POLLINATOR VISITS TO THREATENED SPECIES ARE RESTORED FOLLOWING INVASIVE PLANT REMOVAL

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An indirect consequence of plant invasions is the disruption of native plant-pollinator interactions. We examined effects of invasive baby's breath (*Gypsophila paniculata*) and spotted knapweed (*Centaurea maculosa*) on floral visitors to federally threatened Pitcher's thistle (*Cirsium pitcheri*) in Lake Michigan dunes. In sweep net surveys, abundances of pollinator taxa were five times higher in invaded than in naturally invader-free sites. However, plot-level *G. paniculata* removal treatments increased pollinator visits to *C. pitcheri* relative to invaded plots and restored visitation to levels found in naturally uninvaded plots. Invader removal also increased native plant species richness, which was positively correlated with pollinator visitation to *C. pitcheri*, suggesting an indirect effect on pollinators mediated through invader-altered plant composition. In temporary floral arrays, the rate of pollinator visitation to *C. pitcheri* was not affected by neighbor plant species identity. However, compared with native *Monarda punctata*, invasive *C. maculosa* attracted more total pollinators to the array but reduced the proportion of total visits that were to *C. pitcheri* and increased pollinator movements between plant species. While both *G. paniculata* and *C. maculosa* appear to act as magnet species by attracting more pollinators at the plot level, these invaders have the potential to reduce reproduction of *C. pitcheri* by decreasing pollinator visits and increasing interspecific pollen transfer.

Keywords: *Cirsium pitcheri*, *Gypsophila paniculata*, pollination competition, conservation, restoration, invasive.

Online enhancements: appendix tables.

Introduction

Invasive species pose a threat to the biodiversity of native communities and incur major ecological and economic costs worldwide (Mack et al. 2000; Pimentel et al. 2000; Mitchell et al. 2006). Invaders can exact a heavy toll on biodiversity: competition, predation, parasitism, and herbivory by nonnative species have been estimated to threaten 40% of the species on the U.S. endangered species list (Ricklefs 2001). Most previous studies of invasive plants have focused on their impacts on the native plant community. When possible mechanisms have been explored, prior research has primarily targeted direct, competitive interactions between invasive and native plants (Levine et al. 2003).

One indirect consequence of plant invasions may be the disruption of native plant-pollinator interactions. A recent meta-analysis of plant-plant interactions mediated by pollinators found that nonnative plants have, on average, a negative impact on pollinator visitation to native focal species and that both nonnative and native coflowering plants can reduce the reproductive success of native plants (Morales and Traveset 2009). Some examples deviate from this general pattern. For example, in stands invaded by *Carpobrotus* spp., pollinator

visitation to two coflowering native species was elevated relative to invader-free stands (facilitation; Moragues and Traveset 2005).

Several mechanisms may underlie the effects of invaders on native plant reproduction via altered plant-pollinator interactions. First, nonnative plants may reduce the frequency of pollinator visits to native species, as has been demonstrated for invasive and native loosestrife (*Lythrum* spp.; Brown et al. 2002). Second, invasive plants may act alternatively as pollinator magnets (Thomson 1978), attracting insects to patches including native plants. Third, transfer of nonnative pollen to native plants may interfere with native seed production (Brown and Mitchell 2001; Morales and Traveset 2008; Cariveau and Norton 2009). Interspecific pollen transfer may limit fertilization in the focal species by causing premature stigma closure (Waser and Fugate 1986) or stigma clogging, by reducing the amount of conspecific pollen received by individuals (Campbell and Motten 1985; Cariveau and Norton 2009), or by inhibiting fertilization through allelopathy (Murphy and Aarssen 1995). Fourth, transfer of native pollen to nonnative plants could reduce male fitness of native species through the loss of pollen and female fitness through increased pollen limitation (Morales and Traveset 2008). Finally, the quality of pollination services could decrease if an invasive plant altered pollinator behavior or pollinator community composition; the latter could, for example, result in less efficient pollinators for native species (Dohzono et al. 2008). **Q1**

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The number of studies examining the impacts of invasive plants on pollination of native plants is growing, but thus far, few studies have directly manipulated the presence of the invader (Chittka and Schurkens 2001; but see Aigner 2004; Totland et al. 2006; Cariveau and Norton 2009). Manipulation is necessary to assign causality to the invader. The net effect on a pollinator can derive from a combination of direct effects due to the presence of the invader (i.e., the effect of invader flowers on pollinators) and indirect effects due to invader-mediated changes in the plant community (e.g., if invasion also alters plant competition for resources). To our knowledge, these indirect effects on pollinators, mediated through changes in the plant community, have not been examined to date (see also Levine et al. 2003).

Here, we examined pollination interactions among invasive and native plant species on primary successional sand dunes (Cowles 1899), a system in which plant-pollinator communities have been relatively understudied. On dunes of the Great Lakes in the midwestern United States, our focal native plant species, Pitcher's thistle (*Cirsium pitcheri*), is federally threatened (Pavlovic et al. 2002). Thus, it is important from a conservation standpoint to understand how this plant is affected by nonnative plant invasions, particularly the highly abundant invader baby's breath (*Gypsophila paniculata*). Furthermore, rare species may be particularly susceptible to competition for mutualists (Palmer et al. 2003). The freshwater dune system contains relatively few animal-pollinated plants; thus, high densities of the invader *G. paniculata* may increase the amount of floral resources available to insect pollinators, particularly because *G. paniculata* produces thousands of flowers per individual (Darwent and Coupland 1966). Therefore, we hypothesized that pollinators would be more abundant in invaded areas but that they would switch from *C. pitcheri* to the new resource of *G. paniculata*, thereby reducing visitation to the threatened native plant.

Using field observations, we asked: (1) Are abundances of putative pollinator taxa higher in areas invaded by *G. paniculata* than in uninvaded areas, as predicted by the magnet hypothesis (Laverty 1992; Thomson 1978)? Next, to explicitly quantify effects of *G. paniculata* presence on pollinator visitation to *C. pitcheri*, we conducted a field experiment that addressed the following questions: (2) Are floral visitation rates to *C. pitcheri* higher in areas where *G. paniculata* has been removed compared with invaded areas? (3) Does removal of *G. paniculata* restore floral visitation to *C. pitcheri* to levels found in naturally uninvaded areas? Although *C. pitcheri*'s threatened status precluded our ability to obtain measurements of reproductive success, we evaluated impacts of invader presence on visitation rates and the composition of putative pollinators. While changes in pollination services do not necessarily alter plant reproductive success, Loveless (1984) showed that insect-mediated cross-pollination increased seed set over self-pollinated individuals and also suggested that concurrent declines in insect visitation and seed set over the flowering season of *C. pitcheri* indicated pollinator limitation. We also asked: (4) Do impacts of *G. paniculata* on pollinators of *C. pitcheri* correspond to direct effects of enhanced floral resources and/or to indirect effects of invader-induced changes in the plant community? We addressed this question by comparing plots in which we clipped

the flowers from all *G. paniculata* with plots with *G. paniculata* individuals removed and by evaluating statistical relationships between native plant composition and pollinator visitation. Finally, in a second experiment, we observed pollinator visitation rates to *C. pitcheri* surrounded by temporary experimental arrays of native or nonnative flowers to address the following question: (5) What is the relative importance of floral identity versus floral density in affecting insect visitation to *C. pitcheri* flowers?

Material and Methods

Study Site and Species

Sites were located in Sleeping Bear Dunes National Lakeshore (SBDNL; Leelanau Co., 44°N, 86°W) and the Nature Conservancy's (TNC) Zetterberg Preserve at Point Betsie (Benzie Co., 44°41′N, 86°15′W) in northern Michigan. All sites consisted of open dune habitat. Common grasses included *Ammophila breviligulata*, *Calamovilfa longifolia*, and *Schizachyrium scoparius*, and woody shrubs included *Prunus pumila*, *Juniperus horizontalis*, *Artemisia campestris*, and *Arctostaphylos uva-ursi*. Common insect-pollinated forbs were *Cirsium pitcheri*, *Asclepias syriaca*, *Monarda punctata*, *Lithospermum caroliniense*, *Lathyrus japonicus*, and three nonnative species: *Gypsophila paniculata*, *Centaurea maculosa*, and, less commonly, *Silene vulgaris*.

