Neighborhood-contingent indirect interactions between native and exotic plants: multiple shared pollinators mediate reproductive success during invasions

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Native and exotic plants can influence one another's fecundity through their influence on shared pollinators. Specifically, invasion may alter abundance and composition of local floral resources, affecting pollinator visitation and ultimately causing seedset of natives in more-invaded and less-invaded floral neighborhoods to differ. Such pollinator-mediated effects of exotic plants on natives are common, but native and exotic plants often share multiple pollinators, which may differ in their responses to altered floral neighborhoods. We quantified pollinator-mediated interactions between three common forbs of western Washington prairies (native *Microseris laciniata* and *Eriophyllum lanatum* and European *Hypochaeris radicata*) in three floral neighborhoods: 1) high native and low exotic floral density, 2) high exotic floral density and low native density, and 3) experimentally manipulated low exotic floral density. Pollinator visitation rates varied by floral neighborhood, plant species identity, and their interaction for all three plant species. Similarly, pollinator functional groups (eusocial bees, solitary bees, and syrphid flies) contributed differing proportions of total visitation to each species depending upon neighborhood context. Consequently, in exotic neighborhoods *H. radicata* competed with native *M. laciniata*, reducing seed set, while simultaneously facilitating visitation and seed set for native *E. lanatum*. Seed set of *H. radicata* was also highest in exotic neighborhoods (with high densities of conspecifics), raising the possibility of a positive feedback between exotic abundance and success. Our results suggest that the outcome of indirect interactions between native and exotic plants depends on the density and the composition of the floral neighborhood and of the pollinator fauna, and on context-dependent pollinator foraging.

Conservation of native plants in invaded landscapes requires an integrated understanding of how native and exotic plants interact, including their indirect interactions. Co-occurring native and exotic plants often interact indirectly through shared generalist pollinators. The foraging choices made by pollinators determine the likelihood that a native or exotic individual will receive pollinator visits, as well as the likelihood that conspecific pollen transfer will take place. Exotic plant species' effects on pollinator foraging can thus result in competitive or facilitative effects on native seed production (Caruso and Alfaro 2000, Chittka and Schürkens 2001, reviewed by Bjerknes et al. 2007, Morales and Traveset 2009), potentially influencing plant community composition in future generations. A full understanding of the impacts of exotic species on native plant communities therefore requires understanding the pollinator-mediated effects an exotic species may have on native reproductive success.

How can exotic plant species influence pollinators? Invasion by exotic plant species can alter floral neighborhoods by changing floral density and diversity (Lázaro and Totland 2010b). These neighborhood characteristics are known to influence pollinator foraging behavior (Muñoz and Cavieres 1996, Kunin 1997, Bosch and Waser 2001, Ghazoul 2006, Bartomeus et al. 2008, Flanagan et al. 2010, Yang et al. 2011). Furthermore, foraging behavior in a given floral neighborhood can be contingent on pollinator identity, as pollinator groups may behave differently in the same floral environment (Stout et al. 1998, Lázaro and Totland 2010a, b). Though many studies have documented interaction between native and exotic plants through pollinator services, including the effect of floral density or diversity on pollination (McKinney and Goodell 2001, Moragues and Traveset 2005, Lopezaraiza-Mikel et al. 2007, Gibson et al. 2013), relatively few have examined how floral neighborhood influences multiple shared pollinators to shape the outcome of indirect native/exotic interactions (but see Lázaro and Totland 2010b).

To help fill this gap, we investigated indirect pollinator-mediated interactions between one exotic forb and two native forbs. We examined the effect of native–dense and exotic–dense floral neighborhoods on flower visitation by three groups of pollinators, and tracked plant reproductive success. We asked three questions: 1) does floral

neighborhood affect (a) total pollinator visitation rate and (b) community composition of pollinators visiting a given plant species? 2) Does reproductive success of a given plant species depend on floral neighborhood? 3) Can the relationship between floral neighborhood and reproductive success be predicted by changes to pollinator visitation or pollinator community composition?

Material and methods

Study site

We established a field experiment in Puget Trough prairies (western Washington, USA) in 2010. Formerly covering large areas from Oregon's Willamette Valley through western Washington and southwestern British Columbia, these prairies have undergone extensive fragmentation and habitat conversion, resulting in scattered remnants in small reserves (Dunwiddie et al. 2006). Puget Trough prairies are characterized by shallow, coarse soils with low nutrient levels, and are historically dominated by bunchgrasses and perennial forbs (e.g. *Festuca idahoensis, Camassia quamash*) (Dunwiddie et al. 2006, Ugolini and Schlichte 1973).

