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Rapid Shift in Pollinator Communities Following Invasive Species Removal

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Abstract

Ecological restoration is increasingly used to reverse degradation of rare ecosystems and maintain biological diversity. Pollinator communities are critical to maintenance of plant diversity and, in light of recent pollinator loss, we tested whether removal of invasive glossy buckthorn (*Frangula alnus* L.) from portions of a prairie fen wetland altered plant and pollinator communities. We compared herbaceous plant, bee, and butterfly abundance, diversity, and species composition in buckthorn invaded, buckthorn removal, and uninvaded reference plots. Following restoration, we found striking differences in plant and pollinator abundance and species composition between restored, unrestored, and reference plots. Within 2 years of *F. alnus* removal, plant species diversity and composition in restored plots were significantly different than invaded plots, but also remained significantly lower than reference plots. In contrast, in the first growing season following restoration, bee and butterfly abundance, diversity, and composition were similar in restored and reference plots and distinct from invaded plots. Our findings indicate that a diverse community of mobile generalist pollinators rapidly re-colonizes restored areas of prairie fen, while the plant community may take longer to fully recover. This work implies that, in areas with intact pollinator metapopulations, restoration efforts will likely prevent further loss of mobile generalist pollinators and maintain pollination services. On the other hand, targeted restoration efforts will likely be required to restore populations of rare plants and specialist pollinators for which local and regional species pools may be lacking.

Key words: conservation, plant community, pollination, prairie fen, restoration.

Introduction

Plants and their pollinator communities are inextricably linked. Although restoration efforts have often focused on changes in plant communities, a deeper understating of how pollinator communities respond to restoration efforts is needed to ensure the long-term viability of restored habitats. Declines in pollinator diversity have deepened concerns about the loss of effective pollination in managed crops (McGregor 1976; Klein et al. 2007) and native plant communities (Potts et al. 2010; Winfree 2010). Recent pollinator losses extend beyond the managed honey bee (*Apis mellifera* L.) to key native pollinator groups, including bumblebees, *Bombu*s spp. (Goulson et al. 2008). There are multiple drivers of pollinator diversity loss, including land-use change, introduction of non-native species, and climate change (Kevan 1999; Potts et al. 2010). While habitat loss is considered the primary threat to bee diversity, invasive species exacerbate this threat by reducing habitat quality (Brown & Paxton 2009). Because pollinators and plant populations are tightly linked, pollinator declines and extinctions have the potential to result in trophic cascades that affect plant diversity (Biesmeijer et al. 2006). For example, approximately 87% of angiosperms are animal pollinated (Renner 2006) and over 60% of plant species may be pollen limited (Burd 1994; Ashman et al. 2004). In this light, maintaining or restoring pollinator diversity is an increasing priority for the long-term persistence of imperiled plant communities.

Ecological restoration is increasingly used to reverse losses of rare species and communities and to increase diversity within protected areas (Hobbs & Norton 1996; SER Working Group 2004). Ecosystems are considered restored when the composition, structure, and function have been returned to a goal state, often based on historic conditions (SER Working Group 2004). The positive effect of restoration on plant species diversity is relatively well documented (Ruiz-Jaen & Aide 2005) and plant conservation is well represented in restoration studies (Clark & May 2002). However, whether typical restoration activities lead to effective pollinator conservation is less clear (Winfree 2010).

Two insect groups—bees and butterflies—play an important role in the maintenance of pollination and species diversity. Bee communities are typically species-rich and comprise the dominant pollinators in many regions (Williams et al. 2001). They are well-known for their prevalence as effective pollinators of both crops and wild plants (McGregor 1976;

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Kearns et al. 1998). Butterflies comprise another well-known group of invertebrates and some may be effective umbrella species for conservation, whose protection may lead to the protection of other species (New 1997). Butterfly species range from specialists to generalists and can recover rapidly following restoration (Waltz & Covington 2004). However, little is known about the response of either bee or butterfly communities to restoration efforts (Forup & Memmott 2005; Williams 2011).

Prairie fen is a globally rare wetland ecosystem that occurs in relatively high frequency in the Midwestern United States. Known to harbor extremely high species diversity in small and frequently isolated patches, prairie fens are considered biodiversity hotspots that are threatened by the same factors affecting species diversity globally (Spieles et al. 1999; Amon et al. 2002; Bedford & Godwin 2003; Nekola 2004), e.g. habitat loss, invasive species, and pollution (Wilcove et al. 1998). Prairie fens contain a number of rare and endangered organisms, including 19 plants and 25 insect species, 4 of which are butterflies (MNFI 2007). Many prairie fens in the Midwest are degraded, primarily by invasive species and changes in hydrology (Landis et al. in press). Specifically, glossy buckthorn (*Frangula alnus* L.) is an invasive shrub that is considered a key threat to prairie fen (Fiedler 2010).

We examined concurrent responses of plant and pollinator communities to remove *F. alnus* and other invasives from a prairie fen wetland in Michigan, United States. Our specific goal was to examine the effect of restoration on the diversity, abundance, and structure of both communities in the initial years of a long-term restoration project. We hypothesized that in comparison to untreated controls in restoration treatments (1) forb abundance and plant diversity would increase; (2) bee and butterfly abundance and diversity would increase; and (3) both communities would begin to diverge from untreated plots. We further predicted that (4) neither plant nor pollinator communities would reach reference community states within this short time period. By simultaneously measuring the response of the plant and pollinator communities, we anticipated gaining insight into processes that might guide restoration efforts more broadly.

Methods

Experimental Design

The study was conducted in a prairie fen at the Michigan State University MacCready Reserve in Clarklake, Liberty Township, Jackson County, Michigan. At the beginning of the study, over 75% of the study fen was invaded by mature *Frangula alnus* (Fiedler 2010). The surrounding landscape contains numerous prairie fen wetlands, nearly all in similarly degraded states. In fall 2007, a total of twelve 25 × 25–m plots invaded by *F. alnus* and two uninvaded reference areas were delineated, with an additional reference added in April 2008. In February 2008, *F. alnus* was cleared from six randomly selected plots. We managed invasive plants in removal plots in May 2008 and June 2009. *Phalaris arundinacea*, *Rosa multiflora*, and *Cirsium arvense* were sprayed; *Typha* sp. and *Populus tremuloides* were cut and stem treated with glyphosate 25% active ingredient (Rodeo; Monsanto, St. Louis, MO, U.S.A.). *Frangula alnus* seedlings were flamed with a propane torch.

Sampling

During the 2008 and 2009 growing seasons, we assessed plant diversity and cover within each plot using nine 1 m^2 quadrats in a grid (Fiedler 2010). Three times during each growing season, i.e. 2–6 June, 25–30 July, 5–8 September 2008; 1–5 June, 29 July to 6 August, and 9–11 September 2009, we identified and estimated percent cover of monocotyledonous plants, forbs, and shrubs less than 1.5 m height, for plants rooted within each quadrat.