Our focal native species was *C. pitcheri* (Pitcher's thistle, (Eaton) T. & G., Asteraceae), a monocarpic perennial thistle that flowers after a 5–8-yr juvenile stage, producing a creamy or pink inflorescence 2–5 cm in diameter (Hamze and Jolls 2000). It is listed as federally threatened by the U.S. Fish and Wildlife Service (Pavlovic et al. 2002). Bagging experiments have shown that *C. pitcheri* can self-pollinate, but insect-mediated cross-pollination results in higher seed set (Loveless 1984). Flowering begins in late June and peaks in mid-July, and most individuals have senesced by early August (Loveless 1984). Inflorescences produce pollen and nectar for 3–4 d, and the main pollen vectors include (in no particular order) bumblebees (*Bombus* spp.), megachilid bees (*Megachile*, *Dianthidium*), anthophorid bees (*Melissodes* spp.), halictid bees (*Lasioglossum* spp. and *Agapostemon* spp.), butterflies, and skippers (Loveless 1984, personal observation).

Our focal invasive species was *G. paniculata* L. (Caryophyllaceae), a perennial herb that produces small white flowers (6–8 mm in diameter) arranged in panicle-like compound dichasiums (Darwent and Coupland 1966). An individual is capable of producing >13,000 seeds (Stevens 1957), and the species is listed as a noxious weed in the United States (USDA and NRCS 2009). Flowering begins in late June and mostly ends by early August. Bagging experiments showed that *G. paniculata*'s reproductive success (fertilization rate and seeds per capsule) is significantly enhanced by insect pollination; self-pollination was virtually nonexistent (data not shown). The mean number of flowers per individual observed was 9034 ± 1158 SE in 2008. In some areas of the dunes, *G. paniculata* comprises 80% of all vegetation and may not only outcompete native plants for resources via its deep root system but also overstabilize dune habitat, making it unsuitable for native species (Karamanski 2000). At some of our

sites, densities of *C. pitcheri* were reduced in areas dominated by *G. paniculata* (S. M. Emery, unpublished data).

Pollinator Survey

In July 2007, we established 20×50-m plots across 15 sites: four invaded by *G. paniculata*, five uninvaded by *G. paniculata*, and six invaded by *G. paniculata* but slated for removal treatments in spring 2008 (GPS coordinates provided in table A1 in the online edition of the *International Journal of Plant Sciences*). Initial densities of *G. paniculata* in invaded sites before management ranged from 30% to 70% cover. These plots were part of a larger project to monitor the response of plant, insect, and soil communities following *G. paniculata* removal. For the removal treatment, crews from TNC and SBDNL removed large *G. paniculata* individuals manually with shovels by cutting the taproot below the root crown and used localized herbicide sprays for young individuals in May 2008 (Roundup Weathermax, Monsanto, St. Louis). In Sleeping Bear Dunes National Lakeshore (total area of 288 km^2), *G. paniculata* was estimated to cover 5.6 km^2 in 2007. Crews cleared 0.7 km^2 in 2007 (13.7% of infested area) and 0.82 km^2 in 2008 (14.7% of infested area; S. Yancho, personal communication). In the Nature Conservancy's Zetterberg Reserve at Point Betsie, 0.23 km^2 were treated in 2007 and 2008, out of a total of 1.18 km^2 of infested area (20%; M. Kleitch, personal communication). The treatment itself may have disturbed native communities simply because of workers walking on the dunes. However, plant density is generally low on the dunes (average of 25 individuals/m^2 across all of our plots, including grasses, where a single tiller was counted as an individual), and the removal treatments were kept as localized as possible (i.e., only one individual at a time may be killed with a shovel). One year after removal (2009), *G. paniculata* densities ranged from 2% to 7% cover (S. M. Emery, unpublished data). *Cirsium pitcheri* individuals were relatively rare in *G. paniculata*–invaded sites both before and after management, with an average of 16.8 plants per 100 m^2 in both pretreatment (2007) and posttreatment (2009) surveys (S. M. Emery, unpublished data). Furthermore, we recorded the identities and densities of plant species in each of our plots.

In July 2007 and 2008, we sampled insect communities in each site by taking one sweep net sample (30.5-cm-diameter mesh net with 0.91-m handle) along each of five 20-m transects (spaced 10 m apart) within each plot. Samples were collected by walking along each 20-m transect and swinging the net from side to side at arm's length to collect all insects in nearby air and vegetation. All samples were collected on sunny, low-wind days after morning dew had evaporated. In the lab, we identified all individuals to family and morphospecies. More than 4400 insects representing 95 families were collected and identified. Although sweep net samples are not conventional methods for pollinator surveys (but see Moron et al. 2009), known pollinator families in these samples included a subset of the families we have commonly observed on *C. pitcheri*: Andrenidae, Apidae, Bombyliidae, Colletidae, Crabronidae, Halictidae, Megachilidae, and Syrphidae. Thus, we tested for effects of *G. paniculata* treatment on the abundance of insects in these pollinator families using one-way ANOVA. Data were square root transformed to meet assumptions of normality of residuals and homogeneity of variances.

Gypsophila paniculata *Removal Experiment*

Experimental treatments. To evaluate the effects of *G. paniculata* on pollination services to *C. pitcheri*, we applied four treatments to sites where *C. pitcheri* and *G. paniculata* co-occurred. Treatments manipulated the influence of *G. paniculata*: for the removal treatment we eliminated entire plants, and for the clipped treatment we removed *G. paniculata* flowers only. The invaded treatment consisted of areas with no disturbance or removal, and the uninvaded treatment consisted of naturally invader-free areas with little to no *G. paniculata*. Plot size per treatment ranged from 140 to 460 m^2 (average: 264 ± 20 SE) because in some locations, area was limited by surrounding landscape features (forests, hills, nondune vegetation). All plot-level data were standardized for plot area because we used quadrats to subsample within each plot (see "Plant community surveys"). Plots with the invaded, removal, and clipped treatments were established in each of five locations within TNC and SBDNL properties ($n = 5$ replicate plots per treatment, blocked by location; GPS coordinates provided in table A2 in the online edition of the *International Journal of Plant Sciences*). Naturally uninvaded areas could not be included in this blocked design because none were located near removal areas as a result of the large regional extent of the invasion. Thus, we established five separate plots in uninvaded areas, all of which were <30 km from the invaded areas. Work crews from TNC and SBDNL maintained removals of *G. paniculata* (as described above) for varying lengths of time at each site (table A2). All blocks experienced removal treatment in 2007 and 2008; three sites also had removals in 2005 or 2004. We applied the clipped treatment to remove possible effects of *G. paniculata* flowers on pollinators while keeping plant competition for space and belowground resources relatively intact. To clip the thousands of small *G. paniculata* flowers, stems were cut ~10 cm above the base, which did not kill the individual plants.

Insect observations. In each plot, four *C. pitcheri* individuals were randomly chosen and observed for 15 min each. Pollinator observations were conducted on warm sunny days between 0830 and 1730 hours from July 23 to July 31, 2008, during peak flowering for *G. paniculata*. Half of all trials were conducted before 1230 hours. During the observation period, we recorded the number and identity (family, morphospecies) of pollinators to *C. pitcheri* (visits per plant). For a second round of data collection, two *C. pitcheri* individuals per plot were observed for 15 min each. Within a census period, the order of observations for plots was randomized within a location, but the order of observed locations depended on geographic proximity.

