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dissertation entitled

RESTORATION OF PRAIRIE FEN PLANTS, INSECTS, AND
ABIOTIC PROCESSES

presented by

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has been accepted towards fulfillment
of the requirements for the

Doctoral degree in Entomology

Major Professor's Signature

8/23/2010

Date

RESTORATION OF PRAIRIE FEN PLANTS, INSECTS, AND ABIOTIC PROCESSES

By

Anna Katherine Fiedler

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Entomology

2010

ABSTRACT

RESTORATION OF PRAIRIE FEN PLANTS, INSECTS, AND ABIOTIC PROCESSES

By

Anna Katherine Fiedler

There are growing concerns about biodiversity decline and species extinctions due to habitat fragmentation, invasive species, and climate change. Habitat restoration is increasingly used to reverse degradation of rare ecosystems and maintain biological diversity, species interactions, and ecosystem function. The effects of restoration activities on these properties, however, are often not measured. The Midwestern U.S. has a relatively high density of globally rare prairie fen wetlands which support high plant diversity and support a number of rare and endangered plants, insects, and vertebrates. The most common exotic invasive species in Michigan prairie fens is *Frangula alnus* (glossy buckthorn). *Frangula alnus* invasion is known to alter soil and plant community conditions in fens but changes following restoration have never been quantified. The goal of my research was to assess changes in abiotic conditions, species diversity, and species interactions after restoration, and to assess whether they are on a trajectory toward those in uninvaded fen. Toward that end, I quantified differences in invaded and uninvaded prairie fen before restoration began, as well as tracking shifts in resource availability, plant community, pollinator diversity, plant-pollinator networks, and pollinator function in the two growing seasons following restoration of prairie fen. I found a range of responses to restoration across resources and plant community metrics. Light availability, herbaceous plant cover, and relative graminoid abundance increased in restored plots, while soil pH, surface spatial heterogeneity and floristic quality index were initially greater in uninvaded areas versus invaded fen and remained so in the first two years after restoration. These results indicate that some soil and plant community factors change rapidly while others may remain altered for years.

A diverse community of mobile generalist pollinators rapidly re-colonized restored areas. Bee and butterfly communities were nearly absent in invaded prairie fen and responded rapidly to restoration in abundance, diversity, and composition. However, plant species diversity and composition in restored plots remained significantly different than in reference plots, suggesting the plant community may take longer to recover.

I examined plant–pollinator networks and the ecosystem function of pollination using quantitative food webs describing plant-pollinator interactions, and by assessing pollinator function using sentinel *Asclepias incarnata* plants. Plant-pollinator networks in invaded plots were depauperate, with significantly lower plant and pollinator species richness than restored or reference plots. Network connectance, compartment diversity, generality, and vulnerability did not differ between restored and reference plots, with marginally higher interaction evenness in reference than restored plots. Pollinator function was restored in cleared areas in the first growing season following restoration, with no significant differences in pollinator abundance or diversity between cleared and reference areas. This work indicates that rapid restoration of plant community structure, pollinator diversity, and function are possible in open-structured ecosystems. Combined consideration of species diversity, ecosystem function, and species interactions provides a process-based ecosystem analysis that can inform ecological theory and restoration.

ACKNOWLEDGEMENTS

I am deeply grateful to Dr. Doug Landis for his support through my change in research focus after my Masters degree, his commitment to finding research funding for my project, and for providing the space for me to grow into a colleague over the last four years. Conversations with Dr. Rufus Isaacs, Dr. Patrick Doran, and Dr. Carolyn Malmstrom have helped me to focus and develop my research ideas, as well as provided career direction.

Dave Cuthrell and Ryan O'Conner shared their contagious enthusiasm and love for prairie fens with me. Greg Kowalewski, Steve Woods, Rodolfo Zuniga-Villegas and their crews provided indispensable help with plot establishment and ongoing restoration work. I am grateful to Chris Sebolt for putting himself in very real danger of contracting poison sumac each of the many times he helped with field work and restoration activities.

Jane Memmott and her lab group, especially Jo Brooks, Rachel Gibson, Darren Evans, and Mariano Devoto, made learning about the intricacies of species networks, as well as the meaning of "toodlepip", a joy.

I am extremely grateful for the enthusiastic help that Mitch Lettow provided on this project, and the consistent and humorous assistance that Colin Philippo provided. I simply could not have done this project without their help.

Rob Ahern provided much-needed support and perspective, as well as encouragement to try the parts of this research that I have found most rewarding. I am also grateful to Ben Werling, Mary Gardiner, and Jeff Evans for their input, encouragement, and high fives. Emily Scott and the chocolate chip cookies at Gone Wired provided an impetus to work on weekends to finish this work.

I am indebted to the community of people I have met and become friends with during my time in Lansing. You have been the source of creativity that has kept me interested in, and taking an inspired approach to, this research. Anna Porubcansky has provided constant reminders to take things as they come, Laura Wies has been a safe haven. I am grateful to my family for their continued support of me and interest in this work.

Most of all, I appreciate the support that Jake McCarthy provided, in his near super-human ability to tolerate me after long work days, his interest in my R-values, and his inspiration for ways to clearly communicate my findings to others.

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Chapter 1

LITERATURE REVIEW

Introduction

The retreat of the most recent glaciation from what is now the Northern U.S. approximately 12,000 years ago created a set of abiotic conditions that paved the way for the development of unique communities (Albert 1995). One of these is prairie fen, a unique groundwater fed wetland habitat type in the Midwestern U.S. Prairie fen is exceptional in that it supports very high biodiversity within communities that compose less than 0.1% of the glaciated landscape in the Midwestern U.S. (Nekola 1994). Prairie fen communities in Michigan are home to a suite of rare and endangered plants and animals, including the federally listed Mitchell's Satyr butterfly (*Neonympha mitchellii mitchellii*). The plant community in prairie fen contains many rare species and is increasingly imperiled.

Prairie fen is a fire–dependent community that is typically embedded in a matrix of prairie and savanna habitats. Together, the upland and wetland elements create a landscape of high biodiversity. Since European settlement in the Midwestern U.S., prairie fen and the surrounding matrix have undergone a variety of changes. These changes have resulted in a number of threats to prairie fen, including conversion, fragmentation, hydrological changes, altered disturbance regimes, introduction of non-native species, pollution, and increased nutrient inputs. The result of these combined threats is that a group of plant and animal species endemic to prairie fen are are risk of extinction. Perhaps more importantly, ecosystem functions such as water and nutrient cycling that were once supported by this habitat mosaic may be disrupted. Insects are key to a variety of ecosystem processes: decomposition, insect predation, herbivory, and pollination. Pollinator species loss may represent a direct threat to plant persistence in fen due to decreased seed set, and therefore persistence of already rare plant species. To prevent further species, habitat, and ecosystem function loss and to protect watershed health, an understanding of the importance and restoration of pollinator function in prairie fen communities is vital.

Glacial History

During the Wisconsonian glaciation in the Pleistocene, lobes of glacial ice flowed down from the North, eventually covering all of Michigan and much of Wisconsin and Minnesota (Albert 1995). The advancing glaciers passed over bedrock composed of Paleozoic limestone, dolomite, sandstone, and shale, scouring uplands and carrying soil and rock in and on the ice (Albert 1995). When the glaciers melted about 13,000-16,000 years Before Present (BP), the resulting glacial till was redeposited to form the current landscape. Where glacial lobes meet along their edges, unique processes occur resulting in the formation of interlobate landscapes. These areas are typically of higher relief than the surrounding landscape and contain many ice-contact features, including end-moraine ridges composed of elongate mounds of glacial till at the edge of glaciers, eskers formed of glacial outwash carried by melting water under and between glaciers, and kettlehole lake depressions left by melting ice chunks which often have surrounding wetlands (Albert 1995). The moraine and esker soils are particularly well-drained, but poorly drained soils are typical of the kettlehole depressions (Albert 1995).

Prairie Fen

Unique Wetland Type

Prairie fen habitats are one of the rarest wetland types in the U.S., and occur most commonly in the glaciated Midwest (Spieles et al. 1999, Amon et al. 2002). The difference between current day fen status and that before European settlement is not well known because fen communities were not specifically delineated in early land surveys (Bedford and Godwin 2003). However, prairie fens are undoubtedly much more rare today than they were historically; Pearson and Loeschke (1992) compared the amount of prairie fen in Iowa and determined that nearly 40% had been destroyed by cultivation or drainage. In Michigan, there are currently approximately 130 fens, distributed primarily in the southeastern and southwestern interlobate regions (Spieles et al. 1999). Prairie fens are typically small, those in New York are primarily smaller than 5 hectares (Bedford and Godwin 2003), but contain high plant species diversity. Amon et al. (2002) identified 1169 vascular plant species in Midwestern fens, many of them rare. This combination of small size and high species richness makes fens biodiversity hotspots. In Iowa, New York, and New Jersey, fens compose less than 0.1% of total land, yet contain 7-18% of the rare taxa that occur in those states (Nekola 1994).

The term fen is used to describe a variety of wetland habitats throughout North America and Europe (Amon et al. 2002, Bedford and Godwin 2003). Although they occur across a range of soils, climate, and water availability, fens are distinct from other wetland communities in that all are groundwater fed (Bedford and Godwin 2003) (Fig. 1). Because the primary water input is groundwater, water level variation within undisturbed fens is quite low (Amon et al. 2002, Bedford and Godwin 2003). The resulting system is one where plants grow in constantly saturated soils but are rarely inundated with standing water. The size of the catchment area surrounding a fen is one determinant of how much this water level changes; if the recharge area is small and local, water levels in a fen will drop during extended dry periods (Amon et al. 2002). Water flows through the prairie fen in either diffuse surface flow or in more concentrated stream flow (Spieles et al. 1999). The amount of water that flows from fens into surface lakes and rivers varies greatly, and depends on the amount of water input into the system (Amon et al. 2002).

Fen habitats have a high degree of mineral inflow through groundwater, and the characteristics of the surrounding upland determine the amount and type of nutrients in prairie fens. An alkaline fen results in locations where the surrounding substrate is

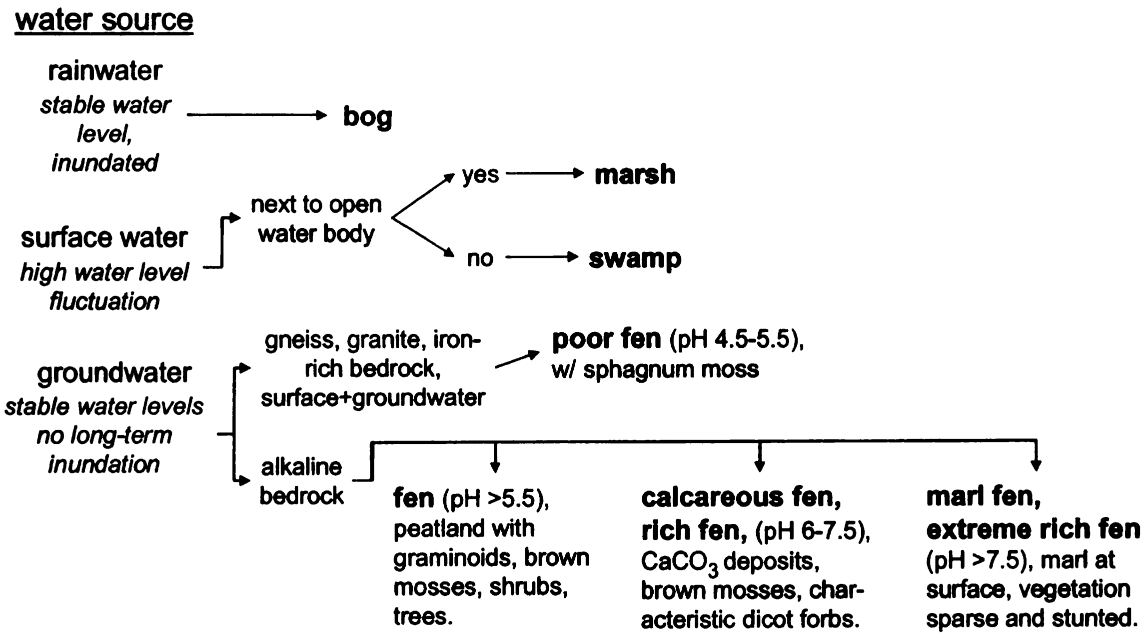

Figure 1. Characterization of wetlands by water source and water level. Fen is defined by groundwater, but poor fen may have a combination of surface and groundwater inflow.

primarily composed of limestone or dolomite bedrock or calcareous rich glacial deposits (Bedford and Godwin 2003). Water flowing through all of these substrates becomes rich in calcium and magnesium. As groundwater flows through surrounding uplands, nutrient availability often decreases because formation of $CaCO_3$, $CaPO_4$ and the presence of iron promote phosphorous adsorption or precipitation into forms of phosphorous that are unavailable to plants (Bedford and Godwin 2003, Grootjans et al. 2006). These communities are often referred to as rich fens due to high species diversity that occurs on soils depauperate in nitrogen and phosphorous. A drop in the partial pressure of CO_2 causes carbonates to form when groundwater rich in calcium bicarbonate reaches the surface (Bedford and Godwin 2003). This causes calcium to precipitate out into $CaCO_3$ deposits, creating a marl substrate that occurs only in alkaline fens. Most commonly this deposit is clay-like marl, however, on occasion $CaCO_3$ precipitates into hard deposits known as tufa (Amon et al. 2002).

In Europe, prairie fens are considered one type of peatland, with peat substrate and occasional mineral soils from $CaCO_3$ deposits (Rydin et al. 2006). In the U.S., however, fens can develop on carbonate or peat substrates, or a combination of the two (Amon et al. 2002). Peat in fens is composed of organic matter provided by brown moss, sedges, and sphagnum moss which break down slowly in the anoxic conditions of the water saturated substrate in prairie fen (Amon et al. 2002, Grootjans et al. 2006). If the water inflow to a fen is small, there may not be sufficient water saturation to lead to peat formation, leading to a fen with mineral substrate only (Amon et al. 2002). Prairie fens, therefore, contain a mosaic with mineral deposits, as well as peat histosols in a progression of decompositional states, including fibric, hemic, and sapric deposits (Buol et al. 1997). Fibric peat is primarily undecomposed brown and sphagnum moss with a tan to light brown color. When water levels drop, sapric peat formed from decomposed brown moss, sedges, and sphagnum is likely to form (Buol et al. 1997, Amon et al. 2002). Sapric peat based soils from 0.5 to >12 m deep are black and high in organic matter, and are the typical prairie fen substrate (Spieles et al. 1999, Amon et al. 2002). Miner and Ketterling (2003) examined the process of marl and peat deposition in a prairie fen in Illinois. They found that basal peat deposits bordering marl flats ranged in age from 14,700 years old to less than 500 years old. This age range and the patterns of peat and marl they found indicate that the formation of peat and marl flats is a cyclic process, with peat erosion forming a marl flat that is subsequently covered by accumulating peat (Miner and Ketterling 2003). Through the process of marl deposition, peat formation, and erosion, a continuum of soils are present within prairie fen that form the substrate for a variety of plant communities.

Plant Community Gradient

The plant community in prairie fen has been characterized as a gradient that includes four (Spieles et al. 1999) to five (Bowles et al. 1996, Bowles et al. 2005) vegetation zones. Here, I use the definitions outlined by Spieles et al. (1999), which include sedge meadow, inundated flats, wooded fen, and marl flat. The occurrence and amount of each vegetation zone varies from fen to fen.

Sedge meadow plant communities primarily occur on sapric peat and have the greatest herbaceous cover and diversity of the plant communities, including shrubs, composites, and grasses (Spieles et al. 1999). The sedge-shrub association contains

Carex stricta (meadow sedge) and *Carex aquatilis*, in addition to low-growing shrubs, especially *Potentilla fruticosa* (shrubby cinquefoil) (Spieles et al. 1999). The sedge-composite association contains *Carex stricta*, *C. saquatilis*, and *C. sterilis*, along with *Aster* spp. (asters), *Eupatorium perfoliatum* (boneset), and *Eupatorium maculatum* (Joe-pye weed) (Spieles et al. 1999). The sedge-grass association is commonly dominated by the same *Carex* species as sedge-composite, as well as *Andropogon gerardii* (big bluestem), *A. scoparious* (little bluestem), and *Sorghastrum nutans* (Indian grass) (Spieles et al. 1999). *Pycnanthemum virginianum* (Virginia mountain mint), *Muhlenbergia glomerata* (marsh wild-timothy), *Thelypteris palustris* (marsh fern), *Solidago ohioensis* (Ohio goldenrod), and *Rudbeckia hirta* (black-eyed Susan) are common species in all of the sedge meadow associations.

The inundated flats zone occurs in depressions near rivers or lakes within the fen, and can be localized around the water body or more expansive. Inundated flat is the wettest area in the fen, with up to 0.3 m of standing water in spring and summer. Dominant plant species include a group of rushes: *Cladium mariscoides* (twig-rush), *Scirpus acutus* (hardstem bulrush), *Eliocharus rostellata* (spike-rush), *E. elliptica* (golden-seeded spike rush), and *Juncus brachycephalus* (Spieles et al. 1999).

Prairie fen may include a wooded zone dominated by shrubs and trees and grading into uplands. In addition, wooded fen zones may also occur in wetter areas, with *Larix laricina* (tamarack) dominating the tree composition. In some cases *Ulmus americana* (American elm) and *Acer rubrum* (red maple) are present in this zone. Common shrub species include *Cornus foemina* (gray dogwood), *C. stolonifera* (red-osier dogwood), *Toxicodendron vernix* (poison sumac), and *Spiraea alba* (meadowsweet) (Spieles et al. 1999).

Areas where calcareous groundwater seepage enters the prairie fen contain marl flat vegetation. Sparse vegetation dominated by calcifiles characterizes these areas, which may be small and broken or broad and flat. Species common in this area include *Lobelia kahlmii* (bog lobelia), *Carex flava* (sedge), *Rhynchospora alba* (beak-rush), and *Parnassia glauca* (grass-of-parnassus). Carnivorous plants, including *Sarracenia purpurea* (pitcher plant) and *Drosera rotundifolia* (round-leaved sundew) may also be found in this plant community.

The result of this soil and vegetation gradient is that the habitat frequently known as prairie fen contains a variety of sub-communities. This continuum is part of the reason for the unusually high species diversity in prairie fens, although all of these plant communities are not present in each prairie fen. In summary, habitats discussed as prairie fen here are groundwater fed, water saturated, alkaline habitats with soils that range from mineral marl to fibric and sapric peat.

In addition to a plant community gradient, tussocks formed by *C. stricta* provide unique microhabitat for a range of plant species occurring from wet to dry. Peach and Zedler (2006) found high species richness on tussocks due to the increased surface area, the seasonal change in composition, and the presence of multiple microhabitats on each tussock. The result was greater species richness per area on tussocks than the fen substrate.

Insects in Prairie Fen

Several studies have examined the insect community in prairie fen. Panzer et al. (1995) reviewed literature and surveyed habitat remnants in the Chicago region to determine a set of remnant-dependant insects associated with the savanna-prairie habitat continuum. They found that Lepidoptera were one of the most remnant-dependant insect groups. Michigan prairie fens alone contain 25 insect species of conservation concern, including 6 moth species in the genus *Papaipema*, ranked as special concern, threatened, or endangered, in large part due to their endemism (Table 1). Of the arthropods in prairie

Table 1. The 25 federally endangered (E), candidate (T), and special concern (SC) insect species in Michigan prairie fen communities (MNFI 2007).

Order	Genus and species	Common Name	State Status
Odonata	*Cordulegaster erronea*	Tiger Spiketail	SC
	Williamsonia fletcheri	Ebony Boghaunter	SC
Orthoptera	*Neoconocephalus lyristes*	Bog Conehead	SC
	Oecanthus laricus	Tamarack Tree Cricket	SC
	Orchelimum concinnum	Red-faced Meadow Katydid	SC
	Paroxya hoosieri	Hoosier Locust	SC
Homoptera	*Flexamia huroni*	Huron River Leafhopper	SC
	Flexamia reflexus	Leafhopper	SC
	Lepyronia angulifera	Angular Spittlebug	SC
	Prosapia ignipectus	Red-legged Spittlebug	SC
Coleoptera	*Liodessus cantralli*	Cantrall's Bog Beetle	SC
	Stenelmis douglasensis	Douglas Stenelmis Riffle Beetle	SC
Lepidoptera	*Calephelis mutica*	Swamp Metalmark	SC
	Euphyes dukesi	Dukes' Skipper	T
	Hemileuca maia	Barrens Buckmoth	SC
	Meropleon ambifusca	Newman's Brocade	SC
	Neonympha mitchelii mitchellii	Mitchell's Satyr	E
	Oarisma poweshiek	Poweshiek Skipperling	T
	Papaipema beeriana	Blazing Star Borer	SC
	Papaipema cerina	Golden Borer	SC
	Papaipema maritima	Maritime Sunflower Borer	SC
	Papaipema sciata	Culvers Root Borer	SC
	Papaipema silphii	Silphium Borer Moth	T
	Papaipema speciosissima	Regal Fern Borer	SC
	Spartiniphaga inops	Spartina Moth	SC

fen, butterfly species are likely the most well-recognized and documented group in Southern Lower Michigan. The greater Washtenaw County butterfly survey has contributed to this knowledge, with documented Lepidopteran sightings from 1994 onward (Kuhlman 2007). Bultman (1992) studied the cursorial spiders associated with prairie fens and oak hickory forest. He found that the spider community in the prairie and seep regions of prairie fen was not the same as that in oak-hickory forest, while the community in forested fen was similar to that in oak hickory forest. Similarly, Lammers-Campbell (1998) examined the community of Chironomidae in a fen and surrounding vegetation. She found that chironomid species and plant community corresponded well with each other, but did not find any chironomid species that were specific to fen only.

Arthropods may not only be indicators of prairie fen community, but also play a key role in formation of fen structure and vegetation. Lesica and Kannowski (1998) examined the role that ants play in forming structure and altering the plant community of fens. They found that while there was more magnesium, phosphate, sodium, and potassium in vegetation hummocks, there were higher nutrient levels in ant mounds, indicating that hummocks may be abandoned ant mounds and providing evidence that ants are key to the formation of soil microtopography. They also found that several grasses, including *Muhlenbergia* sp., grow on active ant mounds. Although each of the experimental studies focuses on a distinct group of insects, it is clear that insects in prairie fen are frequently associated with vegetation structure and type, regardless of whether they are the cause of (or response to) that vegetation.

Historical Disturbance Patterns

Although perennially moist, the large volume of sedge and grass species in prairie fen historically provided enough fuel to support frequent fire (Curtis 1971). Fire maintained the open character of fens, so that while shrubs and trees are part of the system, they did not historically dominate large areas of prairie fens. Fires occurred in the past as a result of drought, lightning strikes and burning by native Americans (Albert 1995, Anderson et al. 2000).

Since about 12,000 BP, with the first evidence of humans in North America, humans have modified the landscape with fire for a variety of purposes (Buckner 2000, Dey and Guyette 2000, Williams 2000a). Paleo-Indian hunter-gatherers used fire indirectly and directly for hunting. Fire was used directly to trap large mammals for hunting, and indirectly to increase the production of forbs and grasses that provide habitat for game (Dey and Guyette 2000). In addition, fire was used to increase the yield of nuts, berries, and acorns, all of which provided food directly to humans and also increased browse for game species (Dey and Guyette 2000). European settlers used fire to clear agricultural fields, as well as to improve the quality of forage for range livestock (Anderson et al. 2000, Dey and Guyette 2000). In a site in Southern Ontario, Dey and Guyette (2000) found that the mean fire return interval in red oak forest was 15 years from 1600-1900, but that varied from 5 to 76 years, illustrating that even with anthropogenic fire regimes, fire frequency was variable.

The General Land Office surveyor notes for the Jackson interlobate region of Michigan in the early 1800's contained historic references to American Indian fires in the oak savanna and barrens (Albert 1995). Even though European settlers used fire for management, fire frequency decreased with European settlement. The average fire return interval in a forest, savanna and fen mosaic in the Missouri Ozarks from 1710 to 1830 ranged from every 3.0 to 4.8 years, while during European settlement that increased to every 6.9-12.5 years (Dey et al. 2004). In the early 20th century, complete fire suppression became the primary mode of land management. The result of lengthening fire return intervals in the 1900's was that the prairie savanna landscape, including prairie fen communities, was colonized by trees and shrubs over time (Buckner 2000, Dey and Guyette 2000). One factor preventing prairie fens from becoming forested since the increase in fire interval is the high water table that prevents most trees, shrubs, and invasive plant species from establishing.

Historic disturbance in prairie fen also included grazing by ungulates, including white-tailed deer, red deer, elk, moose, and auroch (Middleton et al. 2006a, Rydin et al. 2006). In addition, beaver historically created ponds by damming waterways, which after abandonment succeeded to marsh meadows or fens (Rydin et al. 2006). Fire and grazing thus combined to play a role in shaping the Midwestern landscape, with a matrix of open communities and forested habitats in upland areas (Anderson et al. 2000).

Threats to prairie fen systems and their management

There are a number of threats to prairie fen habitats, all of which are either a direct or indirect result of human impacts on the landscape. These include habitat fragmentation, changes in hydrology, invasive species, changes in nutrient inputs and increased pollution, and changes in the fen disturbance regime. In many cases these factors interact to impact prairie fen communities. The effects of these threats both individually and together mean that prairie fen systems will need to be managed for their persistence.

Conversion

Worldwide, the primary threat to prairie fen habitat worldwide is the direct conversion of prairie fens to agricultural and other land uses (Grootjans et al. 2006, van Diggelen et al. 2006). In Europe and Central Asia, wetlands have been drained since the Middle Ages for hay production and cattle grazing. In the 20th century, drainage technology developed further, so that crop production was possible on drained wetlands, leading to a large increase in wetland drainage (van Diggelen et al. 2006). Wetlands are also drained for peat harvest for garden soil enrichment and as a fuel, though bogs are more commonly mined for peat than fens, in areas where peat is rare prairie fen may be used to provide peat. After peat extraction, an area of open water remains (Grootjans et al. 2006), which no longer provides substrate for fen plants. Marl in prairie fens has also been extracted to provide lime on agricultural soils, as well as for cement production (Morrison 1945).

Fragmentation

In addition to direct conversion of prairie fens, the landscape surrounding these habitats in the Midwestern U.S. historically contained oak savanna and upland prairie communities. Both of these community types have been converted to agricultural land since the 1830's. More recently these lands are being intensively developed, so that residential development adjoins prairie fen habitats (Amon et al. 2002) and disturbance has increased or changed in the area between prairie fens (Bedford and Godwin 2003). In many cases, plant and animal species in prairie fen communities, which by their nature were already isolated from each other, have less suitable habitat for dispersal to nearby prairie fen communities. The result of this decreased dispersal is that plant establishment depends on the seed bank exclusively in many cases, rather than on a combination of a seed bank and seed dispersal (Middleton et al. 2006a). Additional negative genetic effects of small populations, such as genetic drift, could be detrimental to fen biodiversity in the long-term.

Hydrological changes

As groundwater-fed communities, prairie fen habitats are extremely sensitive to changes in hydrology. Alteration of groundwater recharge areas surrounding the prairie fen can change the volume of water and nutrient that enter the fen system (Boeye and Verheyen 1992). Quarrying, field tiling, ditching, irrigation, filling, addition of impermeable surfaces (such as roads), and residential development in the uplands bordering prairie fen all disrupt groundwater flow into fens (Amon et al. 2002, Bedford and Godwin 2003). Water withdrawal from aquifers caused by irrigation can alter the depth to the water table, reducing moisture in the plant rooting zone in fens (Amon et al. 2002). In prairie fens with reduced groundwater input, rainwater can flush away minerals key to plant community and soil development (Spieles et al. 1999). Oxygen also becomes more common in soil with depleted water levels, disrupting the anoxic environment characteristic of prairie fen (Amon et al. 2002). Both of these changes lead to succession that is not characteristic of fens.

Changes in disturbance regime

Decreasing frequency of fire, grazing, and mowing have led to a variety of changes in prairie fen communities. All three disturbance types historically created open niches for new plant establishment, and likely played a key role in maintaining high plant diversity in prairie fen. With no grazing, mowing, or fire management, Jensen and

Schrautzer (1999) found that 23 species were likely to become extinct in a German fen system. This group is most likely to include small-seeded species, which depend on bare soil provided by disturbance for establishment and germination.

Several studies indicate that prairie fen plant diversity decreases over time without fire. Kost and De Steven (2000) found increased perennial forb cover in one Wisconsin sedge meadow following a prescribed burn, and their findings indicate that fire provides 1-2 years for forb recruitment due to the decreased litter layer, leading to an increase in plant diversity. Weltzin et al. (2005) examined the effect of litter removal and plant community composition in a fen and found that litter removal increased light availability, soil temperature, and phosphorous in aboveground plant material, along with altering plant communities. Fire burns leaf litter and provides openings in plant communities that likely lead to similar effects on plant communities. Bowles and Jones (2006) examined a group of wetlands in the Chicago region, and found that fens burned every 5 years over a 30 year period maintained species richness, while those burned less frequently did not. In addition, Middleton (2002) performed controlled burns in sedge meadow communities in Wisconsin, and found an increase in forb species richness after burning, including the presence of species that had not been documented in the habitat over the prior 20 years.

While fire may negatively affect insect populations in the short term (Swengel 1998), it is clear that the plant community that provides insect habitat does not persist in the absence of fire. Low-intensity patchy fire, such as that historically present in this landscape, would provide refuges for insect re-population. Panzer and Schwartz (2000) found increased species richness and population densities of most remnant-dependant insect species with rotational burning and fire return intervals of 2-5 years. Williams (2000b) recommends reintroducing fire into the landscape mosaic that includes prairie fen, with the caveat that it be "Indian-type" fire. This type of burn involved a mosaic of habitats that were exposed to low-intensity, patchy fire. Additionally, burns can be timed to avoid periods when insects of concern are in immobile stages, can be carried out in rotating burn units, and burns can be conducted at varying times in the growing season to minimize the effects on one group of insects or plants (Reed 1997, Panzer 2002).

Mowing of prairie fen has been practiced in Europe for hundreds of years for hay production. Beginning in the 1970's many of those fens were no longer mowed, which has led to increased shrub cover and decreased plant diversity (Middleton et al. 2006b). In addition to controlling shrub growth and maintaining high species diversity, mowing has been used effectively as a way to decrease the effects of high nitrogen inputs (Verhoeven et al. 1996).

Prairie fen communities, with their grass and sedge rich flora, presented a habitat for cattle grazing, and fen meadows and partially drained fens were used for this purpose through much of the 20th century in both Europe and North America (Middleton et al. 2006b). Grazing has both positive and negative impacts on prairie fen. Positive impacts include maintenance of open habitat in the absence of fire. On the other hand, cattle can break down the characteristic hummock structure in prairie fens, decreasing the microhabitat variability available to plant species. In addition, when cattle are removed from the habitat, shrubs that cattle grazing had kept small often grow rapidly and become dominant in the fen (Middleton 2002). Reintroducing grazing in prairie fen, however, is not likely to lead to former plant diversity, as species with seeds that do not persist in the seed bank will not return with reintroduction of grazing after long periods (Hald and Vinther 2000).

Pollution, nutrient inputs, and invasive species

A variety of pollution types increasingly enter wetland systems, including chlorine and sodium from road salt, nutrients from septic tanks, herbicide runoff, and fertilizer runoff. Panno et al. (1999) found increased abundance of invasive narrow-leaved cattail and decreasing diversity of native vegetation near a site of nutrient addition and pollution from a nearby septic system and roadway, which contributed Cl- and Na+ to the groundwater. Evidence indicates that pollution leads to changes in the fen plant community.

Changes in nutrient availability may lead to changes in plant dominance within prairie fens. Increased nitrogen deposition in Europe has changed nutrient inputs in wetlands so that some plant communities that were formerly nitrogen limited become phosphorous limited (Verhoeven et al. 1996). Without management such as mowing, plant community succession changes and decreased species diversity often result (Verhoeven et al. 1996).

Prairie fens are increasingly impacted by invasive plant species. Bowles and Jones (2006) compared changes in 31 wetland communities in the Chicago region between 1976 and 2002. They found increased abundance of invasive plant species purple loosestrife (*Lythrum salicaria*), glossy (*Frangula alnus*) and common buckthorn (*Rhamnus cathartica*), and narrow-leaved cattail (*Typha angustifolia*). Additionally, they determined that increased abundance of both invasive narrow-leaved cattail and native broad-leaved cattail (*Typha latifolia*) were associated with significant decreases in native species richness within study plots (Bowles and Jones 2006).

The effects of invasive species are often compounded by increased nutrient availability, which has potential to increase growth of invasive species but not native species, leading to a competitive advantage for the invasive. Woo and Zedler (2002) determined that nitrogen and phosphorous addition to *Typha* x. *glauca* led to increased height, biomass, and ramet density, but had no significant affect on native graminoids. Rickey and Anderson (2004) found a similar pattern with *Phragmites austrailis,* with increased *Phragmites* biomass with nitrogen addition but no significant change in native *Spartina pectinata* biomass. Lindig-Cisneros and Zedler (2002) found that reed canary grass (*Phalaris arundinaceae*) was more likely to establish in areas with fluctuating water levels than static water levels. In addition, they found that *P. arundinaceae* required light availability for germination, which would be caused by a disturbance in prairie fen.

Four changes in environmental conditions are linked to the spread of aquatic invasives: changes in wetland hydrology, increased nutrient levels, increased salinity, and removal of vegetation (Galatowitsch et al. 1999). All of these changes occur with increasing frequency in prairie fens. The result is that a veritable maelstrom of factors is interacting to affect the existence of prairie fen communities. Although the factors threatening prairie fens all stem from human activities, ironically, prairie fens are unlikely to persist without human intervention to maintain them. In Europe, many areas considered natural fens area actually fen meadows that have been slightly drained and used for grazing or mowing, and in North America many prairie fens have been grazed historically (van Diggelen et al. 2006).

Glossy Buckthorn

Life history and arrival in Michigan

Glossy buckthorn (Rhamnaceae: *Frangula alnus* P. Mill. (previously *Rhamnus frangula* L.)) is a shrub of Eurasian origin that is especially aggressive in bogs and fens (Voss 1985). *Frangula alnus* was likely introduced into North America by 1800, cultivated as a hedge plant and for wildlife habitat, but did not naturalize until the 1900's. *Frangula alnus* establishes well in acid to alkaline peat soils with some moisture, although it is does not survive permanent waterlogging (Godwin 1943). In peat soils, the root system grows very near the surface, above the water table (Godwin 1943). *Frangula alnus* forms even-aged stands and individuals grow to 7 m tall; the species is sometimes considered a small tree (Converse 1984). Glossy, smooth, oval leaves with parallel venation open on this shrub earlier than many native woody species in the U.S. Midwest, and stay green late into the fall (Godwin 1943).