We sampled bees and butterflies as representative pollinators using two methods, observational sampling and pollinator bowl traps, from June to September 2008 and 2009 (12 June, 8 August, 6 September 2008; 4 June, 3 July, 5 August, 31 August 2009). Both techniques assess pollinators near ground level where native fen flora is flowering and are unlikely to include pollinators that were active in the *F. alnus* canopy. Both methods were performed on the same days, in sunny calm weather. We performed pollinator observations between 10 am and 3 pm. On each date, two people stood back-to-back in the center of each replicate plot. Observers waited 1 minute after arrival at each sampling location, then observed all bees and butterflies that entered the 2-m radius half-circle surrounding them for 5 minutes. All pollinators entering the sampling area were visually identified to genus and, when possible, unknown species were collected for identification. Although very small pollinators are less likely to be detected using this technique, we did observe small bees including *Hylaeus* and *Lasioglossum* spp.

Pollinator bowl traps consisted of 3.25 oz. white cups (Solo Cup Company, Lake Forest, IL, U.S.A.), one-third painted fluorescent blue, one-third fluorescent yellow (Guerra Paint and Pigment, New York, NY, following Droege 2010), and one-third unpainted. We placed traps in randomized order by color on two sides of all nine plant quadrats, totaling 18 per replicate. Cups were one-third filled with soapy water, placed within 40 cm of the quadrat on the ground where they were not obscured by low growing vegetation, in the field between 8 and 10 am and removed between 4 and 7 pm. Insects were removed from ethanol and samples pooled by replicate. In the laboratory, bees and butterflies were removed, washed (Droege 2010), pinned, and identified to species.

Statistical Analysis

We compared the abundance, diversity, and community similarity of plants, bees, and butterflies in invaded, restored, and uninvaded plots in 2008 and 2009. For plants, we used maximum percent cover per species within a growing season. For bee abundance, we used season-long means per 5-minute observation, and for bee diversity and community similarity we used pollinator bowl data. For butterfly abundance, diversity, and community similarity, we used season-long means per 5-minute observation, calculated by replicate of each treatment. To examine species richness and evenness, we used Simpson's diversity index for plants, bees, and butterflies using $D = 1/\sum(p_i)^2$, where p_i is the proportion of cover of the ith plant species per quadrat or the abundance of a pollinator.

To investigate differences in plant and pollinator abundance and Simpson's diversity, we performed two-way analysis of variances (ANOVAs) for each group with treatment: invaded, removal, and uninvaded reference, and time since restoration: year 1 and year 2 (PROC MIXED, SAS Institute 2010). Bee and butterfly abundance were $\log(x + 1)$ transformed to meet assumptions of normality and homogeneity of variances, with Satterthwaite adjusted degrees of freedom.

To examine community-level shifts in plant, bee, and butterfly abundance following restoration, we created a similarity matrix with square root transformed data using the Bray–Curtis index, which is well suited to species abundance data (Quinn & Keough 2002). So that treatments and replicates with zero insects remained in the analysis, a 1 was added to all insect abundance values. We used nonmetric multidimensional scaling (NMDS) to visualize the differences in treatment and year on community metrics (Waltz & Covington 2004; Williams 2011). The NMDS ordinates data by ranking variables so that the closer their location is in two or three-dimensional space, the more similar they are. We performed the NMDS in 3 and 2 dimensions, with 25 random starting configurations and a minimum stress of 0.01 (Clarke & Gorley 2006). All stress values for two-dimensional figures were 0.14 or less, indicating that two-dimensional representation is a reasonably accurate representation of the relationship between points (Clarke & Gorley 2006).

To examine statistical differences by treatment in community metrics, we performed analysis of similarity (ANOSIM) using the Bray–Curtis resemblance matrix of plant, bee, and butterfly data for year 1 and 2 separately, with 999 random permutations (Clarke & Gorley 2006). Overall tests were significant in all cases, so pairwise tests were appropriate and are reported herein.

Results

Plant Communities

We observed rapid changes in plant abundance, diversity, and community structure within the first two growing seasons following restoration. There was significantly greater percent forb cover in removal and reference plots than in invaded plots in both year 1 and year 2 (Fig. 1a) ($F_{[2,25.3]} = 5.4$, $p = 0.011$), with no significant difference by year ($F_{[1,23.2]} = 3.6$, $p = 0.072$) or treatment × year ($F_{[2,23.2]} = 1.4$, $p = 0.275$). Plant diversity also shifted in the first two growing seasons following restoration, but not as completely (Fig. 1b). We found significant differences among treatments in season-long diversity of all plants less than 1.5 m tall ($F_{[2,11.6]} = 31.9$, $p = 0.013$), with significantly greater diversity in reference than removal plots and significantly greater diversity in removal than buckthorn-invaded plots. There were no significant differences in plant diversity by year ($F_{[1,141} = 3.0$, $p = 0.085$) and no significant year × treatment interaction ($F_{[2,141]} = 1.1$, $p = 0.32$).

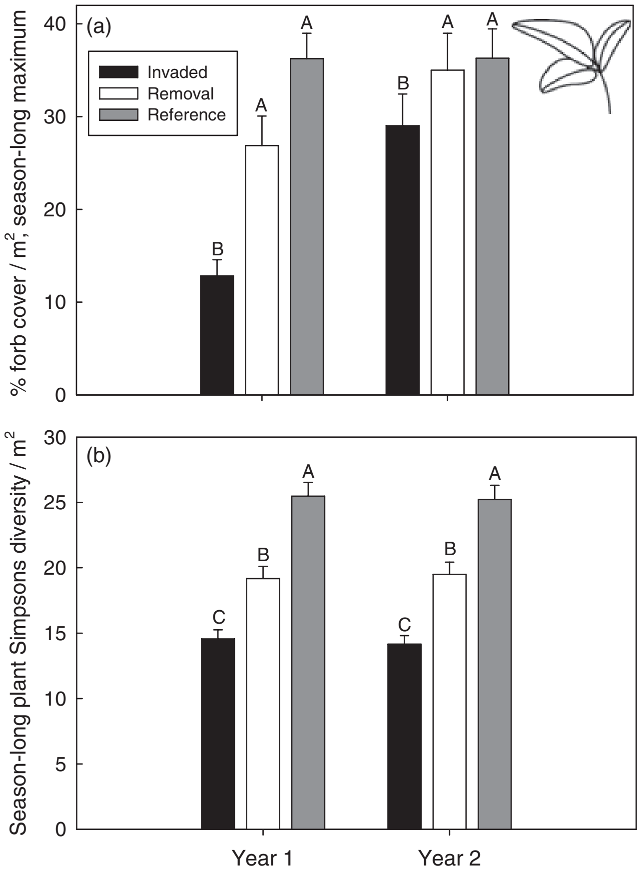

Figure 1. Comparison of (a) percent cover of forbs and (b) season-long plant diversity (Simpson's index) between *Frangula alnus* invaded, removal, and uninvaded fen plots in the first and second years following restoration. Maximum values for percent cover recorded for each growing season are used. Error bars are +SEM, $\alpha = 0.05$. Treatment effects from a two-way ANOVA with treatment and time are shown; year effects were not significant.