Visitors that included potentially pollen-transferring taxa were treated as a proxy for pollinators (Kearns and Inouye 1993); hereafter, we use the term "pollinator" to refer to a visitor. An insect was counted as a pollinator if it landed on an inflorescence, since it was not possible to determine contact with the reproductive organs of the tiny Asteraceae flowers. Insects observed and classified as pollinators included the fol-

lowing orders and families: Hymenoptera, specifically Megachilidae (*Dianthidium simile*), Apidae (*Apis mellifera*, *Bombus* spp.), Colletidae, Crabronidae, Halictidae, and Vespidae; Diptera, specifically Bombyliidae and Syrphidae; and Lepidoptera, specifically Hesperiidae and Nymphalidae. Visits by ants (Hymenoptera: Formicidae) were not included, because ants can have a negligible or negative effect on pollination (Beattie et al. 1984).

Covariates. For each trial, we recorded time, temperature, wind speed (with an anemometer), and the number of *C. pitcheri* inflorescences per plant as potential covariates that may affect pollinators (Kearns and Inouye 1993). Wind speed (m/s) was recorded as an average over 1 min, and trials were not performed when wind speed exceeded 5.5 m/s; maximum wind speed during a trial was 4.6 m/s.

Statistical analyses. The distributions of the residuals of the visitation data were often nonnormal, and nonnormality could not be substantially reduced through transformations. Therefore, we used distribution-free randomization tests with 9999 iterations to evaluate treatment and covariate effects (Edgington 1987; Manly 1991). We applied a randomization test equivalent to a mixed general linear model by encompassing Proc MIXED code within an SAS (ver. 9.1; SAS Institute, Cary, NC) randomization macro program (Cassell 2002).

Two models were used to compare mean responses per plant per plot. In both models, the response variables were the number of pollinator visits per plant, pollinator morphospecies richness per plant, pollinator diversity (Shannon index) per plant, and the number of visits per plant by the most common pollinator, *D. simile*. The first model compared invaded, clipped, and removal plots that were blocked by location. This model included the random effects of location and plot (nested within location × treatment), the repeated factor of time, the fixed effect of treatment (invaded, clipped, or removal), and two covariates: wind speed and the number of inflorescences on the observed *C. pitcheri* plants. Treatment effects were tested over the variation between locations (i.e., $n = 5$ plots for testing the treatment effect). When the treatment effect in this model was significant, we followed up with the randomization test equivalent of a post hoc Tukey's honestly significantly different (HSD) test to determine which treatments significantly differed. We used a second model to compare uninvaded and removal plots. This model included the same factors as the first except that the random effect of location was nested within treatment because uninvaded and removal plots occurred at different locations.

Plant community surveys. Plots were surveyed for differences in plant community composition due to the invader treatments. We counted and identified plants within 1 × 1-m quadrats evenly spaced throughout each plot to survey ~5% of the total plot area. Randomization tests were applied as described for pollinators. The response variables were plant abundance, plant species richness, plant diversity (Shannon index), *C. pitcheri* abundance, and *G. paniculata* abundance. To avoid confounding treatment with plant community measures, these metrics excluded *G. paniculata*. We also tested whether removal of *G. paniculata* affected the number of inflorescences produced by *C. pitcheri* relative to invaded plots.

Direct versus indirect effects models. Effects of the *G. paniculata* removal treatment on pollinators could occur through a direct pathway as a result of the presence of *G.* *paniculata* individuals (e.g., because of its high density of flowers). Alternatively, effects could occur through an indirect pathway mediated by changes in the composition of the local plant community following *G. paniculata* removal. To further separate possible direct and indirect effects for pollinator responses, we added plot-level plant species richness or plant abundance as a covariate to our analysis of treatment effects. In these models with covariates, if the treatment effect remained significant, then results suggest a strong direct effect of the presence of the invader despite variation explained by covarying responses in the plant community (see also Rudgers and Clay 2008). In contrast, if addition of the covariate eliminated the significance of the treatment effect, this would indicate that effects of the treatment occurred largely indirectly through changes in plant community structure. We compared model fit using a model selection procedure and the bias-corrected Akaike's information criterion (AIC$_c$), which is adjusted for small sample sizes. Specifically, we compared the following models: (1) no covariate model, (2) covariate model, and (3) covariate plus covariate interaction with treatment model. We followed methods in Burnham and Anderson (2002) and applied the COMPMIX macro in SAS (ver. 9.1) to determine AIC$_c$.

Experimental Arrays Varying Density and Floral Identity

To compare the relative importance of plant species identity and plant density on pollinator visitation rates to *C. pitcheri*, we constructed temporary experimental flower arrays around naturally occurring *C. pitcheri* individuals in a separate site invaded by *G. paniculata* within SBDNL (Tiessma, 44°43′37N, 86°07′38W). We crossed a plant species identity treatment with a plant density treatment. The three plant species used were *G. paniculata* (nonnative), *C. maculosa* (nonnative), or *M. punctata* (native). *C. maculosa* is also an invasive species of concern on the dunes (Pavlovic et al. 2002) with relatively similar floral morphology to *C. pitcheri* (both are Asteraceae). *Monarda punctata* is common in the dune habitat and overlaps with *C. pitcheri* in flowering phenology more than do other common dune flowers. Plant density treatments consisted of two, four, or eight cut plants placed in PVC pipes around each target *C. pitcheri*. Density levels (1.6, 3.3, and 6.6 individuals/m² for low, medium, and high density, respectively) were chosen to mimic natural levels of variation in plant density at the site; across all of our plant surveys, the average density of each species was between 2 and 4 individuals/m². One control group was a single *C. pitcheri* plant alone (we could not perform density treatments for *C. pitcheri* because we were not permitted to clip the threatened species' inflorescences), and a procedural control consisted of empty PVC pipes arranged at each density to test for possible nontarget effects of PVC presence. Observations took place from late July to mid-August 2007. The use of invaded areas allowed for close proximity of all plant species used in the arrays, including the invader, which minimized wilting.

Arrays consisted of freshly cut stems of the appropriate species placed into 0.61-m-long PVC pipes with a 2.54-cm diameter. Pipes were hammered 0.3 m into the sand to situate the flowers at the same height as *C. pitcheri* flowers and within the range of natural flower heights for all of the plant

species tested. The PVC pipes were arranged around the edge of a 1.22-m^2 grid consisting of nine 0.135-m^2 squares, with *C. pitcheri* located in the center. For two- and four-density treatments, positions for the cut stems on the grid were chosen at random. Extra flowers were cleared from the immediate area surrounding each array (1-m radius). We standardized floral abundance as much as possible; thus, each focal *C. pitcheri* had 2–5 inflorescences at the time of observation, stems of *C. maculosa* had 5 inflorescences, *M. punctata* had two stems with 15–25 inflorescences each, and *G. paniculata* had ~600–750 tiny flowers to approximate natural densities. Treatments were set up 30 min before observation to allow pollinators to acclimate to the presence of new flowers and PVC. Although a longer time would have been preferable, it would also have caused the flowers to wilt. Each treatment combination was replicated four times.

To assess the effects of each plant species on pollinator visitation to *C. pitcheri*, insect visitors were observed for 30 min on clear days between 0900 and 1800 hours. Visits per plant and movements between plants were recorded for each experimental array. Because of nonnormal residuals, we applied a general linear model within a randomization wrapper (Cassell 2002). The model included the fixed effects of array species identity, density, and the species × density interaction, as well as the covariates of time, date, and abundance of *C. pitcheri* inflorescences on the target individual (SAS Institute 2004). We examined both the effects of treatments on visitors to the system as a whole (defined as the array plus target *C. pitcheri*) and the effects on the proportion of total visitors to *C. pitcheri*, because a given plant species (or density) could attract more total pollinators to the system but cause fewer visits to *C. pitcheri*. Response variables thus included total pollinator visits to the system, proportion of system visits to *C. pitcheri*, and pollinator visits to *C. pitcheri* only. Pollinator visits were not significantly different between the PVC procedural control and the no-PVC control ($P = 0.35$); therefore, only the PVC procedural control was used, thus allowing for factorial analysis.