Species

We chose the exotic species *Hypochaeris radicata* and the native species *Microseris laciniata* and *Eriophyllum lanatum* (Asteraceae). All are perennial forbs that are abundant at our field site. *Hypochaeris radicata* thrives even where management by mowing or burning has limited the recruitment of other invasive plants, and is often found in high densities interspersed with native forbs (Waters unpubl.). We expected that these species would interact via their pollinators, because 1) they share similar floral symmetry, as well as capitulum shape, size, color (to the human eye), and reward accessibility (Supplementary material Appendix A1 Fig. A1), 2) they share generalist pollinators, and 3) they overlap in flowering time (*M. laciniata* overlapped in flowering time with *H. radicata* by at least four weeks during spring/summer 2010, while *E. lanatum* overlapped with *H. radicata* by at least six weeks).

Experimental design

We established 30 5 × 5 m plots in an approximately 38-ha area of Glacial Heritage Preserve in Littlerock, Washington, in March 2010 in which to monitor pollinator visitation and seed set of focal species. Plots were no closer to each other than 5 m and no farther than 10 m. The area in which plots were established had been managed by mowing and burning one year previously to reduce densities of other exotic species (not included in this study). At the time of the study, the site was dominated by native forbs (but our focal exotic was still present, occasionally in high abundance). We chose 5 × 5 m plots as a reasonable estimate for the dimensions of a floral neighborhood that would affect reproductive success of focal plants. Tracking of individual bumble bees at the site showed that most bees moved < 3 on average for multiple flower visits before taking longer (>5) flights (Waters and C. Chen unpubl.). We had previously observed eusocial bees, solitary bees, and flies visiting Asteraceae species at the site, and used bumble bee observations to scale neighborhoods because they had some of the largest foraging ranges of our pollinator species. Distances traveled by pollinators between conspecific flowers during a foraging bout are generally small; Waser (1982) found that > 85% of bee individuals visiting three nectar-providing forbs traveled less than 10 m to the next flower, regardless of body size or species. Similarly, Widén and Widén (1990) observed a mean pollen dispersal distance of 5.9 m in an herb visited by bumble bees and syrphids. Finally, Jakobsson et al. (2009) found that a substantial portion (25%) of the variation in pollinator visits and pollen deposition to two forbs was explained by the floral neighborhood within a 3-m diameter circle. We used this information to scale our floral neighborhoods accordingly.

To evaluate the effect of floral neighborhood on pollinator visitation and resulting seed set, we established three treatments (Fig. 1), each with 10 replicate plots: (1) 'Native' neighborhoods with a naturally occurring high density of focal native forbs and low density of *H. radicata*; 2) 'Exotic' neighborhoods with a naturally occurring high density of *H. radicata* and low density of focal native forbs; and 3) 'Clipped exotic' neighborhoods originally with a high density of *H. radicata* and low density of natives, manipulated to produce low *H. radicata* floral density by
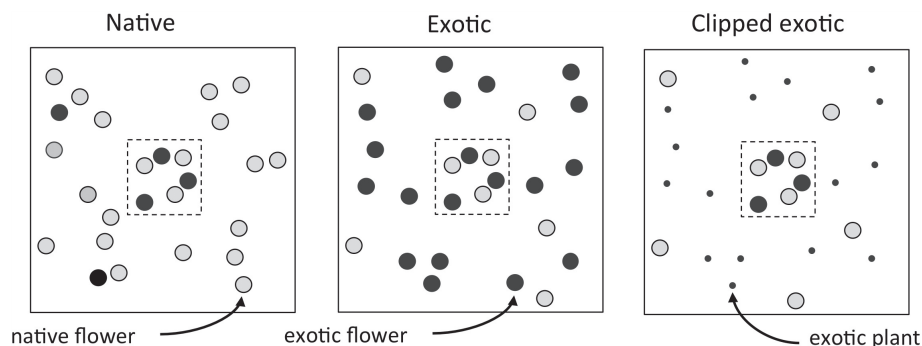

Figure 1. Experimental design, showing focal native and exotic individuals in center of 5 × 5 m plots, in three different floral neighborhoods: native-dominated (high native/low exotic floral density), exotic-dominated (high exotic/low native floral density), or exotic-dominated but clipped (low exotic/low native floral density) neighborhoods.

semiweekly clipping and removal of inflorescences throughout the season. All plots contained both native species, as well as *H. radicata,* and we retained three *H. radicata* individuals, each with a single unclipped inflorescence, in 'Clipped exotic' plots (for experimental treatments). Both types of exotic plots were centered in areas with >10 *H. radicata* individuals m^{-2} (mean inflorescences m^{-2} over season >15.5), and additionally constrained to locations where at least three individuals of *E. lanatum* and *M. laciniata* occurred in the center of the plot. 'Native' plots were randomly interspersed with the 'Exotic' and 'Clipped exotic' plots, but centered in areas with $<$ four *H. radicata* individuals m^{-2} (mean inflorescences m^{-2} over season <5.6), where density of native forbs was concomitantly high.