Reproduction is primarily sexual, although asexual reproduction is reportedly possible in the absence of insect pollination. *Frangula alnus* blooms from the end of May – September, and flowers are visited by bees, wasps, ichneumonids, and beetles (Godwin 1943). Ovate drupes containing 2-3 pyrenes each are produced in large numbers annually (Godwin 1943). Drupes are green when immature, then red changing to black (Converse 1984). A large variety of bird species eat *F. alnus* berries and disperse seeds (Catling and Porebski 1994). Seed dispersal is also carried out by mice and elk, and dispersal in water may also be possible; dry *F. alnus* seeds float for one week, and fruits float up to 19 days (Converse 1984). Seedlings establish most easily in areas with exposed soil and available light (Godwin 1943), and *F. alnus* has greatest seedling density near the source of seed (Converse 1984). Seeds are viable for at least 6 years (Walsh et al. 2003), although if in a dry location for several months the germination rate is very low (Converse 1984).

Frangula alnus is currently widespread in North America, from Nova Scotia west to Manitoba in Canada and in the Eastern U.S. as far south as Kentucky (Sinclair and Catling 1999). *Frangula alnus* was first collected in Michigan in Delta County in the upper peninsula in 1934, although it was likely present in the state before this time (Voss 1985). *Frangula alnus* is most common in Michigan in fens, bogs, disturbed damp to wet areas, lake shores, and thickets along rivers (Voss 1985), although it will survive in forests, as well.

Impacts on habitat

There is evidence that *F. alnus* displaces native plant species in its invasive range. In an Ontario wetland, Sinclair and Catling (1999) compared plant growth in plots with *F. alnus* removed versus beneath *F. alnus* cover. They found both greater herbaceous percent cover and species richness in removal plots. In contrast, Houlahan and Findlay (2004) examined wetlands in Ontario and found that when considering the entire wetland, exotic plant species, including *F. alnus*, were not more likely to be dominant plants than native species. Their results indicate that exotic plant species do not competitively exclude native plant species across wetlands. This pattern is focused on species dominance and not species identification; species composition in the presence of *F. alnus* may change in wetlands. There may also be effects of scale on this pattern, so that at smaller scales native plant diversity is low where exotic plant cover is high.

Frangula alnus may also impact a variety of abiotic factors in prairie fen habitats. Transpiration of *F. alnus* in midsummer has been shown to lower the water table (Godwin 1943), making prairie fen systems increasingly suitable for *F. alnus* and less suitable for native prairie fen species. The organic matter hummocks characteristic of prairie fen communities may provide a wet but not inundated microhabitat conducive to *F. alnus* seedling establishment. In the presence of *F. alnus*, those organic matter hummocks are broken down, reducing microhabitat differences within the fen. This process may be assisted by an overall decrease in the water table. In addition, *F. alnus* may alter nitrogen cycling in prairie fen systems; related common buckthorn (*Rhamnus cathartica* L.) is associated with elevated nitrogen levels in Illinois woodlands (Heneghan et al. 2006). Concurrent with increased nitrogen levels, leaf litter decomposition rates may be altered in the presence of *F. alnus*, resulting in changes in nitrogen mineralization rates. Weltzin et al. (2005) found that the plant community in a northern prairie fen changed with litter removal. This indicates the potential that changes in leaf litter thickness below *F. alnus* lead to changes in plant community composition in prairie fen communities. The potential for *F. alnus* to alter communities that it invades is very real, and exploration of further potential factors affecting prairie fen communities may yield evidence of impacts on a variety of abiotic as well as biotic factors.

Management techniques and implications

A variety of management techniques have been tested for control of adult and seedling *F. alnus*; some have proven more successful than others. Biological control of *F. alnus* and *Rhamnus cathartica* has been investigated but candidate insects did not feed on *F. alnus*. Finding and testing herbivores of *F. alnus* is a current priority (CABI bioscience, www.cabi.org). Oat rust (*Puccina coronata*) does infect *F. alnus*, but it is a secondary host and *P. coronata* does not appear to cause *F. alnus* mortality (Peturson 1949). Cultural control methods of *F. alnus* in wetlands include excavation, mowing, stump cutting, burning, and stem girdling (Converse 1984). *Frangula alnus* resprouts vigorously after top kill or top removal, so that a single cutting results in thick regrowth with more stems than the initial growth. Techniques for herbicide application, however, have been extensively tested to maximize effective control (Converse 1984, Reinartz 1997, Pergams and Norton 2006).

Physical control techniques

Excavation may be useful for small plants and seedlings. With small plants, hand-pulling or removal with a grubbing hoe may be successful. Larger *F. alnus* plants may be pulled out using heavy equipment, but this method results in soil disturbance, not only leaving an open area to be colonized, but also bringing seeds of *F. alnus* or other invasive plants to the surface where they germinate readily (Converse 1984). Repeated mowing or cutting reduces *F. alnus* plant vigor. Sinclair and Catling performed one cutting of *F. alnus* in an invaded Ontario wetland and found greater native plant species cover and diversity after one growing season in the cut area (Sinclair and Catling 1999). Mowing may be a temporary way to increase native plant growth in areas where there aren't resources for herbicide. In addition, annual mowing has been used in European prairie fens to decrease the effect of large nutrient inputs and maintain plant species richness (Gusewell and Le Nedic 2004, Middleton et al. 2006b). Burning is another technique that has been used with relatively low success in an attempt to control *F. alnus*. A burn in late April or early May in the Midwest, when *F. alnus* has leafed out but native plant species have not, has potential to top kill it, eliminating the main growing point, and reduce resprouting. Stem girdling involves destroying the surface of a 2-5 cm band to interrupt cambium flow (Converse 1984). Although girdling doesn't disrupt the soil or require herbicide, Reinartz (1997) found that girdling alone did not cause *F. alnus* mortality in a Midwestern wetland. This method is yet another that suppresses *F. alnus* growth but does not effectively cause mortality.

Chemical control techniques

While physical control techniques may lead to suppression of buckthorn, physical techniques combined with chemical control have proven extremely effective in killing *F. alnus* adults. Herbicide may be applied to uncut stems (basal bark treatment), girdled stems, cut stumps, frilled stems, or foliage, or injected into the trunk. Foliage spray of *F. alnus* requires the largest volume of chemical, and has been carried out with fosamine (ammonium salt) in September with high *F. alnus* mortality rates (Converse 1984). Stem cutting or girdling plus herbicide application lead to high buckthorn mortality rates. The most commonly used herbicides include glyphosate (Rodeo, among others), a non-selective herbicide, and 2-4 D and triclopyr (Garlon and Pathfinder), which are specific to broadleaf plants. Pergams and Norton (2006) performed a comparison of physical and chemical control methods of *R. cathartica* (common buckthorn) and found that girdling or cutting plus stump treatment with herbicide of one stem on the plant usually led to death. Reinartz (1997) compared mortality rates of *F. alnus* using stem girdling and cutting alone versus stem cutting plus glyphosate herbicide treatment. He found that neither girdling or cutting alone led to plant mortality, while cutting plus treatment of 25% concentration glyphosate led to 92 – 100% mortality of individual plants. Herbicide safety in wetlands is of concern, as any surfactant used to increase herbicide penetration into plants will also lead to ready herbicide spread in water. A formulation of glyphosate that is safe for use in wetlands must be used to prevent water contamination. Glyphosate should not be harmful to the surrounding watershed or non-target vegetation without a surfactant, but will degrade more slowly in anaerobic conditions presented by most prairie fen communities (Converse 1984).

Time of year also plays a role in control efficacy of *F. alnus*. Stump cutting plus herbicide treatment of *F. alnus* is known to be highly effective at any time of year except when sap is rising from March – May. In addition, invasive management in prairie fen habitats in winter minimizes trampling to plant communities, making December – February an ideal time to cut and stump treat *F. alnus*. While no references mention disposal of woody material after it is cut, The Nature Conservancy in Michigan uses a method that involves stacking material, allowing it to dry, and burning brush piles (R. Zuniga-Villegas, pers. comm.). This reduces the area where the soil is heat sterilized, which can decrease native plant re-establishment from the seed bank.

Long-term management

Even with herbicide treatment, some stumps resprout and followup treatment is necessary to kill all buckthorn plants. In addition, the prolific production of *F. alnus* seed leads to a large seed bank near adult plants. As seedling density is highest near adult *F. alnus* plants, the target treatment area will be near previous adult populations (Converse 1984). Hand-pulling of seedlings is possible but time-consuming, and also has potential to increase germination of additional *F. alnus* seeds due to disturbance. Use of a propane flame torch in areas with little other plant growth in the first season after treatment of adults is an effective treatment method (R. Zunigo-Villegas, pers. comm). Although the largest flush of seedlings will likely occur in the first year following clearing (Frappier et al. 2004), seedling management will need to continue for several years after adult *F. alnus* management.

The establishment of *F. alnus* monocultures depends on disturbance (Godwin 1943). The reality of prairie fen systems, however, is that they are a community with frequent anthropogenic disturbance and changes in water table. These factors mean that continued management and scouting for *F. alnus* and other invasive species will be necessary in many prairie fen systems. Although there are limited resources to control *F. alnus* and other invasive plant species in natural habitats, the use of several techniques will maximize the effectiveness of those efforts. First, the use of best practices to control invasion will minimize time spent with control followup (Webster et al. 2006). For *F. alnus*, this means cut stump treatment with herbicide rates and formulations that are known to be effective. In addition, prioritizing control areas allows maximum use of resources. Control directed at small satellite populations prevents satellite populations from becoming new populations centers, reducing future control efforts (Webster et al. 2006). During the first and second year of *F. alnus* management, graminoid vegetation is recovering, so that there is often little dry biomass. In subsequent years, fire can be carried through prairie fen systems and prescribed burns every 2-5 growing seasons are a key long-term element of fen management to prevent further invasion of non-natives and maintain plant species diversity and richness.

Conservation of biodiversity and ecosystem function

As human impacts on the biosphere expand, conservation of natural habitats is increasingly vital for the persistence of biodiversity on Earth. The perception of conservation is changing, as well, as we recognize that merely preserving land does not ensure the continued persistence of plant and animal communities and active management is often required to maintain ecosystem services.

Services provided as a result of ecosystem function are known as ecosystem services (Costanza et al. 1997). Ecosystem services fall into four broad categories: supporting, provisioning, regulating, and cultural (Reid et al. 2005). Supporting services include soil formation and nutrient cycling, provisioning include supplying fuel, food, and fresh water, regulating services include regulation of climate, flooding, and disease, and cultural services include educational, spiritual, and aesthetic benefits to humans. Restoration of prairie fen habitats has potential to support and provide many of these services.

Functions of wetlands

Freshwater wetlands provide a variety of ecosystem services which are invaluable to humans. Wetlands specifically provide flood control, nutrient decomposition, waste purification, water supply, and the ability to stabilize and moderate natural and urban microclimates and to retain nutrients and sediments (Moser et al. 1996, Braga 1999, Bedford and Godwin 2003). In addition, wetlands support biodiversity, which humans value for the intrinsic and spiritual worth placed on them and also due to the perception that biodiversity can provide benefits in the future (Thompson and Starzomski 2007).

Healthy prairie fens may be defined by their ability to provide these resources, all of which are dependent on the ecosystem processes of water and mineral cycling, community dynamics, and solar energy flow. Therefore, one measurement of successful prairie fen restoration is that it is a system with key ecosystem processes intact. Reintroduction of the historical disturbance regime and elimination of invasive species are two key steps to restoring that function.

Insect conservation and function

Insects are the most diverse group of taxa on earth, comprising 80% of all metazoan species that have been described (Samways 2005). From 90 to 95% of insect species remain undescribed; estimates of insect diversity on Earth range from 1.8 to 8.8 million species (Samways 1994), with recent estimates placing the total at 3.7 to 5.9 million species (Novotny et al. 2002). Because so many insect species remain undescribed, we do not know current insect extinction rates, but an estimated 11,200 insect species have become extinct since 1600, and 100,000-500,000 more are predicted to become extinct by 2300 (Samways 2005). In North America, an estimated 44% of insects have not been discovered or adequately described (Redak 2000). In 2000, 37 arthropod species were listed as federally endangered in the U.S., and estimates of the actual number of species at risk range from 2000 to 29,000 species (Redak 2000). The same processes that are putting rare habitats and the plant species in them at risk: fragmentation, development, agriculture, pollution, altered disturbance regimes, and nutrient inputs, are also putting insect species endemic to those systems at risk. Insect species extinction may have far-reaching impacts on ecosystem structure and function.

Insects and their activities support a variety of key ecosystem functions and processes. The majority of flowering plants are insect-pollinated (Klein et al. 2006). Detritivores, omnivores, and carrion feeders contribute to decomposition and nutrient cycling (New 2005). Predator and parasitoid insects control herbivore populations, which may be crop pests (Van Driesche and Bellows 1996). Herbivores control plants that may otherwise become weedy (Goeden and Andres 1999).

In addition to these functions that humans value directly, insects also support a multitude of key ecosystem processes. Insects are the primary energy link between plants and other animals, and therefore are the basis for animal food webs. Insects also are habitat architects. Herbivorous insects affect plant community structure, including potential plant species presence or absence, through herbivory. Insects such as termites and ants act as ecosystem engineers by moving and processing large volumes of soil and detritus (Samways 2005). A variety of ecosystem processes, therefore, are dependent on the presence of insects.

Pollination: a key process for ecosystem persistence

Pollination is a key insect-supported ecosystem function (Kevan 1999). Animal pollination is carried out by a diversity of taxa, including bees (which are all obligate flower visitors), flies, butterflies and moths, beetles, birds, bats, and small mammals (Kearns et al. 1998). Insect pollinators, like other arthropods, are threatened by habitat loss, effects of pesticides, increased atmospheric carbon dioxide, and introduction of non-native plants and pollinators (Kearns and Inouye 1997, Memmott and Waser 2002). Pollination has significant direct effects for humans: pollination services are valued at $117/ha/yr (Costanza et al. 1997) and 35% of all crops benefit from insect pollination

(Klein et al. 2006). Beyond direct monetary effects that benefit humans, pollination provides additional indirect effects on gene flow, metapopulation dynamics, and genetic diversity (Neal 1998). The potential negative impacts of decreasing pollinator abundance and diversity are very real. Over 90% of angiosperms are animal pollinated (Kearns et al. 1998). Biesmeijer et al. (2006) found decreased local bee diversity in Britain and the Netherlands after 1980 versus pre-1980. They saw a concomitant decrease in the species diversity of outcrossing plants, a pattern which could result in decreased populations of outcrossing plant species and subsequent reductions in gene flow within a species. It is unclear whether plants or pollinators were lost first; regardless, both groups are key components in the persistence of natural ecosystems.

Declining species diversity and abundance may affect specific organisms in ecosystems differently depending on their origin and habitat specialization. Memmott and Waser (2002) examined the pollinator-plant interaction web of a community in Illinois. They found that, on average, non-native plant species attracted fewer pollinator species than native plants. In addition, generalist pollinators were more likely to visit non-native plants than pollinator specialists. In their study of pollinators in Britain and the Netherlands, Biesmeijer et al. (2006) found a greater decline in species abundance of specialist than generalist bee species. The disappearance of specialist pollinators may or may not have a broad impact on plant community diversity and persistence. Memmott (1999) examined the plant-pollinator food web of a meadow, and found a complex web of interactions dominated by general plant-insect and insect-plant relationships, rather than the specific relationships that are often focused on in pollination biology research. Similarly, Memmott et al. (2004) used a modeling approach to examine the effect of pollinator extinction on plant species diversity. They found that when generalist pollinators were removed from the model system, a more rapid decline in plant species diversity resulted than with specialist pollinators removed. In addition, this decrease was linear, and was not as low as was predicted.

Restoration of prairie fen, as a plant community that commonly occurs in small remnants and contains many rare plant species, may be severely limited by the seed bank and seed dispersal of native plants (Middleton et al. 2006a). Restoration is more likely to be successful with functional interactions in place (Neal 1998). In addition, restoration of prairie fen and other native habitats may help alleviate the pollinator crisis beyond habitat edges, although recent findings indicate that effect of remnant high-quality habitats on agricultural fields extends <150 m from them in an agricultural matrix (Kohler et al. 2008). Many of the rare habitats in the prairie fen continuum contain a diversity of flowering forbs (Spieles et al. 1999), and there has been a call to conserve diverse plant patches to prevent and reverse pollinator decline (Kearns and Inouye 1997, Kearns et al. 1998). In contrast to high quality prairie fen, buckthorn-invaded prairie fen contains very little flowering herbaceous vegetation (pers. obs.).

An additional concern is that while restoration of pollinator richness and abundance may be enough to restore pollinator function, it may not be considered sufficient to restore a resilient habitat. In some cases, systems reach full function at a portion of the total biodiversity (Schwartz et al. 2000). This is related to the concept that species within communities are functionally redundant (Naeem 1998, Wohl et al. 2004). Forup and Memmott (2005) found no significant difference in plant and insect richness or abundance between restored and old hay meadows. Although the old and restored meadows were similar in function, they found that there was a greater proportion of potential species links in the old meadows. This finding suggests that in the case of pollinators, increased species diversity may lead to increased ecosystem stability across functional groups, a relationship that has been found in a number of studies (Peterson et al. 1998, Lhomme and Winkel 2002). The increased species diversity could buffer communities from disturbance and human impacts, indicating that although current ecosystem function is of concern, future resiliency of that function will likely need to be considered.

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Chapter 2

For Natural Areas Journal

BIOTIC AND ABIOTIC CONDITIONS IN MICHIGAN PRAIRIE FEN INVADED BY GLOSSY BUCKTHORN (*FRANGULA ALNUS*)

Anna Katherine Fiedler

Abstract

Michigan prairie fens are unique in their high plant and animal diversity, but many are currently threatened by invasion of exotic glossy buckthorn (*Frangula alnus*). Land managers and conservationists have observed a variety of qualitative changes in prairie fen after *F. alnus* invasion, but the relationship between its presence and biotic and abiotic factors has not been quantified. Here, we compare a set of abiotic factors and the plant community in areas of a Michigan prairie fen invaded by buckthorn with that of uninvaded sites. Many of the conditions typical of fens were different in buckthorn–invaded plots. We found significantly lower soil pH, fewer vegetative hummocks, less light availability, less total plant cover, and lower graminoid relative abundance in invaded versus uninvaded areas. We also examined the buckthorn invasion process by looking at differences from the upland edge to the water's edge of invaded plots. In *F. alnus*-invaded areas, we found significantly greater percent soil organic matter, fewer vegetative hummocks/ m^2 and lower mean coefficient of plant conservatism from upland edge toward the water. Our findings indicate a variety of significant differences in *F. alnus*-invaded areas of prairie fen, which will be useful to wetland managers and conservationists. These differences provide a baseline against which restoration success can be gauged.

Keywords: prairie fen, glossy buckthorn, *Frangula alnus*, restoration, invasive species.

Introduction

The retreat of the most recent glaciation from what is now the northern U.S. approximately 12,000 years ago created a set of abiotic conditions that paved the way for the development of distinctive plant communities (Albert 1995). One of these is prairie fen, a unique groundwater fed wetland habitat found in the Midwestern U.S. Prairie fens, typically less than 5 ha in size (Bedford and Godwin 2003), support very high biodiversity within areas that comprise less than 0.1% of the glaciated landscape in the Midwestern U.S. (Nekola 1994). Prairie fen is one of the rarest wetland types in the U.S., occurring most commonly in the glaciated Midwest (Spieles et al. 1999, Amon et al. 2002). This combination of small size and high species richness makes prairie fens biodiversity hotspots within these landscapes; however, this wetland community and its associated biodiversity are increasingly imperiled.

There are a number of threats to prairie fen habitats, all of which are either a direct or indirect result of human impacts on the landscape. These include habitat fragmentation and conversion (Grootjans et al. 2006, van Diggelen et al. 2006), changes in hydrology (Amon et al. 2002), invasive species (Bowles and Jones 2006), changes in nutrient inputs (Verhoeven et al. 1996), increased pollution (Panno et al. 1999), and changes in the fen disturbance regime (Middleton et al. 2006). In many cases these factors interact to impact prairie fen communities. To minimize the effects of these threats and ensure their persistence, many prairie fens will need to be actively managed. Here, we provide information that will help land managers considering glossy buckthorn removal in prairie fens.

Glossy buckthorn

Glossy buckthorn (Rhamnaceae: *Frangula alnus* P. Mill. (previously *Rhamnus frangula* L.)) is a shrub of Eurasian origin that is especially aggressive in bogs and fens (Galatowitsch et al. 1999). It was introduced in North America, likely before 1800, and was cultivated for forestry uses, wildlife habitat, and as an ornamental hedge plant. It did not become naturalized and exhibit landscape spread until the early 1900's (Converse 1984). *Frangula alnus* is currently widespread in North America, occurring from Nova Scotia west to Manitoba in Canada and in the Eastern U.S. as far south as Kentucky (Sinclair and Catling 1999, USDA 2008).

Frangula alnus tolerates a range of soil and moisture conditions. It establishes well in acid to alkaline peat soils with some moisture, although it is does not survive permanent waterlogging (Voss 1985). This species blooms prolifically and produces abundant fruits, each containing 2-3 seeds, annually (Godwin 1943). A variety of bird species eat *F. alnus* berries and disperse seeds, and seedlings establish best in areas with exposed soil and available light (Converse 1984). *Frangula alnus* is most common in fens, bogs, disturbed damp to wet areas, lake shores, and thickets along rivers (Voss 1985), although it will survive in forests, as well.

Effects on habitat

Frangula alnus may be altering its environment, making it better able to persist in areas where it is established. First, there is evidence that *F. alnus* displaces native plant species in its invasive range. In an Ontario wetland, Sinclair and Catling (1999) compared plant growth in plots with *F. alnus* removed versus beneath *F. alnus* cover. They found both greater herbaceous percent cover and species richness in removal plots.

In addition, Houlahan and Findlay (2004) examined wetlands in Ontario and found that, along with certain natives such as *Salix petiolaris*, exotic plant species, including *F. alnus*, became dominant species in these wetland systems. *Frangula alnus* may also alter a variety of abiotic factors in prairie fen habitats. The organic matter hummocks characteristic of prairie fen communities provide a wet but not inundated microhabitat (Peach and Zedler 2006) that may be conducive to initial *F. alnus* seedling establishment, leading to subsequent breakdown of those hummocks. In addition, *F. alnus* may alter nitrogen cycling in prairie fen systems. Many invasive species are known to alter nitrogen fixation rates and increase nitrogen availability (Ehrenfeld 2003) and *F. alnus* has been associated with elevated soil nitrogen in upland forests (Huebner et al. 2009). In sum, a suite of characteristics may differ between areas with and without *F. alnus* invasion, and characterizing these differences is the first step to understanding invasion.

Land managers concerned with the conservation of prairie fen have observed a variety of changes in prairie fen upon invasion of *F. alnus*. However, the relationship between *F. alnus* presence and these differences in prairie fen has not been quantitatively measured. In addition, baseline data are rarely gathered before restoration, but are crucial to gauging its effectiveness. Therefore, the goal of this study was to quantify the differences in biotic and abiotic factors between invaded and uninvaded prairie fen and examine the importance of glossy buckthorn invasion. Our hypothesis was that biotic and abiotic characteristics would be different in invaded prairie fen, with lower pH and light availability, greater nutrient availability, fewer hummocks, lower herbaceous plant diversity, lower percent cover of herbaceous species, decreased relative abundance of graminoids, and an increased relative abundance of exotic species. A common observation is that *F. alnus* invasions often progress from the drier upland edges of fens towards wetter lowland areas. Therefore, we hypothesized that fens undergoing buckthorn invasion would be the least similar to uninvaded conditions near the upland edge. We anticipated our results would provide information on the potential impacts of glossy buckthorn invasion on wetlands. This information can guide management and restoration efforts to maximize their effects.

Methods

Experimental design

The study took place in Jackson County, Michigan at the Michigan State University MacCready Reserve in Clarklake, Liberty Township. In a single fen, we delineated ten 25 x 25 m replicate plots containing mature glossy buckthorn plants (invaded), as well as two 25 x 25 m uninvaded plots located within 300 m of experimental plots (Figure 2A). Nine 1 m^2 sampling quadrats were established in each plot in Fall 2007. Due to possible effects of slope and position on plant communities and abiotic factors, three transects were established in each plot: 3 m from the upland edge (upland), 3 m from the water edge (water), and in the center of the treatment (center), equidistant to both edges (Figure 2B). All replicates had a distinct upland edge. However, replicates on the East side of the pond lacked a distinct water edge. In these plots the transects began at the upland edge (southwest) and ran down slope (northwest). Each transect contained three replicate quadrats. To further characterize this gradient, we measured the difference in elevation between the center of the "upland" quadrats and center of "water" quadrats (Figure 2C).

Sampling

To assess differences in soil pH and nutrients between buckthorn invaded and uninvaded fen, soil nutrients, organic matter, and pH were measured from soil cores taken at 0-10cm depth. In September–October 2007, two soil samples were taken within 40 cm of each sampling quadrat. Samples from each transect within a plot replicate were homogenized. Samples were sent to the Michigan State University soils lab for measurement of pH (water pH method), percent organic matter (loss on ignition at 500° C), nitrate and ammonia (KCl extraction), phosphorous (Bray P-1 or Olsen in samples with free calcium carbonate) and potassium (neutral 1 normal ammonium acetate procedure).

To assess differences in light availability, microhabitat, and plant community between buckthorn invaded and uninvaded fen, a set of measurements was taken in all nine 1m^2 quadrats in each replicate and treatment in September 2007. Light availability was measured on a clear, sunny day with a 1 m long photosynthetically active radiation (PAR) ceptometer (Sunfleck, Decagon Devices Inc., Pullman, WA) at 100 cm height within each invaded and uninvaded plot. Soil microtopography was measured at the same location by counting the number of vegetation-based hummocks within the 1 m^2 quadrat. In the same 1 m^2 quadrat, we estimated total and species percent cover of forbs, grass, and shrubs less than 1.5 m tall (estimating percent cover including the vertical projection of all vegetation rooted within the quadrat). Mature *Frangula alnus* shrubs were not included in the vegetation analysis. To measure the gradient in soil elevation between upland and water transects within replicates, we used an electronic self-leveling single-beam rotary laser (LMH-C series, CST/Berger, Watseka, IL) on June 15 and 16, 2009.

Statistical analysis

To determine the relative abundance of different plant growth forms per plot, we divided the proportion of graminoid and exotic plant cover, respectively, by total plant cover. These proportion data were arcsin square root transformed for analyses; light availability was log (x+1) transformed to address variance heterogeneity. We calculated diversity indices for within-plot species cover with two metrics: Simpsons diversity index, *D* (using percent cover) (Magurran 2004) and the Floristic Quality Index (FQI). To make the Simpsons index more intuitive, it is expressed here as 1-*D*, so that the value of *D* increases with increasing diversity. Floristic Quality Assessment is performed on a plant species list using the coefficient of conservatism (*C*) assigned to each plant species found in Michigan (Herman et al. 2001). As *C* increases, the probability that a species is likely to occur in intact, uninvaded habitat increases.

To characterize differences between buckthorn invaded and uninvaded areas and examine differences between transects, we performed a 2-way ANOVA on all measured characteristics with treatment (buckthorn-invaded or uninvaded), transect (upland, center, and water), and the interaction between them, including subsamples within transect (SAS Institute 2003, PROC MIXED). Number of live hummocks was non-normally distributed so a poisson distribution with a log link was used (SAS Institute 2003, PROC GLIMMIX). Because transects represent blocks within each replicate, we used a split-plot design with subsampling, with replicate and replicate by treatment as random factors. Due the uneven number of replicates in each treatment, we used Satterthwaite adjusted degrees of freedom (Satterthwaite 1946). Bonferroni adjusted p-values for multiple comparisons are used for transect comparisons.

Results

Differences between invaded and uninvaded plots

Buckthorn-invaded plots differed from uninvaded plots with several key abiotic features altered in buckthorn-invaded habitats. Soil pH, number of vegetative hummocks and light availability were significantly lower in invaded areas (Table 2, Figure 3 a, c, d). There was a trend (p=0.090) toward higher organic matter content in invaded than uninvaded areas (Table 2, Figure 3b). There were no significant differences in soil nitrate, ammonia, phosphorous, or potassium concentrations, although all were numerically greater in buckthorn invaded than uninvaded plots. The transect by treatment interaction was not significant in any of the statistical comparisons (p>0.15).

Buckthorn–invaded plots supported fewer plants characteristic of fens. The mean plant coefficient of conservatism, total plant cover, and graminoid relative abundance were all significantly lower in buckthorn-invaded than uninvaded plots (Table 2, Figure 3 e, f). Although there were no significant differences in plant diversity (Simpsons *D*) or exotic plant relative abundance between invaded and uninvaded areas, there again were numeric differences in the direction we predicted, with lower diversity, greater dominance and greater exotic cover in buckthorn invaded plots (Table 2).

There were marked differences in plant community between buckthorn invaded and uninvaded areas. Shade-tolerant woodland species, including *Lindera benzoin* (L.) Blume, *Rubus strigosus* Michx., *Solanum dulcamara* L., *Rubus pubescens* Raf., *Equisetum arvense* (L.), *Viola nephrophylla* Greene, and *Circaea lutetiana* L., were absent from uninvaded plots but present in at least 10% of buckthorn invaded plots (Table 3). In contrast, light-loving *Pedicularis canadensis* L., *Muhlenbergia glomerata*

(Willd.) Trin., *Scirpus acutus* Muhl. ex Bigelow, *Gentianopsis crinita* (Froel.) Ma, *Rudbeckia hirta* L., *Solidago ohioensis* Frank ex Riddell, *Cladium mariscoides* (Muhl.) Torr., *Sorghastrum nutans* (L.) Nash, and *Potentilla fruticosa* L. were present in 17-50% of uninvaded plots but absent from all buckthorn-invaded plots (Table 3). Several plant species characteristic of prairie fen: *Cirsium muticum* Michx., *Aster lanceolatus* Willd., *Eupatorium macalatum* L., *Thelypteris palustris* Schott, and *Carex stricta* Lam. occurred in 44-100% of uninvaded plots but only 2-24% of buckthorn-invaded plots.

Differences with distance from water's edge

We observed a gradient of increasing graminoid cover and light availability from the upland edge to the water's edge of invaded plots. This plant community gradient coincided with a soil elevational gradient of 16-82 cm from upland plots to those near the water's edge for the replicates on the western side of the lake, and differences of 0-28 cm on the eastern side of the lake (Figure 2c).

Our analysis of habitat factors from the upland to water's edge in invaded areas yielded several interesting patterns in nutrient availability and soil characteristics. There were greater nitrate levels in the center (20.3 ± 4.0 ppm) than water (9.8 ± 3.7 ppm) and upland (8.6 ± 1.1 ppm) transects, while ammonia levels were significantly greater in the water (17.6 ± 1.3 ppm) and center (14.4 ± 2.0 ppm) transects than the upland (9.7 ± 1.3 ppm). Potassium levels, on the other hand, were greater in the water (112.8 ± 11.4 ppm) than center (72.0 ± 8.5 ppm) and upland (70.9 ± 9.6 ppm) transects. There was a significant increase in percent soil organic matter between upland (50.3 ± 7.9) versus center (67.5 ± 6.0) and water (71.5 ± 4.4) in buckthorn-invaded areas, and a similar pattern in uninvaded plots (Table 4, Figure 4a). The number of vegetative hummocks/ m^2

was significantly greater near the water (3.4 ± 0.4) than in the center (0.97 ± 0.27) or upland transects (0.37 ± 0.18) (Figure 4b). There were no significant differences in phosphorous levels, soil pH, or light availability between transect (Table 4). There was the same general trend in number of hummocks in uninvaded areas, but there was a smaller magnitude of difference in hummock density between transects in the uninvaded plots.

Plant community measures also differed by transect within invaded areas, with greater similarity to fen closer to the water's edge. The mean coefficient of conservatism in buckthorn-invaded areas was significantly greater near the water (4.8 ± 0.2) and center (4.5 ± 0.2) than in the upland transect (3.0 ± 0.2) (Table 4, Figure 4c). Again, the differences in plant conservatism for uninvaded plots between blocks were smaller. The relative abundance of graminoids in buckthorn-invaded areas was significantly greater in quadrats near the water (0.25 ± 0.04) than the center (0.05 ± 0.02) and upland (0.02 ± 0.01) areas of the plots (Table 4, Figure 4d), while abundance in uninvaded blocks was much greater overall with less distinct differences between blocks. There were no significant differences in Simpsons D or relative exotic cover by transect (Table 4).

Discussion

In support of our hypotheses (Table 2), we found a number of significant differences in both abiotic and biotic factors between prairie fen invaded by *F. alnus* and nearby uninvaded areas. The differences in uninvaded fen versus buckthorn-invaded areas included significantly greater light availability, higher soil pH, more hummocks, greater plant conservatism, greater percent plant cover, and greater relative graminoid abundance. The primary exception to our predictions was in organic matter content, which we predicted would be lower in invaded areas due to increased decomposition rates. We found a trend toward greater organic matter content in the 0-10 cm soil layer in invaded than uninvaded areas. This either indicates that invasion influences organic matter or that *F. alnus* is better able to invade areas of fen with high organic matter rather than marl-based soils that were more prevalent in the uninvaded areas.

Because we did not follow the entire invasion process in this study we do not know whether *F. alnus* was able to invade areas with different characteristics or if it altered them after its arrival. The study was performed at one buckthorn-invaded site, so we cannot make inferences about patterns between sites. The history of *F. alnus* invasion is not well-documented for this site but we do have access to color photos, likely dating to the 1930's, which show the currently *F. alnus* invaded area with sedge-dominated vegetation and very little shrub growth. We also have a general report from 2002 indicating "minor cover" of *F. alnus* in the fen area. Because shrub-dominated growth in our site was not the historic state and we see buckthorn in areas with peat soils near uplands but not near the water, here we use plot proximity to water as a proxy for understanding the invasion process. While these are critical factors to keep in mind, this study documents a number of striking contrasts between buckthorn-invaded and uninvaded fen which haven not been quantified before. In addition, some patterns, such as differences in herbaceous vegetation and microhabitat, were unlikely to exist pre-invasion.

In addition to differences between buckthorn-invaded and uninvaded areas of a prairie fen, we also found differences in a number of factors between plots nearest the upland edge and water's edge. These differences allow us to examine the possible changes in fen with buckthorn invasion. Within buckthorn invaded replicates, there were areas nearest the water's edge where buckthorn had not established. These areas are likely too wet to allow buckthorn establishment. In the transect nearest the water's edge we found significantly greater potassium levels, hummock abundance, total herbaceous cover, and graminoid relative abundance. A second group of factors, the mean coefficient of conservatism, percent organic matter, and soil ammonia, were all greater near the water and in the center of replicates than near the upland edge. These differences likely represent, in part, a transition to upland soil characteristics and an upland plant community along the upland fen edge.