Results

Are Abundances of Putative Pollinator Taxa Higher in Areas Invaded by Gypsophila paniculata than in Uninvaded Areas?

Fewer potential pollinator species were captured with the sweep net surveys than observed on flowers in the *Gypsophila paniculata* removal experiment, indicating the limitations of sweep net methods for pollinating insects. Despite this limitation, we detected significant differences between invaded and uninvaded sites. Total numbers of potential pollinators were five times more abundant in invaded compared with uninvaded sites in 2008 ($F_{2,12} = 5.58$, $P = 0.022$; fig. 1A) and three times more abundant in 2007, before invader removals ($F_{2,12} = 9.19$, $P = 0.010$; fig. 1A). Sites that had recently been managed by removal of *G. paniculata* had intermediate numbers of pollinators in 2008 (fig. 1A). These differences were mostly due to Halictidae and Syrphidae, which were significantly more abundant in invaded sites than in uninvaded sites in 2008 (Halictidae: $F_{2,12} = 3.99$, $P = 0.047$; Syrphidae: $F_{2,12} = 8.78$, $P = 0.005$; fig. 1B). The abundances of other families did not show significant differences among treatments (Andrenidae, Colletidae, Megachilidae: insufficient sample sizes; Apidae: $F_{2,12} = 0.68$, $P = 0.52$; Bombyliidae: $F_{2,12} = 0.45$, $P = 0.65$; Crabronidae: $F_{2,12} = 2.14$, $P = 0.16$). Syrphidae and Bombyliidae were the most abundant pollinator families collected via sweep nets.

Are Floral Visitation Rates to Cirsium pitcheri Higher in Areas Where Gypsophila paniculata Has Been Removed Compared with Invaded Areas?

Treatment effectiveness on Gypsophila paniculata. The removal treatment was effective. Mean ± SE *G. paniculata* density (individuals/m^2) was 36 times higher in invaded plots (1.23 ± 0.28) and clipped plots (1.12 ± 0.28) compared with removal plots (0.03 ± 0.28; $P = 0.0017$). Uninvaded plots
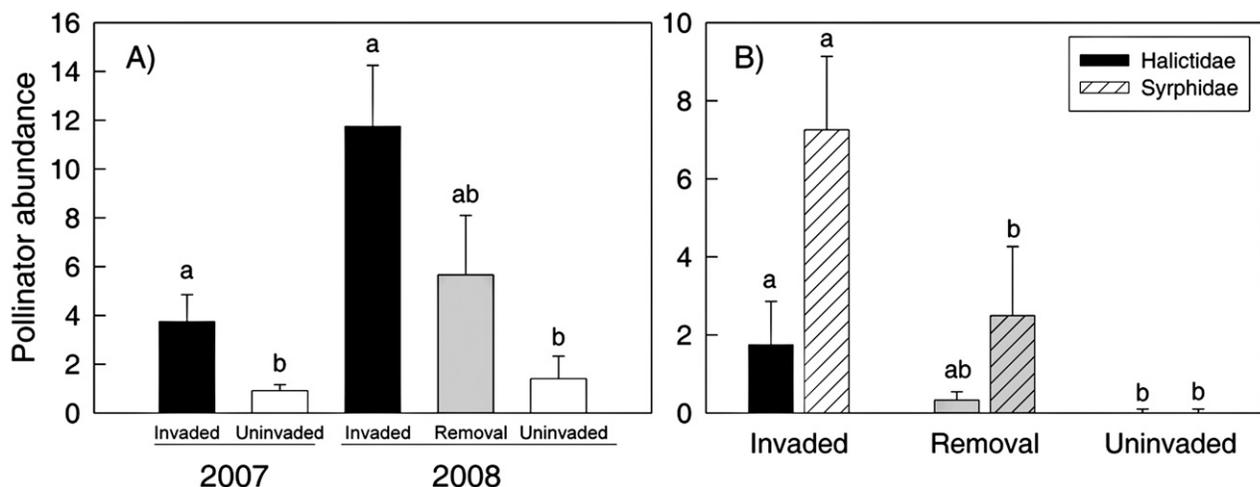

Fig. 1 *A*, July 2007 and 2008 survey of total pollinator abundances from sweep net samples in *Gypsophila paniculata* invaded, removal, or naturally uninvaded sites. *B*, Abundances of two most common pollinator families, Halictidae (solid bars) and Syrphidae (hatched bars). Bars are least squares means ± 1 SE. Different letters indicate significant differences ($P < 0.05$) from Tukey HSD.
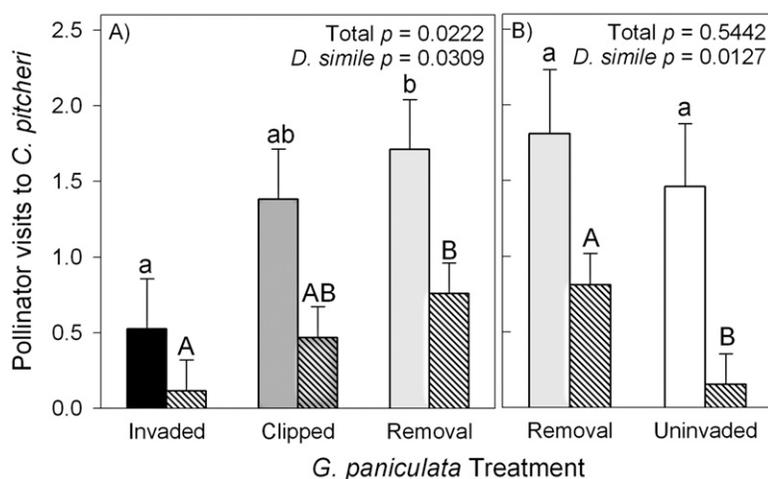
Fig. 2 Net effects of the *Gypsophila paniculata* treatment on total pollinator visits per *Cirsium pitcheri* plant (solid bars; lowercase letters) and on visits by the most common pollinator (*Dianthidium simile*; striped bars; uppercase letters) during 15-min trials for blocked invaded, clipped, and removal treatments (*A*) and removal and uninvaded plots (*B*). Total pollinator visitation was marginally significantly higher for clipped compared with invaded treatments (Tukey HSD, $P = 0.0563$). Bars are least squares means $\pm$ 1 SE. Different letters indicate significant differences ($P < 0.05$) according to randomization Tukey HSD.

(0.33 ± 0.24) and removal plots did not differ significantly in *G. paniculata* density ($P = 0.3323$), although density was not 0 as a result of the presence of newly colonizing individuals.

Floral visitor composition. Out of 199 observed visitors to *Cirsium pitcheri* in the 2008 experiment, three groups were by far the most common: *Dianthidium simile* (26% of visits), small Halictidae (24%), and small Syrphidae (22%). Small halictids and syrphids were not possible to identify to species during pollinator observations and thus were grouped by family. *Dianthidium simile* was also observed on *Centaurea maculosa*, small syrphids were also observed on *G. paniculata*, and small halictids were observed on both invaders. None of these three common *C. pitcheri* visitors was observed on *Monarda punctata*. In total, out of the 25 morphospecies observed visit-

ing *C. pitcheri*, there was substantial overlap with other co-flowering species: six potential pollinator taxa were also observed visiting *G. paniculata*, four were observed visiting *C. maculosa*, and two were observed visiting *M. punctata*.