Clipped treatments allowed us to examine the effects of reduced *H. radicata* floral density when densities of the two native flowers were also naturally low; we did not include a treatment clipping native flowers because of conservation concerns. Our treatments allowed us to compare high native/low exotic floral density, high exotic/low native floral density, and low native/low exotic floral density. By comparing native versus clipped exotic plots, we could investigate the effect of changing native floral density only, while controlling for exotic floral density; by comparing exotic versus clipped exotic, we could similarly investigate the effect of changing only exotic floral density while controlling for native floral density. Biweekly floral censuses of plots verified that clipping treatments and plot selection did result in the desired floral neighborhoods (Supplementary material Appendix A1 Table 1A). Finally, though floral composition was not identical among plots, the three focal species generally occupied the top three abundance ranks during our experiment. The next most abundant species, *Campanula rotundifolia*, did not share pollinators with *E. lanatum*, and reached its peak bloom after *M. laciniata* bloom was over, making it unlikely to interact with either native species through pollinators.

Pollination services

Pollinator visitation was observed in all plots for each species. We counted visitors per 10 minutes within a 1-m^2 square randomly selected in the plot, recording the number of inflorescences watched to estimate visitation per flower. Visits were counted only if there was contact between visitor and stigmas or anthers (Kearns and Inouye 1993). Visitors were categorized as eusocial or solitary bees, or syrphid flies (we observed no other flies and no Lepidoptera visits). Each plot was observed a minimum of three and maximum of five times during the season, on sunny or partly sunny days, when the temperature exceeded 18°C.

To assess the importance of pollinators to plant female fecundity, we asked whether seed production depended on pollinator access to flowers. We did this by comparing seed production of three self-pollinated to three open-pollinated inflorescences for each species in each of the plots. Inflorescences were on different individual plants. The self-pollination (autogamous) treatment consisted of bagging an unopened inflorescence with a breathable nylon bag, securing it with a twist tie, and collecting seed after

ample time for seed maturation. Open pollinated replicate individuals served as controls and were left unbagged. Seed was collected at the end of the season (mid July), when seed from nearby non-experimental individuals at the site had already been released and dispersed by wind. All mature seed (based on seed plumpness in *H. radicata* and on color and plumpness in *E. lanatum* and *M. laciniata),* was counted and weighed.

Statistical analysis

We used generalized linear mixed effects models (R package *lme4*, Bates and Maechler 2008) to test whether pollinator visitation rate depended on the plant species being visited (*E. lanatum* vs *M. laciniata* vs *H. radicata*), the neighborhood treatment in which the plant was growing (native, exotic, clipped exotic), and an interaction between the two. We repeated this analysis for rates of visitation by each pollinator functional group (eusocial bees, solitary bees and flies) as well as for total visitation rate (across all functional groups). Because the total number of flowers we watched in each plot varied, we included this as a covariate in analyses. We used a Poisson distribution (with a log-link), and designated plot as a random effect in these models, to account for non-independence of data collected from the same block and species (Crawley 2007). We explored more complicated random effect structures (e.g. species within plot random effects), as recommended by Zuur et al. (2009), but Akaike information criterion (AIC) values indicated these were not necessary. For each response variable (eusocial bee, solitary bee, fly, total), we constructed five possible mixed effects models representing different combinations of explanatory variables; 1) only flowers watched (the covariate); 2) flowers watched and species identity; 3) flowers watched and neighborhood; 4) flowers watched, species and neighborhood; and 5) flowers watched, species, neighborhood and a species × neighborhood interaction. We selected the model with the lowest AIC value as the best fitting model, and used likelihood ratio tests (LRT) between this best fitting model and models missing only the explanatory variable of interest to determine significance of coefficients. We also performed post hoc general linear hypothesis tests (using function glht in R, allowing for Tukey's HSD comparisons of groups in mixed effects models), to determine which treatment × species combinations were significantly different from each other.