An NMDS ordination of the plant community indicated a shift in the overall community following restoration (Fig. 2). In year 1, analysis of similarity indicated no significant difference between the plant community of removal and buckthorn-invaded plots (R0.17, $p = 0.123$), whereas by year 2, removal and invaded plant communities had significantly diverged (R0.5, $p = 0.002$). In both years, invaded and reference plant communities were significantly different (year 1: R0.86, $p = 0.012$; year 2: R0.82, $p = 0.012$) and the plant community in removal plots remained significantly different than that in reference plots through year 2 post-restoration (year 1: R0.71, $p = 0.012$, year 2: R0.83, $p = 0.012$) (Fig. 2). A number of shade-tolerant species were more common in invaded areas (Table S1). A group of disturbance-tolerant species were more common in recently restored areas, most notably *Carex*

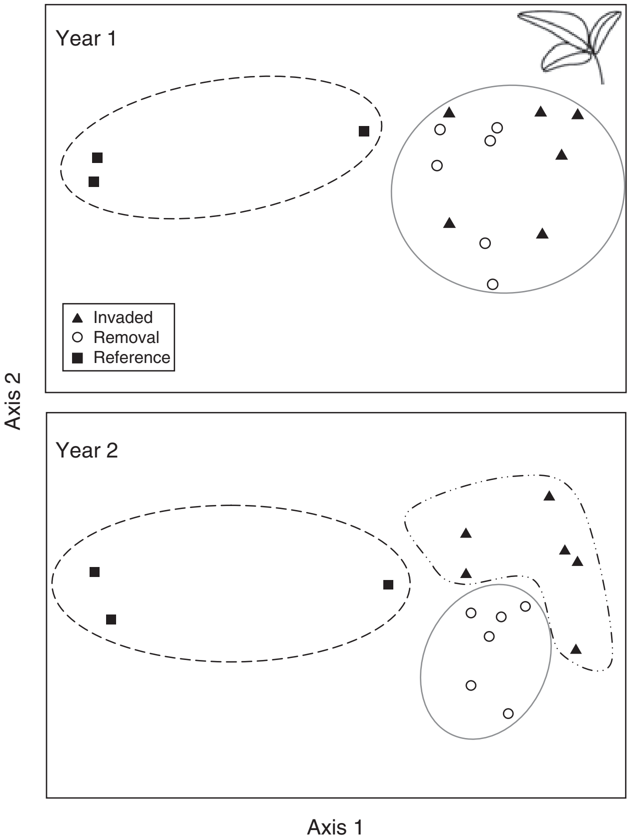

Figure 2. Two-dimensional NMDS ordinations of the plant community show no difference between invaded and removal fen plots in year 1, but a shift in removal plots away from invaded plots by year 2. The ordination is based on a Bray–Curtis dissimilarity matrix for the first and second years following restoration. Maximum values for percent cover recorded for each growing season are used, data were square root transformed. Stress values were 0.08 and 0.09 in years 1 and 2. Lines represent relationships between groups according to ANOSIM.

hystericina, *Epilobium coloratum*, and *Eupatorium perfoliatum* (Table S1). A third group of species were most abundant in reference areas throughout the study (Table S1). While plants with high coefficients of conservatism ($C = 9–10$) sensu Herman et al. (2001) were found in all treatments, 24/34 were only found in the reference plots (Table S1).

Pollinator Communities

Bee abundance and diversity shifted even more rapidly and completely with restoration than the plant community. Bee abundance based on observational sampling was significantly different by treatment ($F_{[2,12]} = 32.8$, $p < 0.001$), year ($F_{[1,12]} = 15.8$, $p = 0.002$), and treatment × year ($F_{[2,12]} = 10.1$, $p = 0.003$), with significantly lower abundances in invaded treatments in both years than all other treatments. In year 1, there were no significant differences between removal and uninvaded reference plots (Fig. 3a), while in year 2, there were significantly more bees in removal than reference or invaded plots. *Apis mellifera* dominated the bee community in observational sampling, followed by *Bombus*, *Hylaeus*, and other Halictidae in year 1. In year 2, *A. mellifera*, *Hylaeus*, and *Bombus* remained dominant groups, with a number of other genera represented by small numbers of insects (Table 1).

We used pollinator trap data to determine bee diversity at the species level and compare it among treatments. Diversity of bees was significantly lower in invaded than removal and reference plots in both study years (Fig. 3b), with no significant differences between removal and reference plots. There were no significant differences in bee diversity by year ($F_{[1,24]} = 0.01$, $p = 0.91$) or treatment × year ($F_{[2,24]} = 2.3$, $p = 0.12$), but there were significant differences by treatment ($F_{[2,24]} = 12.4$, $p = 0.001$). A number of bee species were singletons in both year 1 and year 2, with 31 and 48% of species represented by just one specimen in years 1 and 2, respectively. This means that there is a high likelihood of species turnover based on our sampling technique between years. *Lasioglossum (Dialictus) ephialtum* was more abundant in reference plots in both years than in other treatments (Table 2). Several bee species were more abundant in removal plots in year 2 than in year 1, including *Ceratina calcarata/dupla, Augochlorella aurata*, *L. (Dialictus) ephialtum*, and *L. versatum.*

Patterns of pollinator abundance between observational and pollinator trap data were similar, with the notable exception that *A. mellifera* and *Bombus* spp. were two of the most abundant groups observed, together comprising 51.2 and 49.1% of observed bees in year 1 and 2 after restoration. In contrast, these two groups were less than 4% of total pollinators collected with pollinator traps in both years.

An NMDS analysis of the bee community showed evidence of a shifting pollinator community within the first season following restoration (Fig. 4). There were no significant differences in the bee community between the removal and reference plots (year 1: R0.15, $p = 0.19$; Year 2: R0.24, $p = 0.88$), while the bee community in buckthorn-invaded plots was significantly different than removal plots in both years (year 1: R0.76, $p = 0.001$, year 2: R0.63, $p = 0.004$). Invaded and reference plots remained significantly different from each other (year 1: R0.85, $p = 0.012$, year 2: R0.39, $p = 0.036$). Several of the most abundant pollinators were abundant in both sampling years, including *C. calcarata/dupla*, *L. ephialtum*, and *A. aurata* (Table 2). There were also several notable changes in the bee community across all treatments between years (Table 2).