Nutrient Availability

Nutrient availability in prairie fen is low, a factor that contributes to the high plant species diversity (Boeye et al. 1997, Nekola 2004, Bowles et al. 2005). In our study, we did not find significant differences in soil N, P, or K between invaded and uninvaded fen, although NO_3, NH_4, P, and K levels were all numerically higher in invaded areas. There is evidence that *F. alnus* alters nutrient properties in white-pine dominated uplands (Fagan and Peart 2004) and has been associated with higher nitrogen levels in hardwood dominated uplands (Huebner et al. 2009), but we found no published data on its effect on nutrients in wetlands. Increasing eutrophication of wetlands in North America may lead to decreased species richness within wetlands (Bedford et al. 1999). Increased nutrient availability as a result of *F. alnus* invasion is more likely in this case than larger scale eutrophication leading to decreased species richness, since both uninvaded areas are within 25 m of invaded areas. In our on-going project we are studying differences and changes in soil nutrients after removal of *F. alnus* to examine legacy effects of its invasion on soil properties. This will allow us to examine whether *F. alnus* was able to invade areas with greater soil nutrient availability, lower pH and greater organic matter content, or whether it created these changes after invasion and establishment.

Plant community

We found marked differences in the herbaceous plant community of invaded and uninvaded plots. Specifically, there was significantly more total cover, a significantly greater mean coefficient of conservatism, and higher proportion of graminoid cover in uninvaded than buckthorn-invaded areas. These patterns fit with the sedge and grass-dominated prairie fen, and the higher C indicates a higher quality plant community in uninvaded areas. Common fen species *C. stricta, T. palustris* and *E. maculatum* (Amon et al. 2002) were markedly more abundant in uninvaded areas. Surprisingly, there was no difference in the proportion of exotic herbaceous cover between invaded and uninvaded areas. This indicates that when *F. alnus* is present, it is either preventing establishment or suppressing the presence of smaller non-natives, including *F. alnus* seedlings.

Frangula alnus has been found to have significant negative effects on native herbaceous cover and diversity in pine forests (Frappier et al. 2003). However, we found no significant differences in plant diversity or evenness between buckthorn-invaded and uninvaded herbaceous communities. This result is similar to that of Houlahan and Findlay (2004), who found that invasive species were not more likely to be dominant plants than native wetland species. This suggests that *F. alnus* is likely outcompeting other exotic species, whereas in uninvaded fen, sedges are primarily filling this niche. Similarly, Mills et al. (2009) found that at larger spatial scales *F. alnus* was not associated with decreased herbaceous diversity in a bog community over 15 years, and they found no effect on herbaceous cover of invasion. This may be due to differences in scale and a study site with high initial high shrub cover, whereas in our study the uninvaded plots had low shrub cover.

Patterns in Frangula alnus invasion

Previous reports have observed that *F. alnus* is abundant around the perimeter of prairie fen (McCormac and Schneider 1994) and land managers in Michigan frequently report that their fens are 'ringed' by *F. alnus*. In contrast, areas within fens that are nearest to groundwater inflows appear more resistant to invasion by *F. alnus*. Our examination of biotic and abiotic gradients from the upland toward the water's edge suggests a potential mechanism for such invasion.

Frangula alnus is known to require water during the entire growing season but does not tolerate long periods of inundation. In water-saturated peat soils the root system of *F. alnus* grows very near the surface, above the water table (Godwin 1943). Most fens have a slight to medium slope that permits water drainage, resulting in habitat that is wet but not inundated (Amon et al. 2005). Frequently the drier areas of fens occur near upland edges. For example, the lake-edge fen in our study slopes gradually from a forested upland edge towards the lake (Figure 2). Overhanging tree limbs provide perches from which birds deposit *F. alnus* seeds directly into the fen edge, and the generally drier conditions near the perimeter favor *F. alnus* seedling establishment. We have also observed that *F. alnus* seedlings frequently take root on the top of *Carex spp.* hummocks. Such hummocks have been shown to provide a range of moisture availability to native plants (Peach and Zedler 2006) and may provide a moist but not inundated microhabitat conducive to *F. alnus* seedling establishment.

Once established, *F. alnus* likely facilitates its own further invasion. Transpiration of *F. alnus* in midsummer has been shown to lower the water table in wetlands (Godwin 1943). This would make the portion of fen near *F. alnus* infestations less suitable for native species that require wetter conditions, but increasingly suitable for its own invasion. Finally, with a lowered water table under the mature *F. alnus*, decomposition may be accelerated, leading to breakdown of hummocks and reducing microhabitat differences in the fen. Our data support this pattern of hummock degradation, with significantly fewer hummocks found in *F. alnus* invaded areas.

The patterns we found in this Michigan fen are similar to those that land managers have commonly observed. We have now quantitatively established this set of both abiotic and biotic factors in *F. alnus* invaded and uninvaded fen before restoration activities occur at the site. Several key differences between invaded and uninvaded prairie fen, notably the lack of hummocks, lower plant conservatism, and lower graminoid cover in invaded fen, were unlikely to be present pre-invasion. These findings coupled with those from our on-going restoration efforts at this site will be useful to land managers to determine whether the effects of *F. alnus* are mitigated during restoration. *Frangula alnus* may not only be effectively invading certain areas of fen, it also appears to be facilitating its persistence via microhabitat degradation. While relatively rapid recovery is often seen in prairie fens (e.g. seeding is not a common practice in fen restoration as the existing seed bank appears to be sufficient), *F. alnus* may be altering some conditions over longer periods, leaving a legacy that may increase future fen invasibility.

Acknowledgements

We would like to thank G. Kowalewski, J. Curtis, M. Trimmer and J. Vigneron from MSU forestry, R. Zuniga-Villegas and D. Tison of The Nature Conservancy and the Landis Lab, especially C. Sebolt, for help with plot establishment. D. Cuthrell and R. O'Connor provided invaluable input on research direction. A. Reznicek and R. O'Connor assisted with plant specimen identification. R. Ahern and N. Bello provided significant input on data analysis. B. Werling, P. Doran and two anonymous reviewers helped improve this manuscript. Research funding was provided by the MSU MacCready Endowment and National Fish and Wildlife Foundation. Funding support for A.K.F. was provided through a sustainable agriculture predoctoral fellowship by the C.S. Mott foundation and a MSU Barnett Rosenberg predoctoral fellowship in biological sciences.

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Table 2. Hypothesized and actual differences in abiotic and biotic factors between *Frangula alnus* invaded and uninvaded reference areas of prairie fen. A result in parentheses indicates a marginally significant result.

	Factor	Prediction$^{\#}$	Result^{+}	P	F	DF	Buckthorn invaded	Uninvaded
Soils	pH	-	-	0.001	24.9	1,10	6.77 ± 0.05	7.63 ± 0.16
	NO_3 (ppm)	+	NS	0.146	2.5	1,10	12.89 ± 2.03	5.56 ± 1.13
	NH_4 (ppm)	+	NS	0.194	1.9	1,10	13.92 ± 1.06	9.72 ± 2.49
	P (ppm)	+	NS	0.130	2.4	1,30	9.30 ± 0.88	6.17 ± 1.20
	K (ppm)	+	NS	0.475	0.6	1,10	85.23 ± 6.60	69.17 ± 16.65
	% organic matter	-	(+)	0.090	3.5	1,10	63.07 ± 3.88	35.10 ± 11.60
Microtopography	# hummocks /m^2	-	-	0.004	14.4	1,10	1.60 ± 0.20	5.78 ± 0.66
Light availability	% full sun at 1 m$^{\sim}$	-	-	<0.001	40.4	1,10	9.01 ± 1.53	87.62 ± 6.58
Plant diversity	Simpsons D	-	NS	0.136	2.6	1,10	3.73 ± 0.19	4.67 ± 0.52
Plant quality	Mean C$^{\wedge}$	-	-	0.044	5.3	1,10	4.02 ± 0.14	5.17 ± 0.16
Plant cover	Total % cover	-	-	<0.001	104.1	1,10	20.52 ± 1.92	90.97 ± 5.05
	Relative graminoid cover*	-	-	<0.001	59.3	1,10	0.10 ± 0.02	0.52 ± 0.05
	Relative exotic cover*	+	NS	0.101	3.2	1,10.7	0.15 ± 0.02	0.07 ± 0.04

$^{\#}$ Indicates the predicted direction (- =lower + =higher) in invaded vs. uninvaded plots.

$^{+}$ Parentheses indicate a marginally significant result.

$^{\sim}$ Log(x+1) transformed data used for ANOVA analysis.

$^{\wedge}$ Coefficient of conservatism on a scale of 1 to 10.

* Square root arcsine transformed data used for ANOVA analysis.

Table 3. Plant species identified at research site and the percent of quadrats each species occupied, 112 total.

Family	Genus species	Common Name	C~	All quadrats	Unin-vaded	Invaded
Aceraceae	*Acer rubrum* L.	red maple	7	2.78	0.00	3.33
Scrophulariaceae	*Agalinis purpurea* (L.) Pennell	purple false foxglove	6	5.56	33.33	0.00
Rosaceae	*Agrimonia gryposepala* Wallr.	tall hairy agrimony	2	3.70	11.11	2.22
Fabaceae	*Amphicarpaea bracteata* (L.) Fernald	American hogpeanut	4	0.93	0.00	1.11
Poaceae	*Andropogon gerardii* Vitman	big bluestem	5	0.93	5.56	0.00
Fabaceae	*Apios americana* Medik.	groundnut	7	1.85	0.00	2.22
Asclepiadaceae	*Asclepias incarnata* L.	swamp milkweed	4	2.78	5.56	2.22
Asteraceae	*Aster lanceolatus* Willd.	white panicle aster	3	11.11	50.00	3.33
Asteraceae	*Aster puniceus* L.	purplestem aster	8	11.11	38.89	5.56
Betulaceae	*Betula pumila* (L.)	bog birch	10	0.93	0.00	1.11
Asteraceae	*Bidens frondosa* (L.)	devil's beggartick	1	4.63	0.00	5.56
Asteraceae	*Cacalia plantaginea* Raf.	groovestem Indian plantain	10	0.93	5.56	0.00
Campanulaceae	*Campanula aparinoides* Pursh	marsh bellflower	8	7.41	27.78	3.33
Cyperaceae	*Carex leptalea* Wahlenb.	bristlystalked sedge	10	1.85	0.00	2.22
Cyperaceae	*Carex stipata* Muhl. ex Willd.	awlfruit sedge	3	13.89	0.00	16.67
Cyperaceae	*Carex stricta* Lam.	upright sedge	5	37.04	100.00	24.44
Juglandaceae	*Carya* sp.	hickory	5	1.85	0.00	2.22
Celastraceae	*Celastrus orbiculatus* Thumb	oriental bittersweet	0	0.93	0.00	1.11
Apiaceae	*Cicuta maculata* L.	spotted water hemlock	6	0.93	5.56	0.00
Poaceae	*Cinna arundinacea* L.	sweet woodreed	5	1.85	0.00	2.22
Onagraceae	*Circaea lutetiana* L.	enchanter's nightshade	1	24.07	0.00	28.89
Asteraceae	*Cirsium muticum* Michx.	swamp thistle	10	11.11	44.44	4.44
Cyperaceae	*Cladium mariscoides* (Muhl.) Torr.	smooth sawgrass	10	6.48	38.89	0.00
Ranunculaceae	*Clematis virginiana* L.	western blue virginsbower	4	1.85	0.00	2.22
Cornaceae	*Cornus foemina* Mill.	stiff dogwood	1	7.41	16.67	5.56
Cornaceae	*Cornus stolonifera* Michx.	western dogwood	6	2.78	16.67	0.00
Fabaceae	*Desmodium glutinosum* (Muhl. ex Willd.) Alph. Wood	pointedleaf ticktrefoil	5	0.93	0.00	1.11
Dryopteridaceae	*Dryopteris carthusiana* (Vill.) H.P. Fuchs	spinulose woodfern	8	9.26	0.00	11.11
Onagraceae	*Epilobium coloratum* Biehler	purpleleaf willowherb	3	3.70	11.11	2.22
Equisetaceae	*Equisetum arvense* (L.)	field horsetail	0	12.96	0.00	15.56
Asteraceae	*Eupatorium maculatum* L.	joe-pye weed	4	10.19	50.00	2.22
Asteraceae	*Eupatorium perfoliatum* L.	common boneset	4	12.96	16.67	12.22
Asteraceae	*Euthamia graminifolia* (L.) Nutt.	flat-top goldentop	4	1.85	11.11	0.00
Rhamnaceae	*Frangula alnus* Mill.	glossy buckthorn	0	64.81	61.11	65.56
Oleaceae	*Fraxinus pennsylvanica* Marsh.	green ash	5	2.78	0.00	3.33
Rubiaceae	*Galium boreale* L.	northern bedstraw	7	7.41	11.11	6.67
Rubiaceae	*Galium circaezans* Michx.	licorice bedstraw	10	1.85	0.00	2.22
Rubiaceae	*Galium triflorum* Michx.	fragrant bedstraw	5	12.96	11.11	13.33
Gentianaceae	*Gentianopsis crinita* (Froel.) Ma	greater fringed gentian	10	5.56	33.33	0.00
Rosaceae	*Geum canadense* Jacq.	white avens	1	23.15	5.56	26.67
Boraginaceae	*Hackelia virginiana* (L.) I.M. Johnst.	beggarslice	0	1.85	0.00	2.22
Aquifoliaceae	*Ilex verticillata* (L.) A. Gray	common winterberry	9	0.93	0.00	1.11

Table 3 cont'd.

Family	Genus species	Common Name	C~	All quadrats	Unin-vaded	Invaded
Balsaminaceae	*Impatiens capensis* Meerb.	jewelweed	3	12.96	33.33	8.89
Iridaceae	*Iris versicolor* L.	harlequin blueflag	5	0.93	0.00	1.11
Juncaceae	*Juncus brachycephalus* (Engelm.) Buchenau	smallhead rush	9	0.93	5.56	0.00
Fabaceae	*Lathyrus palustris* L.	marsh pea	8	16.67	27.78	14.44
Poaceae	*Leersia oryzoides* (L.) Sw.	rice cut grass	4	6.48	0.00	7.78
Asteraceae	*Liatris spicata* (L.) Willd.	dense blazing star	6	0.93	5.56	0.00
Lauraceae	*Lindera benzoin* (L.) Blume	northern spicebush	7	7.41	0.00	8.89
Campanulaceae	*Lobelia siphilitica* L.	great blue lobelia	6	3.70	0.00	4.44
Lamiaceae	*Lycopus americanus* Muhl. ex W. Bartram	American water horehound	5	3.70	22.22	0.00
Lamiaceae	*Lycopus uniflorus* Michx.	northern bugleweed	7	19.44	44.44	14.44
Lythraceae	*Lythrum salicaria (L.)*	purple loosestrife	0	1.85	11.11	0.00
Lamiaceae	*Mentha arvensis* L.	wild mint	5	1.85	11.11	0.00
Poaceae	*Muhlenbergia glomerata* (Willd.) Trin.	spiked muhly	10	3.70	22.22	0.00
Poaceae	*Muhlenbergia mexicana* (L.) Trin.	Mexican muhly	5	0.93	5.56	0.00
Poaceae	*Muhlenbergia sylvatica* (Torr.) Torr. ex A. Gray	woodland muhly	10	5.56	0.00	6.67
Dryopteridaceae	*Onoclea sensibilis* L.	sensitive fern	8	14.81	16.67	14.44
Apiaceae	*Osmorhiza claytonii* (Michx.) C.B. Clarke	Clayton's sweetroot	3	1.85	0.00	2.22
Caprifoliaceae	*Oxypolis rigidor* (L.) Raf.	stiff cowbane	7	0.93	0.00	1.11
Poaceae	*Panicum dichotomiflorum* Michx.	fall panicgrass	0	0.93	5.56	0.00
Saxifragaceae	*Parnassia glauca* Raf.	fen grass of parnassus	10	6.48	38.89	0.00
Vitaceae	*Parthenocissus quinquefolia* (L.) Planch.	Virginia creeper	2	24.07	16.67	25.56
Scrophulariaceae	*Pedicularis lanceolata* Michx.	swamp lousewort	9	2.78	16.67	0.00
Crassulaceae	*Penthorum sedoides* L.	ditch stonecrop	5	0.93	0.00	1.11
Poaceae	*Phalaris arundinacea* L.	reed canarygrass	0	12.96	16.67	12.22
Phytolaccaceae	*Phytolacca americana* L.	American Pokeweed	1	0.93	0.00	1.11
Urticaceae	*Pilea pumila* (L.) A. Gray	clearweed	5	68.52	44.44	73.33
Plantaginaceae	*Plantago major* (L.)	common plantain	0	0.93	5.56	0.00
Polygonaceae	*Polygonum amphibium* L.	water knotweed	4	4.63	16.67	2.22
Polygonaceae	*Polygonum punctatum* Elliot	dotted smartweed	6	3.70	0.00	4.44
Polygonaceae	*Polygonum sagittatum* L.	arrowleaf tearthumb	8	8.33	11.11	7.78
Polygonaceae	*Polygonum virginianum* L.	jumpseed	2	6.48	0.00	7.78
Salicaceae	*Populus tremuloides* Michx.	quaking aspen	4	3.70	11.11	2.22
Rosaceae	*Potentilla fruticosa* auct. non L.	shrubby cinquefoil	10	11.11	61.11	1.11
Lamiaceae	*Prunella vulgaris* L.	selfheal	0	0.93	0.00	1.11
Rosaceae	*Prunus serotina* Ehrh.	black cherry	1	6.48	0.00	7.78
Fagaceae	*Quercus* sp.	oak	5	4.63	0.00	5.56
Rhamnaceae	*Rhamnus alnifolia* L'Hér.	alderleaf buckthorn	10	0.93	5.56	0.00
Cyperaceae	*Rhynchospora alba* (L.) Vahl	white beaksedge	10	0.93	5.56	0.00
Grossulariaceae	*Ribes cynosbati* L.	eastern prickly gooseberry	5	4.63	0.00	5.56
Rosaceae	*Rosa multiflora* Thunb.	multiflora rose	0	14.81	5.56	16.67
Rosaceae	*Rosa palustris* Marsh.	swamp rose	7	0.93	0.00	1.11
Rosaceae	*Rubus pubescens* Raf.	dwarf red blackberry	10	12.04	0.00	14.44
Rosaceae	*Rubus strigosus* Michx.	grayleaf red raspberry	3	6.48	0.00	7.78
Asteraceae	*Rudbeckia hirta* L.	blackeyed Susan	1	5.56	33.33	0.00

Table 3 cont'd.

Family	**Genus species**	**Common Name**	**C~**	**All quadrats**	**Unin-vaded**	**Invaded**
Salicaceae	*Salix discolor* Muhl.	pussy willow	2	5.56	33.33	0.00
Caprifoliaceae	*Sambucus canadensis* L.	American black elderberry	1	2.78	0.00	3.33
Poaceae	(Michx.) Nash	little bluestem	5	4.63	27.78	0.00
Cyperaceae	*Scirpus acutus* Muhl. ex Bigelow	hardstem bullrush	6	3.70	22.22	0.00
Lamiaceae	*Scutellaria galericulata* L.(17)	marsh skullcap	5	3.70	0.00	4.44
Asteraceae	*Senecio aureus* L.	golden ragwort	7	27.78	11.11	31.11
Asteraceae	*Senecio pauperculus Michx.*	balsam groundsel	6	5.56	22.22	2.22
Smilacaceae	*Smilax tamnoides* L.	bristly greenbrier	5	6.48	0.00	7.78
Solanaceae	*Solanum americanum* Mill.	American black nightshade	0	6.48	0.00	7.78
Asteraceae	*Solidago altissima* L.	Canada goldenrod	1	2.78	5.56	2.22
Asteraceae	*Solidago ohioensis* Frank ex Riddell	Ohio goldenrod	9	5.56	33.33	0.00
Asteraceae	*Solidago patula* Muhl. ex Willd.	roundleaf goldenrod	9	31.48	38.89	30.00
Asteraceae	*Solidago riddellii* Frank ex Riddell	Riddell's goldenrod	7	6.48	38.89	0.00
Asteraceae	*Solidago rugosa* Mill.	wrinkleleaf goldenrod	6	25.93	22.22	26.67
Asteraceae	*Solidago uliginosa* Nutt.	bog goldenrod	10	0.93	0.00	1.11
Poaceae	*Sorghastrum nutans* (L.) Nash	indiangrass	5	8.33	50.00	0.00
Araceae	*Symplocarpus foetidus* (L.) Salisb. ex Nutt.	American skunk cabbage	8	3.70	0.00	4.44
Ranunculaceae	*Thalictrum dasycarpum* Fisch. & Avé-Lall.	purple meadow-rue	5	1.85	0.00	2.22
Thelypteridaceae	*Thelypteris palustris* Schott	eastern marsh fern	6	17.59	66.67	7.78
Anacardiaceae	*Toxicodendron radicans* (L.) Kuntze	eastern poison ivy	2	6.48	11.11	5.56
Liliaceae	*Triantha glutinosa* (Michx.) Baker	sticky tofieldia	10	0.93	5.56	0.00
Typhaceae	*Typha* L.	cattail	1	0.93	0.00	1.11
Ulmaceae	*Ulmus* sp.	elm	3	5.56	0.00	6.67
Poaceae	unknown grass			7.41	0.00	8.89
Urticaceae	*Urtica dioica* L.	stinging nettle	0	7.41	0.00	8.89
Violaceae	*Viola nephrophylla* Greene	northern bog violet	9	21.30	0.00	25.56
				Mean richness / m^2	**14.8±0.7**	**7.8±0.3**

~Coefficient of conservatism from Herman et al. (2001)

Table 4: Differences in abiotic and biotic factors between upland and water's edge transects in prairie fen. P-values are bolded where less than 0.10.

	Factor	Result°	DF	Water vs. Center		Water vs. Upland		Center vs. Upland	
				t	P	t	P	t	P
Soils	pH	NS	2,20	-1.7	0.318	-0.3	>0.50	-1.4	>0.50
	NO_3 (ppm)	ctr>wat=up	2,20	2.5	**0.062**	-0.3	>0.50	2.8	**0.032**
	NH_4 (ppm)	wat=ctr>up	2,20	-1.9	0.239	-4.5	**0.002**	2.7	**0.044**
	P (ppm)	NS	2,30	-0.7	>0.50	1.3	>0.50	-2.0	0.169
	K (ppm)	wat>ctr=up	2,20	-5.0	**0.001**	-5.1	**0.001**	0.1	>0.50
	% organic matter	wat=ctr>up	2,20	-0.9	>0.50	-4.6	**0.001**	3.7	**0.004**
Microtopography	# hummocks /m^2	wat>ctr=up	2,20	-4.8	**0.003**	-5.9	**0.003**	-1.2	>0.50
Light availability	% full sun at 1 m~	NS	2,20	-0.5	>0.50	-0.6	>0.50	0.2	>0.50
Plant diversity	Simpsons D	NS	2,20	-1.2	>0.50	-2.5	0.066	1.3	>0.50
Plant quality	Mean C^	wat=ctr>up	2,20	-0.4	>0.50	-3.1	**0.019**	2.7	**0.043**
Plant cover	Total % cover	wat>ctr=up	2,20	-2.5	**0.062**	-2.7	**0.040**	0.2	>0.50
	Relative graminoid cover*	wat>ctr=up	2,20	-0.8	>0.50	-0.2	>0.50	-0.5	>0.50
	Relative exotic cover*	NS	2,91	-0.8	>0.50	-0.2	>0.50	-0.5	>0.50

~ Log(x+1) transformed data used for ANOVA analysis.

^ Coefficient of conservatism on a scale of 1 to 10.

* Square root arcsine transformed data used for ANOVA analysis.

° Treatments on opposite sides of > or < signs are significantly different.

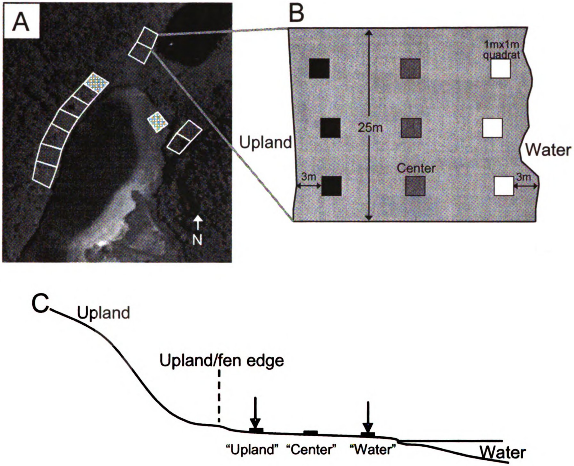

Figure 2. Layout of research plots at MacCready Reserve, Clarklake, MI. A: Ten 25 x 25m replicates of buckthorn invaded plots are shown as outlined rectangles and two uninvaded areas as white filled rectangles. B: Quadrats in black lie 3m from the upland edge (upland). White quadrats lie 3m from the water's edge (water) and dark grey quadrats are in the center of plots (center). C: Schematic of typical elevational differences within plots, arrows showing where elevation was measured.

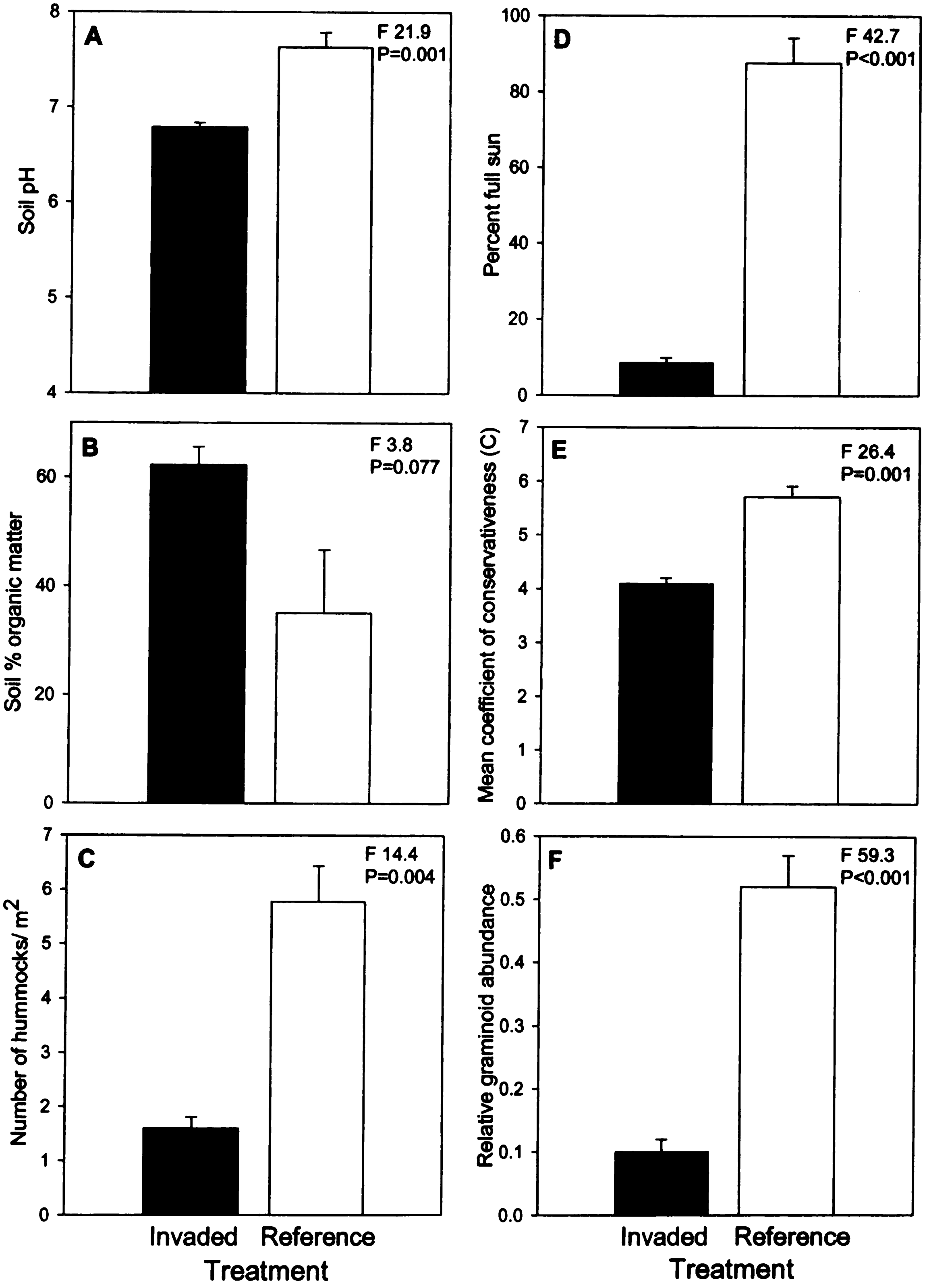

Figure 3. Comparisons of abiotic and biotic factors between *F. alnus* invaded and uninvaded plots. Error bars are +SEM, α=0.05. Treatment effects from a 2-way ANOVA with treatment and transect are shown here.

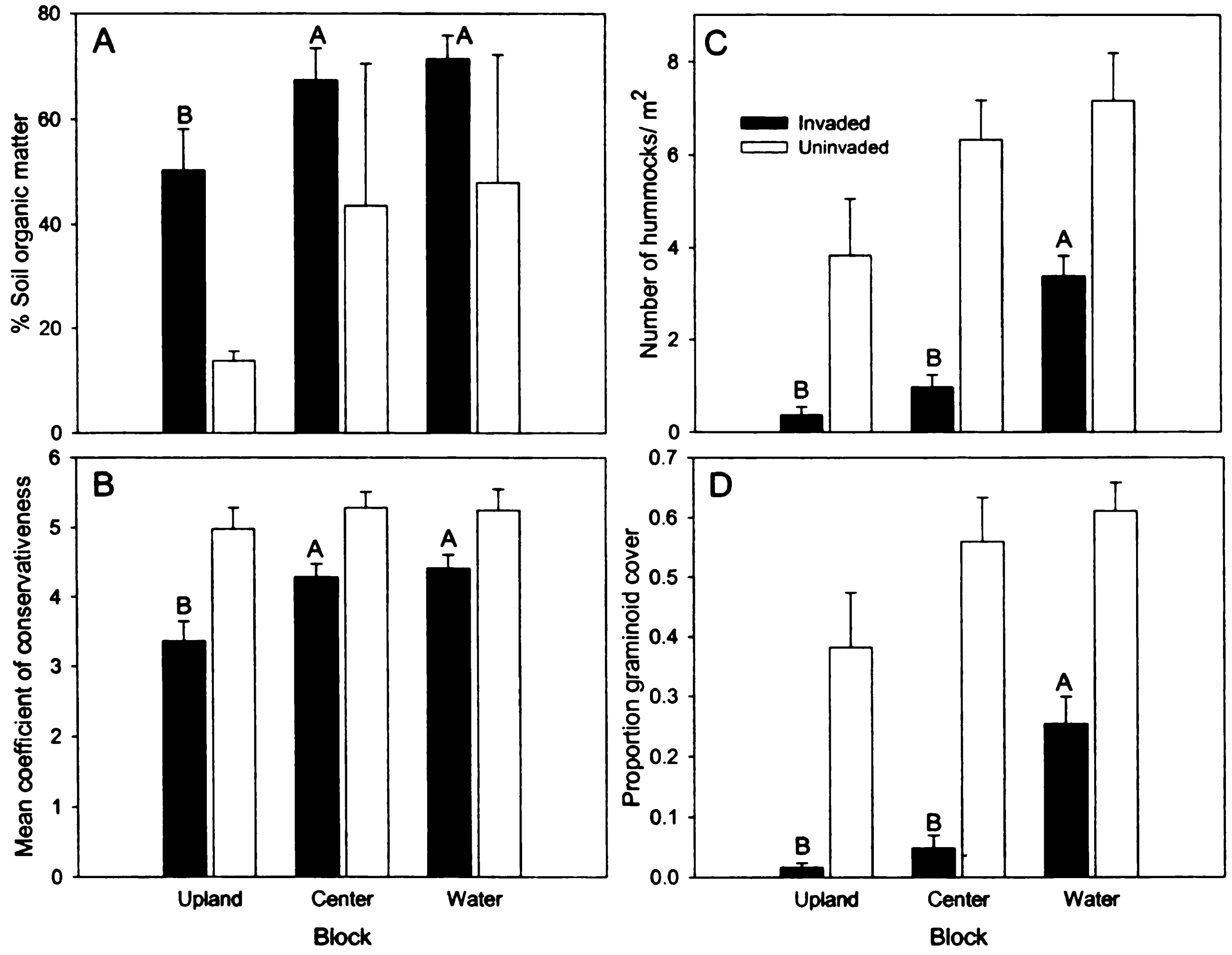

Figure 4. The effect of distance to the upland/water's edge on abiotic and biotic factors in *F. alnus* invaded plots. Patterns in uninvaded plots are shown for comparison; no statistical tests were performed on these data. Error bars are +SEM. Bars with different letters within a figure are significantly different using Bonferonni adjusted LS means comparisons (p<0.05).

Chapter 3

For Ecological Restoration

DIFFERENTIAL SHIFTS IN RESOURCE AVAILABILITY AND PLANT COMMUNITY STRUCTURE FOLLOWING PRAIRIE FEN RESTORATION

Anna Katherine Fiedler

Abstract

Restoration activities frequently involve removal of exotic invasive species, but subsequent changes in resource availability and the plant community are rarely quantified. The exotic invader glossy buckthorn (*Frangula alnus*) is known to alter soil and plant community conditions in rare prairie fen wetlands; here, we ask whether its removal leads to shifts in resource availability and plant communities. We examined availability of light, soil nutrients, and spatial heterogeneity, and the resulting changes in herbaceous cover and diversity in *F. alnus* invaded, removal, and uninvaded areas of prairie fen over two years. We found rapid increases in light availability, herbaceous plant cover, and relative graminoid abundance in restored plots. There were no significant differences in soil organic matter, nitrate, ammonia, potassium, and phosphorous, plant diversity or plant species dominance between treatments before or after restoration. Other factors, such as soil pH, surface spatial heterogeneity, and floristic quality index, were initially greater in uninvaded areas versus invaded fen, and remained so in the first two years after restoration. An NMDS analysis considering soil and plant factors simultaneously showed *F. alnus* removal plots were on a trajectory toward uninvaded reference areas by end of year one, with continued shifts towards reference conditions in year two. Our results show that in prairie fen some soil and plant community factors change rapidly while others may remain altered for years, potentially leading to alternative stable states. We conclude that while short-term success can be achieved, long-term efforts are likely required for successful restoration and invasive management.

Keywords: prairie fen, restoration, *Frangula alnus*, glossy buckthorn, invasive species.