Analysis for seed production was carried out similarly, also comparing five models: 1) a null model with only random effects; 2) neighborhood only as an explanatory variable; 3) plant species only; 4) neighborhood and species; and 5) species, neighborhood, and their interaction. Finally, we also used mixed effects models to test whether the production of seed in controls versus pollinator exclusion treatments differed across treatment groups, again with plot as a random effect.

Generalized linear models described above allow us to determine how individual pollinator functional group visitation or total visitation is influenced by native versus exotic floral neighborhoods, but do not allow us to determine how and whether pollinator community composition is influenced by neighborhoods (regardless of impacts on the number of visits). Therefore, we also used multinomial

likelihood model fitting to determine how floral neighborhoods and species identity influenced the proportion of eusocial bees versus solitary bees versus flies visiting each plant species. This could only be done for pollinator visitation data where at least one pollinator was observed, reducing our data set by approximately half. We constructed four models; 1) a null model where the proportion of pollinator functional group visits did not vary by species or neighborhood; 2) a model in which pollinator functional groups varied across species (but not neighborhoods); 3) a model in which pollinator functional groups varied across neighborhoods (but not species), and 4) a model in which the probability of observing pollinator functional groups depended both on the identity of the flower visited and on the surrounding neighborhood. We used AIC values to assess which of these four models best explained observed pollinator communities.

All analyses were performed in R ver. 2.14.2 using the lmer function in the lme4 package (for mixed effects models), glht in the multcomp package (for post hoc tests) and dmvt in the mvtnorm (for maximum likelihood model fitting).

Results

Inflorescences in native floral neighborhoods were visited at a higher rate than in exotic neighborhoods (Fig. 2). Pollinator visitation rates were generally low, and varied by plant species, by neighborhood, and by their interaction (likelihood ratio test (LRT), $p < 0.001$, Table 1, Fig. 3). For example, *Microseris laciniata* received significantly more pollinator visits per inflorescence per hour than *Eriophyllum lanatum* and *Hypochaeris radicata* in all neighborhoods ($p < 0.001$, Tukey's HSD test for both pairwise comparisons, Fig. 3h vs 3d, l), and clipped exotic neighborhoods tended to have lower visitation per hour than both native and exotic neighborhoods, though visitation differed significantly only between clipped exotic and exotic (clipped exotic vs exotic, $p = 0.021$; clipped exotic vs native, $p = 0.359$; Tukey's HSD test, Fig. 2). However, neighborhood effects on pollinator visitation varied by species: visitation rates to *E. lanatum* and exotic *H. radicata* were higher in exotic neighborhoods (Fig. 3), while visitation rate to *M. laciniata* was significantly higher in native neighborhoods (Tukey's HSD test, native vs exotic, $p < .001$; native vs clipped exotic, $p = 0.015$; Fig. 3a–c). Including Shannon–Wiener floral
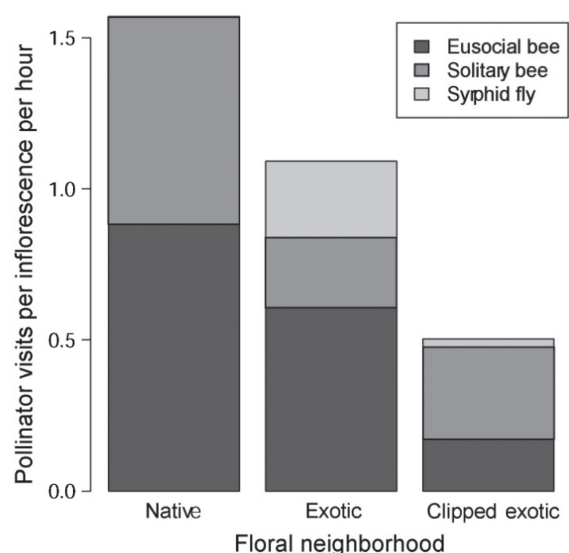

Figure 2. Mean pollinator visitation rates per inflorescence per hour by three pollinator functional groups: eusocial bees (black), solitary bees (gray), and syrphid flies (light gray) in three floral neighborhoods (Native: high native floral density; Exotic: high exotic floral density; and Clipped exotic: low exotic floral density produced by clipping exotic inflorescences). Visitation differed significantly between neighborhoods for most groups ($p = 0.049$ eusocial bees; $p = 0.933$ solitary bees; $p = 0.044$ syrphid flies; $p = 0.013$ all pollinators).

diversity in models of pollinator visitation did not improve model fit (LRT, $p = 0.746$).