Net effects of Gypsophila paniculata *on* Cirsium pitcheri *floral visitation.* Insect visitation to *C. pitcheri* flowers was 3.2 times higher in *G. paniculata* removal plots compared with invaded plots (fig. 2*A*; table 1, model A). For *D. simile*, the most common pollinator to *C. pitcheri*, visits were 6.5 times higher in removal than in invaded areas (fig. 2*A*). Because we lack a measure of *D. simile* abundance that is independent of the pollination visits, we cannot tease apart whether this effect reflects a change in abundance and/or a change in behavior. In our study, the mean number of inflo-

Table 1

Results (*P* Values) from Randomization Tests Using Mixed-Model General Linear Models for the Responses of Pollinators to *Cirsium pitcheri* Plants during 15-min Observation Periods

Response	Treatment	Wind speed	Floral abundance	Time
A:				
Total visits/plant	.0222*	.7466	.0001**	.3195
Morphospecies richness/plant	.0671	.1607	.0017**	.1809
Shannon index/plant	.2627	.5190	.0007**	.5303
Dianthidium simile visits/plant	.0309*	.9794	.0058**	.6730
B:				
Total visits/plant	.5442	.9189	<.0001**	.2243
Morphospecies richness/plant	.6351	.9449	<.0001**	.1145
Shannon index/plant	.9976	.1714	.0042**	.4209
D. simile visits/plant	.0127*	.1619	.0008**	.9688

Note. Model A compares *Gypsophila paniculata* treatments: invaded, clipped, and removal plots, blocked by location (location effect not shown). Model B compares the *G. paniculata* removal treatment to naturally uninvaded plots. Diversity was calculated as the Shannon diversity index. Floral abundance refers to the number of inflorescences per individual *Cirsium pitcheri* observed.

* $P < 0.05$.

** $P < 0.01$.

rescences per individual observed was 2.9 in 2007 and 2.5 in 2008. The number of *C. pitcheri* inflorescences was positively correlated with all response variables (table 1, model A), showing that visitation additionally depended on floral abundance of the target plant. However, the removal treatment had no effect on the number of *C. pitcheri* inflorescences per plant relative to invaded plots (mean ± SE number of inflorescences per *C. pitcheri*; removal: 2.7 ± 0.8; invaded: 2.6 ± 0.3; $P = 0.8159$). Wind speed and time had no significant effects in any analysis (table 1, model A). Despite treatment effects on total visitation to *C. pitcheri*, there was only a marginally significant treatment effect on insect richness per *C. pitcheri* individual ($P = 0.0671$; mean ± SE; invaded: 0.45 ± 0.20; clipped: 0.86 ± 0.20; removal: 0.94 ± 0.20) and no significant effect on the Shannon diversity of floral visits (table 1, model A).

Does Removal of Gypsophila paniculata Restore Floral Visitation to Cirsium pitcheri to Levels Found in Naturally Uninvaded Areas?

Visitation to *C. pitcheri* was not significantly different between experimental *G. paniculata* removal plots and naturally uninvaded areas (fig. 2B; table 1, model B). However, *D. simile* visitation was 5.3 times higher in removal compared with uninvaded plots (fig. 2B). Again, the number of *C. pitcheri* inflorescences was positively related to visitation and did not differ between invaded and uninvaded plots (invaded: 2.6 ± 0.3; uninvaded: 2.7 ± 0.4; $P = 0.8420$). Wind speed and time had no significant effects (table 1, model B). There were no significant differences between removal and uninvaded plots in the richness or diversity of visiting insects (table 1, model B).

Do Impacts of Gypsophila paniculata on Pollinators of Cirsium pitcheri Correspond to Direct Effects of Enhanced Floral Resources and/or to Indirect Effects of Invader-Induced Changes in the Plant Community?

Our clipping treatment suggested a direct effect of *G. paniculata* floral presence on pollinators to *C. pitcheri*. Floral visitation by insects was 2.6 times higher in clipped compared with invaded plots (marginally significant; Tukey HSD $P = 0.0563$; fig. 2A), and visitation was not significantly higher in removal compared with clipped plots (Tukey HSD $P = 0.4564$). Thus, *G. paniculata* had stronger negative effects on putative pollinators when it had flowers than when flowers were removed.

In addition to this evidence for a direct effect, *G. paniculata* removals also increased native plant species richness and abundance, suggesting potential for an indirect effect on pollinators. Plant abundance per square meter (excluding *G. paniculata*) was 41% higher in removal plots than in invaded plots (fig. 3A) and 94% higher in naturally uninvaded than in removal plots (fig. 3B), suggesting that either removal treatments have not had sufficient time to return to natural levels of plant abundances or naturally uninvaded areas may resist the invader as a result of the high abundances of native plants. Similarly, plant species richness per square meter was on average 22% higher in removal plots than in invaded
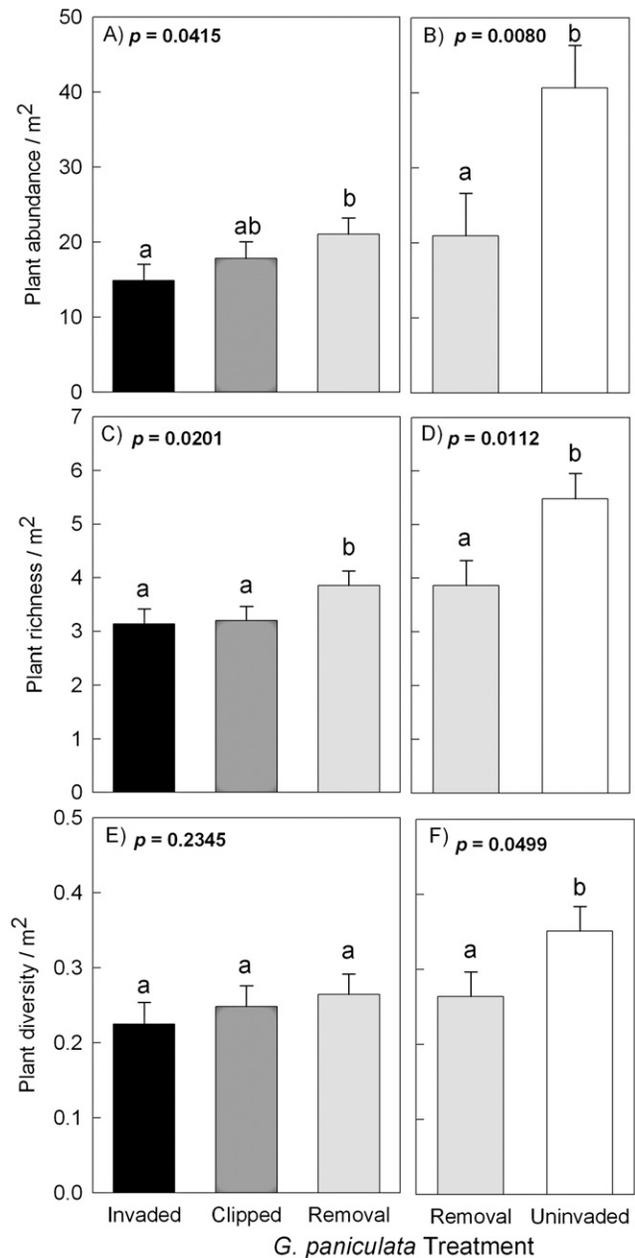

Fig. 3 Effects of *Gypsophila paniculata* treatments on the plant community. Plant abundance (*A*, *B*), richness (*C*, *D*), and diversity (*E*, *F*) calculated with the Shannon diversity index. *A*, *C*, and *E* show blocked invaded, clipped, and removal treatments; *B*, *D*, and *F* compare removal and naturally uninvaded plots. Bars are least squares means ± 1 SE. Different letters indicate significant differences ($P < 0.05$) according to randomization Tukey HSD.

