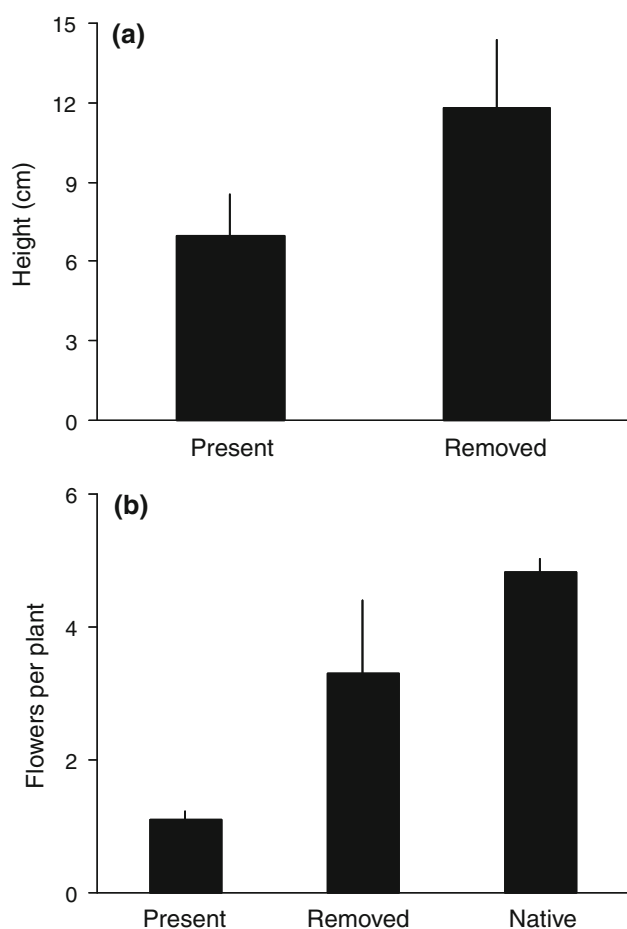


Fig. 3 Response of *C. pulchella* to removal of *E. esula* **a** height, **b** flower number, as well as flower number in native sites. Bars mean + SE

increased potential recruitment from 1.22 plants to 1.37, an increase of 12.3 % (Table 1). In contrast, using treatment means to simulate amelioration of direct competitive effects on flower number and recruitment rates resulted in expected recruitment of 8.25 plants, an increase of 574 %.

Discussion

The sharing of pollinators with co-flowering species has the potential to reduce or even increase pollinator visitation (Levin and Anderson 1970; Waser 1983; Campbell 1985; Moeller 2004; Ghazoul 2006). While interactions between natives that share pollinators with invasive species, on average, reduce visitation and seed production (Morales and Traveset 2009), whether this indirect competition is meaningful for native plant populations has remained untested. This is particularly important in the case of interactions between native and invasive plant species, because direct competitive effects of invasive plants are often strong (Levine et al. 2003; Maron and Marler 2008). *E. esula* competes with *C. pulchella* for both pollinator visits and resources. However, because plants were only weakly pollen-limited, competition for pollinators has limited potential to influence *C. pulchella* abundance. In contrast, competition for resources strongly reduced both the number of *C. pulchella* plants that recruit into the population and flower production. Ameliorating direct effects of resource competition on recruitment and adult performance could increase future abundance by 574 %.

The number of studies demonstrating competitive effects of exotics on natives for pollinators has increased dramatically over the last decade (reviewed in Morales and Traveset 2009; Bartomeus et al. 2010; Flanagan et al. 2010; McKinney and Goodell 2011; Takakura et al. 2011). However, we have lacked studies examining whether changes in pollinator visitation and its effects on seed input have significant impacts on plant abundance. Changes in seed production may not translate into changes in plant abundance due to a number of compensatory, density-dependent processes (Ashman et al. 2004; Price et al. 2008; Feldman and Morris 2011; Horvitz et al. 2011). We found that pollinator visitation to *C. pulchella* was greatly reduced in sites containing *E. esula* compared to native-dominated sites. Reductions in visitation could contribute to reduced seed production in invaded sites, because, in

Table 1 Reproductive output, recruitment rate, and projected future number of recruits (assumes $n_t = 1$) for *C. pulchella* in native and invaded plots with ambient or supplemental pollen (i.e., with and

without competition for pollinators) and when *E. esula* is present or removed from within 1.0 m (i.e., with and without competition for resources)

Invasion status	± Supp. pollen	± <i>E. esula</i>	Flowers/plant	Seeds/flower	Seeds/plant	Recruitment	$n_t + 1$
Native	–	–	4.82	41.28	198.97	0.053	10.55
Invaded	–	+	1.14	41.28	47.06	0.026	1.22
Invaded	+	+	1.14	46.38	52.87	0.026	1.37
Invaded	–	–	3.77	41.28	155.63	0.053	8.25
Invaded	+	–	3.77	46.38	174.85	0.053	9.27

Recruitment is the mean number of seeds added that survived to flower across seed densities. Because no seed additions were performed in native sites, recruitment rate from *E. esula* removal plots in invaded sites is used

general, reproduction of *C. pulchella* is limited by pollen receipt, and because increases in seed input increased *C. pulchella* recruitment. However, because the magnitude of pollen limitation in our system is relatively weak, and because *E. esula* suppresses *C. pulchella* recruitment, increases in abundance are small.