Visitation rates to each plant species by individual pollinator functional groups, as well as by all pollinator groups together, were affected by plant species, by floral neighborhood, and by their interaction (Table 1). In addition, pollinator functional group composition varied by treatment: for each plant species, neighborhood had a significant effect on the community of visiting pollinators observed (LRT, Table 1, Fig. 4). For example, flies preferentially visited *E. lanatum*, but their visitation rate depended on neighborhood. Thus, a much higher proportion of visits to *E. lanatum* in exotic neighborhoods than in other neighborhoods came from flies (Fig. 3c). Eusocial bees also visited *H. radicata* and *M. laciniata* in a neighborhood-dependent fashion. *H. radicata* received the most frequent eusocial bee visits in exotic floral neighborhood treatments

Table 1. AIC values for alternative models explaining pollinator visitation rate[a] (number of visits per inflorescence per hour by solitary bees, euscocial bees, syrphid flies or all pollinators) and pollinator communities[b] (proportion of visits by solitary bees, eusocial bees or flies) as a function of plant species identity and floral neighborhood (and their interaction). AIC values of best fitting models in bold.

Model	Pollinator visitation rate[a] (number of flowers watched as a covariate)				Pollinator communities[b]
	Solitary bees	Eusocial bees	Syrphid flies	Total visits	
1. Null (intercept only)	257.79	681.40	137.03	765.17	678.42
2. Plant species	256.08	390.93	97.89	543.72	494.64
3. Neighborhood	261.31	684.38	135.73	768.42	636.46
4. Plant species + Neighborhood	259.76	391.18	95.03	544.15	NA
5. Plant species × Neighborhood	**245.66**	**353.71**	**91.09**	**499.29**	**436.67**

[a]Pollinator visitation rate models are generalized linear models with a Poisson distribution and log link, using plot as a random effect.
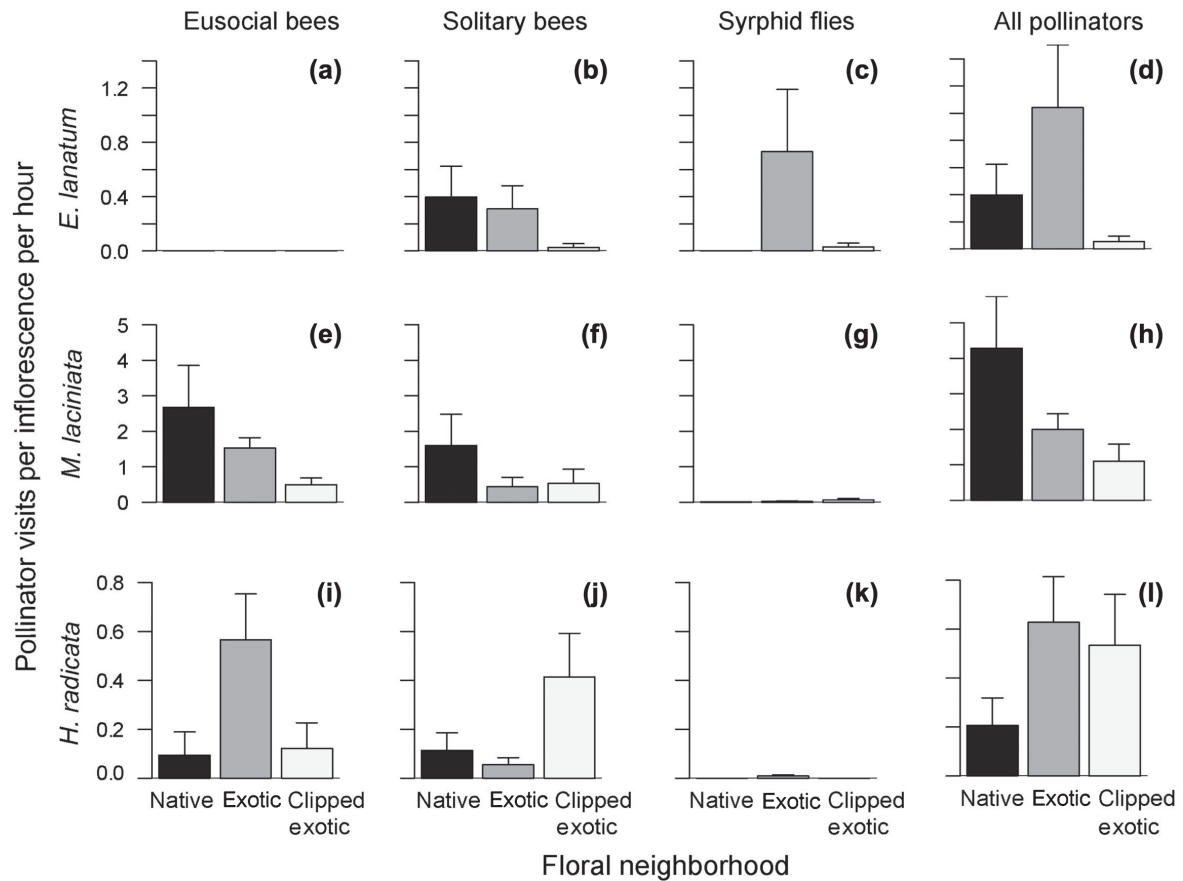[b]Pollinator community models are fit using multinomial likelihood methods.