Introduction

Non-native invasive species are one of the greatest threats to native communities in the U.S. (Wilcove et al. 1998). Once established, many exotic plant species can alter ecosystem processes. For example, systems invaded by non-native plants tend to have greater standing crop biomass, more rapidly decaying litter, shifts in the timing of nutrient cycling, greater inorganic nitrogen levels, and increased nitrogen mineralization rates (Ehrenfeld 2003). Wetlands are particularly invasible by non-native plants (Zedler and Kercher 2005). In the less than 9% of earth's land area that wetlands occupy (Zedler and Kercher 2005), they support a number of ecosystem functions, including water filtration and purification, flood control, and function as carbon sinks (Baron et al. 2002). These functions, however, as well as biodiversity, are degraded in many wetland ecosystems (Zedler and Kercher 2005).

Prairie fens are a globally rare wetland community that is most abundant in the glaciated Midwestern U.S. These groundwater–fed systems were always historically small and isolated (Bedford and Godwin 2003), yet contain very high plant diversity per unit area (Nekola 1994). Both rare and endangered insects and plants occur in this habitat type, making its protection a primary concern (Spieles et al. 1999). Like many natural areas globally, prairie fen habitats are under pressure from a number of threats. These include changes in nutrient inputs (Verhoeven et al. 1996), increased pollution (Panno et al. 1999), changes in hydrology (Amon et al. 2002), habitat fragmentation and conversion (Grootjans et al. 2006, van Diggelen et al. 2006), alteration of fen disturbance regimes (Middleton et al. 2006), and invasive species (Bowles and Jones 2006). These factors often interact to alter the plant and animal communities within prairie fen.

The most common invasive species in Midwestern U.S. wetlands include reed canarygrass (*Phalaris arundinaceae* L.) (Galatowitsch et al. 1999), purple loosestrife (*Lythrum salicaria* L.), cattail (*Typha* sp.), glossy (*Frangula alnus* Mill.), and common buckthorn (*Rhamnus cathartica* L.) (Bowles and Jones 2006). Reed canarygrass and native cattail (*Typha latifolia* L.) have both been shown to tolerate a wider range of moisture conditions than non invasive wetland species (Kercher and Zedler 2004a) and reed canarygrass tolerates multiple disturbances more readily than native wet prairie species (Kercher and Zedler 2004b). Additionally, there is evidence that the native-non-native hybrid cattail *Typha* x *glauca* acts as an ecosystem engineer, with greater soil organic matter, nitrogen, and litter mass and lower plant species richness in densely invaded areas than in recently invaded areas (Tuchman et al. 2009). Common buckthorn has been associated with a number of changes in soils in upland habitats, including elevated pH, higher percent nitrogen, and altered nitrogen mineralization rates (Heneghan et al. 2006). Glossy buckthorn (Rhamnaceae: *Frangula alnus* (previously *Rhamnus frangula* L.)) has also been associated with elevated soil nitrogen levels in uplands (Huebner et al. 2009). Such changes in resource availability may create a legacy of invasion which needs to be addressed in ecosystem restoration.

Glossy buckthorn is a Eurasian shrub that was introduced in North America, becoming naturalized by the early 1900's (Converse 1984). It is currently widespread, occurring in the Northeastern and western plains states of the US, as well as Eastern Canada (Sinclair and Catling 1999, USDA 2010). Glossy buckthorn establishes well in soils with a wide pH range and is aggressive in fens and bogs (Galatowitsch et al. 1999). It is most commonly found in wet areas as it requires moist sites, but does not survive permanent waterlogging (Voss 1985). Mature individuals can survive in forested areas given adequate moisture. *Frangula alnus* blooms prolifically and produces abundant fruits annually (Godwin 1943). A number of bird species eat the berries, effectively dispersing seeds, which germinate most successfully on exposed soils with available light (Converse 1984).

Frangula alnus is considered a key threat to prairie fens due to its ability to invade and alter resource availability. Once established, it frequently becomes an additional dominant species in prairie fen (Houlahan and Findlay 2004) and alters the open sedge-dominated structure to one dominated by up to 7m tall shrubs, with shade-tolerant species in the herbaceous layer. In areas with *F. alnus* removed, herbaceous plant growth and species richness are greater than in areas where it remains (Sinclair and Catling 1999). This pattern is well understood by land managers, and the typical means of restoration include removal of adult glossy buckthorn and subsequent control of reprouts and seedlings (Converse 1984). In comparison to uninvaded reference areas, invaded areas of prairie fen differ in plant, soil, and abiotic factors (Chapter 2). However, it is currently unknown if such features pre-exist, are caused by glossy buckthorn invasion, or a combination of both. Because plant invasions may result in long-term shifts in resource availability that lead to alternative stable states (Suding et al. 2004), understanding if *F. alnus* removal from ecosystems allows a return towards reference conditions is of significant concern.

The goal of this study was to assess the success of habitat restoration by determining whether restored areas of prairie fen approach uninvaded reference areas in resource availability and resultant plant community indices. Specifically, we examined changes in soil resources, light availability, microhabitat, and plant diversity, functional group, and quality over two growing seasons in buckthorn invaded, removal, and uninvaded areas. Our hypotheses were that 1) soil nutrients would be greatest in invaded plots, would decrease in removal plots, and be lowest in uninvaded plots, 2) neither soil pH nor organic matter would shift over time, 3) light availability would increase in removal plots to a level near that of the uninvaded plots, 4) microhabitat availability would remain high in uninvaded plots, and low in both removal and invaded plots, 5) native herbaceous cover, grass and sedge cover, plant species diversity, and plant quality would be greatest in uninvaded plots, would increase in removal plots, and remain low in buckthorn invaded plots, and 6) exotic invasive plant species cover would be greatest in invaded plots, followed by removal plots, followed by the uninvaded reference.

Methods

Experimental design

The study was conducted in a *F. alnus* invaded prairie fen on the Michigan State University MacCready Reserve, in Clarklake, Liberty Township, Jackson County, Michigan. In September 2007, we assessed the site for potential restoration of prairie fen habitats, delineating twelve 25 x 25 m replicate plots containing mature *F. alnus* plants, on hydric soils and with plant species characteristic of prairie fen at the invasion margins. In 2008, we began restoration of six of these plots, following current best management practices (The Nature Conservancy, R. Villegas, pers. comm.). In February, we cut *F. alnus* and treated cut stumps with herbicide, using glyphosate 25% AI (Rodeo, Monsanto, St. Louis, MO) plus Cide Kick II surfactant, adjuvant, and penetrator (Brewer

International, Vero Beach, FL). Cut stumps were treated within 15 minutes of cutting, brush was piled and burned in April-June 2008. Brush piles were located at plot margins, outside of future sampling areas. In May 2008 and June 2009, we managed invasive plants in the restored plots in the following ways. Using glyphosate (25% active ingredient) and Cide Kick II, we sprayed glossy buckthorn re-sprouts and patches of *P. arundinacea* L., *Rosa muliflora* Thunb., and *Cirsium arvense* (L.) Scop. We cut and treated cut stems of *Typha* sp. and *Populus tremuloides* Michx. within restored plots, and used a propane torch to flame *F. alnus* seedlings. None of these activities was required more than once in a growing season within a particular area.

These restoration activities created two treatments among areas that were initially invaded by *F. alnus*: 1) invaded, a control where glossy buckthorn remained unmanaged, and 2) restored, where glossy buckthorn was removed and invasives were managed during 2008 and 2009. We also delineated two 25 x 25 m uninvaded reference plots located within 300 m of experimental plots in Fall 2007, and a third uninvaded plot in May 2008. We established nine 1 m^2 sampling quadrats in each plot, laid out on a grid across each replicate (Chapter 2).

Sampling

Soil characteristics were measured in each replicate from soil cores (0-10 cm depth) collected 6-7 Oct. 2007, 29 Sept. 2008, and 14 Sept. 2009. We collected two soil samples near each sampling quadrat, and sent them to the Michigan State University soils lab for measurement of pH (water pH method) percent organic matter (loss on ignition at 500 ° C) phosphorous (Bray P-1 or Olsen in samples with free calcium carbonate) potassium (neutral 1 normal ammonium acetate procedure), nitrate, and ammonia (KCl extraction) (Brown 1998).

To assess changes in plant community, light availability, and microhabitat between buckthorn invaded, restored, and uninvaded fen, we measured the following parameters in all quadrats in September 2007, 2008, and 2009. We estimated species percent and total cover of graminoids (including Poaceae, Cyperaceae and Juncaceae), forbs, and shrubs less than 1.5 m tall including all vegetation rooted within the quadrat. We use summed cover by species for total herbaceous cover, not including mature *F. alnus* shrubs. Light availability at 100cm height was measured on a clear, sunny day with a 1 m long photosynthetically active radiation (PAR) ceptometer (Sunfleck, Decagon Devices Inc., Pullman, WA), using the average of three measurements from each quadrat. Soil microtopography was measured in Sept. 2007, June 2008 and June 2009 by counting the number of vegetative hummocks of 5 cm or more in height within each quadrat.

Statistical analysis

To account for shifts in total cover, we standardized the grass and sedge cover and exotic cover as proportions of total cover. We calculated Simpsons Diversity Index $D=1/\sum(p_i)^2$ where p_i is the proportion of cover of the *i*th plant species per quadrat (using 1/D so that the value increases with diversity) to examine the interaction of species abundance and evenness, and the Berger Parker index of dominance to examine patterns of plant species dominance (Magurran 2004). We used coefficients of conservatism (C) for each plant species (Herman et al. 2001) and species richness (S) within a quadrat to calculate the floristic quality index (FQI) (Swink and Wilhelm 1994) per m^2 quadrat using: $FQI= \text{Mean } C * \sqrt{S}$. Higher values indicate a plant community that is more likely to be found in high quality, undisturbed habitats. To address heterogeneity of variances the following variables were transformed for ANOVA analyses: light availability, nitrate levels, and number of hummocks/m^2 were log(x+1) transformed, the proportion of graminoid and exotic cover were arcsin(square root) transformed, and phosphorous and Simpsons diversity were square root transformed.

To characterize differences in removal versus buckthorn invaded and uninvaded plots over time, we performed a 2-way ANOVA on all of the measured characteristics with treatment (invaded, removal, and uninvaded), time: pre restoration, year 1, year 2 (Sept. 2007, 2008, and 2009, except for hummocks, which were measured in Sept. 2007, June 2008, and June 2009), and the interaction between them (SAS Institute 2003, PROC MIXED). The model included subsamples within treatment and replicate, with each replicate of a treatment as the experimental unit. We specified a compound symmetry covariance structure and used Satterthwaite adjusted degrees of freedom to account for the uneven number of replicates between reference (n=2-3) and other treatments (n=6) (Satterthwaite 1946).

To examine shifts in suites of characteristics over time, we used nonmetric multidimensional scaling (NMDS). NMDS creates an ordination of data quadrats by ranking each variable relative to the others, adjusting quadrats to minimize the stress between them on a two-dimensional surface. Using untransformed data for all factors, we calculated a mean by transect, then by row, for each variable, with one value per treatment and replicate for each date. The analysis included all resource and plant variables mentioned above, as well as percent bare ground /m^2 quadrat, and exchangeable soil calcium and magnesium (ppm) (neutral 1 normal ammonium acetate procedure).

Because factors were on different scales, data for each time were normalized before performing the NMDS; for each value, the mean is subtracted and divided by the standard deviation for that variable (Clarke and Gorley 2006a). We used a Euclidian distance resemblance matrix, which is appropriate for data without zeroes and on similar scales (Quinn and Keough 2002). The NMDS was performed using 2 and 3 dimensions, with 25 random starting configurations and a minimum stress of 0.01 (Clarke and Gorley 2006a). To compare differences by time we performed an analysis of similarity (ANOSIM) using the resemblance matrix for each time period with 999 random permutations (Clarke and Gorley 2006b).

Results

Resource availability

We observed shifting patterns in soil characteristics, but never a significant treatment by time interaction (Fig. 5, Table 5). Soil pH was significantly greater in uninvaded plots than invaded plots at the beginning of the study, and did not change following *F. alnus* removal (Fig. 5A). There were no significant differences by treatment or time in percent organic matter (Fig. 5B), although levels of both were numerically lower in the uninvaded reference plots than in removal or invaded replicates on all dates. Nitrate, ammonia, and potassium levels varied significantly by time but not by treatment (Table 5, Appendix A). There were no significant differences by treatment or over time in phosphorous (Table 5, Appendix A).

Initially, light availability at 1m height was significantly greater in uninvaded replicates than invaded replicates (Fig. 5C, Table 5), but increased after buckthorn removal with no significant differences between removal and uninvaded references in year 1 and year 2 after removal. The number of vegetative hummocks was significantly greater on all dates in the uninvaded replicates than either the invaded or removal, and there were significant differences by year on this metric, with more in both the invaded and removal treatments in year 1 and year 2 than pre-restoration (Fig. 5D, Table 5).

Plant community characteristics

We observed varying responses of the plant community to fen restoration. Percent herbaceous cover was significantly greater in uninvaded reference plots than invaded plots on all dates (Fig 6A, Table 6). Herbaceous cover increased rapidly in removal plots, becoming equivalent to reference plots by year 2. The floristic quality index per m^2 was significantly greater on all dates in the uninvaded plots, with no significant treatment differences between invaded and removal treatments (Fig. 6B, Table 6). The index was significantly greater in year 1 and 2 than pre-restoration. There were no significant differences in Simpsons diversity index by treatment, but there were significant differences in D by year, with the greatest values in year 2, followed by year 1 and pre-restoration (Fig. 6C, Table 6). The Berger Parker index of dominance was greatest pre-restoration, followed by year 1, with significantly lower plant dominance in year 2 than pre-restoration (Fig. 6D, Table 6). The index was numerically lower in uninvaded reference areas, with the value in removal areas decreasing over time. The proportion of graminoid (Poaceae, Cyperaceae, and Juncaceae) cover was significantly greater in uninvaded reference than invaded plots before treatment establishment and remained significantly lower in invaded plots (Fig. 6E, Table 6). Graminoid cover increased in removal plots in years 1 and 2 (Fig. 6E). Finally, proportion of exotic cover was significantly greater in invaded and removal plots versus reference areas pre-restoration and remained significantly higher in invaded and removal plots through year 2 (Fig. 6F, Table 6), although there was a numeric decrease in cover in restored plots.

An NMDS analysis that included all of the resources and plant factors above, as well as percent bare ground and soil Ca and Mg, revealed a shift in treatments over time. Before restoration, *F. alnus* invaded and removal plots were similar to each other and significantly different from reference plots (Fig. 7A, Table 7). In year 1 the removal plots began to shift toward reference plots, with significant differences between all treatments (Fig. 7B, Table 7). In year 2 post-restoration, the level of similarity continued to decrease between the invaded and removal treatments (Fig 7C). Stress values for the 2-dimensional plot were under 0.1 in all years, indicating that these figures accurately represent the relationship between points.

Discussion

Shifts in resource availability that occurred with habitat degradation may alter the course of habitat restoration, but exactly how resources shifted with degradation is rarely known. Incorporating measurements of resource availability with plant community metrics post-restoration allows for better assessment of potential limiting factors for restoration, and has potential to alter the course of restoration efforts. In this study, we found that plant community structure recovered rapidly with removal of invasive *F. alnus*, while plant diversity and resource availability did not. Specifically, total herbaceous cover and proportion graminoid cover rapidly rebounded to near or above reference levels in restored plots. In contrast, there was no evidence for change in soil microhabitat or nutrient availability, with most factors not different initially between invaded and uninvaded plots. We also found no significant change in plant diversity; however, we did observe rapid increases in light availability and plant structural response. Examination of all factors combined (NMDS) showed that after the first growing season, restored areas were distinct from invaded areas and continued to shift towards reference conditions in the second growing season, suggesting that restored areas are on an initial trajectory toward conditions found in the uninvaded reference plots. Individual metrics, however, may take longer to recover, if at all.

Resource Availability

We measured soil nutrients and microhabitat availability, as well as light availability, as a result of restoration, but found significant differences only in light availability. This manifested as an immediate shift in light availability at 1m height after restoration activities. This is not surprising, given that *F. alnus* provided nearly full shade in densely invaded areas. This finding indicates that current prairie fen restoration practices are effective at restoring this key resource for the herbaceous plant community. However, many wetlands in North America are also limited by nitrogen or phosphorous availability (Bedford et al. 1999). There were no initial differences in soil nitrate, ammonia, potassium, or phosphorous levels between *F. alnus* invaded and uninvaded areas, and no changes by treatment emerged in the first two years after restoration. This finding was contrary to our hypothesis that soil nutrients would differ by treatment over time. It may be that the groundwater inputs continue to supply these nutrients or that they simply shift more slowly than our 2-year timeframe. Wetland eutrophication is a persistent concern in Europe (Bakker and Berendse 1999) and a growing one in the U.S., especially near urban areas where greater nitrogen levels are associated with greater non-native plant cover (Matthews et al. 2009b). Agriculture is another source of nutrient input, either via overland flow or groundwater infiltration (Drexler and Bedford 2002). These potential patterns point to the need for long-term monitoring of soil resources after wetland restoration.

Results of soil pH and microhabitat support our hypothesis that neither would change over the timeframe of this study. Soil pH was markedly lower in *F. alnus* invaded areas before restoration and remained lower in removal areas in the first two years after *F. alnus* removal. Either *F. alnus* is more readily able to invade areas with pH near neutral or it is causing shifts in alkaline soil pH toward neutral over time. Related species are known to shift soil pH, although not necessarily in the same direction: invasion of related *R. cathartica* has been associated with increases in soil pH in uplands (Heneghan et al. 2006). We also found significantly fewer vegetative hummocks in *F. alnus* invaded areas, both before and in the two years following restoration. These hummocks of undecomposed sedge litter are known to provide suitable microhabitat for plants with a variety of moisture and light tolerances, and are one mechanism for supporting high plant diversity in prairie fens (Peach and Zedler 2006). Degraded hummocks may take tens or even hundreds of years to re-form (Zedler 2000) so this shift is likely to remain in the long term in areas of prairie fen where mature *F. alnus* was established. Invasive species may be drivers leading to change or may enter a system subsequent shifts in it (MacDougall and Turkington 2005). While we do not have causal evidence for shifts in pH and microhabitat resulting from *F. alnus* invasion, we do not have any reason to believe there are systematic differences between the reference and invaded areas in either of these factors.

Plant Community Structure and Diversity

We found that herbaceous plant cover in restored areas rapidly recovered to levels similar to those in uninvaded references. The proportion of graminoid cover in restored areas also appeared to recover in the first year following restoration and decreased in the second year, likely due to a greater increase in perennial forb cover. The proportion of herbaceous exotic cover was initially significantly greater in invaded than in reference plots and remained greater in removal plots, but numerically decreased over time. Contrary to our hypothesis, there were no significant shifts by treatment in plant diversity metrics during the first two years following restoration. We did observe an increase in the floristic quality and Simpsons diversity indices over time and a decrease in plant dominance; however, these patterns are likely due to repeated sampling, increasing the likelihood of finding easily overlooked species. While we did not find significant differences by treatment in Simpsons diversity and plant dominance, the floristic quality index was significantly greater in uninvaded reference plots than either the *F. alnus* removal or invaded plots.

Similar patterns in plant cover have been found in other wetland restorations. In 76 constructed and restored wetlands, the goal of minimum percent plant cover was more frequently met than goals regarding overall plant structure or nativeness (Matthews and Endress 2008). In contrast to our findings, the floristic quality index also increased rapidly in these restorations, which included seed additions and was calculated on a site-wide basis rather than in m^2 plots (Matthews and Endress 2008). Even mined peatlands with the surface peat removed have been shown to revegetate rapidly with seed additions (Cobbaert et al. 2004). Prairie fen restorations focused on invasive species control do not typically include seed addition. Our study provides evidence that seed addition is unnecessary to regain herbaceous plant cover in this type of habitat. If, however, the floristic quality index in *F. alnus* removal areas doesn't begin to move on a trajectory toward that in the uninvaded areas within 5 years of clearing, seeding or planting of key species might be required. The native species pool in wetlands has been found to be landscape-limited (Matthews et al. 2009a), pointing to the low likelihood of propagules entering isolated prairie fen systems without assistance if they do not remain in the seedbank at a site.

We found evidence that in the methods typically used to restore prairie fens invaded by non-native *F. alnus* were successful in the short-term. The long-term success of prairie fen restorations, however, will depend on a number of factors. Further plant succession will be determined in part by the longevity and species present in the soil seed bank, which may be limited at the landscape, rather than local, scale. Additionally, plant community metrics of wetland restoration success may improve over the short term, then decrease over the longer term (Matthews et al. 2009c). There is evidence for greater seed production in more disturbed fen communities, with few plant species producing the majority of seeds (Klimkowska et al. 2009), thereby limiting the number of plant species that can arise from the seed bank itself.

Through the use of uninvaded references at the same site, we have evidence that a number of factors are on a trajectory toward that in the reference areas. The use of references in restoration provides metrics against which restoration success may be measured (Brinson and Rheinhardt 1996, SER Working Group 2004) but there are difficulties inherent in finding sites that match the exact conditions expected in a restored area (White and Walker 1997). This is of particular relevance in prairie fens, which contain regionally variable plant species (Amon et al. 2002) several plant subcommunities, and the potential for shifts in the entire plant community across a single fen (Bowles et al. 2005). One of the three references in our site, in particular, differs in soil characteristics and is characterized as a marl flat subcommunity, while the remaining two references and the areas invaded by *F. alnus* are characterized as sedge meadow. Although the marl flat reference is useful in considering plant characteristics broadly, we do not expect that *F. alnus* removal areas will move toward conditions in that reference in the long term, unless they occur in a specific area of mineral-rich groundwater upwelling.

Long-term Restoration Success

Invasive species management is a continued concern in many restorations. Invasives have become increasingly common in wetlands since the 1970's (Bowles and Jones 2006). We do not know the exact history of invasion at the study site, but photos from the 1930's show it as a sedge-dominated community and *F. alnus* may have been present at this site for upwards of 60 years. Propagules for *F. alnus* remain in the seed bank, and other invasives, including *P. arundinaceae*, *Typha* sp., and *L. salicaria*, are all present at the site. In addition to occurring locally, these species are now part of the regional species pool and can readily be brought to the site by wildlife and humans. To prevent re-invasion of non-native species, both the local and regional species pool will need to be managed (Matthews et al. 2009b) in the long term or expectations for successful restoration may need to shift to include patches of non-native invasives. North American prairie fens are historically fire-adapted systems (Curtis 1971) and re-introduction of periodic, patchy fire (Williams 2000) has been shown to help remove litter buildup and maintain species diversity in fen communities (Middleton et al. 2006) and other wetlands (Bowles and Jones 2006). Once sedge and grass material have begun to grow in prairie fens after *F. alnus* removal, fire is part of the long-term management scheme for fen restoration, and it helps prevent re-invasion of *F. alnus*, which is not fire tolerant.

Despite restoration of the historic disturbance regime, some changes in previously invaded prairie fen may lead them to alternative stable states (Suding et al. 2004). We found evidence that soil structure and pH are altered in prairie fens; each of these factors is likely to change only over long periods of time, and may make restoration more difficult (Zedler 2000). Our study reinforces the need to measure multiple metrics across trophic levels in assessment of restoration success (Ruiz-Jaen and Aide 2005). If we had measured only plant structure, we would have classified this restoration as a success, and would not have had evidence pointing toward longer-term microhabitat and plant diversity changes in this ecosystem. We have performed top-down removal of invasive species, but have not addressed possible bottom-up factors that could shift the plant community in the long term (D'Antonio and Chambers 2006). One solution to nutrient-based alternative stable states is to put greater inputs into a system for a greater amount of time, in hopes of shifting community dynamics. However, this approach has had little evidence of long-term success (Lindig-Cisneros et al. 2003, Corbin and D'Antonio 2004).

Finally, while we found evidence of conditions in restored plots moving in the direction of those in references, there are a number of considerations in measuring the long-term success of restoration. Novel approaches to restoration which involve changes that are not part of the historic disturbance regime may be required to shift the restoration toward the goal and away from an alternative stable state (Firn et al. 2010). In this case, continued site-wide *F. alnus* removal and management will be required to ensure the persistence of prairie fen. The research site currently is an ideal area for performing adaptive restoration research (Hobbs and Harris 2001, Zedler and Kercher 2005), and management practices into the future could include novel, lower input methods to support plant diversity.

Implications for practice

- Best practice methods used for invasive species removal and control of prairie fen wetlands were successful in the short-term.
- Mid- and long-term restoration success will likely be based on continued invasive control.
- Rare and special concern plant species may require seeding/planting if the local species pool cannot provide these sources.

Acknowledgements

We would like to thank G. Kowalewski, J. Curtis, M. Trimmer and J. Vigneron from MSU forestry, R. Zuniga-Villegas and D. Tison of The Nature Conservancy and the Landis Lab, especially C. Sebolt, for help with plot establishment. We greatly appreciate the field assistance provided by C. Phillippo and M. Lettow. A. Reznicek and R. O'Connor assisted with plant specimen identification. P. Doran, R. Isaacs, and C. Malmstrom reviewed and helped improve this manuscript. Research funding was provided by the MSU MacCready Endowment and National Fish and Wildlife Foundation. Funding support for A.K.F. was provided through a sustainable agriculture

predoctoral fellowship by the C.S. Mott foundation and a MSU Barnett Rosenberg predoctoral fellowship in biological sciences.

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Table 5. Differences in resource availability between invaded, removal, and uninvaded treatments pre-restoration and year 1 to 2 post-restoration (September 2007, 2009, and 2009, respectively). Significant p-values (α=0.05) are bolded. Treatment*time interactions not shown if neither treatment nor time were significant.

Factor		Treatment		Time		Treatment * time	
		F	**P**	**F**	**P**	**F**	**P**
Light availability	% full sun at 1 m~	47.6	**<.001**	11.9	**<.001**	8.9	**<.001**
Soils	pH	15.7	**0.001**	0.5	0.585	0.3	0.905
	NH_4 (ppm)	2.5	0.126	13.4	**<.001**	2.5	0.068
	NO_3 (ppm)~	0.7	0.500	8.1	**0.001**	0.9	0.486
	Phosphorous (ppm)^	2.2	0.153	0.2	0.808	-	-
	Potassium (ppm)	0.5	0.612	9.8	**0.001**	0.7	0.599
	% organic matter	1.4	0.278	0.6	0.548	-	-
Microtopography	# hummocks /$m^{2\sim}$	13.3	**0.001**	5.8	**0.009**	3.2	**0.031**

~ Log(x+1) transformed data used for ANOVA analysis.

^ Square root transformed data used for analysis.

Table 6. Differences in plant community metrics between invaded, removal, and uninvaded treatments pre-restoration and year 1 to 2 post-restoration (September 2007, 2009, and 2009, respectively). Significant p-values (α=0.05) are bolded.

Factor	Treatment		Time		Treatment * time	
	F	P	F	P	F	P
% herbaceous cover	22.9	**<.001**	40.0	**<.001**	19.8	**<.001**
Relative graminoid cover*	25.7	**<.001**	1.3	0.301	3.5	**0.023**
Relative exotic cover*	6.11	**0.003**	0.8	0.452	1.8	0.125
Plant species richness	32.6	**<.001**	70.0	**<.001**	8.8	**<.001**
Mean C∞	16.6	**0.001**	1.3	0.28	0.5	0.772
Floristic quality index	39.7	**<.001**	20.8	**<.001**	1.6	0.190
Simpsons D^	2.9	0.098	9.5	**0.001**	1.8	0.132
Berger-Parker dominance	1.7	0.219	5.4	**0.005**	1.3	0.263

* Square root arcsine transformed data used for analysis.

^ Square root transformed data used for analysis.

∞ Coefficient of conservativeness on a scale of 1 to 10.

Table 7. ANOSIM based on similarity matrix by time. All resource factors and plant factors presented in tables 1 and 2 included, plus % bare ground, soil Ca and Mg. Significant p-values are bolded. R ranges up to 1, a value closer to 1 indicates greater between treatment differences.

Time	**Overall Test**		**Invaded: Removal**		**Invaded: Reference**		**Removal: Reference**	
	R	**P**	**R**	**P**	**R**	**P**	**R**	**P**
Pre restoration	0.31	**0.017**	-0.07	0.693	0.92	**0.036**	0.92	**0.036**
Year 1	0.50	**0.001**	0.27	**0.043**	0.88	**0.012**	0.67	**0.012**
Year 2	0.66	**0.001**	0.58	**0.002**	0.96	**0.012**	0.79	**0.012**

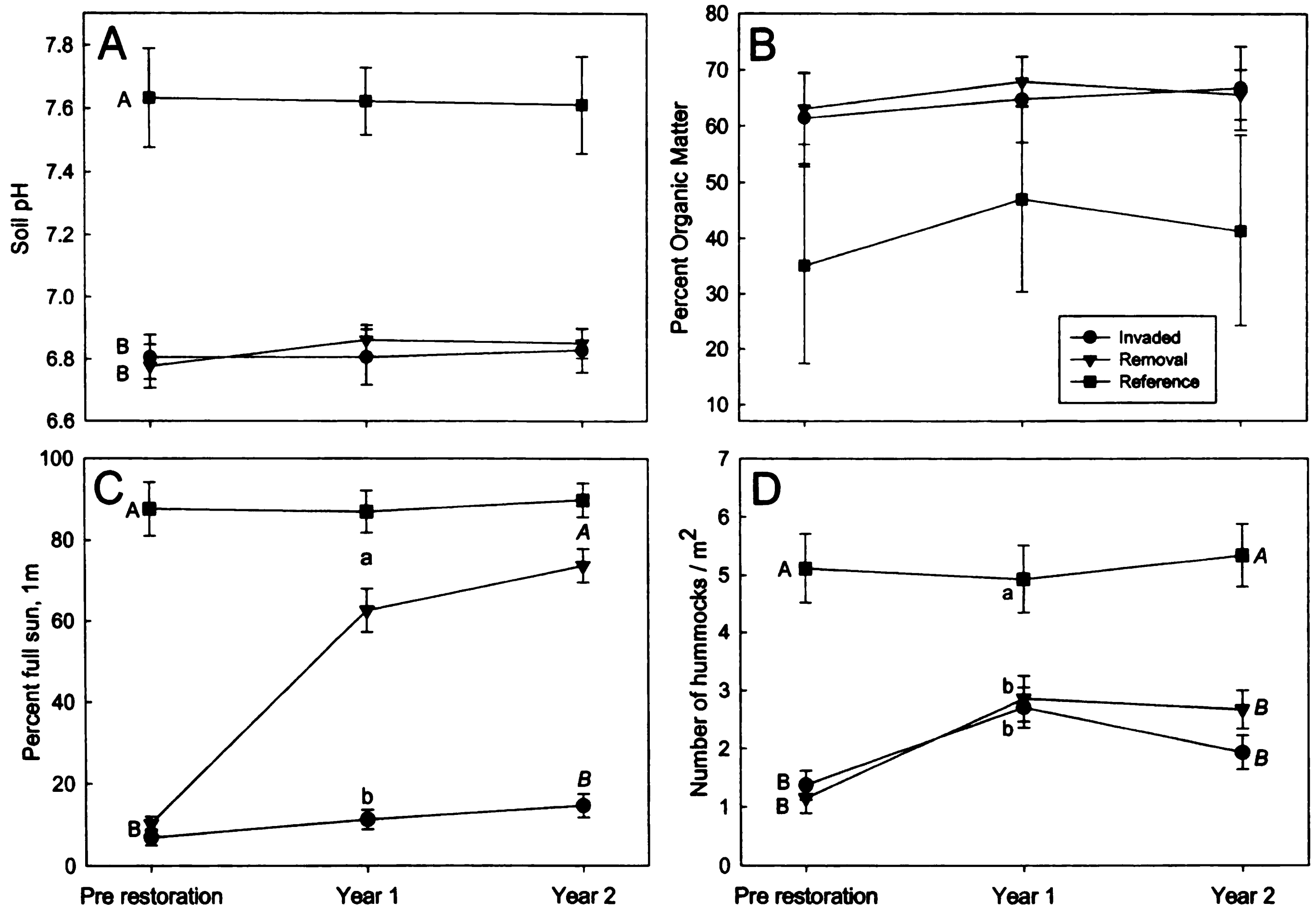

Figure 5. Comparisons of soil resource availability, light and microhabitat between *F. alnus* invaded, removal, and uninvaded plots. Error bars are +SEM, α=0.05. Where treatment or treatment*time were significantly different using LS means separations, letters of significance are shown.

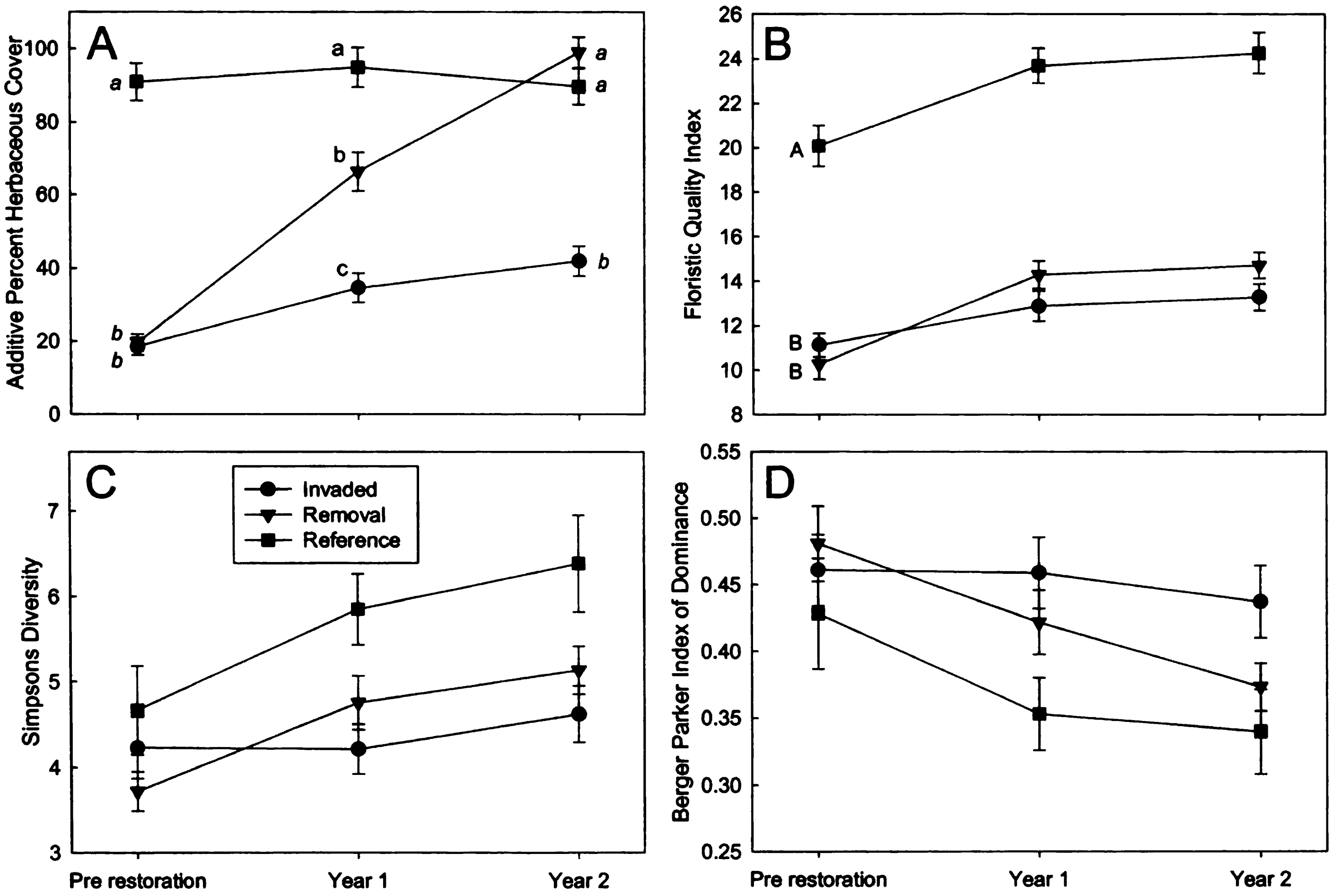

Figure 6. Comparisons of plant metrics between *F. alnus* invaded and uninvaded plots. Error bars are +SEM, α=0.05. Treatment effects from a 2-way ANOVA with treatment and transect are shown. Additive herbaceous cover represents the sum of individual plant species cover/m^2 plot. Where treatment or treatment*time were significantly different using LS means separations, letters of significance are shown.