Butterfly abundance and diversity also shifted rapidly post-restoration. We found significant differences in butterfly abundance by treatment ($F_{[2,12]} = 8.4$, $p = 0.005$) but not by year ($F_{[1,12]} = 0.1$, $p = 0.35$) or treatment × year ($F_{[2,12]} = 1.3$, $p = 0.32$). Although there were significantly fewer butterflies in invaded plots than other treatments in both study years, there was no significant difference between removal and reference plots (Fig. 3c). There were significant differences in butterfly diversity among treatments ($F_{[2,12]} = 10.3$, $p = 0.003$), years ($F_{[1,12]} = 7.1$, $p = 0.021$), and their interaction ($F_{[2,12]} = 4.2$, $p = 0.041$). Patterns of butterfly diversity mirrored butterfly abundance, with significantly lower diversity in invaded plots than in other treatments in both years, but no significant

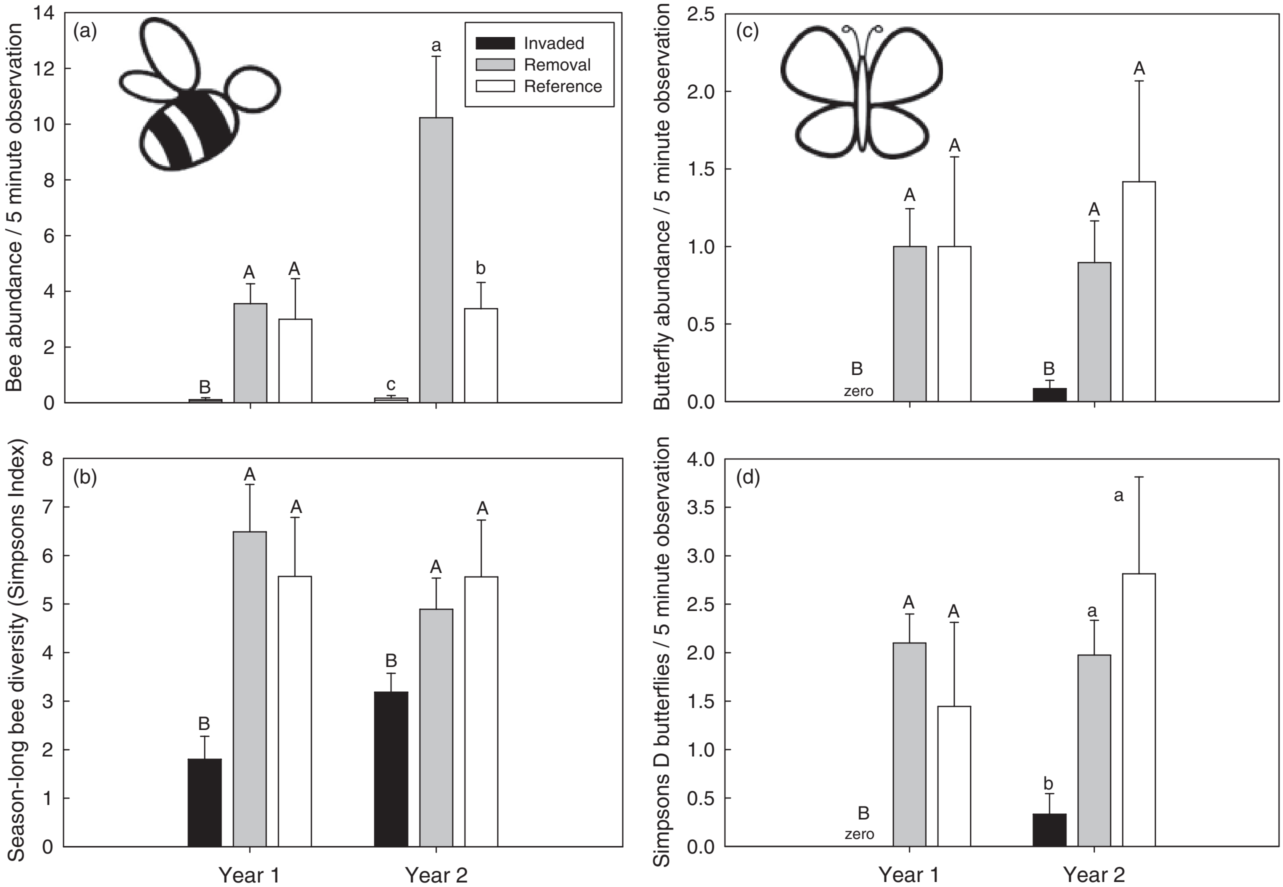

Figure 3. Comparisons of (a) bee abundance, (b) bee diversity, (c) butterfly abundance, and (d) butterfly diversity in the first and second seasons following fen restoration. Bee abundance, butterfly abundance, and diversity are based on the season-long mean number of individuals observed in 5-minute observational sampling periods in invaded, removal, and on-site reference (reference). Bee diversity is based on bees collected with bowl sampling in invaded, removal, and reference plots. Treatment effects from two-way ANOVAs with treatment and time are shown. Upper and lower case letters within the same figure indicate that differences in abundance or diversity vary between treatments by year, as is the case with (a) and (d).

differences between restored and reference plots (Fig. 3d). Across treatments, a number of butterfly species were singletons in both study years, with 62.5 and 46% of species represented by one individual in years 1 and 2, respectively. At the species level, *Pieris rapae* was more abundant than any other butterfly in year 1, while in year 2 *Phyciodes tharos* and *Poanes massasoit* composed a greater proportion of butterflies observed.

An NMDS analysis on the butterfly community also indicated a rapid response to restoration (Fig. 4c & 4d). The butterfly community in invaded plots was significantly different than that in the plots where buckthorn was removed in years 1 and 2 (year 1: R0.44, $p = 0.02$; year 2: R0.40, $p = 0.002$). In year 1, removal and reference plots had similar butterfly communities (R0.17, $p = 0.79$), as did invaded and reference plots (R0.50, $p = 0.083$), with zero butterflies collected in invaded areas. In year 2, the butterfly community was significantly different in invaded plots than both the removal (R0.40, $p = 0.002$) and reference (R0.74, $p = 0.012$) plots and was not different in removal versus reference plots (R0.21, $p = 0.17$). The only butterfly species seen in invaded plots was *Megisto cymela* (Table 3). Despite no significant community-wide differences in butterflies in year 2 between reference and removal plots, *Epargyreus clarus* and *Speyeria cybele cybele* were more abundant in removal than reference plots, while *Ancyloxypha numitor*, *P. massasoit*, and *P. tharos* were more abundant in reference than removal plots (Table 3).

Discussion

There are increasing concerns that loss of pollinators and pollination services could lead to degradation of rare plant communities. Therefore, restoration efforts need to consider not only plant abundance and diversity but also that of their pollinators, and ultimately the provision of pollination services (Fiedler 2010). In this study, we examined plant and pollinator communities following restoration of prairie fen, documenting rapid responses among both taxa. While *Frangula alnus*-invaded plots supported lower diversity and abundance of plants and pollinators, both communities changed rapidly following *F. alnus* removal.

Table 1. Number of bees seen using observational sampling per replicate and treatment in years 1 and 2 post-restoration.