plots (fig. 3C) and was 42% higher in uninvaded plots than in removal plots (fig. 3D). There was no treatment effect on plant diversity per square meter among the invaded, clipped, and removal plots (fig. 3E), but plant diversity was 33% higher in uninvaded plots than in removal plots (fig. 3F). Finally, invaded, clipped, and removal treatments did not differ in the density of *C. pitcheri* ($P = 0.1640$) or in the density of another invasive plant, *C. maculosa* ($P = 0.3893$). There
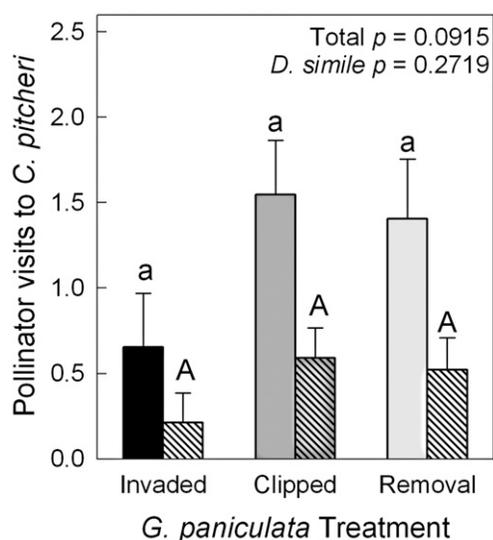
Fig. 4 Direct effects of *Gypsophila paniculata* treatment on total pollinator visits to *Cirsium pitcheri* (solid bars; lowercase letters) and visits by the most common pollinator (*Dianthidium simile*; striped bars; uppercase letters) during 15-min trials. Indirect effects of treatment on plant community composition are removed by including plot-level plant species richness as a covariate. Bars are least squares means ± 1 SE (adjusted for presence of the covariate). Different letters indicate significant differences ($P < 0.05$) according to randomization Tukey HSD.

were also no differences in the density of *C. pitcheri* ($P = 0.4457$) or *C. maculosa* ($P = 0.4654$) between removal plots and naturally uninvaded plots, although a larger survey showed reduced *C. pitcheri* in some *G. paniculata*–invaded areas (S. M. Emery, unpublished data).

When plant species richness was added as a covariate to our general linear models, effects of the *G. paniculata* treatment became weaker (e.g., the effect size for pollinator visitation was reduced by 50%) and nonsignificant (fig. 4; table 2). Importantly, the best fit model included the covariate of plant species richness ($AIC_c = 326.0$), which fit the data marginally better than the covariate + treatment × covariate interaction model ($AIC_c = 326.5$, $\Delta_i = 0.5$) and substantially

better than the model lacking the plant species richness covariate ($AIC_c = 330.5$, $\Delta_i = 4.5$; larger AIC_c indicates worse fit, and a difference in AIC_c >2 indicates a better model fit). Analysis of model fit for *D. simile* response showed a similar pattern (data not shown). Thus, indirect changes in plant richness were correlated with, and may be partly responsible for, the net effects of complete *G. paniculata* removal on floral visitor responses (cf. figs. 2, 4). Plant abundance did not have a similar effect on visitation, and neither plant species richness nor plant abundance significantly interacted with invader treatment in our analyses (table 2). Plant species abundance and richness were marginally positively correlated across plots (Spearman $r = 0.42$, $P = 0.063$, $n = 20$ plots).

What Is the Relative Importance of Floral Identity versus Floral Density in Affecting Pollinator Visitation to Cirsium pitcheri?

In our array experiment, insect visitation to the entire floral system (focal *C. pitcheri* inflorescence plus flowers in arrays) was 3.3 times higher for *G. paniculata* and *C. maculosa* arrays compared with arrays of the native species, *M. punctata*, or to control (empty) arrays (fig. 5A). However, the proportion of putative pollinators that visited the focal species (*C. pitcheri*) was 2.2 times higher in *M. punctata* compared with *C. maculosa* arrays (fig. 5B), although the effect of species identity was only marginally significant ($P = 0.0575$). For both nonnative species, combining these two responses—increased visitation to the whole system but reduced proportion of visits to *C. pitcheri*—resulted in no significant effect of species identity on the absolute number of insects visiting *C. pitcheri* flowers (fig. 5C). In addition, absolute visitation to *C. pitcheri* was no higher in the presence of other species than in the presence of the empty PVC control (fig. 5C). Time and date were significantly associated with the abundance of floral visits to the system, and time affected both the abundance of visits to *C. pitcheri* and the number of interspecific movements (i.e., between *C. pitcheri* and another plant species; table 3). The species × density interaction was significant for the number of interspecific movements; this was driven solely by a high number of interspecific movements for medium-density *C. maculosa* trials (data not shown). Finally, the number of interspecific move-

Table 2

Statistical Models to Separate Potential Direct and Indirect Effects of *Gypsophila paniculata* Treatments (Invaded, Clipped, and Removal Plots) on Pollinator Visitation to *Cirsium pitcheri* Plants

Response	Treatment	Wind speed	Floral abundance	Time	Plot-level plant richness	Plot-level plant abundance
Total visits/plant	.0915	.6213	.0001**	.6598	.0459*	
Dianthidium simile visits/plant	.2719	.8600	.0046**	.6890	.0066**	
Total visits/plant	.0354*	.7233	.0002**	.3207		.6292
D. simile visits/plant	.0528	.9898	.0062**	.6720		.6332

Note. Results are from randomization tests using mixed-model general linear models for the responses of pollinators to *C. pitcheri* when two plant community measures were included in analysis: plant species richness or plant abundance (number/m^2). Floral abundance refers to the number of inflorescences per individual *C. pitcheri* observed. Compare with table 1.
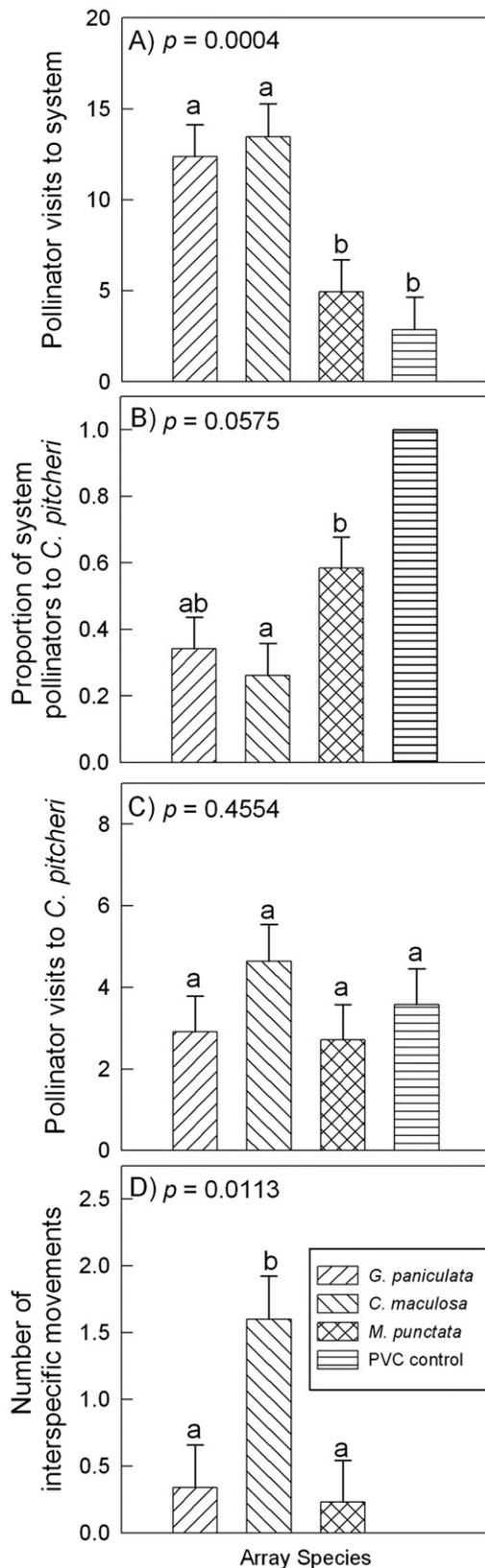
* $P < 0.05$.
** $P < 0.01$.