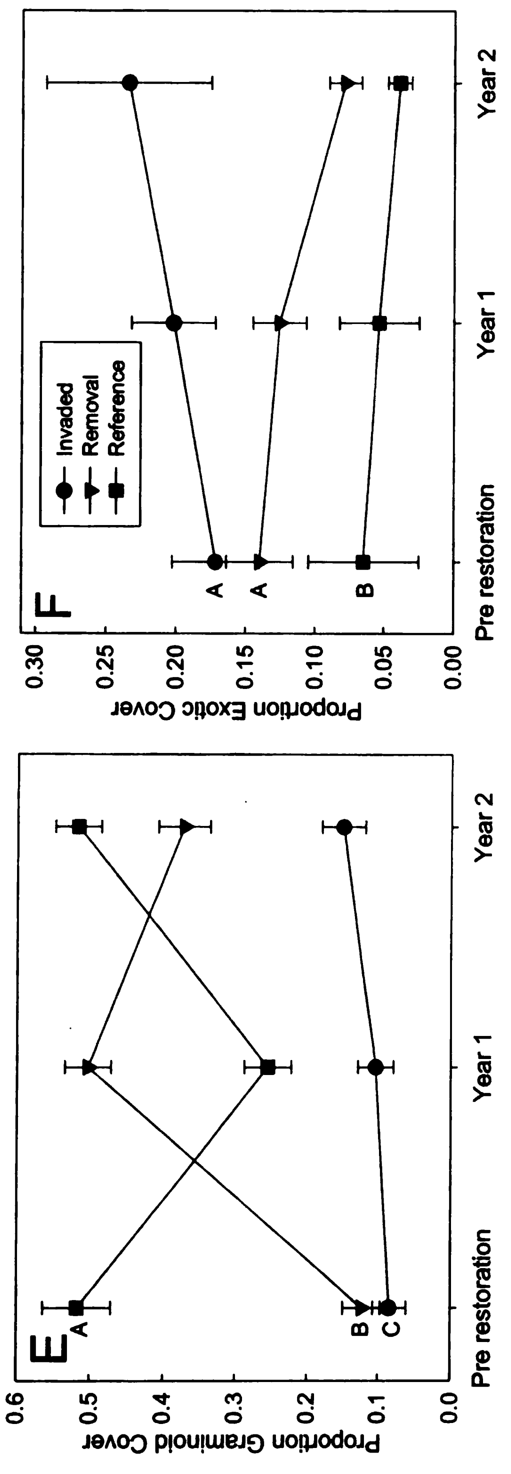

Figure 6 cont'd.

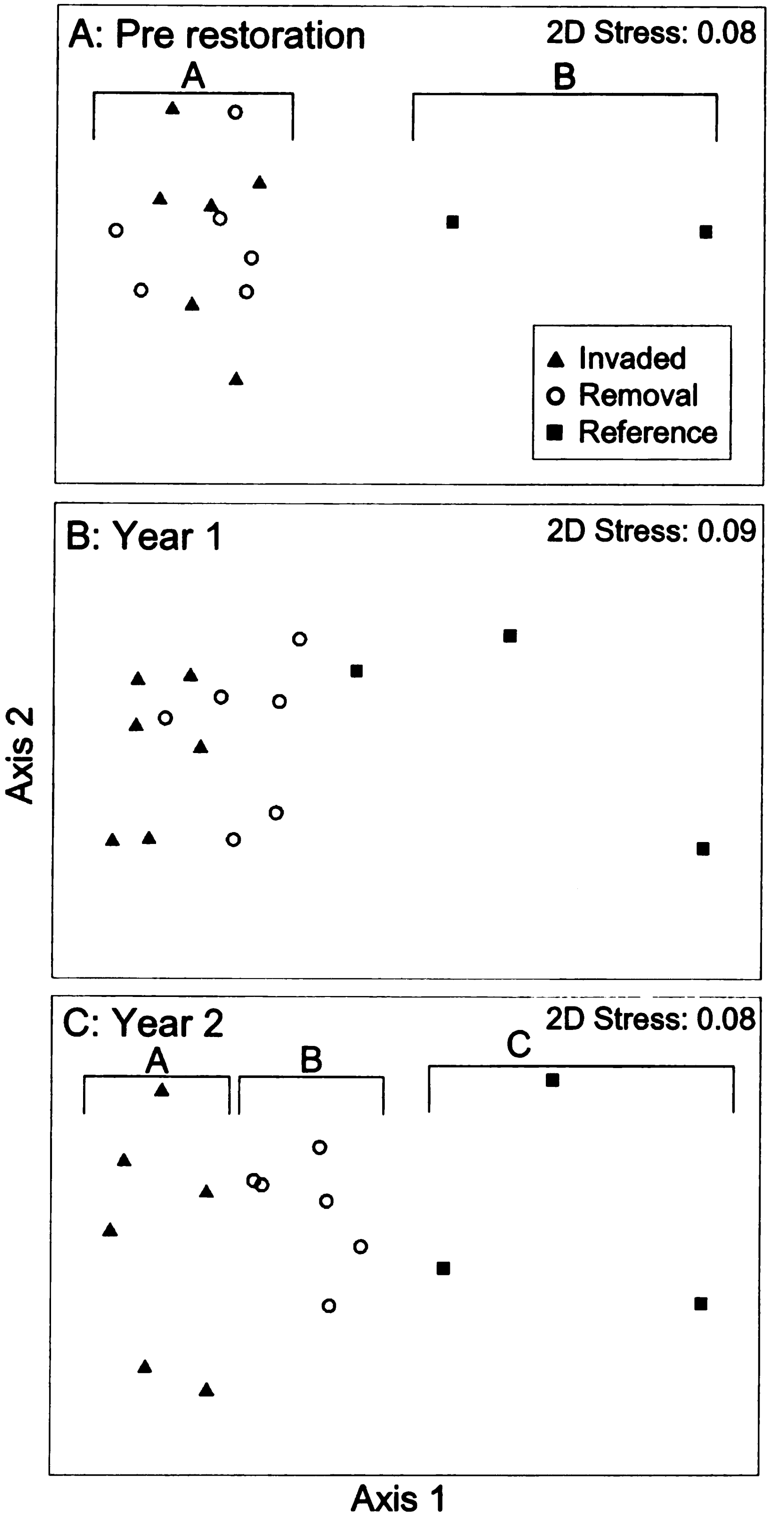

Figure 7. Two dimensional NMDS plots based on a mean of each resource and plant metric by treatment and replicate using the Euclidian dissimilarity index. There were two reference plots pre-restoration; a third was added before year 1. Pre-restoration and year 2 statistical differences by treatment are shown with letters.

Chapter 4

For Restoration Ecology

INVASIVE SPECIES REMOVAL LEADS TO RAPID RECOVERY OF POLLINATOR COMMUNITIES IN PRAIRIE FEN

Anna Katherine Fiedler

Abstract

Habitat restoration is increasingly used to reverse degradation of rare ecosystems and maintain biological diversity. In the face of increasing concerns about overall biodiversity decline, and specifically pollinator loss, we ask whether restoration of a prairie fen wetland increases plant and pollinator diversity. Here, we compare herbaceous plant, bee, and butterfly abundance, diversity, and species composition in prairie fen invaded by glossy buckthorn (*Frangula alnus*), in restored areas where glossy buckthorn was removed, and in uninvaded reference areas. We found striking differences between invaded and uninvaded prairie fen in pollinator abundance and species composition. Plant species diversity and composition in restored plots were significantly different than invaded plots two years after restoration, but also remained significantly lower than reference plots over this time period. In contrast, bee and butterfly abundance, diversity, and composition were similar in restored and reference plots, and distinct from invaded plots, in the second growing season following restoration. Our findings indicate that a diverse community of mobile generalist pollinators rapidly re-colonizes restored areas, while the plant community may take longer to recover. This work implies that, in areas with intact pollinator metapopulations, restoration will likely prevent further loss of mobile generalist pollinators. On the other hand, targeted efforts will likely be required to restore populations of rare insects.

Keywords: conservation, restoration, pollinator, prairie fen, plant community.

Introduction

In recent years, concerns about losses of pollinator diversity have mounted. Bees have long been considered important crop pollinators (Klein et al. 2007), but their importance in natural areas is also increasingly recognized (Potts 2010, Winfree 2010), and pollinator losses extend beyond the managed honeybee, *Apis mellifera* L., to key native pollinator groups, e.g. *Bombus* sp. (Goulson et al. 2008). There are likely multiple drivers of pollinator diversity loss, including land-use change, introduction of non-native plants, pollinators, grazers, and pathogens, altered hydrology, and climate change (Kevan 1999, Potts 2010). The primary threat to bee diversity is habitat loss, with invasive species, parasites, and disease as secondary factors (Brown and Paxton 2009). Because pollinators and wild plant populations are tightly linked, pollinator declines and extinctions have the potential to result in trophic cascades that affect plant diversity. About 90% of angiosperms are animal pollinated (Nabhan and Buchmann 1997) and over 60% of plant species are dependent on pollination by insects for maximal fruit and seed set (Burd 1994, Ashman et al. 2004). Concomitant, large-scale declines have been found in pollinator abundance and insect-pollinated plant diversity pre- versus post-1980 in England and the Netherlands (Biesmeijer et al. 2006). With multiple lines of evidence for losses in both plants and pollinators, maintaining species diversity and pollination is an increasing priority for the long-term persistence of rare communities and habitats.

The use of habitat restoration to reverse losses of rare communities and the species within them is rising. One of the primary goals of ecosystem restoration is to increase diversity within protected areas (Hobbs and Norton 1996, SER Working Group 2004). Ecosystems are considered restored when the structure, function, and composition are returned to a goal state, often based on historic conditions (SER Working Group

2004). The effect of restoration on plant species diversity is relatively well-documented (Ruiz-Jaen and Aide 2005) and plant conservation is well-represented in scientific studies (Clark and May 2002). However, the effects of restoration on the pollinator community are less well known.

Because pollinators are infrequently considered in restoration, we do not know whether typical restoration activities prevent further pollinator species losses, and there is concern that they do not (Dixon 2009). Two insect groups, bees and butterflies, play an important role in maintenance of pollination and species diversity. Bees are a species-rich group, and the dominant group of pollinators in many regions (Williams et al. 2001). They are well known for their prevalence as effective pollinators of both crops and wild plants (Kearns et al. 1998). Butterflies comprise a well-known, charismatic group of invertebrates and some may be effective umbrella species for conservation whose protection may lead to protection of other species (New 1997). Because butterflies are herbivorous as larvae and nectivarous as adults, they provide a potential link between ecosystem functions of herbivory and pollination (Waltz and Covington 2004). In addition, butterfly species range from specialists to generalists, and are known to recover rapidly following restoration (Waltz and Covington 2004). Finally, in the Midwestern U.S., butterflies and skippers form the most prevalent group of insects that are strongly dependent on remnant savanna and prairie ecosystems (Panzer et al. 1995).

In the Midwestern U.S., there is a relatively high frequency of globally rare prairie fen wetlands. These ecosystems contain extremely high species diversity in small, isolated patches, and are threatened by the same factors affecting species diversity globally, (Spieles et al. 1999, Amon et al. 2002, Bedford and 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 plant species and 25 insect species, 4 of which are butterflies (MNFI 2007). Many of the fens in the Midwest are degraded, primarily by invasive species and changes to hydrology. Restoration activities in prairie fen frequently involve removal of invasive species, but the effect on pollinators and the plants on which they depend has not been studied.

Measuring changes in plants and insects is important to gain an understanding of whether restoration activities lead to restoration of pollinator communities. In addition, patterns in prairie fen provide an indication of what is likely in other restored ecosystems. We examined plant and pollinator response to removal of invasive *Frangula alnus* L. (glossy buckthorn) from a prairie fen wetland in Michigan, USA. Our goal was to examine the effect of restoration on the diversity, abundance, and community of both plants and pollinators in the first two years of a long-term restoration project. We hypothesized that under restoration treatments 1) forb abundance and plant diversity would increase and 2) bee and butterfly abundance and diversity would increase, with the community becoming distinct from that in invaded plots but remaining distinct from uninvaded plots. We also predicted that plant and pollinator communities would not reach reference community states within this short time period.

Methods

Experimental design

We conducted this study in a prairie fen at the Michigan State University MacCready Reserve in Clarklake, Liberty Township, Jackson County, Michigan. In

25x25 m plots, we cleared invasive *F. alnus* from 6 replicate plots, left *F. alnus* in 6 replicate plots, and delineated three 25x25 m uninvaded reference areas (Chapter 2). We cleared *F. alnus* in February 2008, following best management practices (The Nature Conservancy, R. Villegas pers. comm.) of cutting and treating *F. alnus* stumps with herbicide (glyphosate 25% AI, Rodeo, Monsanto, St. Louis, MO) with Cide Kick II surfactant, adjuvant, and penetrator (Brewer International, Vero Beach, FL), and stacked brush piles outside of sampling areas (Chapter 2). Brush was burned in early spring 2009. During the 2008 and 2009 growing seasons, we applied foliar herbicide to *F. alnus* re-sprouts, *P. arundinacea* L., *Rosa muliflora* Thunb., and *Cirsium arvense* (L.) Scop., and cut and treated cut stems of *Typha* sp. and *Populus tremuloides* Michx. within restored plots.

Sampling

During the 2008 and 2009 growing seasons, we assessed plant diversity and cover in 9 m^2 quadrats laid out on a grid within each plot (Chapter 2) three times during the growitng season: 2-6 June 2008, 1-5 June 2009, 25-30 July 2008, 29 July-6 August 2009, 5-8 Sept. 2008, and 9-11 Sept. 2009. We identified and estimated percent cover of each monocot, forb, and shrub less than 1.5 m height that was rooted within each quadrat.

We sampled pollinators using two methods, observational sampling and pollinator bowl traps, monthly from June-September 2008 and 2009 (12 June, 8 August, 6 Sept. 2008 and 4 June, 3 July, 5 August, and 31 August 2009). Both techniques were performed on the same day, in sunny, calm weather, when insects are most likely to be active. We performed pollinator observation between 10am and 3pm EST. On each date, two people stood back to back in the center of each replicate plot. Upon arrival at the location, observers waited 1 minute, noting plant species blooming within 2 m of the sample point. Each then observed all bees and butterflies that entered a 2 m radius half circle around them for 5 minutes (10 minutes in June 2009), identifying all pollinators in the sampling area within that time to genus and, when possible, collecting unknowns for identification. Although small pollinators are less likely to be detected using this technique we did observe small bees including *Hylaeus* and *Lasioglossum* sp. using this method.

Pollinator traps consisted of 3.25 oz. white cups (Solo Cup Company, Lake Forest, IL). One third of the cups were painted blue fluorescent, and one third were painted yellow fluorescent (Guerra Paint and Pigment, New York, NY, Droege 2010). We placed two traps on opposite sides of all 9 plant quadrats per replicate, with starting cup color randomized on each date and color alternating in the order: blue, white, yellow. Cups were placed within 40 cm of the quadrat on the ground in locations where they were not obscured by low growing vegetation. Each cup was filled 1/3 full with soapy water (Droege 2010) and placed in the field between 8-10am. Cups were removed in the same order they were placed in the field, from 4-7pm on a given sampling day, soap water was strained out, and all insects were strained into ethanol into samples pooled by replicate. All bees and butterflies were removed from samples, 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. In all cases season-long means were calculated by sampling date and replicate of each treatment. Pollinator abundance during the 10-minute sampling period in June 2009 was divided by 2 to make this sampling effort comparable with those on other dates. Bees in pollinator bowls were summed per replicate on a given date. We used Simpsons diversity of each plants, bees, and butterflies as a metric representing both species richness and evenness, using $D=1/\sum(p_i)^2$ where p_i is the proportion of cover of the *i*th plant species per quadrat or the abundance of a pollinator (Magurran 2004).

To investigate differences in plant and pollinator abundance and Simpsons diversity, we performed 2-way 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, and we used Satterthwaite adjusted degrees of freedom to account for the unequal number of replicates between treatments (Satterthwaite 1946).

To examine community-level shifts in plant, bee, and butterfly abundance with 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 and Keough 2002). In the case of insect abundances, a "dummy variable" of 1 was added to all values, so that treatments and replicates with zero insects stayed in the analysis. We used nonmetric multidimensional scaling (NMDS) to visualize the differences by treatment and year on community metrics. The NMDS ordinates data by ranking variables so that the closer their location is in 2 or 3 dimensional space, the more similar they are. We performed the NMDS with 2 and 3 dimensions, 25 random starting configurations and a minimum stress of 0.01 (Clarke and Gorley 2006a). All stress values for 2-dimensional figures were 0.14 or less. Values under 0.10 indicate that 2-dimensional representation is an accurate representation of the relationship between points. Values from 0.10 to 0.20, while still representative, will not likely accurately show the small-scale relationships between points (Clarke and Gorley 2006b). 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 and Gorley 2006b). Overall tests were significant in all cases, so pairwise tests were appropriate and are reported herein.

Results

We observed rapid changes in plant and pollinator abundance, diversity, and communities within the first two years of restoration. We examined forb cover as an indicator of potential flowering resources for pollinators. There was significantly greater percent forb cover in removal and reference plots than in invaded plots in both year 1 and year 2 (Figure 8A) (P=0.011, F $5.4_{2,25.3}$), with no significant difference by year (P=0.072, F $3.6_{1,23.2}$) or treatment by year (P=0.275, F $1.4_{2,23.2}$). Plant diversity also shifted in the first two growing seasons following restoration, but not as completely. We found significant differences by treatment in season-long Simpsons diversity of all plants less than 1.5m tall (P=0.013, F $31.9_{2,11.6}$), with significantly greater diversity in uninvaded reference plots than removal plots, and significantly greater diversity in removal plots than those that remained invaded by buckthorn. There were no significant differences in plant diversity by year (P=0.085, F $3.0_{1,141}$) or treatment by year (P=0.32, F $1.1_{2,141}$).

An NMDS ordination of the plant community indicated a shift in the overall community following restoration (Figure 9). In year 1, there was no significant difference between the plant community of removal and buckthorn invaded plots (R 0.17, P=0.123) while by year 2, removal and invaded plant communities were significantly different (R 0.5, P=0.002). In both years, there were significant differences between the invaded and reference plant communities (Year 1: R 0.86 P=0.012, Year 2: R 0.82 P=0.012) and the plant community in removal plots remained significantly different than that in reference plots through year 2 after restoration (Year 1: R 0.71 P=0.012, Year 2: R 0.83 P=0.012) (Figure 9). A number of shade-tolerant species were more common in invaded areas; forbs included *Circaea lutetiana, Symplocarpus foetidus, Rosa multiflora,* and *Viola nephyrophylla* (Table 8). A second group of disturbance tolerant species were more common in recently restored areas, including monocots *Carex bebbii, C. hystericina, C. stipata* and *Leersia oryzoides* and forbs *Bidens frondosa, Epilobium coloratum, Erechtites hieraciifolia, Eupatorium perfoliatum, Senecio aureus, Solanum dulcamara*, and *Pilea pumila* (Table 8). A number of species remained far more abundant in uninvaded areas, including monocots *Calamagrostis canadensis, Carex stricta, C. tetanica, Muhlenbergia glomerata, Schizachyrium scoparium, Scirpus acutus, S. americanus,* and *Sorghastrum nutans*, as well as forbs *Aster lanceolatus, Eupatorium maculatum, Gentianopsis crinita, Hypoxis hirsuta, Lycopus americanus, Lysimachia quadriflora, Polygonum amphibium, Potentilla fruticosa, Rudbeckia hirta*, and *Zigadenus elegans*, and the fern *Thelypteris palustris* (Table 8).

Bee abundance and diversity shifted rapidly and more completely with restoration than the plant community. Bee abundance based on observational sampling was significantly different by treatment ($P<0.001$, F $32.8_{2,12}$), year ($P=0.002$, F $15.8_{1,12}$), and treatment*year ($P=0.003$, F $10.1_{2,12}$), 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 (Figure 10A). In year 2, there were significantly more bees in removal than reference plots (Figure 10A). *Apis mellifera* dominated the bee community according to observational sampling, followed by *Bombus*, *Hylaeus*, and other Halictidae in year 1. In year 2, *Apis mellifera*, *Hylaeus*, and *Bombus* remained dominant groups, with a number of other genera represented by small numbers of insects (Table 9).

We used pollinator trap data to assess bee diversity at the species level. Diversity of bees was significantly lower in invaded than removal and reference plots in both study years (Figure 10B), with no significant differences between removal and reference plots. There were no significant differences in bee diversity by year ($P=0.91$, F $0.01_{1,24}$) or treatment*year ($P=0.12$, F $2.3_{2,24}$), but there were significant differences by treatment ($P=0.001$, F $12.4_{2,24}$). A number of bee species were represented by only one individual in both year 1 and year 2, with 31% (9 of 29) of species (range in abundance 1-24) and 46% (23 of 50) of bee species (range in abundance 1-84) represented by 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* sp. 2 was more abundant in reference plots in both years than in other treatments (Table 10). Several bee species were more abundant in removal plots in year 2 than in year 1, including *Ceratina* *calcarata/dupla, Augochlora pura, Augochlorella aurata*, *Lasioglossum Dialictus* sp. 2 and *Lasioglossum rohweri*.

Patterns of pollinator abundance between observational and pollinator trap data were similar with the notable exception that *Apis mellifera* and *Bombus* species were two of the most abundant groups observed, for a combined total of 51.2 and 49.1 of observed pollinating bees in year 1 and 2 after restoration. In contrast, these two groups comprised less than 4% of total pollinators collected with pollinator traps in both year 1 and 2.

An NMDS analysis of the bee community showed evidence of a shifting pollinator community within the first season following restoration (Figure 11). There were no significant differences in the bee community between the removal and reference plots (Year 1: R 0.15 P=0.19, Year 2: R -0.24 P=0.88), while the bee community in buckthorn invaded plots was significantly different than removal plots in both years 1 and 2 (Year 1: R 0.76 P=0.001, Year 2: R 0.63 P=0.004). Invaded and reference plots remained significantly different (Year 1: R 0.85 P=0.012, Year 2: R 0.39 P=0.036). Several of the most abundant pollinators were abundant in both sampling years, including *Ceratina calcarata/dupla*, *Lasioglossum Dialictus* sp. 2, and *Augochlora aurata* (Table 10). There were also several notable changes between years. *Lasioglossum rohweri* increased in relative abundance in year two. There was a nearly complete shift in Megachilidae species between years 1 and 2 so that species represented in year 1 were absent or nearly so in year 2, with others collected in year 2 (Table 10). In addition, a greater number of *Lasioglossum Dialictus* sp. and *Andrena* species were collected in year 2 than in year 1. The only species which decreased greatly in abundance between year 1 and year 2 was *Augochlora pura* (Table 10).

Butterfly abundance and diversity also shifted rapidly post-restoration. We found significant differences in butterfly abundance by treatment (P=0.005, F $8.4_{2,12}$) but not by year (P=0.35, F $0.1_{1,12}$) or treatment*year (P=0.32, F $1.3_{2,12}$). There were significantly fewer butterflies in invaded plots than other treatments in both study years, and no significant difference between removal and on-site reference plots (Figure 10C). There were significant effects on butterfly diversity by treatment (P=0.003, F $10.3_{2,12}$), year (P=0.021, F $7.1_{1,12}$), and treatment*year (P=0.041, F $4.2_{2,12}$). Butterfly diversity was significantly lower in invaded plots than in restored and uninvaded reference plots in both years, with no significant differences between restored and reference plots (Figure 10D). A number of butterfly species were singletons in both study years, with 45.5% (5 of 11) of species (range in abundance 1-22) and 40% (6 of 15) of species (range in abundance 1-15) 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 (Figure 12). The butterfly community in invaded plots was significantly different than that in the removal in years 1 and 2 (Year 1: R 0.44 P=0.02, Year 2: R 0.40 P=0.002). In year 1, removal and reference plots had similar butterfly communities (R -0.17 P=0.79), as did invaded and reference plots (R 0.50 P=0.083). No butterflies were collected in invaded areas, with a mean of 1±0.58 butterflies/5 minute sampling collected in uninvaded references. In year 2, the butterfly community was significantly different in invaded than both the removal (R 0.40 P=0.002) and reference (R 0.74 P=0.012) plots and was not different in removal versus reference plots (R 0.21 P=0.17). The only butterfly species seen in invaded plots was *Megisto cymela* (Table 11). 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*, *Poanes Massasoit*, and *Phyciodes tharos* were more abundant in reference than removal plots (Table 11).

Discussion

There are increasing concerns about ecosystem degradation and loss of the plants and pollinators within ecosystems. The assessment of flowering plant resources as well as pollinator diversity, abundance, and community recovery are vital to evaluating the long-term stability of pollinator populations in degraded and restored ecosystems. In this study, we examined plant and pollinator communities with restoration of prairie fen wetland, and found rapid responses in both species groups. We found distinctly lower abundance and diversity of plants, bees, and butterflies in areas of the fen invaded by *F. alnus*, while the plant and pollinator communities in restored areas shifted rapidly toward those in uninvaded reference plots. Our results indicate that, within two years of *F. alnus* removal, generalist pollinator community and diversity were restored in this ecosystem. In contrast, forb abundance, plant diversity, and the plant community in restored areas were intermediate between invaded and reference plots.

We did find 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 uninvaded 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. 2009c). Remnant ecosystems frequently have greater native plant species richness and diversity than restored or re-created systems (Polley et al. 2005, Shepherd and Debinski 2005). Even if the local plant community is manipulated, the plant species pool and quality are limited by landscape structure and mesoscale dynamics (Matthews et al. 2009a). For plants, regional pools also determine the likelihood of reinvasion by non-natives (Matthews et al. 2009b). This points to the potential need for management of regional plant species pools in restoration.

There may be multiple factors playing a role in the rapid insect response to restoration in this prairie fen. The primary one is likely the fact that areas of intact, uninvaded fen were within 300m of invaded areas, so that there were existing floral resources nearby at a scale within foraging distance for even the smallest pollinators we collected (Steffan-Dewenter et al. 2002, Greenleaf et al. 2007). 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 and Boeke 2006, Tuell et al. 2008) and landscape scales (Steffan-Dewenter and Tscharntke 1999, Steffan-Dewenter et al. 2002, Potts et al. 2003). For butterflies, availability of both nectar resources and larval host plants affect their distribution (Pywell et al. 2004).

While we did not measure floral resources directly in this study, we found that in restored areas, forb cover rapidly increased to levels similar to those in uninvaded plots. Inasmuch as percent cover of forbs may act as a proxy for floral resources this may indicate that floral abundance increased in restored areas. Light availability has been documented to affect butterfly abundance in other restorations with no changes in nectar plant species richness (Waltz and Covington 2004). Our previous work shows that light availability increased rapidly to reference conditions following removal treatments (Chapter 3). Butterflies are known to use habitat openings (Pollard et al. 1975) and butterfly richness is greatest in the open-structured phase of grassland clearing (Erhardt 1985). In Mediterranean systems, bee abundance of common species was greater in areas with more recent disturbance (Potts et al. 2003). In time, fewer pollinators may be found in restored fen plots if they are again encroached by shrubs and light availability decreases.

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 fact, all pollinator community metrics became similar to those in uninvaded fen within the first year following restoration. In our study, bee abundance in restored plots surpassed that in reference plots in the second year after restoration. We did not see the same pattern in bee diversity, however, indicating a potential maximum bee diversity was reached within a plot even as bee abundance continued to increase. Similarly, Ebeling et al. (2008) found a leveling off in pollinator species richness with plant species richness and floral area, but a continued increase in the frequency of pollinator visits to flowers.

In addition to resource density, habitat size and quality play a role in pollinator abundance and diversity. Habitat area influences which pollinator species use a patch. In calcareous grasslands in Europe, increased species richness of monophagous butterflies in calcareous grasslands with habitat area (Steffan-Dewenter and Tscharntke 2000) provide evidence that specialists may be more likely to find the resources they require in larger areas. Scale also affects wild, solitary bees at much smaller scales than bumble bees and honeybees (Steffan-Dewenter et al. 2002). Our study site includes a relatively small total area and many intact prairie fen wetlands are small, isolated communities; it would be interesting to see whether there is a relationship between the size of calcareous grasslands in North America and insect diversity, especially of rare species.

The regional species pool is also a key element of species diversity and abundance. In general, animals are more mobile than plants. However, fauna also have a range of responses to restoration due to differences in their mobility and habitat requirements, the presence of predators, and the rate of revegetation (Nichols and Nichols 2003). For more mobile flying insects, the regional species pool and quality of the landscape surrounding restored areas may also be key factors (Summerville et al. 2005). More mobile, common insects are likely to recolonize restored areas more rapidly than rare species. None of the six butterfly species of concern that inhabit prairie fens were found at our study site, despite the presence of small intact fen patches throughout the study area. For those species of concern, habitat suitability is clearly not the only factor determining their presence at a site, and larger scale restoration and connection of currently disparate metapopulations, or even assisted migration, may be necessary for rare species to inhabit this prairie fen and other restored areas.

Despite evidence of increased flowering plant and pollinator diversity and abundance following habitat restoration and the prevalence of generalization in pollination systems (Waser et al. 1996) we do not know whether the plant-pollinator interactions that lead to persistence of insect and plant diversity have been restored. Plant-pollinator communities may be successfully restored but species interactions may remain more complex on remnant than restored habitat (Forup et al. 2008). Different species may be carrying out pollination, with unknown long-term repercussions. For example, plant abundance and insect richness and abundance are restored in old field meadows, although the species comprising each system are distinct (Forup and Memmott 2005). In addition, pollinator, especially bee, communities vary in species composition and abundance by year (Williams et al. 2001, Petanidou et al. 2008). Patterns of bee abundance in our study matched that pattern; a large proportion of species collected in both years were singleton species. This means that longer-term studies of pollination will more likely assess the ability of plants and pollinator communities to persist in restored habitats. Insect pollinators may be required in the long term to maintain genetic variability in plant populations, as mobile insects can function as mobile link organisms, linking genetic material through pollination (Lundberg and Moberg 2003).

Our study indicates that, in a landscape with intact habitat patches, mobile insect abundance, diversity, and community were actually more rapidly restored than plant communities in the short term. At our study site, patches of degraded habitat were interspersed with patches of intact prairie fen, as well as neighboring undeveloped uplands. This landscape likely provided sufficient resources for the persistence of generalist pollinators (Winfree et al. 2009), which readily re-colonized restored areas. In an area without generalist pollinators, we would expect to see cascading effects on plant community diversity over time (Memmott et al. 2004). Finally, whether current restoration activities are sufficient for conservation of both plants and pollinators that are endemic to this habitat will need to be assessed over decades.

Implications for practice

- Current restoration best practices for prairie fen restoration are sufficient for restoration of the insect pollinator community in the short-term.
- Rare plants may require re-introduction and long-term monitoring to ensure their persistence in this habitat.
- Rare and endangered insects may require well-maintained corridors or even relocation assistance to enter this site in the medium-term, and continued monitoring will be required to assess long-term persistence.

Acknowledgements

C. Phillippo and M. Lettow provided invaluable field assistance. We are grateful to T. Reznicek for plant identification and B. DeMarco, J. Tuell and M. Nielsen for insect identification. Thanks to J. McCarthy for creating the bee, butterfly, and plant symbols. Research funding was provided by National Fish and Wildlife Foundation, the MSU MacCready Endowment, and a Hanes Trust Fellowship of the Michigan Botanical Society. Funding support for A.K.F. was provided through a sustainable agriculture predoctoral fellowship by the C.S. Mott foundation, a MSU Barnett Rosenberg predoctoral fellowship in biological sciences, and a MSU College of Agriculture dissertation completion fellowship.

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Table 8. Plant species identified at research site and the percent of quadrats each species occupied in year 2 (2009), 177 total. Bolded values are species whose frequency varied most by treatment, Inv=Invaded, Remo=Removal and Ref=Reference.