		Year 1				*Year 2*			
Family	*Genus*	*% Observed*	*Invaded*	*Removal*	*Reference*	*% Observed*	*Invaded*	*Removal*	*Reference*
Andrenidae									
	Andrena	0	—	—	—	1.8	0	0	0.25
Apidae									
	Apis mellifera	30.5	0	1.22	0.78	36.8	0	3.90	1.17
	Anthophora	0	—	—	—	0.3	0	0.04	0
	Bombus	21.2	0.06	0.56	0.78	12.3	0.10	1.33	0.25
	Ceratina	0	—	—	—	7.1	0	0.52	0.46
	Xylocopa	0	0	0	0	0.9	0	0.13	0
Colletidae									
	Hylaeus	16.9	0	0.44	0.67	15.6	0.02	1.83	0.29
Halictidae									
	Agapostemon		—	—	—	0.6	0	0.08	0
	Augochlora	0	—	—	—	5.9	0	0.65	0.17
	Augochlorella	1.7	0	0.11	0	7.0	0.02	0.90	0.04
	Halictus	0	—	—	—	1.7	0	0.06	0.17
	Lasioglossum	2.5	0	0.06	0.11	7.1	0	0.69	0.29
	Other Halictidae[a]	23.7	0.06	1.06	0.44	0	—	—	—
Megachilidae									
	Heriades	0	—	—	—	1.5	0	0.04	0.17
	Hoplitus	0	—	—	—	0.2	0	0.02	0
	Megachile	0	—	—	—	0.6	0	0	0.08
	Osmia	0	—	—	—	0.2	0	0.02	0
	Perdita	0	—	—	—	0	0	0	0
	Other[a]	3.4	0	0.11	0.11	0.6	0.02	0.02	0.04
Genus richness		7	2	7	6	17	4	15	12

The first column for years 1 and 2 shows the percent of bees each genus comprised of the total number observed. Dashes indicate that no insects of that species were seen in a given year. Values are by replicate and treatment, averaged over sample dates.
[a] Bees that were not identified to genus; may be composed of more than one genus and family.

We found support for our hypothesis that plant diversity would increase in restored *F. alnus* removal plots, although in the short-term, season-long plant diversity remained lower in removal than reference plots. This is similar to other findings in wetland restorations, where goals related to percent cover are more frequently met than those of species diversity (Matthews et al. 2009*b*). Moreover, the most conservative plant species were most likely to be found only in reference plots, suggesting that restoration of plant diversity is incomplete. Remnant ecosystems frequently have greater native plant species richness and diversity than restored or re-created systems (Polley et al. 2005; Shepherd & Debinski 2005). Even if the local plant community is manipulated, the plant species pool and quality are limited by landscape structure and mesoscale dynamics so that regional pools determine the likelihood of reinvasion by non-natives (Matthews et al. 2009*a*). This suggests the potential need for management of regional plant species pools in fen restoration.

Rapid shifts in the pollinator community contradicted our hypothesis that the pollinator community in restored areas would remain distinct from that in uninvaded areas. In this study, all pollinator community metrics became similar to those in uninvaded fen within the first year following restoration. Bee abundance in restored plots even surpassed that in reference plots in the second year after restoration. We did not see the same pattern in bee diversity, however, suggesting that maximum bee diversity was reached within a plot while bee abundance continued to increase. Similarly, Ebeling et al. (2008) found an asymptotic relationship between pollinator species richness and plant species richness and floral area, but a continued increase in the frequency of pollinator visits to flowers.

Multiple factors may contribute to the rapid insect response to restoration in this prairie fen. The primary factor may be that areas of intact fen were present within 300 m of all invaded areas, providing floral, nesting, and structural resources within foraging distance of even the smallest pollinators we collected (Steffan-Dewenter et al. 2002; Greenleaf et al. 2007). Restoration of invaded plots led to an opening in the canopy and subsequent increases in flower abundance and diversity, a resource which the pollinator community rapidly found. The link between plants and pollinators is well-known; a number of studies have found positive relationships between richness or abundance of floral resources and pollinator diversity or activity at local (Erhardt 1985; Hegland & Boeke 2006; Tuell et al. 2008) and landscape scales (Steffan-Dewenter & Tscharntke 1999; Potts et al. 2003). For butterflies, availability of both nectar resources and larval host plants affects their distribution (Pywell et al. 2004). Light availability has also been documented to affect butterfly abundance in other restorations, even with no changes in nectar plant species richness (Waltz & Covington 2004). Our recent work at the same site shows that light availability increased rapidly to reference conditions following removal treatments (Fiedler 2010). Butterflies are

Table 2. Number of bees collected using pollinator bowl sampling per replicate and treatment in years 1 and 2 post-restoration.

		Year 1				Year 2			
Family	*Genus Species*	*% Trapped*	*Inv*	*Remo*	*Ref*	*% Trapped*	*Inv*	*Remo*	*Ref*
Andrenidae									
	Andrena allegheniensis Viereck	0	—	—	—	0.2	0	0.04	0
	A. carlini Cockerell	0	—	—	—	0.2	0	0.04	0
	A. cressonii Robertson	0	—	—	—	0.6	0	0.04	0.08
	A. nasonii Robertson	0	—	—	—	0.6	0	0.04	0.08
	A. perplexa Smith	0.6	0	0.06	0	0	—	—	—
Apidae									
	Anthophora terminalis Cresson	0.6	0.06	0	0	0.6	0.04	0	0.08
	A. ursina Cresson	0	—	—	—	0.2	0	0.04	0
	A. mellifera L.	3.2	0	0.06	0.22	2.0	0	0.17	0.25
	Bombus impatiens Cresson	0	—	—	—	0.2	0	0.04	0
	B. vagans Smith	0	—	—	—	0.2	0	0.04	0
	Ceratina calcarata/dupla[a]	**18.2**	0.11	**1.00**	0.44	**19.9**	0.33	**1.83**	**1.92**
	C. strenua Smith	1.9	0	0.06	0.11	1.6	0	0.17	0.17
Colletidae									
	Hylaeus affinis Smith	0	—	—	—	0.2	0	0.04	0
	Hylaeus sp. 1	5.8	0	0.17	0.33	3.9	0.04	0.33	0.42
	Hylaeus sp. 3	0	—	—	—	0.6	0	0.04	0.08
Halictidae									
	Agapostemon sericeus (Forster)	0	—	—	—	0.4	0	0	0.08
	Ag. virescens (F.)	1.3	0	0.11	0	0.0	—	—	—
	Augochlora pura (Say)	8.4	0.06	**0.56**	0.11	0.4	0.04	0.04	0
	Aug. aurata (Smith)	7.8	0.06	**0.50**	0.11	**11.2**	0.08	**1.54**	0.67
	Augochloropsis metallica (F.)	0	—	—	—	0.4	0	0.08	0
	Halictus confusus Smith	1.3	0	0.11	0	4.5	0	0.33	0.58
	Halictus ligatus Say	1.3	0	0.11	0	1.0	0	0.04	0.17
	Lasioglossum (Dialictus) atwoodi Gibbs	4.5	0	0.17	0.22	0.8	0.13	0.04	0
	L. (D.) bruneri (Crawford)	0	—	—	—	0.2	0.04	0	0
	L. (D.) cressonii (Robertson)	0.6	0	0.06	0	0.6	0.04	0.08	0
	L. (D.) divergens (Lovell)	0.6	0.06	0	0	0	—	—	—
	L. (D.) ephialtum Gibbs	**11.0**	0	0.06	**0.89**	**14.0**	0.42	**0.96**	**1.50**
	L. (D.) illinoense (Robertson)	0	—	—	—	0.2	0.04	0	0
	L. (D.) macoupinense (Robertson)	0	—	—	—	0.2	0.04	0	0
	L. (D.) mitchelli Gibbs	3.9	0	0.11	0.22	0.2	0	0.04	0
	L. (D.) oceanicum (Cockerell)	0	—	—	—	0.4	0	0.08	0
	L. (D.) paradmirandum (Knerer & Atwood)	1.3	0	0.11	0	0	—	—	—
	L. (D.) pectorale (Smith)	2.6	0	0.11	0.11	1.0	0	0.13	0.08
	L. (D.) pilosum (Smith)	1.3	0	0	0.11	0.8	0	0	0.17
	L. (D.) sp. 3	0	—	—	—	3.3	0.13	0.21	0.33
	L. (D.) sp. 4	0	—	—	—	0.2	0	0.04	0
	L. (D.) sp. 5	0	—	—	—	0.4	0	0	0.08
	L. (D.) sp. 6	0	—	—	—	0.2	0.04	0	0
	L. (D.) sp. 7	0	—	—	—	0.2	0.04	0	0
	L. (D.) sp. 8	0	—	—	—	0.4	0	0	0.08
	L. (D.) spp.	1.9	0	0.17	0	1.2	0.04	0.04	0.17
	L. (D.) versans (Lovell)	3.2	0.06	0.22	0	0	—	—	—
	L. (D.) versatum (Robertson)	5.2	0	0.22	0.22	**21.1**	0.04	**2.63**	**1.67**
	L. coriaceum (Smith)	5.2	0.28	0.06	0.11	1.4	0.13	0.08	0.08
	L. leucozonium (Schrank)	1.9	0	0.17	0	0.2	0	0.04	0
	L. nelumbonis (Robertson)	0.6	0	0.06	0	0	—	—	—
Megachilidae									
	Hoplitis producta (Cresson)	0	—	—	—	0.6	0	0.13	0
	H. spoliata (Provancher)	0	—	—	—	0.4	0	0.08	0
	Megachile campanulae (Robertson	0	—	—	—	0.4	0	0	0.08
	M. inermis Provancher	0	—	—	—	0.2	0	0.04	0
	M. montivaga Cresson	0	—	—	—	0.2	0	0.04	0
	M. pugnata Say	0.6	0	0.06	0	0	—	—	—
	M. relative Cresson	0.6	0	0.06	0	0	—	—	—
	Osmia georgica Cresson	0	—	—	—	0.6	0	0.13	0
	O. michiganensis Mitchell	0	—	—	—	0.6	0	0.04	0.08
	O. pumila Cresson	2.6	0	0.22	0	0.2	0	0.04	0
	O. simillima Smith	1.3	0	0	0.11	0	—	—	—
Species richness		29	7	25	14	48	17	37	23