Fig. 5 Experimental arrays around *Cirsium pitcheri*. Effects of species identity on total pollinator abundance to the system (*A*), proportion of total pollinator visits to *C. pitcheri* (*B*), total pollinator visits to *C. pitcheri* (*C*), and number of interspecific movements during 30-min trials (*D*). The control treatment (PVC only) was not included in the analysis for *B* or *D*, but for *B* the bar is included as a reference at 1 (i.e., all visits occurred to *C. pitcheri*). For *D*, there were no possible interspecific movements in the PVC-only treatment. Bars show least squares means ± 1 SE. Different letters indicate significant differences ($P < 0.05$) according to randomization Tukey HSD.

ments was 5.6 times higher in *C. maculosa* arrays than in *G. paniculata* or *M. punctata* arrays (fig. 5*D*), which could reduce fitness of *C. pitcheri* through conspecific pollen loss or heterospecific pollen deposition. Consistent with these patterns, in our 2008 plot-level experiment, mean visits to *C. pitcheri* were 0.52 ± 0.14 (mean ± SE) floral visitors per plant in plots where *C. maculosa* was present and 1.7 ± 0.35 in plots with no *C. maculosa* (square root transformed, $t = -3.08$, $P = 0.0067$).

Discussion

Altogether, our results suggest that the large displays of *Gypsophila paniculata* are highly attractive to pollinators, leading to elevated abundances of pollinating taxa in invaded areas but attracting insects away from flowers of the threatened native plant, *Cirsium pitcheri*. Our results support the magnet hypothesis (Thomson 1978; Laverty 1992) because the abundance of insects in pollinator families was five times greater in the invaded plots than in uninvaded plots. Similarly, our array experiment showed that both invasive species (*G. paniculata* and *Centaurea maculosa*) attracted more pollinators to the whole system (*C. pitcheri* plus the array species) than did the native *Monarda punctata* or control PVC grid. This is among the first evidence supporting the hypothesis proposed by Bjerknes et al. (2007) that invasive species may have a positive impact on pollinator populations as a result of an increase in landscape-level resource availability (see also Tepedino et al. 2008). Our result contrasts with the negative responses of pollinator groups in areas invaded by *Solidago canadensis* (de Groot et al. 2007; Moron et al. 2009).

Our results also support the hypothesis that native and invasive plants compete for pollinator visitation, a pattern similar to observations in other systems. Despite higher abundances of pollinators in invaded areas compared with uninvaded areas, rates of floral visitation to *C. pitcheri* were 70% lower in invaded plots than in *G. paniculata* removal plots. Our findings are most similar to effects observed by Totland et al. (2006), who found that the nonnative plant *Phacelia tanacetifolia* reduced pollinator visitation to the native *Melampyrum pratense* but increased the abundance of pollinators entering plots. Similarly, in our array experiment, despite local increases in the abundance of pollinators, both *G. paniculata* and *C. maculosa* reduced the proportion of visits to *C. pitcheri*, although this did not ultimately reduce the absolute number of insect visits to *C. pitcheri*, as we observed in the experimental field plots. The relatively small size of the array experiments compared with our plot level manipulations may have produced weaker effects on pollinator behaviors. In addition, array experiments were conducted within invaded areas, and we may have observed different

Table 3

Results from Randomization Tests Using Mixed-Model General Linear Models for the Response of Pollinators to
***Cirsium pitcheri* during 30-min Observation Periods**

Response	Species	Density	Species × density	Time	Date	Floral abundance
No. visits to system	.0004**	.0792	.1494	.0003**	.0194*	.9640
Proportion of system visits to *C. pitcheri*	.0575	.1453	.9869	.5616	.8114	.0527
No. visits to *C. pitcheri* plant	.4554	.6056	.9100	.0001**	.1030	.1005
No. interspecific movements	.0113*	.6461	.0428*	.0069**	.2570	.2465

Note.   Treatments consisted of arrays around *C. pitcheri* containing flowers of *Gypsophila paniculata*, *Centaurea maculosa*, *Monarda punctata*, or PVC control and crossed with low (2), medium (4), or high (8) floral density. Floral abundance refers to the number of inflorescences per individual *C. pitcheri* observed.

* $P < 0.05$.

** $P < 0.01$.

impacts of invader presence if arrays had occurred in areas free of the invader.

It remains unclear what the consequences of reduced pollination may be for the reproductive success of *C. pitcheri* because a reduction in pollinator visitation does not necessarily translate to a reduction in reproductive success (Ghazoul 2004; Totland et al. 2006). However, Loveless (1984) suggested that *C. pitcheri* is pollinator limited, since open-pollinated flowers set significantly more seed than self-pollinated flowers. In addition, pollen limitation has been documented in another thistle species, *Cirsium arvense* (Lalonde and Roitberg 1994). Future studies in our system could provide greater insight into the temporal dynamics of altered pollinator visitation by extending observation through more than one season. It would also be useful to explore the spatial scale at which altered visitation is the strongest (Cariveau and Norton 2009). Finally, prior work has documented strong effects of insect herbivory on the demography of *C. pitcheri* (Bevill et al. 1999; Louda et al. 2005), and it could be interesting to examine whether *G. paniculata* alters rates of herbivory on this threatened plant.

We suggest that removal of *G. paniculata* is an effective strategy for restoring floral visitation to *C. pitcheri*, since visitation rates by insects did not significantly differ between experimental removal plots and naturally uninvaded plots. Effective restoration of plant-pollinator interactions has also been observed in hay meadows and heathlands following plant restoration efforts (Forup and Memmott 2005; Forup et al. 2008), although the time elapsed since beginning invader removal treatments was much shorter in our system (2–4 yr) than in the heathlands and meadow restorations (10–20 yr). In addition, from a conservation perspective, studies are needed on other potential impacts of *G. paniculata* on *C. pitcheri*, including competitive effects for nutrients and water.

Removal of *G. paniculata* significantly increased visits by the most commonly observed floral visitor, *Dianthidium simile*, which may be an important pollinator of *C. pitcheri*. This bee is a ground nester (O'Brien 2007), but it is not known how it is affected by disturbance; perhaps the ground disturbance caused by workers removing the invasive plant actually promotes or recruits *D. simile*. Alternatively, this result could reflect different pollinator communities between the geographic locations, since removal and uninvaded sites were located in different areas because of the large extent of invasion. However, it may also indicate higher *D. simile* abundance in removal plots as a result of the regional pres-

ence of *G. paniculata*. To fully understand the consequences of restoration via invader removal, future work should evaluate responses in both the abundance and effectiveness of individual pollinator species.

Effects of *G. paniculata* on pollinators appear to derive from both direct and indirect effects of the invasion. Pollinator visitation was marginally higher in clipped than in invaded areas and not significantly different between clipped and removal areas. This result indicated that the impact of *G. paniculata* on *C. pitcheri* pollinators was directly due to the presence of flowers on the invader, because removing only the flowers had effects similar to removing entire plants. However, the resident plant community was also altered by the removal of *G. paniculata* individuals: invaded plots supported lower plant abundance and native plant species richness (both measures excluded *G. paniculata*) compared with sites where *G. paniculata* had been removed, although removal plots had lower abundance and richness than naturally invader-free areas. Plant species richness per plot was positively correlated with pollinator visitation to *C. pitcheri*, evidence for an indirect effect that has occurred through invader-caused reductions in plant diversity. Similarly, Fontaine et al. (2006) manipulated both plant and pollinator functional diversity, and when both were high, they observed recruitment of more diverse plant communities. We did not find a significant relationship between plant abundance (excluding *G. paniculata*) and insect visitation to *C. pitcheri* flowers, and this result was consistent with the lack of effect of plant density in our array experiment. Thus, we hypothesize that higher plant richness may increase pollinator visitation to *C. pitcheri* in uninvaded and invader-removal areas, although the mechanism driving such an effect remains unclear, since the total pollinator abundances were higher in invaded areas. To our knowledge, this is the first evidence to suggest that invasive plants may affect pollinators by reducing the richness of the native plant community.