Family	Genus species	Common Name	C~	Native	Inv	Remo	Ref
Aceraceae	*Acer rubrum* L.	red maple	7	Y	27.78	37.04	29.63
Asteraceae	*Achillea millefolium* L.	common yarrow	0	N	1.85	1.85	0.00
Ranunculaceae	*Actaea rubra*	red baneberry	10	Y	1.85	0.00	0.00
Scrophulariaceae	*Agalinis purpurea* (L.) Pennell	purple false foxglove	6	Y	0.00	3.70	0.00
Rosaceae	*Agrimonia gryposepala* Wallr.	tall hairy agrimony	2	Y	0.00	0.00	3.70
Rosaceae	*Agrimonia parviflora* Aiton	harvestlice	7	Y	5.56	7.41	7.41
Poaceae	*Agropyron trachycaulum* (Link) Malte ex H.F. Lewis	slender wheatgrass	8	Y	0.00	0.00	3.70
Fabaceae	*Amphicarpaea bracteata* (L.) Fernald	American hogpeanut	4	Y	12.96	12.96	14.81
Poaceae	*Andropogon gerardii* Vitman	big bluestem	5	Y	0.00	0.00	11.11
Fabaceae	*Apios americana* Medik.	groundnut	7	Y	3.70	11.11	0.00
Araceae	*Arisaema triphyllum* (L.) Schott	jack in the pulpit	4	Y	7.41	1.85	0.00
Asclepiadaceae	*Asclepias incarnata*	swamp milkweed	4	Y	1.85	12.96	25.93
Asclepiadaceae	*Asclepias syriaca*	common milkweed	0	Y	1.85	0.00	0.00
Asteraceae	*Aster lanceolatus* Willd.	white panicle aster	3	Y	0.00	5.56	**55.56**
Asteraceae	*Aster puniceus* L.	purplestem aster	8	Y	12.96	24.07	48.15
Asteraceae	*Aster umbellatus* Mill.	parasol whitetop	9	Y	1.85	0.00	7.41
Asteraceae	*Bidens coronata (L.) Britton*	crowned beggarticks	9	Y	0.00	3.70	7.41
Asteraceae	*Bidens frondosa* (L.)	devil's beggartick	1	Y	25.93	27.78	0.00
Urticaceae	*Boehmeria cylindrica* (L.) Sw.	false nettle	2	Y	35.19	50.00	29.63
Poaceae	*Bromus ciliatus* L.	fringed brome	10	Y	0.00	1.85	14.81
Poaceae	*Calamagrostis canadensis* (Michx.)	bluejoint	3	Y	0.00	1.85	**51.85**
Ranunculaceae	*Caltha palustris* L.	yellow marsh marigold	5	Y	3.70	3.70	7.41
Convolvulaceae	*Calystegia sepium* (L.) R. Br.	hedge false bindweed	1	Y	0.00	1.85	11.11
Campanulaceae	*Campanula aparinoides* Pursh	marsh bellflower	8	Y	7.41	12.96	33.33
Brassicaceae	*Cardamine bulbosa* (Schreb. ex Muhl.) Britton, Sterns & Poggenb.	bulbous bittercress	6	Y	0.00	11.11	0.00
Cyperaceae	*Carex bebbii* Olney ex Fernald	Bebb's sedge	6	Y	1.85	**16.67**	0.00
Cyperaceae	*Carex cryptolepis* Mack.	northeastern sedge	9	Y	0.00	0.00	3.70
Cyperaceae	*Carex flava L.*	yellow sedge	10	Y	0.00	0.00	7.41
Cyperaceae	*Carex granularis* Muhl. ex Willd.	limestone meadow sedge	4	Y	1.85	1.85	0.00
Cyperaceae	*Carex hystericina* Muhl. ex Willd.	bottlebrush sedge	5	Y	0.00	**38.89**	3.70
Cyperaceae	*Carex leptalea* Wahlenb.	bristlystalked sedge	10	Y	3.70	14.81	0.00
Cyperaceae	*Carex pellita* Muhl. ex Willd.	woolly sedge	4	Y	3.70	5.56	29.63
Cyperaceae	*Carex prairea* Dewey ex Alph. Wood	prairie sedge	10	Y	0.00	0.00	25.93
Cyperaceae	*Carex sartwellii* Dewey	Sartwell's sedge	6	Y	0.00	0.00	14.81
Cyperaceae	*Carex sterilis* Willd.	dioecious sedge	10	Y	1.85	0.00	44.44
Cyperaceae	*Carex stipata* Muhl. ex Willd.	awlfruit sedge	3	Y	**33.33**	**42.59**	0.00
Cyperaceae	*Carex stricta* Lam.	upright sedge	5	Y	25.93	27.78	**92.59**
Cyperaceae	*Carex tetanica* Schkuhr	rigid sedge	9	Y	0.00	3.70	**40.74**
Cyperaceae	*Carex vulpinoidea* Michx.	fox sedge	2	Y	1.85	5.56	11.11
Juglandaceae	Carya seedling	pignut or shagbark	5	Y	3.70	5.56	0.00
Celastraceae	*Celastrus orbiculatus* Thumb	oriental bittersweet	0	N	14.81	1.85	7.41
Apiaceae	*Cicuta maculata* L.	spotted water hemlock	6	Y	0.00	1.85	0.00
Poaceae	*Cinna arundinacea* L.	sweet woodreed	5	Y	9.26	7.41	3.70
Onagraceae	*Circaea lutetiana* L.	broadleaf enchanter's nightshade	1	Y	**59.26**	**48.15**	11.11
Asteraceae	*Cirsium arvense* (L.) Scop.	Canada thistle	0	N	0.00	9.26	0.00
Asteraceae	*Cirsium muticum* Michx.	swamp thistle	10	Y	7.41	14.81	51.85
Asteraceae	*Cirsium vulgare* (Savi) Ten.	bull thistle	0	N	0.00	1.85	0.00
Cyperaceae	*Cladium mariscoides* (Muhl.) Torr.	smooth sawgrass	10	Y	0.00	0.00	62.96
Ranunculaceae	*Clematis virginiana* L.	western blue virginsbower	4	Y	0.00	3.70	0.00

Table 8 cont'd.

Family	**Genus species**	**Common Name**	**C~**	**Native**	**Inv**	**Remo**	**Ref**
Asteraceae	*Conyza canadensis* (L.) Cronquist	Canadian horseweed	0	Y	0.00	3.70	0.00
Cornaceae	*Cornus foemina* Mill.	stiff dogwood	1	Y	16.67	5.56	14.81
Cornaceae	*Cornus stolonifera* Michx.	redosier dogwood	6	Y	1.85	7.41	37.04
Dryopteridaceae	*Dryopteris carthusiana* (Vill.) H.P. Fuchs	spinulose woodfern	8	Y	7.41	3.70	0.00
Dryopteridaceae	*Dryopteris cristata* (L.) A. Gray	crested woodfern	10	Y	9.26	3.70	0.00
Cyperaceae	*Eleocharis elliptica* Kunth	elliptic spikerush	8	Y	0.00	1.85	40.74
Cyperaceae	*Eleocharis rostellata* (Torr.) Torr.	beaked spikerush	10	Y	0.00	9.26	3.70
Onagraceae	*Epilobium coloratum* Biehler	purpleleaf willowherb	3	Y	24.07	**64.81**	11.11
Equisetaceae	*Equisetum arvense* (L.)	field horsetail	0	Y	27.78	37.04	11.11
Asteraceae	*Erechtites hieraciifolia* (L.) Raf. ex DC.	American burnweed	2	Y	18.52	29.63	0.00
Asteraceae	*Erigeron annuus* (L.) Pers.	eastern daisy fleabane	0	N	1.85	7.41	0.00
Asteraceae	*Erigeron philadelphicus* L.	Philadelphia fleabane	4	Y	0.00	3.70	0.00
Asteraceae	*Eupatorium maculatum* L.	spotted joe pye weed	4	Y	5.56	18.52	**55.56**
Asteraceae	*Eupatorium perfoliatum* L.	common boneset	4	Y	29.63	**72.22**	44.44
Asteraceae	*Euthamia graminifolia* (L.) Nutt.	flat-top goldentop	4	Y	0.00	5.56	7.41
Rosaceae	*Fragaria virginiana* Duchesne	Virginia strawberry	1	Y	5.56	1.85	7.41
Rhamnaceae	*Frangula alnus* Mill.	glossy buckthorn	0	N	79.63	79.63	48.15
Oleaceae	*Fraxinus pennsylvanica* Marsh.	green ash	5	Y	1.85	0.00	0.00
Rubiaceae	*Galium boreale* L.	northern bedstraw	7	Y	7.41	5.56	7.41
Rubiaceae	*Galium circaezans* Michx.	licorice bedstraw	10	Y	1.85	5.56	0.00
Rubiaceae	*Galium triflorum* Michx.	fragrant bedstraw	5	Y	18.52	16.67	7.41
Gentianaceae	*Gentianopsis crinita* (Froel.) Ma	greater fringed gentian	10	Y	0.00	0.00	**18.52**
Geraniaceae	*Geranium maculatum* L.	spotted geranium	4	Y	0.00	1.85	0.00
Rosaceae	*Geum canadense* Jacq.	white avens	1	Y	25.93	14.81	11.11
Poaceae	*Glyceria striata* (Lam.) Hitchc.	fowl mannagrass	4	Y	31.48	57.41	48.15
Boraginaceae	*Hackelia virginiana* (L.) I.M. Johnst.	beggarslice	0	Y	1.85	1.85	0.00
Asteraceae	*Helenium autumnale* L.	common sneezeweed	5	Y	0.00	0.00	18.52
Asteraceae	*Helianthus giganteus* L.	giant sunflower	9	Y	0.00	1.85	0.00
Poaceae	*Hierochloe odorata* (L.) P. Beauv.	sweetgrass	9	Y	0.00	5.56	3.70
Liliaceae	*Hypoxis hirsuta* (L.) Coville	common goldstar	9	Y	0.00	0.00	**48.15**
Aquifoliaceae	*Ilex verticillata* (L.) A. Gray	common winterberry	9	Y	3.70	1.85	0.00
Balsaminaceae	*Impatiens capensis* Meerb.	jewelweed	3	Y	22.22	24.07	22.22
Iridaceae	*Iris versicolor* L.	harlequin blueflag	5	Y	0.00	0.00	3.70
Juncaceae	*Juncus brachycephalus* (Engelm.) Buchenau	smallhead rush	9	Y	0.00	0.00	11.11
Juncaceae	*Juncus dudleyi* Wiegand	Dudley's rush	4	Y	1.85	18.52	7.41
Cupressaceae	*Juniperus virginiana* L.	eastern redcedar	2	Y	3.70	0.00	0.00
Fabaceae	*Lathyrus palustris* L.	marsh pea	8	Y	5.56	16.67	22.22
Poaceae	*Leersia oryzoides* (L.) Sw.	rice cut grass	4	Y	16.67	**38.89**	7.41
Asteraceae	*Liatris spicata* (L.) Willd.	dense blazing star	6	Y	0.00	0.00	11.11
Lauraceae	*Lindera benzoin* (L.) Blume	Northern spicebush	7	Y	18.52	7.41	0.00
Campanulaceae	*Lobelia kalmii* L.	Ontario lobelia	10	Y	0.00	0.00	11.11
Campanulaceae	*Lobelia siphilitica* L.	great blue lobelia	6	Y	9.26	11.11	0.00
Caprifoliaceae	*Lonicera* L.	honeysuckle	0	N	0.00	1.85	0.00
Lamiaceae	*Lycopus americanus* Muhl. ex W. Bartram	American water horehound	5	Y	11.11	12.96	**66.67**
Lamiaceae	*Lycopus uniflorus* Michx.	northern bugleweed	7	Y	18.52	33.33	55.56
Primulaceae	*Lysimachia quadriflora* Sims	fourflower yellow loosestrife	9	Y	0.00	3.70	**48.15**
Lythraceae	*Lythrum salicaria (L.)*	purple loosestrife	0	N	5.56	24.07	18.52
Lamiaceae	*Mentha arvensis* L.	wild mint	5	Y	3.70	5.56	22.22
Poaceae	*Muhlenbergia glomerata* (Willd.) Tri	spiked muhly	10	Y	0.00	0.00	**48.15**
Poaceae	*Muhlenbergia mexicana*	Mexican muhly	5	Y	7.41	18.52	22.22
Dryopteridaceae	*Onoclea sensibilis* L.	Sensitive fern	8	Y	27.78	12.96	11.11

Table 8 cont'd.

Family	**Genus species**	**Common Name**	**C~**	**Native**	**Inv**	**Remo**	**Ref**
Apiaceae	*Osmorhiza claytonii* (Michx.) C.B. Clarke	Clayton's sweetroot	3	Y	7.41	3.70	0.00
Apiaceae	*Oxypolis rigidor* (L.) Raf.	stiff cowbane	7	Y	5.56	3.70	14.81
Poaceae	*Panicum capillare* L.	witchgrass	1	Y	0.00	1.85	0.00
Saxifragaceae	*Parnassia glauca*	grass of parnassus	10	Y	0.00	0.00	**37.04**
Vitaceae	*Parthenocissus quinquefolia* (L.) Planch.	Virginia creeper	2	Y	27.78	29.63	22.22
Scrophulariaceae	*Pedicularis lanceolata* Michx.	swamp lousewort	9	Y	0.00	0.00	7.41
Crassulaceae	*Penthorum sedoides* L.	ditch stonecrop	5	Y	5.56	16.67	0.00
Poaceae	*Phalaris arundinacea* L.	reed canarygrass	0	N	16.67	25.93	18.52
Phytolaccaceae	*Phytolacca americana* L.	American pokeweed	1	Y	1.85	0.00	0.00
Urticaceae	*Pilea pumila* (L.) A. Gray	clearweed	5	Y	68.52	**81.48**	18.52
Plantaginaceae	*Plantago major* (L.)	common plantain	0	N	0.00	0.00	3.70
Poaceae	*Poa pratensis* L.	Kentucky bluegrass	0	N	1.85	1.85	3.70
Polygonaceae	*Polygonum amphibium* L.	water knotweed	4	Y	3.70	11.11	**55.56**
Polygonaceae	*Polygonum hydropiperoides* Michx.	swamp smartweed	7	Y	0.00	1.85	0.00
Polygonaceae	*Polygonum punctatum* Elliot	dotted smartweed	6	Y	11.11	12.96	3.70
Polygonaceae	*Polygonum sagittatum* L.	arrowleaf tearthumb	8	Y	14.81	27.78	7.41
Polygonaceae	*Polygonum virginianum* L.	jumpseed	2	Y	7.41	5.56	0.00
Salicaceae	*Populus tremuloides* Michx.	quaking aspen	4	Y	5.56	24.07	7.41
Rosaceae	*Potentilla fruticosa* auct. non L.	shrubby cinquefoil	10	Y	0.00	0.00	**62.96**
Lamiaceae	*Prunella vulgaris* L.	selfheal	0	Y	0.00	3.70	0.00
Rosaceae	*Prunus serotina* Ehrh.	black cherry	1	Y	24.07	12.96	3.70
Lamiaceae	*Pycnanthemum virginianum* (L.) T. Dur. & B.D. Jacks. ex B.L. Rob. &	Virginia mountainmint	5	Y	1.85	0.00	14.81
Fagaceae	*Quercus* sp.	oak	5	Y	3.70	3.70	0.00
Ranunculaceae	*Ranunculus recurvatus* Poir.	blisterwort	5	Y	12.96	0.00	0.00
Rhamnaceae	*Rhamnus alnifolia* L'Hér.	alderleaf buckthorn	10	Y	0.00	0.00	3.70
Rhamnaceae	*Rhamnus cathartica* L.	common buckthorn	0	N	18.52	9.26	7.41
Cyperaceae	*Rhynchospora alba* (L.) Vahl	white beaksedge	10	Y	0.00	0.00	7.41
Grossulariaceae	*Ribes cynosbati* L.	eastern prickly gooseberry	5	Y	5.56	3.70	0.00
Brassicaceae	*Rorippa palustris* (L.) Besser	bog yellowcress	4	Y	5.56	3.70	0.00
Rosaceae	*Rosa multiflora* Thunb.	multiflora rose	0	N	**27.78**	7.41	3.70
Rosaceae	*Rosa palustris* Marsh.	swamp rose	7	Y	1.85	5.56	3.70
Rosaceae	*Rubus pubescens* Raf.	dwarf red blackberry	10	Y	20.37	3.70	3.70
Rosaceae	*Rubus strigosus* Michx.	grayleaf red raspberry	3	Y	16.67	18.52	14.81
Asteraceae	*Rudbeckia hirta* L.	blackeyed Susan	1	Y	0.00	1.85	**40.74**
Polygonaceae	*Rumex orbiculatus* A. Gray	greater water dock	8	Y	1.85	3.70	3.70
Salicaceae	*Salix discolor* Muhl.	pussy willow	2	Y	0.00	38.89	33.33
Caprifoliaceae	*Sambucus canadensis* L.	American black elderberry	1	Y	9.26	3.70	3.70
Apiaceae	*Sanicula gregaria*	black snakeroot	2	Y	0.00	12.96	0.00
Lauraceae	*Sassafras albidum* (Nutt.) Nees	sassafras	3	Y	0.00	1.85	0.00
Poaceae	*Schizachyrium scoparium* (Michx.) Nash	little bluestem	5	Y	0.00	0.00	**37.04**
Cyperaceae	*Scirpus acutus* Muhl. ex Bigelow	hardstem bullrush	6	Y	0.00	0.00	**33.33**
Cyperaceae	*Scirpus americanus* Pers.	threesquare	5	Y	0.00	0.00	**33.33**
Cyperaceae	*Scirpus atrovirens* Willd.	green bulrush	4	Y	0.00	27.78	0.00
Lamiaceae	*Scutellaria galericulata* L.	marsh skullcap	5	Y	3.70	20.37	11.11
Lamiaceae	*Scutellaria lateriflora* L.	blue skullcap	5	Y	3.70	1.85	3.70

Table 8 cont'd.

Family	Genus species	Common Name	C~	Native	Inv	Remo	Ref
Asteraceae	*Senecio aureus* L.	golden ragwort	7	Y	38.89	**51.85**	18.52
Asteraceae	*Senecio pauperculus Michx.*	balsam groundsel	6	Y	0.00	0.00	33.33
Liliaceae	*Smilacina stellata* (L.) Desf.	starry false lily of the valley	5	Y	5.56	3.70	0.00
Smilacaceae	*Smilax tamnoides* L.	bristly greenbrier	5	Y	12.96	1.85	0.00
Solanaceae	*Solanum dulcamara* L.	climbing nightshade	0	Y	11.11	**29.63**	0.00
Asteraceae	*Solidago altissima* L.	Canada goldenrod	1	Y	1.85	9.26	11.11
Asteraceae	*Solidago gigantea* Aiton	giant goldenrod	4	Y	3.70	3.70	11.11
Asteraceae	*Solidago ohioensis* Frank ex Riddell	Ohio goldenrod	9	Y	0.00	0.00	**33.33**
Asteraceae	*Solidago patula* Muhl. ex Willd.	roundleaf goldenrod	9	Y	35.19	37.04	33.33
Asteraceae	*Solidago riddellii* Frank ex Riddell	Riddell's goldenrod	7	Y	1.85	1.85	**37.04**
Asteraceae	*Solidago rugosa* Mill.	rough-leaved goldenrod	6	Y	35.19	31.48	18.52
Poaceae	*Sorghastrum nutans* (L.) Nash	indiangrass	5	Y	0.00	0.00	**33.33**
Poaceae	*Sphenopholis intermedia* (Rydb.) R)	slender wedgescale	4	Y	0.00	0.00	7.41
Rosaceae	*Spiraea alba* Du Roi	white meadowsweet	7	Y	0.00	0.00	3.70
Araceae	*Symplocarpus foetidus* (L.) Salisb. ex Nutt.	American skunk cabbage	8	Y	**24.07**	14.81	3.70
Asteraceae	*Taraxacum officinale* F.H. Wigg.	common dandelion	0	N	0.00	5.56	0.00
Ranunculaceae	*Thalictrum dasycarpum* Fisch. & Avé-Lall.	purple meadow-rue	5	Y	5.56	3.70	11.11
Thelypteridaceae	*Thelypteris palustris* Schott	eastern marsh fern	6	Y	14.81	9.26	**70.37**
Anacardiaceae	*Toxicodendron radicans* (L.) Kuntze	Eastern poison ivy	2	Y	3.70	3.70	3.70
Anacardiaceae	*Toxicodendron vernix (L.) Kuntze*	poison sumac	10	Y	1.85	5.56	0.00
Clusiaceae	*Triadenum fraseri* (Spach) Gleason	Fraser's marsh St. Johnswort	8	Y	0.00	0.00	3.70
Fabaceae	*Trifolium repens* L.	white clover	0	N	0.00	1.85	0.00
Typhaceae	*Typha latifolia* L.	broadleaf cattail	1	N	3.70	**20.37**	7.41
Ulmaceae	Ulmus sp.	elm	3	Y	24.07	27.78	3.70
Urticaceae	*Urtica dioica* L.	stinging nettle	0	N	5.56	12.96	0.00
Verbenaceae	*Verbena hastata* L.	swamp verbena	4	Y	0.00	5.56	0.00
Verbenaceae	*Verbena urticifolia* L.	white vervain	5	Y	0.00	3.70	0.00
Violaceae	*Viola nephrophylla* Greene	northern bog violet	9	Y	**50.00**	35.19	7.41
Vitaceae	*Vitis riparia* Michx.	riverbank grape	2	Y	5.56	7.41	0.00
Liliaceae	*Zigadenus elegans* Pursh ssp. *glaucus* (Nutt.) Hultén	mountain deathcamas	10	Y	0.00	0.00	**18.52**

~Coefficient of conservatism from Herman et al. (2001)

Table 9. Number of bees observed using observational sampling per replicate and treatment in years 1 and 2 post restoration. The percent of bees each genus composed of the total number observed 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.

		Year 1				**Year 2**			
Family	**Genus**	**% obs**	**Invaded**	**Removal**	**Reference**	**% obs**	**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
	Xylocopa	0	0	0	0	0.9	0	0.13	0
Colletidae									
	Ceratina	0	-	-	-	7.1	0	0.52	0.46
Halictidae									
	Hylaeus	16.9	0	0.44	0.67	15.6	0.02	1.83	0.29
	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*	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	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

*Represents bees that were not identified to genus; may be composed of more than 1 genus and family.

Table 10. Number of bees collected using pollinator bowl sampling per replicate and treatment, Inv=Invaded, Remo=Removal and Ref=Reference, in years 1 and 2 post restoration. The percent of bees each species composed 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.

		Year 1				Year 2			
Family	**Genus species**	**% trapped**	**Inv**	**Remo**	**Ref**	**% trapped**	**Inv**	**Remo**	**Ref**
Andrenidae									
	Andrena alleghenіensis 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
	Apis 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 affinus 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 atlanticum (Mitchell)	3.9	0	0.11	0.22	0.2	0	0.04	0
	L. bruneri (Crawford)	0	-	-	-	0.2	0.04	0	0
	L. coriaceum (Smith)	5.2	0.28	0.06	0.11	1.4	0.13	0.08	0.08
	L. cressonii (Robertson)	0.6	0	0.06	0	0.6	0.04	0.08	0
	L. Dialictus sp. 1	4.5	0	0.17	0.22	0.8	0.13	0.04	0
	L. Dialictus sp. 2	**11.0**	0	0.06	**0.89**	**14.0**	0.42	**0.96**	**1.50**
	L. Dialictus sp. 3	0	-	-	-	3.3	0.13	0.21	0.33
	L. Dialictus sp. 4	0	-	-	-	0.2	0	0.04	0
	L. Dialictus sp. 5	0	-	-	-	0.4	0	0	0.08
	L. Dialictus sp. 6	0	-	-	-	0.2	0.04	0	0
	L. Dialictus sp. 7	0	-	-	-	0.2	0.04	0	0
	L. Dialictus sp. 8	0	-	-	-	0.4	0	0	0.08
	L. Dialictus spp.	1.9	0	0.17	0	1.2	0.04	0.04	0.17
	L. divergens (Lovell)	0.6	0.06	0	0	0	-	-	-
	L. illinoense (Robertson)	0	-	-	-	0.2	0.04	0	0
	L. leucozonium (Schrank)	1.9	0	0.17	0	0.2	0	0.04	0
	L. macoupinense (Robertson)	0	-	-	-	0.2	0.04	0	0
	L. nelumbonis (Robertson)	0.6	0	0.06	0	0	-	-	-
	L. nymphaearum (Robertson)	0	-	-	-	0.4	0	0.08	0

Table 10 cont'd.

		Year 1				Year 2			
Family	**Genus species**	**% trapped**	**Inv**	**Remo**	**Ref**	**% trapped**	**Inv**	**Remo**	**Ref**
Halictidae									
	L. paradmirandum (Knerer & Atwood)	1.3	0	0.11	0	0	-	-	-
	L. pectorale (Smith)	2.6	0	0.11	0.11	1.0	0	0.13	0.08
	L. pilosum (Smith)	1.3	0	0	0.11	0.8	0	0	0.17
	L. rohweri (Ellis)	5.2	0	0.22	0.22	**21.1**	0.04	**2.63**	**1.67**
	L. versans (Lovell)	3.2	0.06	0.22	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. relativa 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. similima Smith	1.3	0	0	0.11	0	-	-	-
Species richness		29	7	25	14	48	17	37	23

[a] females of these species, *C. calcarata* Robertson and *C. dupla* Say, are morphologically indistinguishable; only 1 male of each species was collected.

Table 11. Number and identity of butterflies seen during 5 minute observational sampling in years 1 and 2 post restoration, % obs=percent of total observed per year, Inv=Invaded, Remo=Removal and 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.

			Year 1				Year 2			
Family	**Genus species**	**Common name**	**% 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
	Poanes 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
	Papilio 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

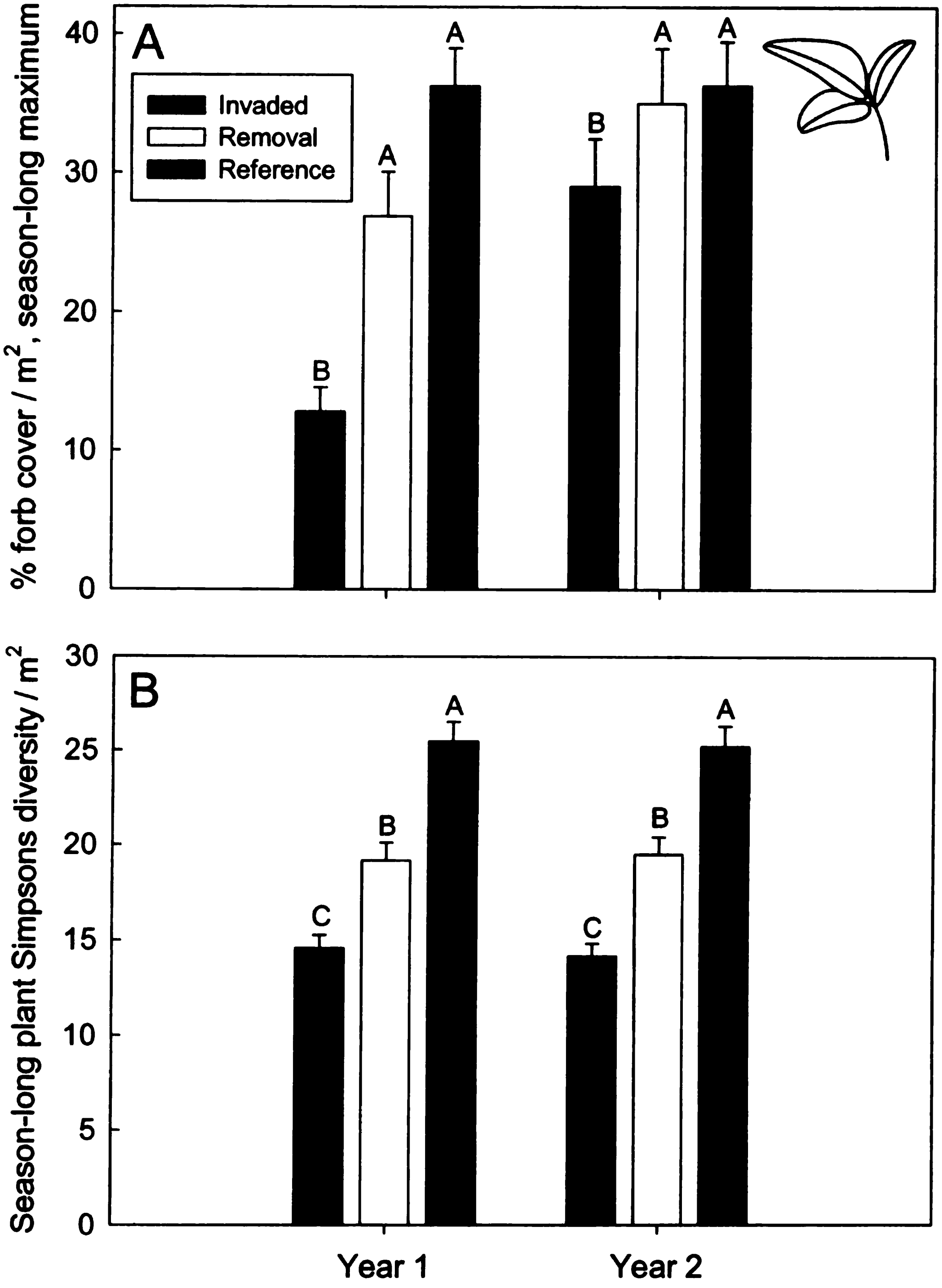

Figure 8. Comparisons of A) percent cover of forbs and B) Simpsons diversity between *F. alnus* invaded, removal, and uninvaded plots in the first and second years following restoration. Maximum values for percent cover recorded for each growing season are used. Error bars are +SEM, α=0.05. Treatment effects from a 2-way ANOVA with treatment and time are shown; year effects were not significant.

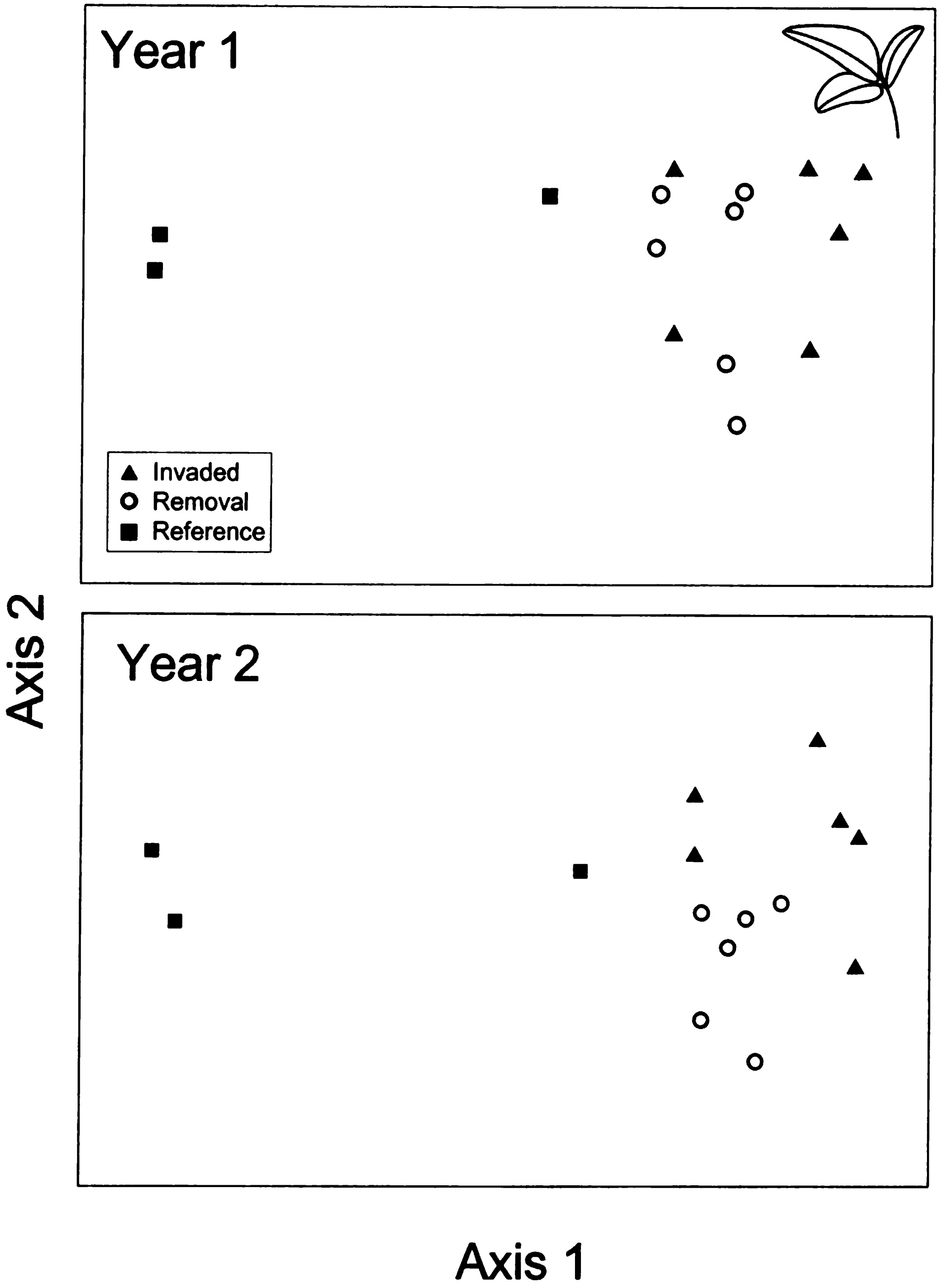

Figure 9. Two dimensional NMDS ordinations of the plant community show no difference between invaded and removal plots in year 1 but a shift in removal plots away from invaded plots by year 2. The ordination is based a Bray-Curtis dissimilarity matrix for the first and second years following restoration. 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.

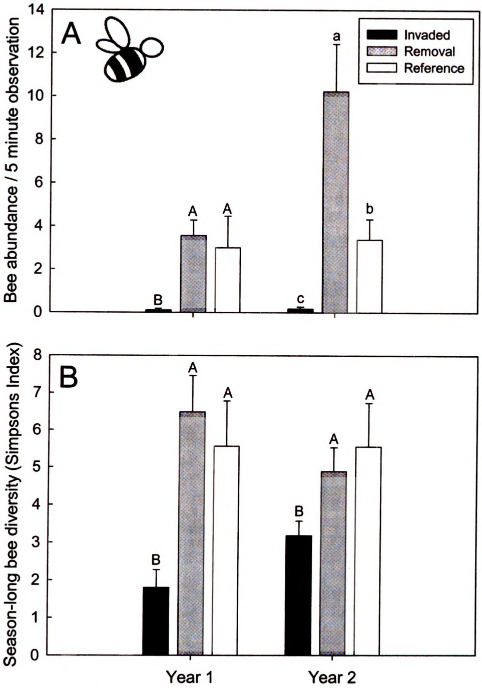

Figure 10. Comparisons of A) bee abundance B) bee diversity C) butterfly abundance and D) butterfly diversity in the first and second seasons following restoration. Bee abundance, butterfly abundance, and diversity are based on the season-long mean number of individuals observed in 5-minute observational sampling periods in invaded, removal, on-site reference (reference) and off-site reference (off-site). Bee diversity is based on bees collected with bowl sampling in invaded, removal, and on-site reference plots. Treatment effects from 2-way ANOVAs with treatment and time are shown. Letters in upper and lower case within the same graph indicate that treatments differed by year or treatment*year.

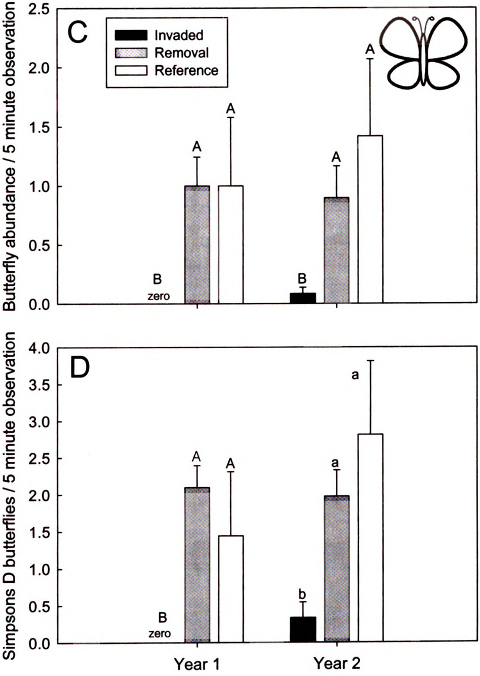

Figure 10 cont'd.