The percent of bees each species comprised of the total number trapped is in the first column for years 1 and 2. Bolded values are the most common species whose abundance varied most by treatment. Dashes indicate no insects of that species were seen in a given year. Values are by replicate and treatment, averaged over sample dates.
[a] Females of these species, *C. calcarata* Robertson and *C. dupla* Say, are morphologically indistinguishable; only 1 male of each species was collected.

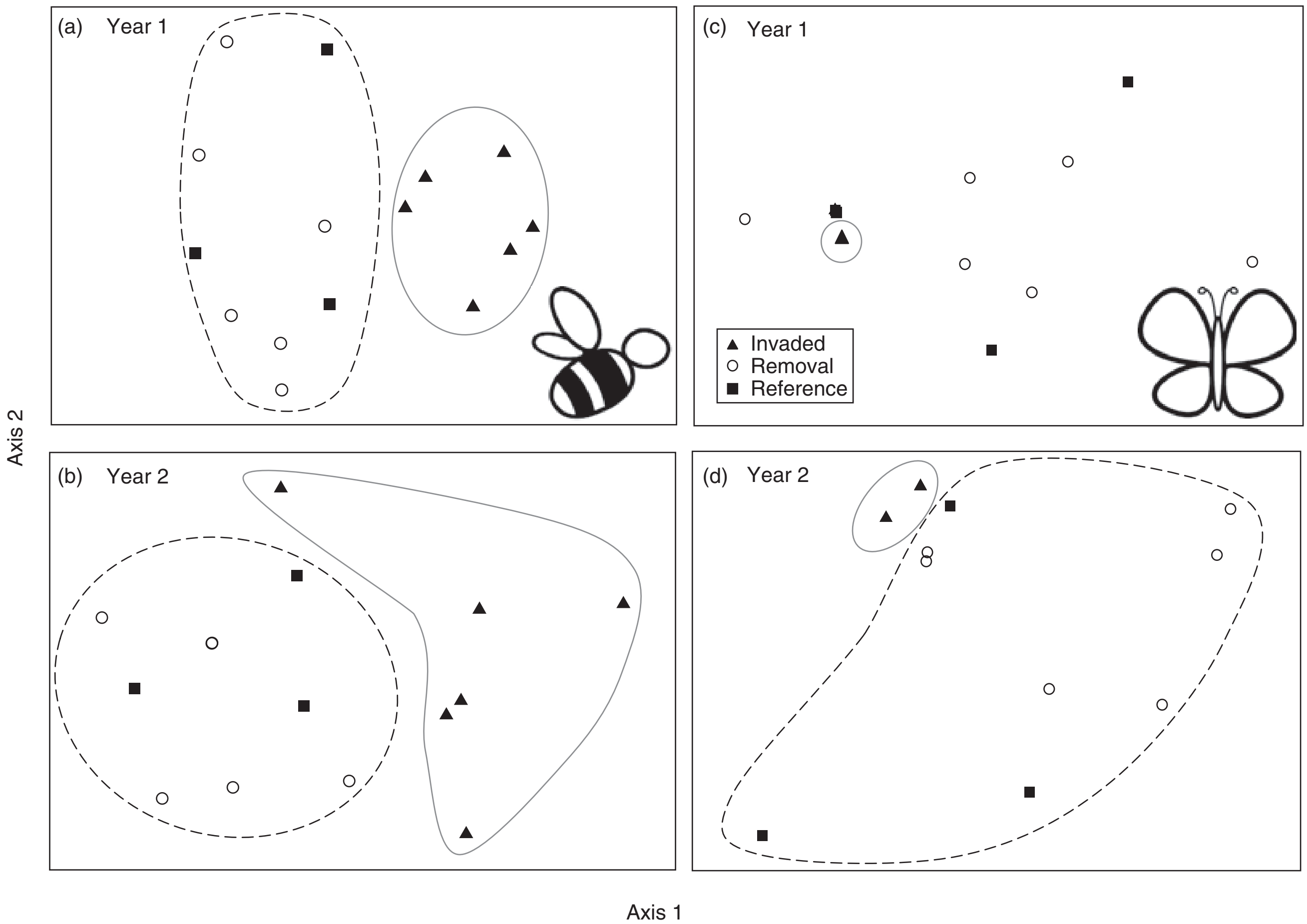

Figure 4. Two-dimensional NMDS ordinations of the bee (a, b) and butterfly community (c, d) following restoration. (a) and (b) show distinct bee communities in invaded plots in both years 1 and 2, with bee communities in removal and reference plots overlapping. (c) and (d) show that the invaded and removal butterfly communities differ in both years 1 and 2. In year 1, all six replicates of invaded contained zero butterflies and all points overlap. In year 2, one butterfly was seen in invaded plots and five of the six points overlap. The ordination is based a Bray–Curtis dissimilarity matrix (using $n + 1$), using mean values per replicate and treatment; data were square root transformed. Stress values were as follows: (a) 0.14, (b) 0.14, (c) 0.04 and (d) 0.11. Lines represent relationships between groups according to ANOSIM.

also known to use habitat openings and butterfly richness is greatest in the open-structured phase of grassland clearing (Erhardt 1985; Potts et al. 2003). The increase in flowering plant abundance and diversity that occurred immediately following invasive removal was primarily of short-lived, ruderal species. We anticipate a continued shift in plant species toward a sedge-dominated community and it is likely that pollinator abundance will also decrease over time in removal plots.