Conclusions

The invasive plant, *Gypsophila paniculata*, attracts pollinators to invaded areas, but this increase in pollinator abundance does not translate to increased insect visitation to the flowers of a rare, native plant. In fact, the federally threatened thistle, *Cirsium pitcheri*, experienced lower visitation rates in invaded areas compared with uninvaded areas, where

pollinators were less abundant overall. Conservation efforts to remove the invader quickly and successfully restored rates of insect visitation to the threatened thistle. While some concerns have been raised that pollinator populations may crash following the widespread removal of invaders or other common species (Gibson et al. 2006; Carvalheiro et al. 2008), our results suggest that *C. pitcheri* will receive higher visitation following removal, despite any reductions in total pollinator abundances.

Acknowledgments

Literature Cited

Aigner PA 2004 Ecological and genetic effects on demographic processes: pollination, clonality and seed production in *Dithyrea maritima*. Biol Conserv 116:27–34.

Beattie AJ, C Turnbull, RB Knox, EG Williams 1984 Ant inhibition of pollen function: a possible reason why ant pollination is rare. Am J Bot 71:421–426.

Bevill RL, SM Louda, LM Stanforth 1999 Protection from natural enemies in managing rare plant species. Conserv Biol 13:1323–1331.

Bjerknes AL, O Totland, SJ Hegland, A Nielsen 2007 Do alien plant invasions really affect pollination success in native plant species? Biol Conserv 138:1–12.

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

Brown BJ, RJ Mitchell, SA Graham 2002 Competition for pollination between an invasive species (purple loosestrife) and a native congener. Ecology 83:2328–2336.

Burnham KP, DR Anderson 2002 Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Campbell DR, AF Motten 1985 The mechanism of competition for pollination between two forest herbs. Ecology 66:554–563.

Cariveau DP, AP Norton 2009 Spatially contingent interactions between an exotic and native plant mediated through flower visitors. Oikos 118:107–114.

Carvalheiro LG, ERM Barbosa, J Memmott 2008 Pollinator networks, alien species and the conservation of rare plants: *Trinia glauca* as a case study. J Appl Ecol 45:1419–1427.

Cassell D 2002 A randomization-test wrapper for SAS PROCs. Proceedings of the Twenty-Seventh Annual SAS Users Group International Conference Paper 251-27. SAS Institute, Cary, NC.

Chittka L, 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.

Q3 Cowles HC 1899 The ecological relations of the vegetation on the sand dunes of Lake Michigan. Bot Gaz 27:95–117, 167–202, 281–308, 361–391.

Darwent AL, RT Coupland 1966 Life history of *Gypsophila paniculata*. Weeds 14:313–318.

de Groot M, D Kleijn, N Jogan 2007 Species groups occupying different trophic levels respond differently to the invasion of semi-natural vegetation by *Solidago canadensis*. Biol Conserv 136:612–617.

Dohzono I, YK Kunitake, J Yokoyama, K Goka 2008 Alien bumble bee affects native plant reproduction through interactions with native bumble bees. Ecology 89:3082–3092.

Edgington ES 1987 Randomization tests. Dekker, New York.

Fontaine C, I Dajoz, J Meriguet, M Loreau 2006 Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. PLoS Biol 4:129–135.

Forup ML, KSE Henson, PG Craze, J Memmott 2008 The restoration of ecological interactions: plant-pollinator networks on ancient and restored heathlands. J Appl Ecol 45:742–752.

Forup ML, J Memmott 2005 The restoration of plant-pollinator interactions in hay meadows. Restor Ecol 13:265–274.

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

Gibson RH, IL Nelson, GW Hopkins, BJ Hamlett, J Memmott 2006 Pollinator webs, plant communities and the conservation of rare plants: arable weeds as a case study. J Appl Ecol 43:246–257.

Hamze SI, CL Jolls 2000 Germination ecology of a federally threatened endemic thistle, *Cirsium pitcheri*, of the Great Lakes. Am Midl Nat 143:141–153.

Karamanski TJ 2000 A nationalized lakeshore: the creation and administration of Sleeping Bear Dunes National Lakeshore. National Park Service, Department of the Interior, Washington, DC.

Kearns CA, DW Inouye 1993 Techniques for pollination biologists. University Press of Colorado, Niwot.

Lalonde RG, BD Roitberg 1994 Mating system, life-history, and reproduction in Canada thistle (*Cirsium arvense* Asteraceae). Am J Bot 81:21–28.

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

Levine JM, M Vila, CM D'Antonio, JS Dukes, K Grigulis, S Lavorel 2003 Mechanisms underlying the impacts of exotic plant invasions. Proc R Soc B 270:775–781.

Louda SM, TA Rand, AE Arnett, AS McClay, K Shea, AK McEachern 2005 Evaluation of ecological risk to populations of a threatened plant from an invasive biocontrol insect. Ecol Appl 15:234–249.

Loveless MD 1984 Population biology and genetic organization in *Cirsium pitcheri*, an endemic thistle. PhD diss. University of Kansas, Lawrence.

Mack RN, D Simberloff, WM Lonsdale, H Evans, M Clout, FA Bazzaz 2000 Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710.

Manly BFJ 1991 Randomization and Monte Carlo methods in biology. Chapman & Hall, London.

Mitchell CE, AA Agrawal, JD Bever, GS Gilbert, RA Hufbauer, JN Klironomos, JL Maron, et al 2006 Biotic interactions and plant invasions. Ecol Lett 9:726–740.

Moragues E, A Traveset 2005 Effect of *Carpobrotus* spp. on the

pollination success of native plant species of the Balearic Islands. Biol Conserv 122:611–619.

Morales CL, A Traveset 2008 Interspecific pollen transfer: magnitude, prevalence and consequences for plant fitness. Crit Rev Plant Sci 27:221–238.

——— 2009 A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. Ecol Lett 12:1–13.

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

O'Brien MF 2007 Notes on *Dianthidum simile* (Cresson) (Hymenoptera: Megachilidae) in Michigan. Great Lakes Entomol 40:23–28.

Pavlovic NB, ML Bowles, SR Crispin, TC Gibson, KD Herman, RT Kavetsky, AK McEachern, MR Penskar 2002 Pitcher's thistle (*Cirsium pitcheri*) recovery plan. US Fish and Wildlife Service, Fort Snelling, MN.

Pimentel D, L Lach, R Zuniga, D Morrison 2000 Environmental and economic costs of nonindigenous species in the United States. BioScience 50:53–65.

Ricklefs R 2001 The economy of nature. WH Freeman, New York.

Rudgers JA, K Clay 2008 An invasive plant-fungal mutualism reduces arthropod diversity. Ecol Lett 11:831–840.

SAS Institute 2004 SAS, version 9.1.3. SAS Insitute, Cary, NC.

Stevens OA 1957 Weights of seeds and numbers per plant. Weeds 5:46–55.

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

Thomson JD 1978 Effects of stand composition on insect visitation in two-species mixtures of *Hieracium*. Am Midl Nat 100:431–440.

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

USDA, NRCS 2009 The PLANTS database. National Plant Data Center, Baton Rouge, LA. http://plants.usda.gov.

Waser NM, ML Fugate 1986 Pollen precedence and stigma closure: a mechanism of competition for pollination between *Delphinium nelsonii* and *Ipomopsis aggregata*. Oecologia 70:573–577.

Queries

Q1 Murphy and Aarssen 1995 is not listed in the literature cited. Please provide reference information.
Q2 Palmer et al. 2003 is not listed in the literature cited. Please provide reference information.
Q3 I added page numbers for Cowles 1899. Are changes correct?