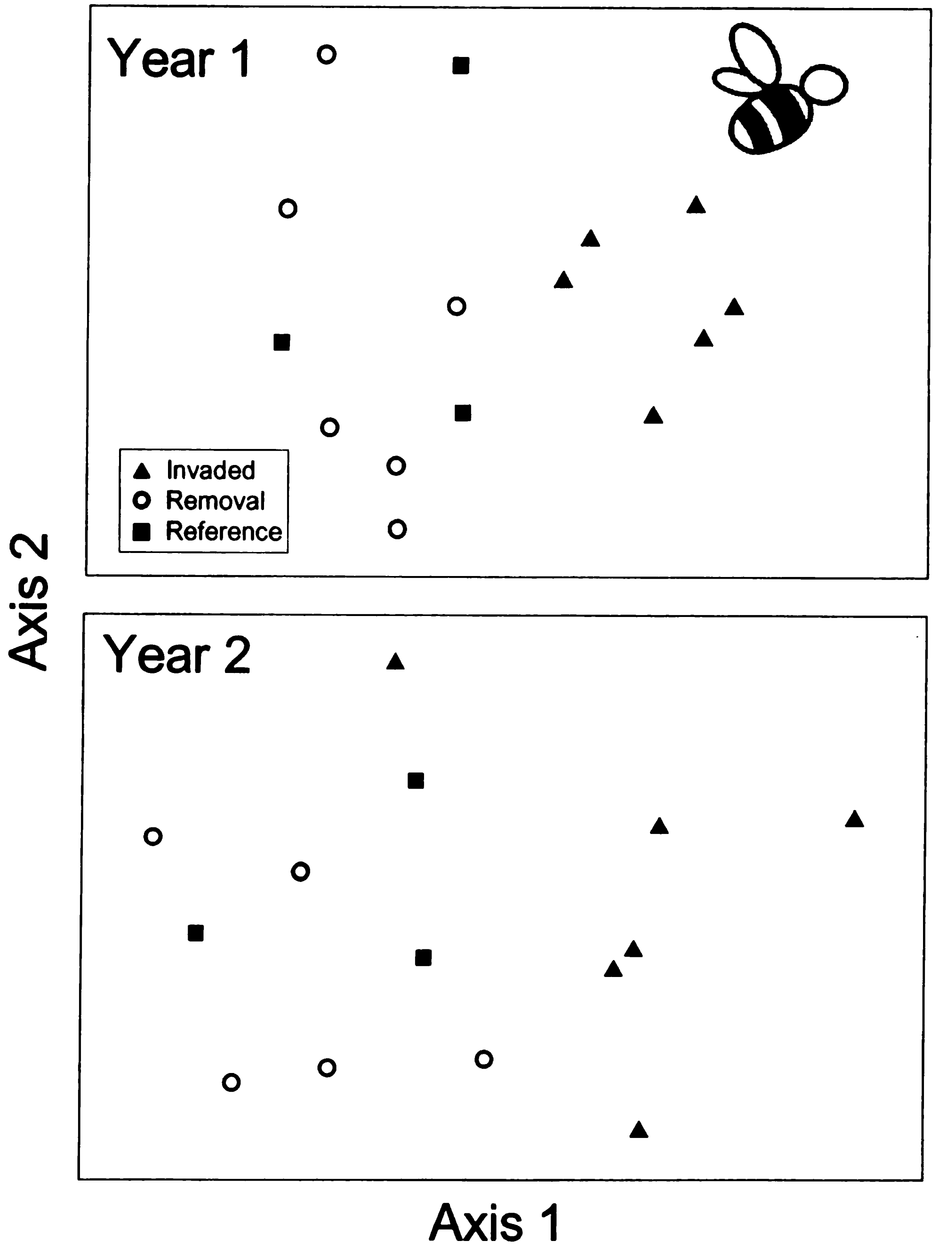

Figure 11. Two dimensional NMDS ordinations of the bee community show distinct bee communities in invaded plots in both years 1 and 2, with bee communities in removal and reference plots overlapping. The ordination is based a Bray-Curtis dissimilarity matrix (using n+1), using mean values per replicate and treatment; data were square root transformed. Stress values were 0.14 in both years.

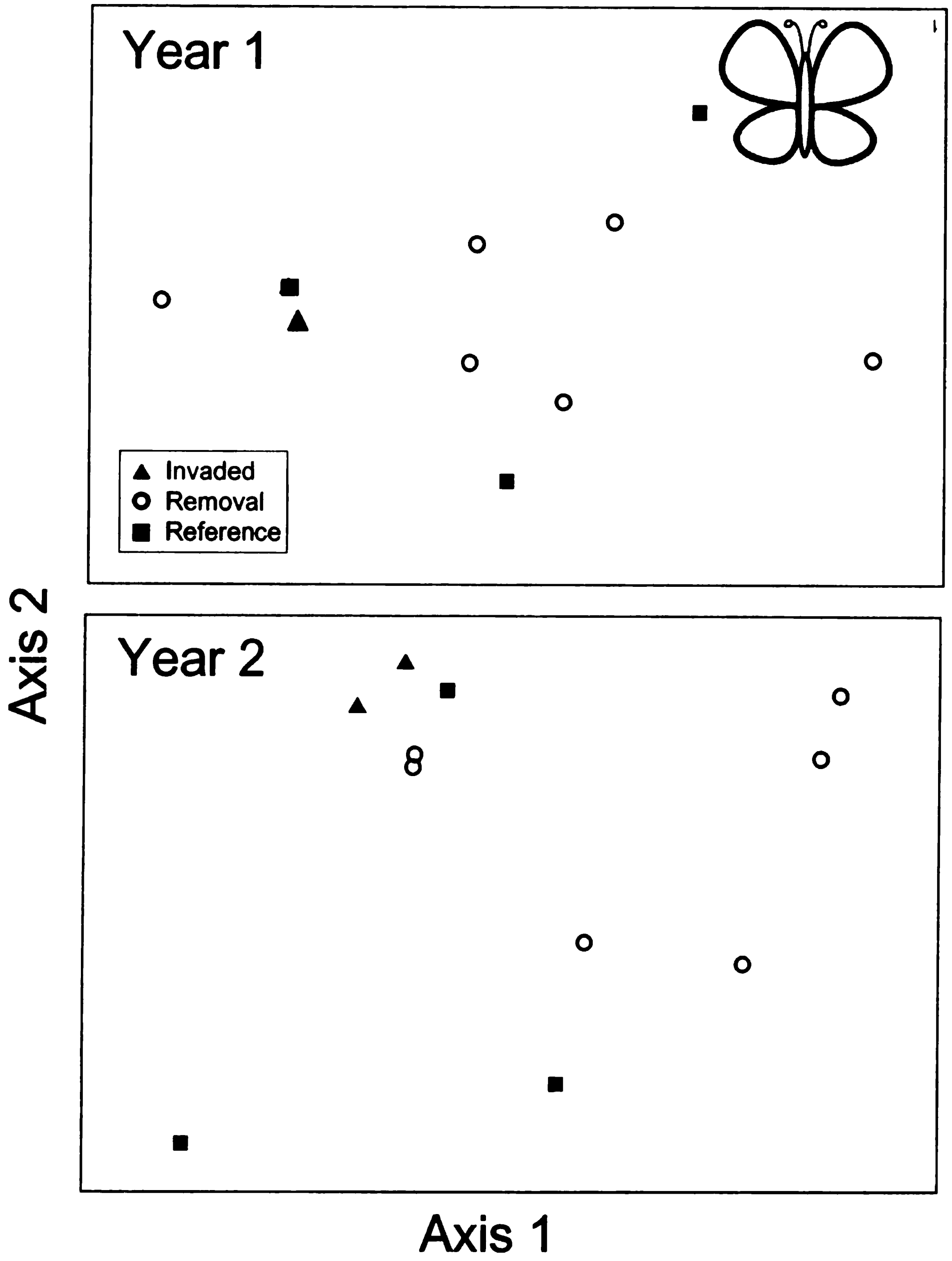

Figure 12. Two dimensional NMDS ordinations of the butterfly community show that the invaded and removal butterfly communities differ in both years 1 and 2. In year 2, all six replicates of invaded contained 0 butterflies, and all points overlap. In year 2, 1 butterfly was seen in invaded plots and 5 of 6 points overlap. The ordination is based a Bray-Curtis dissimilarity matrix (using n+1), with mean values per replicate and treatment; data were square root transformed. Stress values were 0.04 for year 1 and 0.11 for year 2.

Chapter 5
For Oecologia

RAPID RESTORATION OF PLANT-POLLINATOR NETWORKS AND FUNCTION FOLLOWING HABITAT RESTORATION

Anna Katherine Fiedler

Abstract

Species diversity is often used as the primary indicator of successful habitat restoration; however, it is also critical that species interactions for long–term ecosystem persistence are restored. Here, we determine whether plant–pollinator networks and the key ecosystem function of pollination are restored following invasive species removal from a degraded prairie fen wetland. We examined 1) quantitative food webs describing plant–pollinator interactions, 2) pollinator diversity and abundance, and 3) pollinator function using sentinel plant species, *Asclepias incarnata,* in invaded, uninvaded reference, and restored plots, following invasive species removal. Plant–pollinator networks in invaded plots were highly depauperate, with significantly lower plant and pollinator species richness than restored or reference plots. In contrast, network connectance, compartment diversity, generality, and vulnerability did not differ between restored and reference plots, with marginally higher interaction evenness in reference than restored plots. Moreover, pollinator function was restored in cleared areas in the initial growing season following restoration. We found no significant differences in pollinator abundance or diversity between cleared and reference areas, while these remained low in uncleared areas. In the second year following restoration, we found no significant differences in pollinator function or abundance, potentially due to spillover effects of restoration or stochastic pollination by year. Pairing plant–pollinator networks with measures of pollination shows that, although plant and insect community composition are not yet fully restored, function has been. Consideration of ecosystem function and species interactions in combination provide a more process–based analysis that can inform both ecological theory and restoration.

Introduction

Habitat loss is the number one cause of species extinctions in North America (Wilcove et al. 1998), as well as the leading cause of pollinator extinctions globally (Brown and Paxton 2009). Drivers of global environmental change, including land use, elevated CO_2, and biotic invasions, lead not only to species extinctions but also changes in species interactions within ecosystems (Tylianakis et al. 2008). Plant–pollinator interactions are of particular concern as evidence mounts that pollinators are under threat (Potts et al. 2010, Winfree 2010). Over 90% of angiosperms are animal–pollinated (Nabhan and Buchmann 1997), and the fossil record indicates that major plant extinctions in the past led to a decline in insect diversity (Bascompte and Jordano 2007). Recent documentation of concomitant declines in both pollinators and insect–pollinated plants (Biesmeijer et al. 2006) has reinforced the need to address plant and pollinator populations in tandem.

Construction of quantitative plant–pollinator networks is one way to assess the structure, and stability, of plant–pollinator interactions. Quantitative interaction networks are increasingly used to examine similarities and differences between species interactions across taxa and trophic levels (Bascompte and Jordano 2007). This characterization of networks has resulted in the identification of recurring patterns which facilitate species persistence and long-term maintenance of biodiversity (Bascompte et al. 2006). Such patterns include: 1) asymmetry, where specialist insects tend to visit generalist plants and specialist plants tend to be visited by generalist insects, 2) nestedness, with specialist species interacting with a subset of those in generalist interactions and 3) heterogeneity, with the majority of species linked in few interactions, but a few species more connected than expected by chance (Bascompte and Jordano 2007). Due to the prevalence of generalist interactions between pollinators and plants (Waser et al. 1996, Olesen et al. 2008), plant–pollinator networks are likely to be relatively stable over time. However, if generalist pollinator species are lost, additional plant extinctions are more likely than if specialist pollinators become locally extinct (Memmott et al. 2004).

An increasingly common solution to habitat degradation is to restore fragmented habitats, removing invasive species and reintroducing historic disturbance regimes. The plant community is commonly the focus of restoration (Young et al. 2005), with species diversity the primary metric of success (Ruiz-Jaen and Aide 2005). Diversity metrics, however, cannot assess whether recovery of species interactions and ecosystem function have occurred. In contrast, a quantitative evaluation of species interactions could reveal such patterns and help determine. Ecosystem function is rarely accounted for in restoration (but see: Lomov et al. 2009, Lomov 2010, in press), and structure and function may not be on the same trajectory.

Whether species network properties in restored systems are comparable to those in intact ecosystems has been examined in only a handful of cases (Forup and Memmott 2005, Forup et al. 2008). Species interactions were found to be more complex in ancient than restored areas in heathlands with low plant diversity (Forup et al. 2008). In old field hay meadows, there were no differences in insect richness or abundance between old and restored meadows, but there was a greater proportion of potential species links in old than restored meadows (Forup and Memmott 2005). In both cases, not all differences in species identity between restored and reference sites that resulted in differences in network structure.

Over 60% of plant species are dependent on pollination by insects for maximal fruit and seed set (Burd 1994, Ashman et al. 2004). The removal of obligate pollinators from an ecosystem may result in populations which persist but cannot reproduce (Eriksson 2000). Plants may be pollen limited over long timeframes due to random fluctuations in populations and weather, plant adaptation to stochastic pollinator communities, or habitat alteration (Ashman et al. 2004). Invasive plants may also lead to increased competition for pollinators (Bartomeus et al. 2008) and affect pollination rates at related native species (Brown et al. 2002). Assessing pollen limitation at the population level, however, is extremely difficult due to plant reproductive tradeoffs. For example, many self–incompatible plants compensate for dependence on pollination by reproducing vegetatively, rather than depending exclusively on seeds for reproduction (Bond 1994). However, in systems without this compensation the risk for plant extinction is high (Bond 1994). Habitat fragmentation can negatively effect pollination and plant reproduction, with self–incompatible species more negatively affected by fragmentation (Aguilar et al. 2006). In degraded, fragmented ecosystems, the soil seed bank is often lost and seed dispersal is limited, so that plant reproduction is entirely dependent on the species that remain or are reintroduced (Bakker and Berendse 1999). Given this overall pattern and the prevalence of habitat fragmentation worldwide, it is vital that we gain a better understanding of whether pollinator function is re–established following habitat restoration and how function relates to plant–pollinator network structure.

Pollen transport webs assessing the likelihood that flower–visiting insects are potential pollinators have been previously studied (Forup and Memmott 2005, Forup et al. 2008). However, the question of whether network properties and pollen transport webs actually translate into the key ecosystem function of pollination has never been explored in a restoration context. Our goal was to document the effect of a non–native invasive plant on plant–pollinator networks in prairie fen wetlands (Chapters 2–4). Here we examine the effect of restoration on plant–pollinator networks, the function of pollination, and their interactions.

Methods

Study system and experimental design

This study took place in prairie fen, a globally rare groundwater fed wetland ecosystem with high species density (Nekola 1994, Amon et al. 2002). Parts of the glaciated Midwestern US, where prairie fens have the highest density on Earth, fens contain from 7– 18% of the rare taxa occurring in their respective states. Threats to prairie fen include habitat fragmentation, invasive species encroachment, hydrological changes, and pollution (Spieles et al. 1999, Bedford and Godwin 2003). The primary invasive species in North American prairie fens is *Frangula alnus* L. (glossy buckthorn). This species can form a 7 m tall closed-canopy system that alters the typical sedge-meadow nature of prairie fen (Sinclair and Catling 1999). The conservation and restoration of fens is paramount to survival of the species within them, as well as the water filtration and flood control services these wetlands provide.

The study sites were two prairie fens in Jackson County, Liberty Township, Michigan: the Michigan State University MacCready Reserve in Clarklake, MI, and the Grand River Fen, in Liberty MI. At the MacCready Reserve, we established six replicate plots containing mature *F. alnus* plants (invaded), six replicate plots where mature *F.*

alnus plants were removed in February 2008 (restored), and three replicate uninvaded plots (on–site reference) (Fiedler and Landis in review). Four replicate plots separated by a minimum of 15m were also laid out at the Grand River Fen as a larger, contiguous reference area (off–site reference). All plots measured approximately 25x25 m.

Sampling

Pollinator networks

We established four circular sampling areas of 2 m diameter on a grid within each replicate. We sampled for plant–pollinator interactions every three weeks throughout the 2009 growing season, on 15 June, 6 July, 27 July, 19 August, and 1 September. Sampling was performed between 1000 and 1600 EST on clear, calm, sunny days, with the initial replicate for sampling rotated on each date. All flowering forbs within each sampling area were identified, and the number of floral units counted using the method of Dicks et al. (2002). Upon arrival at a sampling plot, we waited one minute for insects to resume normal activity, then counted and identified all flower–visiting arthropods during a 5–minute period, noting the plant species they visited. Flower–visiting species were collected using a Bioquip Insect Vac (Rancho Dominguez, CA) or visually identified to species in the case of *Apis mellifera, Agapostemon sericeus, Ceratina calcarata/dupla, Augochlorella aurata, Dolichovespula maculata, Hylaeus* sp., *Toxomerus sp., Gymnosoma occidua, Plagiognathus politis, Phymata pennsylvanica*, and Lepidoptera. All identified species were subsequently included in plant–pollinator networks.

Pollinator function

In April 2008, we tested three species for their potential use as pollination sentinel plants: *Asclepias incarnata* L., *Lobelia siphilitica*, and *Eupatorium perfoliatum*. All three species are native to Michigan prairie fens, are known to be attractive to a number of pollinators (Tuell et al. 2008), and have short lifespans which allow successful propagation and reliable flowering. To test for pollinator dependency, we grew each species obtained as plant plugs (Wildtype Native Plant Nursery, Mason MI) in a greenhouse, watered with 100 ppm N (Peters Professional 20-20-20, Scotts, Maryville, OH) and 24/22 degrees C day/night and 20/4 hours light/dark. When plants were flowering, we placed them into a 2x2 m mesh cage in the greenhouse, 3 without and 3 with mesh bags over inflorescences to exclude pollinators. We placed a "research mini" hive of *Bombus impatiens* (Koppert, Romulus, MI) in the cage with flowering plants of A. incarnata, *L. siphilitica* and *E. perfoliatum* for 17, 22, and 35 days, respectively, during April-May 2008. We then allowed plants to develop, and counted seeds and fruits after fruits matured. We found no significant differences using a 2-tailed, paired t-test in the number of seeds per flower on *L. siphilitica* (P=0.556) or *E. perfoliatum* with versus without pollination, but did find significant differences in *A. incarnata* (P=0.012). We therefore used paired sentinel *A. incarnata* L. plants to assess the level of pollination in the field. There is some controversy regarding the degree to which *A. incarnata* is a self–incompatible species (Lipow and Wyatt 2000), but at minimum pollinia must be transferred within a flower for pollination to occur, so insects are key to pollination of this species (Judd 2002).

The field study was carried out in 2008 and 2009 using *A. incarnata* plants of genotypes originally collected from Jackson and Ingham counties in Michigan (Wildtype Native Plant Nursery, Mason, MI). Plants were potted into 2.5 gallon pots and individuals with similar numbers of buds were paired. Plants were placed in all 15 plots at the

MacCready site, near the center of each replicate, and in 4 replicates 15 m from each other at the Grand River site from 8 – 22 July 2008 and 13 – 30 July 2009. In both years timing of the field experiment corresponded with natural flowering phenology of A. *incarnata* at these sites. All open flowers were removed before placement in the field and one plant was bagged with no–see–um netting (Skeeta, Bradenton, FL) to exclude pollinators while the paired plant was left unbagged to allow full access by pollinators. This design accounts for any incidental self–pollination within plants. In 2009, we also sprayed Tangle–trap insect trap coating (Tanglefoot Company, Grand Rapids, MI) on all plant stems of pollinator excluded plants to prevent small insects from climbing the stems and accessing flowers.

We counted the number of flower clusters that opened on each plant during its time in the field. When most plants had finished blooming, all plants were removed from the field, and unopened buds were excised and plants were bagged to prevent insect visitation so that subsequent fruit set was due to field pollination only. Bagged plants were held outdoors while fruits developed. Fruits were collected when mature but before dehiscence, dried, and frozen for 24h to kill seed–feeding insects. The length and weight of each pod, and number of viable seeds produced were measured for each fruit. In 2009, a systemic insecticide was applied to all plants after removal from the field site at a rate of 0.37g/liter (imidacloprid, Marathon granular, OHP Inc, Mainland, PA) on 1 August to prevent oleander aphid (*Aphis nerii* Boyer de Fonscolombe) feeding on plants.

During *A. incarnata* deployment in the field, we observed all flower–visiting insects for 10 minutes/ replicate three times during each field season (10, 14–15, and 17 July 2008, 16, 20, and 24 July 2009) between 1000 and 1600 EST on calm, sunny days.

To prevent bias, the starting replicate for sampling was rotated on each date. Insects were collected whenever possible and identified to species and to genus when only observed in the field.

Statistical analysis

Pollinator networks

We condensed all species interactions into one plant–pollinator network per replicate of each treatment, and created one matrix for each, representing the number of visits at each plant species by a particular insect species. Due to the low number of sample replicates and uneven sample sizes, all 7 replicates were included together in the plant–pollinator network analyses. We calculated a set of quantitative network parameters for each matrix using R (Bipartite v. 1.11, R Project 2009). Metrics included: 1) connectance, a measure of the proportion of possible links that were actually observed, 2) compartment diversity, Shannon's diversity index across compartment sizes, 3) vulnerability, the mean number of links per plant, 4) generality, the mean number of plants per pollinator and 5) interaction evenness, based on Shannon's diversity with matrix cells as species and interactions as abundance (Tylianakis et al. 2007). A number of metrics examining the topology of plant–pollinator networks are correlated (Tylianakis et al. 2007, Dormann et al. 2009). We performed a Pearson correlation between values for these metrics, eliminating those that were significantly correlated at a Bonferroni–adjusted P of 0.0021. Although we used weighted, quantitative metrics in all cases (Banasek-Richter et al. 2004), a number of metrics are known to be affected by the richness of both lower and higher trophic levels in the web. We accounted for these effects by performing an ANCOVA with treatment as the main effect and the number of plant and pollinator species within the network as covariates (JMP v. 8.0.2, SAS Institute 2009). We report p-values for treatment effects using type III sums of squares, accounting for the effect of the number of species in the web. We assessed residuals for adherence to the assumption of homogeneity of variances, and performed reciprocal transformations on connectance and vulnerability to meet this assumption.

Because plant–pollinator interactions were nearly absent in unrestored areas, we could not calculate quantitative parameters on these networks. To examine differences in fundamental properties of the webs, including: observed flowering plant richness, proportion of plant species not visited by pollinators, pollinator richness, sampling time, and floral density per replicate, we performed ANOVAs with treatment as the main effect (SAS Institute 2010). To examine differences in the insect and plant community between treatments, we created a Bray–Curtis similarity matrix using square root transformed data, adding 1 to all values so that replicates with low insect and plant abundance remained in the analysis. This matrix was used in non–metric multidimensional scaling (NMDS) to examine the relationships between treatments, with points closer to each other in 2–dimensional space being more similar. We performed the NMDS using 2 and 3 dimensions, with a minimum stress of 0.01 and 25 random starting configurations (Clarke and Gorley 2006a). Stress values for 2–dimensional figures were 0.14 or less, indicating that the 2–dimensional representation shown is an accurate representation of the relationship between the points overall, although likely not necessarily between clustered points (Clarke and Gorley 2006b). We compared treatments using analysis of similarity (ANOSIM) with the resemblance matrix for each treatment, including 999 random permutations (Clarke and Gorley 2006b).

Pollinator function

We compared treatment and time effects on two characteristics of *A. incarnata* plants open to pollinators: the number of seeds/fruit and the number of fruits/flower cluster open during deployment (accounting for incidental pollination on paired, pollinator exclusion plants). We also compared treatment and time effects on flower–visiting insect richness and abundance, as well as bee and butterfly abundance, standardizing all values by the number of flower clusters open during sampling. We used 2–way ANOVAs with treatment (invaded, restored, on–site reference, off–site reference) and time (i.e. growing season since restoration; year 1 and year 2), as well as their interaction (PROC Mixed, SAS Institute 2010).

Results

Plant–pollinator networks

We observed a total of 684 plant–insect interactions in 19 plant–insect webs, including 100 insect and 52 flower species (Table 12, Table 13). We found striking differences in plant–pollinator web structure between invaded and both restored and uninvaded plots. Networks at the herbaceous plant level were greatly simplified, and nearly absent, in invaded plots (Figure 13A), with few plants in the web, as well as low floral density (Table 14). In restored and reference plots, there were a greater number of interactions, as well as more species of both plants and pollinators (Figure 13B,C). Interestingly, the restored replicates contained greater plant species richness, floral density, and a greater number of plant–pollinator interactions than the uninvaded reference plots (Table 14).

Analyses of a number of network factors, accounting for the number of pollinators and plants in the network, show no significant differences between the interactions within restored and uninvaded reference networks (Table 15). There was, however, a marginally significant difference in interaction evenness between restored (0.843 ± 0.025) and reference networks (0.940 ± 0.019) with greater evenness in reference networks, indicating increased uniformity of interactions between trophic levels along different pathways in reference networks.

An NMDS ordination of the plant and insect communities shows that both the insect and plant communities differ between the reference and restored plots (Figure 14). The reference and restored areas cluster separately and are significantly different in both plant (R 0.96, P=0.012) and insect (R 0.81, P=0.012) species identity and abundance. The flowering plant (R 0.74, P=0.002) and insect (R 0.96, P=0.002) communities in restored plots are distinct from those in invaded plots, as well. The two reference sites (on– and off–site), which were lumped for the prior analysis, are not significantly different in their plant communities (R 0.00, P=0.486). Notably, the flowering shrub *Potentilla fruticosa* auct. non L. was the most abundant and most visited plant species in all but one of the reference replicates (Figure 13C), while it was entirely absent from the restored replicates. The on–and off–site references differed in insect communities (R 0.56, P=0.029), and the insect communities in them were more similar to each other than the references were to the restored or invaded treatments (Figure 14B).

Pollinator function

We observed 202 total insects in 40 genera in 2008, and 96 insects in 26 genera in 2009, with a total of 329 *A. incarnata* flower clusters blooming on uncaged plants in the field in 2008 and 403 flower clusters in 2009. We found significant differences in the number of fruits produced in 2008, but not in 2009 (Table 16, Figure 15A). In 2008, we found significantly greater number of fruits per flower cluster in the restored, on– and off–site reference than the invaded plots, indicating that pollinator function was fully restored in the first year following invasive removal. We found no significant differences in the abundance of seeds per fruit by treatment or year, with a mean of 50.1± 2.4 seeds per fruit (Table 14), indicating that the number of fruits produced does, in fact, represent plant reproductive output.

We found differences by treatment in the rate of insect visitation at flowers (Table 14, Figure 15B), with significantly greater insect density at the off–site reference than all other treatments, no significant difference between the on–site reference and restored plots, and a significantly lower flower–visiting insect density in the invaded plots. This difference indicates that flower–visiting insect rates we observed in the off–site reference may be greater than those required for pollen saturation at *A. incarnata*. In 2009, we observed no significant differences in rates of insect visitation by treatment (Figure 15B), which fits with the similar rates of fruit production in that year (Figure 15A).

We examined pollinator species richness to assess whether fruit set was affected by the number of flower–visiting insect species. We found significant differences in pollinator richness by treatment and by year, with no significant treatment*year interaction (Table 16, Figure 15C) with greatest richness at on–site reference plots, followed by the off–site reference, restored, and invaded plots.

We also assessed whether restoration had differential effects on different key pollinator groups; hymenoptera have been shown to be the most abundant and effective pollinators of related *Asclepias* species, with *Apis mellifera* inefficient at pollen transfer (Theiss et al. 2007). Lepidoptera were less abundant and less likely to pick up *Asclepias* pollinia, so were overall less effective pollinators (Theiss et al. 2007). Therefore, we examined the visitation rates of Lepidoptera and bees separately. We found significant differences in butterfly abundance by treatment and time (Table 16). Bee abundance differed significantly by treatment, but not by year (Table 16, Figure 15D), with significantly greater bee visitation rates at flowers at the off–site reference than the restored and invaded plots, and intermediate rates at the on–site reference. There were no significant differences in the evenness of plant–visiting insects by treatment or year, based on the Berger–Parker index of dominance (Table 16).

Discussion

Incorporation of plant-pollinator networks and the resultant levels of pollination function could greatly strengthen our ability to assess the success of ecological restorations. Our examination of shifts in a plant–pollinator networks under restoration indicated a near complete absence of plant–pollinator interactions in invaded areas, with rapid network recovery following restoration. We found that although both plant and insect identities varied between restored and uninvaded reference plots, plant–pollinator network topologies were similar. In addition, we linked these findings to pollination of one species within that web, *A. incarnata*, and found recovery of pollinator function in restored areas within the first growing season following restoration.

We found no significant differences in network properties between restored and reference webs, in properties including web connectance, compartment diversity, the generalization of pollinators, and vulnerability of plants. We did find marginally greater interaction evenness in reference plots. Our findings match those of other plant–pollinator networks in restored areas, including heath (Forup et al. 2008) and old field hay meadows (Forup and Memmott 2005), where no significant differences in network topologies were found between restored and reference areas, although there were trends in both studies toward greater connectance and more complex species interactions in reference than restored areas. Our study also indicated subtle differences between network structures in restored and intact ecosystems. Despite finding no differences in network structure between restored and reference plots, we did find significant differences in both the plant and pollinator communities between restored and reference plots, indicating that species interactions were restored independent of species identity. This finding is also consistent with other restorations in which network structure is restored while species identities remain distinct (Forup and Memmott 2005, Forup et al. 2008).

One unique component of our findings was the near complete lack of a plant–pollinator web under *F. alnus*. The fact that *F. alnus* is not wind-pollinated and produces seed readily suggests that pollinators are visiting its flowers in the canopy, however this network does not extend to the understory under *F. alnus*. One caveat is that there may be a network of pollinators visiting the shade-tolerant herbaceous plants that bloom earlier in the growing season than we measured. In other plant–pollinator networks, invasive plants have similar growth habits to the natives, and their effects on plant–pollinator webs have been measured directly (Aizen et al. 2008, Bartomeus et al. 2008) and vary, depending on their flowering phenology compared to the native community (Bartomeus et al. 2008). In addition, non–native plant species have been found to be potential stabilizers of plant–pollinator networks, even as they fundamentally modify their structure (Aizen et al. 2008, Valdovinos et al. 2009). The drastic and rapid modification of the plant–pollinator web at ground level that we found with restoration indicates that in cases where invasive plants alter plant community structure, plant–pollinator networks between multiple species may be less likely to persist.

Our examination of pollination on the sentinel plant *A. incarnata* indicated that pollinator function was rapidly restored in this system. In the first year following restoration we saw greater fruit set in restored and reference than invaded plots. The significantly greater pollinator visitation rates at off–site reference plots indicated that *A. incarnata* may have a fruit production threshold that was reached at a fraction of the pollinator density. The insect species richness patterns that only loosely match patterns in fruit production also fit with prior findings that, for *A. incarnata*, pollinator effectiveness, rather than the rate of insect visitation, is the best predictor for pollination (Sahli and Conner 2006). Pollinator constancy at *A. incarnata* is known to be high, but pollinator effectiveness is determined both by an insect's ability to remove pollinia and the proportion of pollinia removed that are inserted into the flower (Theiss et al. 2007). Therefore, low pollinator diversity can lead to high rates of pollination when pollinators that are most effective are also most abundant (Perfectti et al. 2009).

We found no significant differences in fruit production or pollinator visitation rates between *A. incarnata* in restored or invaded plots in the second season following restoration even though pollinator networks remained nearly absent in invaded plots. There are several, related, possible explanations for these patterns. The first is that both plant and pollinator species in networks are known to vary from year to year, although web properties can remain consistent between years (Alarcon et al. 2008, Olesen et al.

2008, Petanidou et al. 2008). Thus, our finding of varying pollinator function between year 1 and year 2 may have been driven by stochastic factors alone. A second explanation is that flower density changed in restoration plots over time, influencing pollinator behavior. In the first growing season, vegetative cover and flowering plant density remained low in restored plots, while by the second growing season, flowering plant density in restored plots was greater than that in reference plots. This could have led to greater competition between plants for pollinators in the restored plots (Sargent and Ackerly 2008). Finally, there are known, positive spillover effects on plant diversity beyond the edges of restored areas (Brudvig et al. 2009). In this case, we may have measured a spillover effect of restoration on pollinator function as pollinators became more likely to search for floral resources in invaded areas that neighbored restored areas greater floral densities.

Generalist pollinators may be playing a key role in our system which in the initial phases of restoration represents an early successional plant community (Chapter 3). Many early successional species have adaptations, including self–compatibility and wind–dispersed seeds, that may lead to lower likelihood of pollen limitation (Bond 1994, Ashman et al. 2004). In contrast, the plant community of high quality fens may be reproducing vegetatively (Klimkowska et al. 2009), so that fen species that did not persist with *F. alnus* invasion may no easily return to restored areas. Determining potential mechanisms for patterns of restored function even as differences in plant communities persist would also allow for explicit restoration of pollinator function in communities with plant species that are likely to be pollen–limited (Bond 1994) and could increase relocation success of pollinator–dependent plant species. In our study, intact areas of prairie fen were within 400m of restored areas, so that in a landscape context, there was a potential source of both plants and pollinators nearby (Pauw 2007).

Our approach combining functional elements of restoration with plant–pollinator network structure allows potential assessment of the mechanisms of pollinator limitation, as well as providing a meaningful metric for the recovery of function with restoration. Assessment of function and species networks approached in tandem with species diversity measurements could provide mechanisms for assessing why restorations aren't successful, as well as providing a more complete understanding of ecosystem processes in degraded and restored habitats.

Acknowledgements

Research funding was provided by National Fish and Wildlife Foundation, the MSU MacCready Endowment, and a Hanes Trust Fellowship of the Michigan Botanical Society. We are grateful to The Nature Conservancy of Michigan for allowing our use of the Grand River fen as a field site. Funding support for A.K.F. was provided through a sustainable agriculture predoctoral fellowship by the C.S. Mott foundation a MSU Barnett Rosenberg predoctoral fellowship in biological sciences, and a MSU College of Agriculture dissertation completion fellowship. T. Rezniceck provided valuable plant identification, M. Arduser, J. Tuell, G. Parsons, B. DeMarco, F. C. Thompson, and M. Neilsen provided valuable insect identifications.

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Table 12. Plant species in quantitative flower visitation webs included in Figure 13.