Figure 3. Pollinator visitation rates per flower (mean + SE) to native prairie forbs *E. lanatum* (a–d) and *M. laciniata* (e–h) and exotic prairie forb *H. radicata* (i–l) by large eusocial bees, small solitary bees, flies, and all pollinators in the three floral neighborhoods (black: Native, high native floral density; gray: Exotic, high exotic floral density; and light gray: Clipped exotic, low exotic floral density produced by clipping exotic inflorescences). Total pollinator visitation differed significantly by floral neighborhood, plant species, and their interaction ($p < 0.001$ for all explanatory variables).
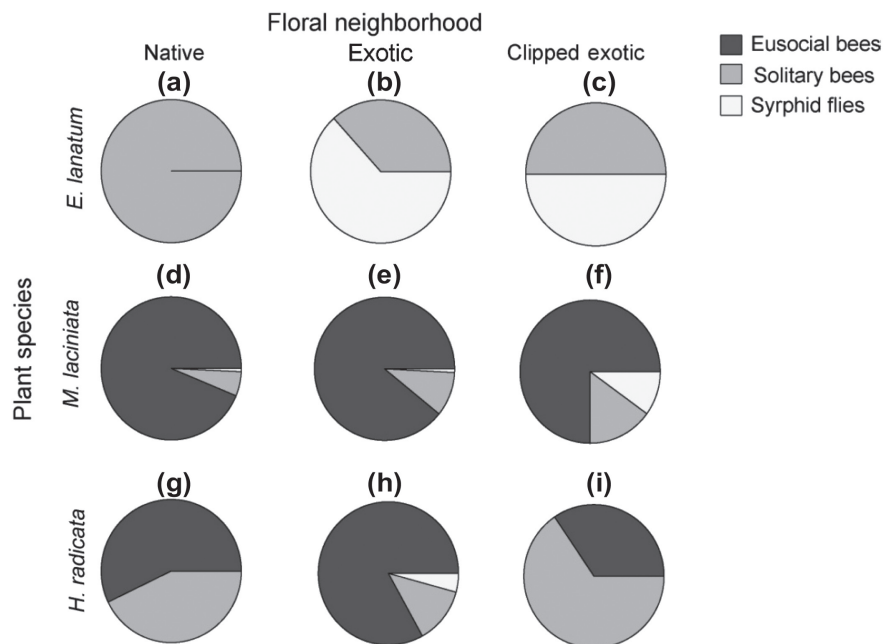
Figure 4. Pollinator communities visiting natives *E. lanatum* (a–c) and *M. laciniata* (d–f) and exotic *H. radicata* (g–i). Pie charts represent the proportion of eusocial bees (black), solitary bees (gray) and flies (light gray) visiting each plant species in Native (a, d, g), Exotic (b, e, h) and Clipped exotic neighborhoods (c, f, i).

(Fig. 3h vs 3g,i), while eusocial bee visitation to *M. laciniata* was most frequent in native neighborhoods (Fig. 3d).

Seed set per inflorescence also varied by floral neighborhood, plant species, and their interaction (p < 0.001 for all explanatory variables). Mean seed set for *M. laciniata* differed significantly in all neighborhoods and was higher in native than exotic and clipped exotic neighborhoods (Fig. 5, Tukey's HSD test, native vs exotic, p < 0.001, native vs clipped exotic, p = 0.015, exotic vs clipped exotic, p = 0.003). Mean seed set of *E. lanatum* was highest in exotic neighborhoods, which differed significantly from clipped exotic (p < 0.001), but not native (p = 0.276) neighborhoods (Tukey's HSD test, Fig. 5). Mean seed set of *H. radicata*, by contrast, did not vary significantly among floral neighborhoods (Fig. 5).