Across sites, supplemental pollen increased seed set for *C. pulchella* by only 10.6 %, compared to an average increase of 42 % for studies generally examining the magnitude of pollen limitation (Ashman et al. 2004). Few studies investigating the influence of plant invasion on seed production have estimated pollen limitation. Rather, most studies have compared seed production for natives growing near and at varying distances from an invader. However, these results may be confounded with direct effects of competition for soil resources. Reductions in seed production may result from competition for pollinators; however, it is also possible that resource competition limits seed production. Of the few studies using potted plants to isolate indirect effects of competition for pollinators, results have ranged from no effect on seed set (Cariveau and Norton 2009; Bartomeus et al. 2010) to reductions of 25–40 % (Chittka and Schürkens 2001; Brown et al. 2002; Flanagan et al. 2010).

The relatively small effect of supplementing pollen to *C. pulchella* may be the result of self-pollination in invaded sites where visitation was rare. Though *C. pulchella* has morphological features that promote outcrossing, flowers may self-pollinate in the absence of pollinators (Newman and Pilson 1997), and competition for pollinator services can select for self-pollination (Levin 1972; Fishman and Wyatt 1999; Moeller and Geber 2005). Both reduced visitation and interspecific pollen transfer have the potential to select for traits that favor self-pollination (Fishman and Wyatt 1999; Knight 2004), such as reduced herkogamy (spatial separation of anthers and stigma), reduced dichogamy (temporal separation of anther dehiscence and stigma receptivity), and reduced corolla size (Wyatt 1983). If rates of self-pollination are greater in invaded sites where pollinator visits are rare, there may be consequences for population persistence in invaded sites due to reductions in genetic variation. Newman and Pilson (1997) found that genetic variation strongly influenced germination and survival for *C. pulchella*, and that decreased genetic effective population size increased the probability of population extinction over only three generations.

We assessed pollinator visitation and pollen limitation in different years (2010 and 2011, respectively). It is possible that the degree of pollen limitation did not differ between invaded and native sites in 2011 because pollinator visitation patterns between site types were equivalent in 2011. However, we tested whether relative pollinator visitation rates were consistent between years by re-observing visitation at a

subset of sites in 2011 (three native and three invaded), and found that visitation rates did not differ between years (J.D. Palladini, unpublished data). In addition, *C. pulchella* abundance was notably lower at two invaded sites used to assess pollen limitation. Because floral density can influence pollination success (Groom 1998; Knight 2003), it is possible that the pollen limitation we observed was influenced by plant density. However, the site with the lowest abundance showed no evidence of pollen limitation, suggesting the plant abundance per se is not a primary factor influencing pollen limitation across sites.

In contrast to indirect effects, direct effects of competition with *E. esula* were strong. Both recruitment and the number of flowers per plant increased when *E. esula* was removed. Vilá et al. (2011) found that only 14 % of field investigations of impacts of exotic plant used manipulative experiments. However, when examined, exotic plants significantly reduced growth and reproduction of native plant species (Levine et al. 2003; MacDougall and Turkington 2005; Biggerstaff and Beck 2007; Coleman and Levine 2007; Denoth and Myers 2007; Cipollini et al. 2008; Vilá et al. 2011). Our study is unique in that we use experimental removals to examine not only the impacts of *E. esula* on adult plant fitness but also its effects on subsequent recruitment and abundance of *C. pulchella*. Strong resource competition reduced recruitment and also lowered flower number, with much greater consequences for whole plant seed production than limited pollen receipt, consistent with research demonstrating that resource levels strongly influence plant fitness (Campbell and Halama 1993; Munoz et al. 2005; Ne'eman et al. 2006; Burkle and Irwin 2008). Because reduced recruitment and adult performance are likely outcomes of competition between exotics and invasive forbs, even changes in the number of seeds per fruit of 25–40 % (Chittka and Schürkens 2001; Brown et al. 2002; Flanagan et al. 2010), may result in only trivial changes in plant abundance. For example, in order for the effects of competition for pollinators to equal effects of resource competition, *E. esula* would need to reduce ambient seed production by *C. pulchella* to 7 seeds per fruit, 83 % fewer than we observed.

This study demonstrates that indirect interactions involving competition for shared pollinators between an invasive and native plant may have consequences for plant abundance. However, these effects are weak compared to the effects of direct resource competition. Thus, restoration efforts that ameliorate resource competition would likely benefit *C. pulchella*. Future studies that examine the relative importance of indirect and direct effects will provide further insight into the mechanisms by which invasives reduce native abundance and enable managers to better predict how native plants will respond to restoration efforts.

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