In addition to resource density, habitat size and quality play important roles in pollinator abundance and diversity. Habitat area influences which pollinator species use a patch. In calcareous grasslands in Europe, species richness of monophagous butterflies increased with habitat area (Steffan-Dewenter & Tscharntke 2000), providing evidence that specialists may be more likely to find the resources they require in larger areas.

Even when plant–pollinator communities are successfully restored, species interactions may remain less complex than in remnant habitats (Forup et al. 2008), potentially affecting pollination in the long term. For example, in old field meadows plant abundance and insect richness and abundance were restored, although the species comprising each system are distinct (Forup & Memmott 2005). In addition, pollinator, especially bee, communities vary in species composition and abundance by year (Williams et al. 2001). Patterns of bee abundance in our study matched that pattern, with a large proportion of singleton species collected in both years.

Our study indicates that following removal of *F. alnus*, pollinator abundance, diversity, and community structure rapidly became similar to those in reference conditions. In contrast, while plant communities rapidly became distinct from unrestored plots, they did not approach reference conditions within the timeframe of our study. Surprisingly, these rapid pollinator responses occurred within a landscape containing relatively little intact habitat. This landscape likely provided sufficient resources for the persistence of generalist pollinators, which readily re-colonize restored areas. In landscapes lacking resources for generalist pollinators, there are likely cascading effects on plant community diversity over time (Memmott

Table 3. Number and identity of butterflies seen during the 5-minute observational sampling in years 1 and 2 post-restoration.

Family	Genus Species	Common Name	Year 1				Year 2			
			% obs	Inv	Remo	Ref	% obs	Inv	Remo	Ref
Danaidae										
	Danaus plexippus (Linnaeus)	Monarch	3.8	0	0.06	0	0	—	—	—
Hesperiidae										
	—	Unidentified skipper	11.5	0	0.06	0.11	4.3	0	0.02	0.08
	Ancyloxypha numitor (Fabricius)	Least skipper	3.8	0	0.06	0	8.7	0	0.04	**0.17**
	Epargyreus clarus (Cramer)	Silver spotted skipper	0	—	—	—	5.2	0	**0.13**	0
	Poanes hobomok (Harris)	Hobomok skipper	0	—	—	—	0.9	0	0.02	0
	P. massasoit (Scudder)	Mulberry wing skipper	3.8	0	0.06	0	13.9	0	0	**0.33**
Lycaenidae										
	Celastrina neglecta (W. H. Edwards)	Summer azure	0	—	—	—	1.7	0	0.04	0
Nymphalidae										
	Boloria selene myrina (Cramer)	Silver bordered fritillary	0	—	—	—	1.7	0	0	0.04
	Phyciodes tharos (Drury)	Pearly crescent	0	—	—	—	20.9	0	0.08	**0.42**
	Speyeria cybele cybele (Fabricius)	Great spangled fritillary	15.4	0	0.11	0.11	20.9	0	**0.42**	0.08
	Vanessa cardui (Linnaeus)	Painted lady	0	—	—	—	3.5	0	0	0.08
Papilionidae										
	Papilio glaucus (Linnaeus)	Tiger swallowtail	3.8	0	0.06	0	3.5	0	0.08	0
	P. troilos (Linnaeus)	Spicebush swallowtail	11.5	0	0.06	0.11	6.1	0	0.06	0.08
Pieridae										
	Pieris rapae (Linnaeus)	Cabbage white	46.2	0	**0.44**	**0.22**	0	—	—	—
Satyridae										
	Megisto cymela (Cramer)	Little wood satyr	0	—	—	—	8.7	0.08	0	0.13
Species richness			8	0	8	5	13	1	9	9

obs, percent of total observed per year; Inv, Invaded; Remo, Removal; Ref, Reference.
Bolded values are the most abundant species whose abundance varied by treatment. Dashes indicate no insects of that species were seen in a given year. Values are by replicate and treatment, averaged over sample dates.

et al. 2004). Here and elsewhere, the most conservative plants may not return to restored areas and seed additions may be required. Only continued study will reveal whether the current restoration activities will be sufficient for long-term conservation of endemic plants and pollinators.

Implications for Practice

- Restoration activities targeted to areas with intact habitat patches may assist in community persistence and recovery of generalist pollinators.
- Rare plants may require seed additions and long-term monitoring to ensure their persistence in prairie fen habitats.
- Assessment immediately following restoration is not sufficient to include the trajectory of the plant and pollinator community through plant succession.

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LITERATURE CITED

Amon, J. P., C. A. Thompson, Q. J. Carpenter, and J. Miner. 2002. Temperate zone fens of the glaciated Midwestern USA. Wetlands **22:**301–317.

Ashman, T. L., T. M. Knight, J. A. Steets, P. Amarasekare, M. Burd, D. R. Campbell, et al. 2004. Pollen limitation of plant reproduction: Ecological and evolutionary causes and consequences. Ecology **85:**2408–2421.

Bedford, B. L., and K. S. Godwin. 2003. Fens of the United States: distribution, characteristics, and scientific connection versus legal isolation. Wetlands **23:**608–629.

Biesmeijer, J. C., S. P. M. Roberts, M. Reemer, R. Ohlemuller, M. Edwards, T. Peeters, et al. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science **313:**351–354.

Brown, M. J. F., and R. J. Paxton. 2009. The conservation of bees: a global perspective. Apidologie **40:**410–416.

Burd, M. 1994. Bateman principle and plant reproduction—the role of pollen limitation in fruit and seed set. Botanical Review **60:**83–139.

Clark, J. A., and R. M. May. 2002. Taxonomic bias in conservation research. Science **297:**191–192.

Clarke, K. R., and R. N. Gorley. 2006. Primer v6. Primer-E, Plymouth, United Kingdom.

Droege, S. 2010. The very handy manual: how to catch and identify bees and manage a collection (available from ftp://ftpext.usgs.gov/pub/er/md/laurel/Droege/).

Ebeling, A., A. M. Klein, J. Schumacher, W. W. Weisser, and T. Tscharntke. 2008. How does plant richness affect pollinator richness and temporal stability of flower visits? Oikos **117:**1808–1815.

Erhardt, A. 1985. Diurnal Lepidoptera: sensitive indicators of cultivated and abandoned grassland. Journal of Applied Ecology **22:**849–861.

Fiedler, A. K. 2010. Restoration of prairie fen plants, insects, and abiotic processes. PhD dissertation. Department of Entomology, Michigan State University, East Lansing.