Data from pollinator exclusion treatments showed that pollinator services increased *M. laciniata* and *H. radicata*

Figure 5. Effect of floral neighborhood on seed production (mean ± SE) for three species of prairie forbs in spring and summer 2010: (a) native *E. lanatum;* (b) native *M. laciniata*; (c) exotic *H. radicata*. Black: Native neighborhood, high native floral density; gray: Exotic neighborhood, high exotic floral density; and light gray: Clipped exotic neighborhood, low exotic floral density produced by clipping exotic inflorescences). Seed production differed significantly by neighborhood for *M. laciniata* and *E. lanatum,* but not for *H. radicata*. Different letters indicate significant differences between neighborhoods calculated using glht/Tukey's HSD test.

seed set regardless of neighborhood (Tukey's HSD test, selfing vs other treatments p < 0.001 *H. radicata*, p < 0.001 *M. laciniata*). When excluding pollinators, seed production was minimal for *H. radicata* in all neighborhoods (mean = 0.30 + 0.14 seeds per capitulum) and reduced by more than half for *M. laciniata* (mean 11.0 + 2.3 seeds per capitulum). Pollinator exclusion treatments were not successful for *E. lanatum* because wet nylon bags broke fragile stalks, and this data was eliminated from analysis.

Discussion

Overall, our study demonstrates that pollinator-mediated interactions between native and exotic plants are influenced by floral neighborhoods, affecting seed set, and consequently that neighborhood-contingent interactions are likely to be important to the conservation and restoration of native plants. Specifically, we found that pollinator visitation to co-occurring native and exotic plants varied by floral neighborhood, with exotic floral neighborhoods having both competitive and facilitative effects on pollinator visitation to natives. In addition, major pollinator functional groups shifted their visitation patterns individualistically by floral neighborhood. As a result, seed set of both native species was neighborhood-contingent.

We found opposite effects of the exotic floral neighborhood on visitation and seed set of the two native species (Fig. 3d, h, i). Others have found that plants sharing pollinators can have negative, positive or neutral indirect effects on each other's pollinator visitation (Laverty 1992, Aigner 2004, Moeller 2004, Ghazoul 2006, Hegland and Boeke 2006, Bjerknes et al. 2007, Hegland et al. 2009, Kaiser-Bunbury 2009, Morales and Traveset 2009); we observed a single exotic species exerting both positive and negative indirect effects simultaneously. Our results must be viewed with caution because our study encompasses a single pollinator community, and further studies are needed to document this phenomenon across multiple locations. However, such mixed responses by natives, if applicable across many sites and communities, could complicate restoration, as removal of exotics will therefore not necessarily benefit all native species.