Fiedler, A. K., and D. A. Landis. 2011. Biotic and abiotic conditions in Michigan prairie fen invaded by glossy buckthorn (*Frangula alnus*). Natural Areas Journal. In press.

Forup, M. L., K. S. E. Henson, P. G. Craze, and J. Memmott. 2008. The restoration of ecological interactions: plant-pollinator networks on ancient and restored heathlands. Journal of Applied Ecology **45:**742–752.

Forup, M. L., and J. Memmott. 2005. The restoration of plant-pollinator interactions in hay meadows. Restoration Ecology **13:**265–274.

Goulson, D., G. C. Lye, and B. Darvill. 2008. Decline and conservation of bumble bees. Annual Review of Entomology **53:**191–208.

Greenleaf, S. S., N. M. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. Oecologia **153:**589–596.

Hegland, S. J., and L. Boeke. 2006. Relationships between the density and diversity of floral resources and flower visitor activity in a temperate grassland community. Ecological Entomology **31:**532–538.

Herman, K. D., L. A. Masters, M. R. Penskar, A. A. Reznicek, G. S. Wilhelm, W. W. Brodovich, and K. P. Gardiner. 2001. Floristic quality assessment with wetland categories and examples of computer applications for the state of Michigan. Michigan Department of Natural Resources Wildlife Division, Natural Heritage Program, Lansing, Michigan.

Hobbs, R. J., and D. A. Norton. 1996. Towards a conceptual framework for restoration ecology. Restoration Ecology **4:**93–110.

Kearns, C. A., D. W. Inouye, and N. M. Waser. 1998. Endangered mutualisms: the conservation of plant-pollinator interactions. Annual Review of Ecology and Systematics **29:**83–112.

Kevan, P. G. 1999. Pollinators as bioindicators of the state of the environment: species, activity and diversity. Agriculture Ecosystems & Environment **74:**373–393.

Klein, A. M., B. E. Vaissiere, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B-Biological Sciences **274:**303–313.

Landis, D. A., A. K. Fiedler, C. A. Hamm, D. L. Cuthrell, E. H. Schools, D. R. Pearsall, M. E. Herbert, and P. J. Doran. 201x. Insect conservation in prairie fen: addressing the challenge of global change. Journal of Insect Conservation. In press. DOI: 10.1007/s10841-011-9398-3.

Matthews, J. W., A. L. Peralta, A. Soni, P. Baldwin, A. D. Kent, and A. G. Endress. 2009*a*. Local and landscape correlates of non-native species invasion in restored wetlands. Ecography **32:**1031–1039.

Matthews, J. W., G. Spyreas, and A. G. Endress. 2009*b*. Trajectories of vegetation-based indicators used to assess wetland restoration progress. Ecological Applications **19:**2093–2107.

McGregor, S. E. 1976. Insect pollination of cultivated crop plants. USDA Agricultural Handbook #496. U.S. Government Printing Office, Washington, D.C.

Memmott, J., N. M. Waser, and M. V. Price. 2004. Tolerance of pollination networks to species extinctions. Proceedings of the Royal Society of London Series B-Biological Sciences **271:**2605–2611.

MNFI (Michigan Natural Features Inventory). 2007. Species explorer (available from http://web4.msue.msu.edu/mnfi/explorer/index.cfm2010).

Nekola, J. C. 2004. Vascular plant compositional gradients within and between Iowa fens. Journal of Vegetation Science **15:**771–780.

New, T. R. 1997. Are lepidoptera an effective 'umbrella group' for biodiversity conservation? Journal of Insect Conservation **1:**5–12.

Polley, H. W., J. D. Derner, and B. J. Wilsey. 2005. Patterns of plant species diversity in remnant and restored tallgrass prairies. Restoration Ecology **13:**480–487.

Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. Trends in Ecology & Evolution **25:**345–353.

Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'eman, and P. Willmer. 2003. Linking bees and flowers: how do floral communities structure pollinator communities? Ecology **84:**2628–2642.

Pywell, R. F., E. A. Warman, T. H. Sparks, J. N. Greatorex-Davies, K. J. Walker, W. R. Meek, C. Carvell, S. Petit, and L. G. Firbank. 2004. Assessing habitat quality for butterflies on intensively managed arable farmland. Biological Conservation **118:**313–325.

Quinn, G. P., and M. J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, United Kingdom.

Renner, S. S. 2006. Rewardless flowers in the angiosperms and the role of insect cognition in their evolution. Pages 123–144 in N. M. Waser and J. Ollerton, editors. Chapter 6, Plant-pollinator interactions: from specialization to generalization. University of Chicago Press, Chicago, Illinois.

Ruiz-Jaen, M. C., and T. M. Aide. 2005. Restoration success: how is it being measured? Restoration Ecology **13:**569–577.

SAS Institute. 2010. SAS/STAT user's guide for personal computers. SAS Institute, Cary, North Carolina.

SER Working Group. 2004. The SER international primer on ecological restoration. Society for Ecological Restoration International, Tucson, Arizona (available from www.ser.org).

Shepherd, S., and D. M. Debinski. 2005. Evaluation of isolated and integrated prairie reconstructions as habitat for prairie butterflies. Biological Conservation **126:**51–61.

Spieles, J. B., P. J. Comer, D. A. Albert, and M. A. Kost. 1999. Natural community abstract for prairie fen. Michigan Natural Features Inventory, Lansing, Michigan.

Steffan-Dewenter, I., U. Munzenberg, C. Burger, C. Thies, and T. Tscharntke. 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology **83:**1421–1432.

Steffan-Dewenter, I., and T. Tscharntke. 1999. Effects of habitat isolation on pollinator communities and seed set. Oecologia **121:**432–440.

Steffan-Dewenter, I., and T. Tscharntke. 2000. Butterfly community structure in fragmented habitats. Ecology Letters **3:**449–456.

Tuell, J. K., A. K. Fiedler, D. Landis, and R. Isaacs. 2008. Visitation by wild and managed bees (*Hymenoptera*: *Apoidea*) to eastern US native plants for use in conservation programs. Environmental Entomology **37:** 707–718.

Waltz, A. E. M., and W. W. Covington. 2004. Ecological restoration treatments increase butterfly richness and abundance: mechanisms of response. Restoration Ecology **12:**85–96.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. Bioscience **48:**607–615.

Williams, N. M. 2011. Restoration of nontarget species: bee communities and pollination function in riparian forests. Restoration Ecology **19:**450–459.

Williams, N. M., R. L. Minckley, and F. A. Silveira. 2001. Variation in native bee faunas and its implications for detecting community changes. Conservation Ecology 5 (available from http://www.consecol.org/vol5/iss1/art7/).

Winfree, R. 2010. The conservation and restoration of wild bees. Year in Ecology and Conservation Biology 2010 **1195:**169–197.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Plant species ($n = 177$) and the percent of quadrats occupied by each species in *Frangula alnus* invaded, *F. alnus* removal, and uninvaded reference plots in a prairie fen wetland, Clarklake, Michigan 2009. Values in italicized bold varied greatly between treatments.

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