The visitation and seed set patterns we observed can be explained by floral neighborhood treatments affecting pollinator groups differently, as others have also observed (Lázaro and Totland 2010b, Sieber et al. 2011, Yang et al. 2011). Syrphid flies demonstrated foraging preferences at the neighborhood level, entering only exotic neighborhoods, where they solely visited native *Eriophyllum lanatum*. In contrast, eusocial bees showed less preferential selection of foraging neighborhood, but once present, their foraging behavior differed in neighborhoods of different composition. These pollinator-specific, neighborhood-contingent behaviors resulted in opposite effects of *Hypochaeris radicata* on the two natives: *H. radicata* competed with *Microseris laciniata* for eusocial bee pollinators, and simultaneously attracted syrphid flies to the neighborhood, where they visited only *E. lanatum*. Neighborhood-specific visitation rates by different pollinator types probably also resulted in differential pollinator contributions to seed production in different neighborhoods.
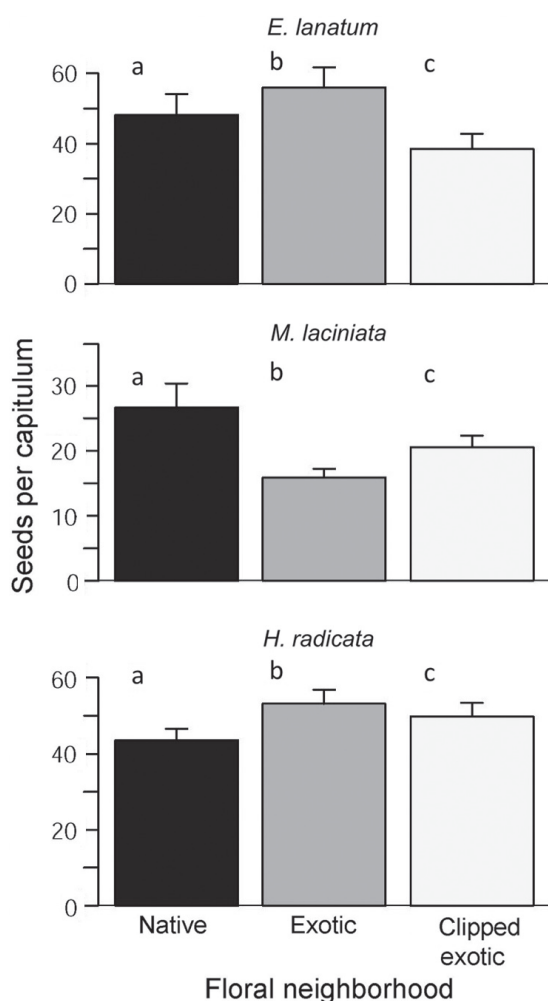
Though conspecific floral density is known to affect pollinator visitation, it is unlikely that it was the only aspect of floral neighborhood responsible for visitation to the two native species. Native plots had higher densities of *E. lanatum* and *M. laciniata* (Supplementary material Appendix A1 Table 1A), and these more attractive floral displays could attract more pollinators, particularly for *M. laciniata.* However, *E. lanatum* received significantly fewer visits in Native plots, despite higher floral densities there (Supplementary material Appendix A1 Table 1A). If this resulted from increased intraspecific competition (Wirth et al. 2011) we would have expected higher visitation in both Exotic and Clipped exotic plots, not just the Exotic treatment, since *E. lanatum* density was low in both. Thus, we believe floral neighborhood differences in exotic, not conspecific, floral density were responsible for the patterns of pollinator visitation to *E. lanatum.* Pollinator visitation to the exotic species, *H. radicata,* was also contingent on floral neighborhood, but appeared independent of exotic (conspecific) floral density, since visitation was almost as frequent in the Clipped exotic (low exotic/low native floral density) as in the Exotic (high exotic/low native floral density) treatments.

Neighborhood effects on seed production suggest that the net indirect effect of *H. radicata* invasions could be negative for native Puget Trough plant communities, for two reasons. First, the impacts of *H. radicata* on *M. laciniata* seed production were more strongly negative than the positive impacts of *H. radicata* on *E. lanatum* seed set. Second, the influence of exotic *H. radicata* on pollinators could result in increasingly greater per capita seed production as its invasion proceeds, as its seed production per inflorescence was greater in exotic (already invaded) neighborhoods. Increased seed production will not necessarily lead to *H. radicata* population increase unless rates of other key processes such as seed predation, germination, seedling survival, and density-dependent flower and seed production permit (Price et al. 2008, Waser et al. 2010), but an increased seed supply nevertheless creates a potential for future population expansion. Finally, the influence of *H. radicata* invasion is not limited to the pollinator-mediated indirect interactions we have documented here, since *H. radicata*, is also known to be a strong competitor with native plant species for soil resources (Fisher unpubl.). This could result in a positive feedback that increases invasion rates over time.

Our data paint a picture of a network in which plant-pollinator interaction strengths could be highly spatially variable and mediated by neighborhood-contingent, individualistic pollinator behaviors. One implication is that shifts in abundance of pollinator types could result in flipping of the native/exotic plant indirect interaction sign, changing the local effect of the exotic species on natives. The composition of pollinator fauna shared by coflowering plant species (including natives and exotics) is known to vary substantially from season to season (Alarcón et al. 2008, Petanidou et al. 2008), suggesting that variation in this interaction sign could be common; for example, a season with low syrphid abundance would switch the effect of exotic neighborhoods on *E. lanatum* from positive to neutral (Fig. 3b–d). More broadly, this suggests that recent pollinator declines could interact synergistically with invasion to produce complex and potentially unexpected impacts on native plant communities.

From an applied perspective, these neighborhood effects imply that restoration planners should consider whether exotic plants have both competitive and facilitative indirect effects on native plants of management concern. Indiscriminate elimination of an exotic species could lead to unintentional creation of floral neighborhoods not conducive to pollination of some native species, some of which may be rare to start with. This is an especially important consideration when insect-pollinated native plant populations are seed limited, as is often the case with rare plants. Removal of exotic floral resources could also have negative demographic effects on pollinators that could feed back to affect native plants in unexpected ways. Conservation practitioners should endeavor to consider pollinator-mediated indirect interactions between native and exotic plants when creating conservation and restoration plans.

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