Code	**Family**	**Genus species**	**Common Name**
ASTLAN	Asteraceae	*Aster lanceolatus* Willd.	white panicle aster
BOECYL	Urticaceae	*Boehmeria cylindrica* (L.) Sw.	false nettle
CIRLUT	Onagraceae	*Circaea lutetiana* L.	broadleaf enchanter's nightshade
CIRMUT	Asteraceae	*Cirsium muticum* Michx.	swamp thistle
EPICOL	Onagraceae	*Epilobium coloratum* Biehler	purpleleaf willowherb
EUPPER	Asteraceae	*Eupatorium perfoliatum* L.	common boneset
FRAALN	Rhamnaceae	*Frangula alnus* Mill.	glossy buckthorn
GALBOR	Rubiaceae	*Galium boreale* L.	northern bedstraw
GEUCAN	Rosaceae	*Geum canadense* Jacq.	white avens
HYPHIR	Liliaceae	*Hypoxis hirsuta* (L.) Coville	common goldstar
IMPCAP	Balsaminaceae	*Impatiens capensis* Meerb.	jewelweed
LOBKAH	Campanulaceae	*Lobelia kalmii* L.	Ontario lobelia
LOBSIP	Campanulaceae	*Lobelia siphilitica* L.	great blue lobelia
LYSQUA	Primulaceae	*Lysimachia quadriflora* Sims	fourflower yellow loosestrife
LYCUNI	Lamiaceae	*Lycopus uniflorus* Michx.	northern bugleweed
MENARV	Lamiaceae	*Mentha arvensis* L.	wild mint
MIMRIN	Scrophulariaceae	*Mimulus ringens* L.	Allegheny monkeyflower
PARGLA	Saxifragaceae	*Parnassia glauca* L.	grass of parnassus
PEDLAN	Scrophulariaceae	*Pedicularis lanceolata* Michx.	swamp lousewort
PENSED	Crassulaceae	*Penthorum sedoides* L.	ditch stonecrop
POTFRU	Rosaceae	*Potentilla fruticosa* auct. non L.	shrubby cinquefoil
POLPUN	Polygonaceae	*Polygonum punctatum* Elliot	dotted smartweed
POLSAG	Polygonaceae	*Polygonum sagittatum* L.	arrowleaf tearthumb
ROSMUL	Rosaceae	*Rosa multiflora* Thunb.	multiflora rose
SCUGAL	Lamiaceae	*Scutellaria galericulata* L.	marsh skullcap
SOLDUL	Solanaceae	*Solanum dulcamara* L.	climbing nightshade
SOLOHI	Asteraceae	*Solidago ohioensis* Frank ex Riddell	Ohio goldenrod
SOLPAT	Asteraceae	*Solidago patula* Muhl. ex Willd.	roundleaf goldenrod
SOLRUG	Asteraceae	*Solidago rugosa* Mill.	rough-leaved goldenrod
VALULI	Valerianaceae	*Valeriana uliginosa* (Torr. & A. Gray) Rydb.	mountain valerian

Table 13. Insect species in quantitative flower visitation webs included in Figure 13.

Code	Order	Family	Genus species
	Hymenoptera		
1		Apidae	*Anthophora terminalis* Cresson
2		Apidae	*Apis mellifera* L.
3		Apidae	*Bombus fervidus* (F.)
4		Apidae	*Bombus impatiens* Cresson
5		Apidae	*Bombus vagans* Smith
6		Apidae	*Ceratina calcarata/dupla* [a]
7		Colletidae	*Hylaeus* sp.
8		Halictidae	*Augochlora pura* (Say)
9		Halictidae	*Augochlorella aurata* (Smith)
10		Halictidae	*Augochloropsis metallica fulgida* (Smith)
11		Halictidae	*Halictus rubicundus* (Christ)
12		Halictidae	*Lasioglossum lineatulum* (Crawford)
13		Ichneumonidae	"ichneum2"
14		Tiphiidae	*Myzinum* sp.
15		Vespidae	*Dolichovespula arenaria* (Fabricius)
16		Vespidae	*Dolichovespula maculata* (Linnaeus)
	Diptera		
17		Syrphidae	*Sphaerophoria* sp.
18		Syrphidae	*Syrphus ribesii* (Linnaeus)
19		Syrphidae	*Toxomerus marginatus* Say
20		Tachinidae	*Jurinopsis adjusta* Van der Wulp
21		Tephritidae	*Urophora* sp.
	Coleoptera		
22		Cerambycidae	*Euderces picipes* (F.)
23		Chrysomelidae	*Diabrotica undecimpunctata* (Barber)
24		Coccinellidae	*Harmonia axyridis* (Pallas)
25		Mordellidae	*Mordella atrata* (Melsheimer)
26		Mordellidae	*Mordella marginata* (Melsheimer)
	Hemiptera		
27		Miridae	*Neurocolpus nubilis* (Say)
28		Miridae	*Plagiognathus* sp.
29		Phymatidae	*Phymata pennsylvanica* (Handlirsch)
30		Reduviidae	*Zelus luridus* Stal

Table 14. Characterization of plant–pollinator networks in invaded, restored, and uninvaded reference treatments. Mean ±SEM.

Treatment	Plant richness	Insect richness	% of plants not visited	Floral density~	# of interactions
Invaded	1.2 ± 0.5	1.7 ± 0.9	59.7 ± 15.0	1.3 ± 0.4	2.0 ± 1.1
Restored	9.8 ± 1.5	22.5 ± 2.9	32.6 ± 9.3	14.1 ± 1.7	77.5 ± 18.4
Reference	5.6 ± 0.8	13.6 ± 1.2	55.5 ± 5.1	5.2 ± 0.8	25.9 ± 4.9

~Per m^2

Table 15. Differences in plant–pollinator network structure metrics between restored and uninvaded reference plots, based on an analysis of covariance with the number of plant and pollinator species in each network accounted for, with DF 3,9.

Factor	**F**	**P**	**R^2**
Connectance*	0.3	0.580	0.958
Compartment diversity	0.2	0.652	0.172
Generality	3.0	0.796	0.894
Vulnerability*	0.5	0.484	0.662
Interaction evenness	4.4	0.066	0.447

* Reciprocal transformation performed for data analysis

Table 16. Differences in pollinator function and insect visitation at *A. incarnata* plants between invaded, restored, and uninvaded treatments. Insect abundances are scaled by the number of *A. incarnata* flower clusters open during sampling. Significant p-values (α=0.05) are bolded.

Factor	Treatment		Year		Treatment * year	
	F	**P**	**F**	**P**	**F**	**P**
Seeds/fruit	0.5	0.664	2.4	0.134	2.0	0.147
Fruits/flower cluster*~	12.5	**<.001**	3.3	0.081	4.9	**0.007**
Total insect abudance*	8.0	**0.001**	10.2	**0.004**	4.9	**0.008**
Bee abundance*	3.1	**0.042**	0.1	0.911	1.6	0.214
Butterfly abundance*	3.9	**0.019**	4.8	**0.037**	1.1	0.371
Pollinator species richness	5.5	**0.005**	4.4	**0.047**	0.7	0.577
Berger-Parker dominance	0.3	0.852	2.1	0.156	1.5	0.238

* log(x+1) transformed data used for analysis.

^Square root transformed data used for analysis.

~Accounting for pods produced in the unpollinated pair (i.e. incidental pollination)

Figure 13. Quantitative flower visitation webs for representative replicates of the A) invaded, B) restored, and C) reference prairie fen plots. Plant species are represented by rectangles on the bottom of the figure, insects are shown on the top level. The width of a bar represents the relative abundance of pollinators or plants and the frequency of the interaction is represented by the width of the line from pollinators to plants. Flowers that were observed but no pollinators were observed at are present in these webs, but with no line connecting them to pollinators. Hymenopteran flower–visitors are shown in black, insects from all other orders are in grey.

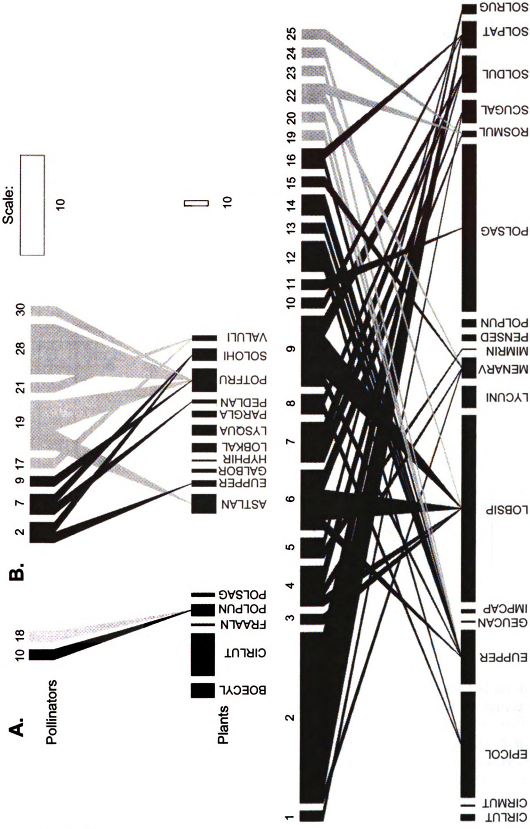
A.
Pollinators
Plants
10
18
BOECYL
CIRLUT
FRAALN
POLPUN
POLSAG
B.
2
7
9
17
19
21
28
30
ASTLAN
EUPPER
GALBOR
HYPHIR
LOBKAL
LYSQUA
PARGLA
PEDLAN
POTFRU
SOLOHI
VALULI
Scale:
10
10
C.
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
19
20
22
23
24
25
CIRLUT
CIRMUT
EPICOL
EUPPER
GEUCAN
IMPCAP
LOBSIP
LYCUNI
MENARV
MIMRIN
PENSED
POLPUN
POLSAG
ROSMUL
SCUGAL
SOLDUL
SOLPAT
SOLRUG

Figure 13.

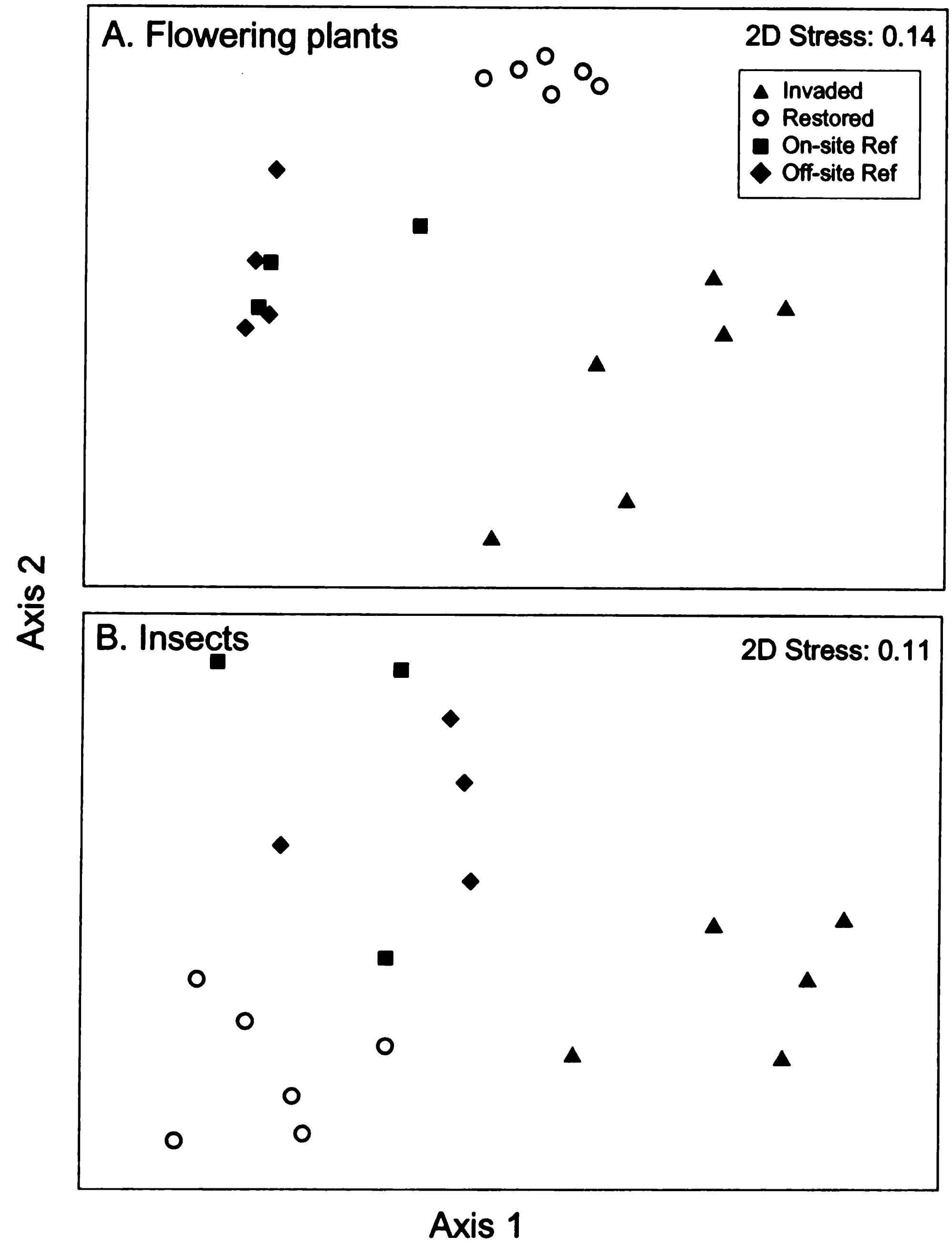

Figure 14. Two dimensional NMDS ordinations of A) the flowering plant and B) flower–visiting insect communities in plant–pollinator interactions. Both A) and B) indicate that there are distinct plant and pollinator communities at the uncleared and cleared plots. A) shows no distinction between the plant communities in the on– and off–site references, while B) reveals significantly different plant–visiting insect communities between on– and off–site references. The ordination is based on a Bray–Curtis dissimilarity matrix (using n+1) with mean values per replicate and treatment; data were square root transformed. Stress values were 0.14 and 0.11 for flowering plants and insects, respectively.

Figure 15. Patterns of A) pollinator function and at *A. incarnata* flower–visiting B) insect richness C) insect abundance and D) bee abundance in the first and second seasons following restoration. Insect richness and abundances are based on means by treatment and replicate over three sampling dates. Error bars are +SEM, □=0.05. Treatment effects from a 2–way ANOVA with treatment and time are shown where significant. Letters in upper and lower case within the same graph indicate that treatments differed by year or treatment*year.

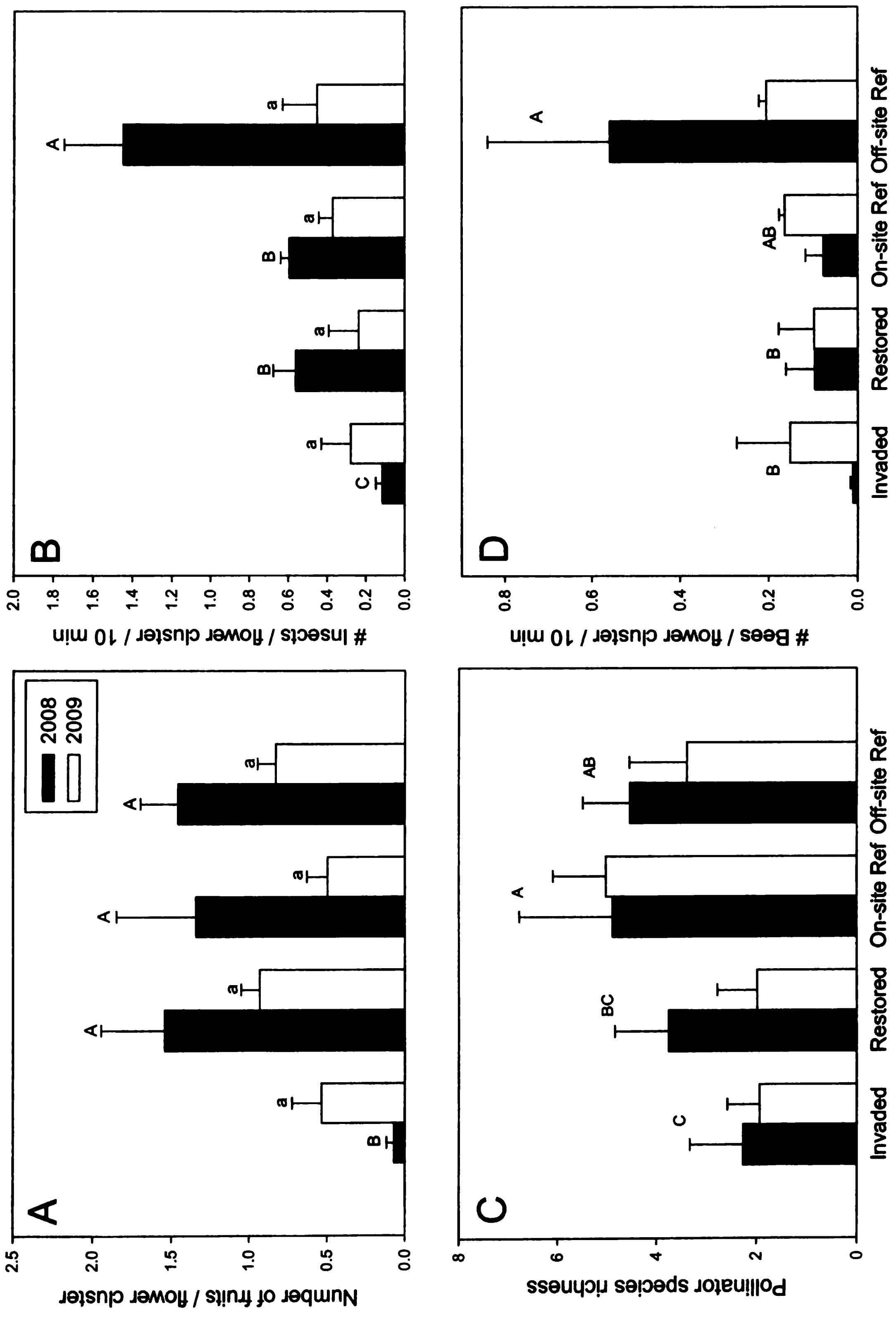
A
Number of fruits / flower cluster
0.0
0.5
1.0
1.5
2.0
2.5
2008
2009
B
a
A
a
A
a
A
a
B
Insects / flower cluster / 10 min
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
C
a
B
a
B
a
A
a
C
Pollinator species richness
0
2
4
6
8
C
BC
A
AB
D
Bees / flower cluster / 10 min
0.0
0.2
0.4
0.6
0.8
B
B
AB
A
Invaded
Restored
On-site Ref
Off-site Ref
Invaded
Restored
On-site Ref
Off-site Ref

Figure 15.

Chapter 6

CONCLUSION

IMPROVING THE PRACTICE OF RESTORATION THROUGH RESTORATION ECOLOGY

Ecosystem restoration was first practiced in the 1940's with Aldo Leopold's pioneering prairie restoration efforts in Wisconsin (Jordan et al. 1987). The subsequent emergence of ecosystem restoration as a science is, in fact, a measure of our increasing understanding of complex ecological systems (Jordan et al. 1987) as well as a means to uncover gaps in our scientific knowledge. The practice of ecosystem restoration provides a unique opportunity to address those knowledge gaps through development of ecological theory and paradigms. The applied aspects of restoration dominated the science until the 1990's so that the branch of ecology that has stemmed from ecosystem restoration, restoration ecology, is relatively young (Young et al. 2005). The goal of ecosystem restoration is the recovery of an ecosystem toward a healthy, functional system (SER Working Group 2004). Therefore, ecosystem restoration involves manipulating species and processes within ecosystems and by its very nature provides potential for large-scale experimental and observational studies that inform basic questions about community and ecosystem ecology. My PhD research spans several areas of ecological theory that could be informed through restoration, including species competition, succession, examination of mutualisms, recruitment limitation, and ecosystem function (Young et al. 2005).

This study is unique within a restoration ecology context in two ways. First, it includes low-quality invaded areas and high-quality uninvaded reference areas in addition to restored areas. In many cases restoration projects are performed in areas where there is no available reference community, so historic conditions are used instead (White and Walker 1997). In other cases, the comparisons lie between areas that have already been restored and high quality references (e.g. Forup and Memmott 2005, Forup et al. 2008) which do not provide an indication of the change since factors degrading the system were removed or altered. Second, it incorporates a multi-faceted assessment of restoration including conditions in invaded and high quality areas before restoration began (Chapter 2) resource availability and plant community structure (Chapter 3), pollinator and plant diversity (Chapter 4), and plant-pollinator network structure and pollination in invaded, restored, and uninvaded plots (Chapter 5). This is the first study, to my knowledge, that incorporates examination of all of these facets within a single ecosystem.

This cross-cutting approach not only provides a more nuanced assessment of restoration success, it combines two areas of ecology that were, until recently, seen as distinct: community and ecosystem ecology. The community ecology paradigm includes a smaller-scale focus on species diversity and constraints that lead to greater or lower diversity, as well as species interactions (Loreau 2010). The ecosystem ecology paradigm includes a larger-scale focus on energy flow and nutrient cycling, with biogeochemical processes as the primary focus (Loreau 2010). The new paradigm, incorporating the strengths of both community and ecosystem ecology, is one focused on biodiversity and ecosystem functioning (Schwartz et al. 2000, Naeem 2002, Loreau 2010).

My study incorporates plant and pollinator diversity, as well as examination of the community-based ecosystem function of pollination. Although I do not incorporate explicit examination of the relationship between biodiversity and ecosystem function in my study (Loreau et al. 2001), I found no significant differences in pollinator diversity (Chapter 4) plant-pollinator network properties, or pollinator function (Chapter 5) between restored and reference communities. Using this approach, I can assess whether functional elements of a system are consistent over time even if there are shifts in species diversity and identity, and incorporate a more current, Gleasonian understanding of plant communities as dynamic, rather than moving toward equilibrium after restoration (Gleason 1926). Because I have characterized abiotic factors in the system, I also have an understanding of what the biotic limitations may be.

A number of the factors I measured yielded different trajectories toward restoration. Interestingly, factors related to resource availability, including soil pH and microhabitat, showed no change in the first two growing seasons post-restoration (Chapter 2). Plant diversity and quality had also not changed in restored areas. On the other hand, a number of factors shifted rapidly post-restoration. Plant community structure had recovered broadly after 2 growing seasons. All metrics based on the pollinator community, including diversity, plant-pollinator networks, and pollination, recovered nearly immediately following restoration.

While it is clear that the restored areas are broadly on a trajectory toward the state in reference areas, I do not know whether the shift will continue over time. There may be biotic or abiotic thresholds in this system, so that the changes I have observed plateau or conditions shift in the direction of the invaded system (Suding et al. 2004, Suding and Hobbs 2009). Although my study has been relatively comprehensive in the factors measured post-restoration, the findings are limited by the short timescale represented, with two growing seasons post-restoration. Continued monitoring would not only assess whether the restoration is successful in the long-term, it could provide a link between elements of ecosystem theory and restoration (Young et al. 2005). These include 1) assessing dispersal or recruitment limitation of key fen species, especially sedges, 2) determining whether the lack of microtopography limits plant diversity and if microtopographic variability increases over scales of tens, rather than hundreds, of years,

3) tracking whether plant succession moves in the direction of species found in intact prairie fens, and 4) examination of plant-pollinator mutualisms and pollinator function over time, to determine whether structure and function of the pollinator system are stable across growing seasons.

This work also informs timescales for restoration in different ecosystems. The goal state for prairie fens is essentially one of arrested succession, with relatively frequent disturbance preventing extensive shrub growth. As a result, prairie fens are dominated by herbaceous perennial sedges, forbs, and grasses, as well as shrubs, resulting in a rapidly restorable community structure. This community structure is also part of the reason for the rapid plant and insect response; the primary plants are herbaceous perennial species, rather than much longer-lived trees. Timescales for restoration in open-structured ecosystems are likely to be shorter than those in which longer-lived trees are an important part of the structure.

Although the metrics of restoration success I measured broadly indicate success in terms of restoration, there are a number of factors which remain to be addressed. The research design of this site, with restoration of intentionally fragmented patches, would take a great deal of effort to maintain in the long-term. Even in more contiguous restored tracts, long-term control of invasive species will be required, as invasives are part of the regional species pool and can disperse into the restored area (Matthews et al. 2009). Studies on habitat restoration typically focus on restoration of single habitat types, despite the fact that habitats occur on gradients and were historically interconnected. There is mounting evidence that species will be more likely to persist in landscapes that facilitate dispersal among habitat patches (Ricketts 2001, Franklin and Lindenmayer

2009). Explicit tests of the effect of restoration across habitats (e.g. of prairie fens and neighboring upland prairie and oak savanna systems) would provide ideal conditions to assess whether there are positive effects of restoration in linked habitats, including increased native plant diversity within and outside of restored areas (Brudvig et al. 2009).

Because research related to restoration is performed with limited resources, on-ground restoration that incorporates any type of monitoring is relatively rare. I call for clear communication of restoration research findings as a vital component of improving the practice of ecosystem restoration. This extends beyond scientific publications to workshops, web-based tools, and contacts with conservation organizations. Both restoration ecology and ecosystem restoration would be advanced if restoration were regularly carried out in both the context of ecological and practical questions that need addressing, in collaboration with land managers.

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Appendix A. Soil nutrient levels (Mean ± SEM) from 1-10 cm soil depth cores.

Factor	**Time**	**Invaded**	**Removal**	**Reference**
NH_4 (ppm)	Pre-restoration	14.74 ± 1.33	14.52 ± 1.37	9.72 ± 2.49
	Year 1	9.16 ± 0.81	9.79 ± 1.08	6.13 ± 1.00
	Year 2	17.77 ± 2.07	12.85 ± 1.29	8.17 ± 1.49
NO_3 (ppm)	Pre-restoration	12.73 ± 2.42	17.83 ± 3.26	5.56 ± 1.13
	Year 1	6.70 ± 1.02	10.40 ± 1.72	6.92 ± 2.00
	Year 2	13.34 ± 2.87	13.45 ± 2.33	8.86 ± 3.09
Phosphorous (ppm)	Pre-restoration	7.78 ± 0.77	9.67 ± 1.30	6.17 ± 1.19
	Year 1	8.83 ± 1.35	9.06 ± 1.34	7.50 ± 1.35
	Year 2	10.17 ± 0.78	11.39 ± 1.08	4.78 ± 1.31
Potassium (ppm)	Pre-restoration	88.96 ± 8.30	79.12 ± 7.97	69.17 ± 16.65
	Year 1	104.36 ± 10.05	103.46 ± 10.14	94.47 ± 11.96
	Year 2	101.98 ± 8.32	85.89 ± 6.76	80.59 ± 10.07

Appendix B.

Plant Voucher Data

Page 1 of 5 Pages

Collection #	Family	Scientific Name	Date	Collection location
151	Euphorbiaceae	*Acalypha rhomboidea* Raf.	9/10/2008	Block 5
163	Aceraceae	*Acer rubrum* L.	5/30/2009	near Ref 1
103	Asteraceae	*Achillea millefolium* L.	6/6/2008	Block 6
157	Ranunculaceae	*Actaea rubra*	5/27/2009	Block 1 cleared
34	Scrophulariaceae	*Agalinis purpurea* (L.) Pennell	9/11/2007	interlake fen
133	Rosaceae	*Agrimonia parviflora* Aiton	8/14/2008	N of Block 1
189	Poaceae	*Agropyron trachycaulum* (Link) Malte ex H.F. Lewis	8/3/2009	Ref 3
164	Brassicaceae	*Alliaria petiolata* (M. Bieb.) Cavara & Grande	5/30/2009	Block 3 cleared
96	Fabaceae	*Amphicarpaea bracteata* (L.) Fernald	6/5/2008	Block 3
225	Poaceae	*Andropogon gerardii* Vitman	8/24/2009	Ref 3
156	Araceae	*Arisaema triphyllum* (L.) Schott	5/27/2009	Block 1 uncleared
248	Asclepiadaceae	*Asclepias incarnata*	7/16/2009	Ref 2
197	Asclepiadaceae	*Asclepias syriaca*	8/6/2009	interlake fen
16	Asteraceae	*Aster lanceolatus* Willd.	9/9/2007	Ref 1
12	Asteraceae	*Aster puniceus* var. firmus	9/9/2007	Ref 1
18	Asteraceae	*Aster umbellatus* Mill.	9/9/2007	Ref 1
257	Betulaceae	*Betula pumila* (L.)	7/3/2009	Ref 3
14	Asteraceae	*Bidens coronata (L.) Britton*	9/9/2007	Ref 1
13	Asteraceae	*Bidens frondosa* (L.)	9/9/2007	Ref 1
90	Urticaceae	*Boehmeria cylindrica* (L.) Sw.	6/5/2008	Block 2
143	Poaceae	*Bromus ciliatus* L.	9/5/2008	Ref 3
144	Poaceae	*Calamagrostis canadensis* (Michx.) P. Beauv.	9/5/2008	Ref 3
137	Ranunculaceae	*Caltha palustris* L.	5/15/2008	near Ref 1
57	Convolvulaceae	*Calystegia sepium* (L.) R. Br.	6/2/2008	Ref 3
246	Campanulaceae	*Campanula aparinoides* Pursh	7/27/2009	interlake fen
140	Brassicaceae	*Cardamine bulbosa* (Schreb. ex Muhl.) Britton, Sterns & Poggenb.	5/15/2008	Block 2 cleared
123	Cyperaceae	*Carex bebbii* Olney ex Fernald	7/30/2008	Block 5 cleared
101	Cyperaceae	*Carex blanda* Dewey	6/6/2008	Block 6
190	Cyperaceae	*Carex cryptolepis* Mack.	8/3/2009	Ref 3
52	Cyperaceae	*Carex flava* L.	6/2/2008	Ref 3
179	Cyperaceae	*Carex granularis* Muhl. ex Willd.	6/5/2009	Block 5 cleared
74	Cyperaceae	*Carex hystericina* Muhl. ex Willd.	6/4/2008	Ref 1
42	Cyperaceae	*Carex leptalea* Wahlenb.	9/11/2007	Block 1
73	Cyperaceae	*Carex pellita* Muhl. ex Willd.	6/4/2008	Ref 1
66	Cyperaceae	*Carex prairea* Dewey ex Alph. Wood	6/3/2008	Ref 2
60	Cyperaceae	*Carex sartwellii* Dewey	6/2/2008	Ref 3
51	Cyperaceae	*Carex sterilis* Willd., ♀	6/2/2008	Ref 3
54	Cyperaceae	*Carex sterilis* Willd., ♂	6/2/2008	Ref 3
78	Cyperaceae	*Carex stipata* Muhl. ex Willd.	6/4/2008	Block 1
72	Cyperaceae	*Carex stricta* Lam.	6/4/2008	Ref 1
53	Cyperaceae	*Carex tetanica* Schkuhr	6/2/2008	Ref 3

Appendix B

Plant Voucher Data

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Collection #	Family	Scientific Name	Date	Collection location
198	Cyperaceae	*Carex vulpinoidea* Michx.	8/6/2009	Block 5 cleared
154	Juglandaceae	*Carya* sp.	5/27/2009	Block 3 uncleared
51	Celastraceae	*Celastrus orbiculatus* Thumb	9/13/2007	Block 5
175	Apiaceae	*Cicuta maculata* L.	6/2/2009	Block 1 cleared
21	Poaceae	*Cinna arundinacea* L.	9/9/2007	Block 1
251	Onagraceae	*Circaea lutetiana* L.	7/3/2009	Block 2 cleared
150	Asteraceae	*Cirsium arvense* (L.) Scop.	9/9/2008	Block 6
213	Asteraceae	*Cirsium muticum* Michx.	8/17/2009	near 5 cleared
244	Asteraceae	*Cirsium vulgare* (Savi) Ten.	9/11/2009	Block 5 cleared
110	Cyperaceae	*Cladium mariscoides* (Muhl.) Torr.	7/28/2008	Ref 3
224	Ranunculaceae	*Clematis virginiana* L.	8/24/2009	Block 5 uncleared
62	Cornaceae	*Cornus foemina* Mill.	6/2/2008	Ref 3
63	Cornaceae	*Cornus stolonifera* Michx.	6/2/2008	Ref 3
254	Fabaceae	*Desmodium glutinosum* (Muhl. ex Willd.) Alph. Wood	7/16/2009	1 cleared
196	Poaceae	*Dichanthelium acuminatum* (Sw.) Gould & C.A. Clark var. *fasciculatum* (Torr.) Freckmann	8/6/2009	Block 6 cleared
46B	Dryopteridaceae	*Dryopteris carthusiana* (Vill.) H.P. Fuchs	9/12/2008	Block 1
102	Dryopteridaceae	*Dryopteris cristata* (L.) A. Gray	6/6/2008	Block 5
55	Cyperaceae	*Eleocharis elliptica* Kunth	6/2/2008	Ref 3
149	Cyperaceae	*Eliocharis elliptica* Kunth	9/8/2008	Block 4
41	Equisetaceae	*Equisetum arvense* (L.)	9/11/2007	Block 1
119	Asteraceae	*Erechtites hieraciifolia* (L.) Raf. ex DC.	7/29/2008	Block 6 cleared
162	Asteraceae	*Erigeron annuus* (L.) Pers.	5/27/2009	Block 1 cleared
161	Asteraceae	*Erigeron philadelphicus* L.	5/27/2009	Block 1 cleared
8	Asteraceae	*Eupatorium maculatum* L.	9/9/2007	Ref 1
260	Asteraceae	*Eupatorium perfoliatum* L.	9/14/2009	Near Ref 1
24	Asteraceae	*Euthamia graminifolia* (L.) Nutt.	9/11/2007	
259	Rosaceae	*Fragaria virginiana* Duchesne	9/14/2009	Upland near ref 1
153	Rhamnaceae	*Frangula alnus* Mill.	5/27/2009	Block 3 uncleared
50B	Oleaceae	*Fraxinus pennsylvanica* Marsh.	9/17/2007	Block 6
80	Rubiaceae	*Galium boreale* L.	6/4/2008	Block 1
100	Rubiaceae	*Galium circaezans* Michx.	6/6/2008	Block 6
1	Rubiaceae	*Galium triflorum* Michx.	9/9/2007	Ref 1
239	Gentianaceae	*Gentianopsis crinita* (Froel.) Ma	9/10/2009	Ref 3
159	Geraniaceae	*Geranium maculatum* L.	5/27/2009	Block 2 cleared
124	Rosaceae	*Geum canadense* Jacq.	7/30/2008	Block 5 cleared
61	Poaceae	*Glyceria striata* (Lam.) Hitchc.	6/2/2008	Ref 3
118	Boraginaceae	*Hackelia virginiana* (L.) I.M. Johnst.	7/29/2008	Block 2cleared, out
145	Asteraceae	*Helenium autumnale* L.	9/5/2008	Ref 3
236	Asteraceae	*Helianthus giganteus* L.	9/9/2009	Block 3 cleared
141	Liliaceae	*Hypoxis hirsuta* (L.) Coville	5/22/2008	Ref 3
56	Aquifoliaceae	*Ilex verticillata* (L.) A. Gray	9/17/2007	Block 5
203	Balsaminaceae	*Impatiens capensis* Meerb.	8/6/2009	Block 2 cleared
155	Iridaceae	*Iris versicolor* L.	5/27/2009	Block 1 cl

Appendix B
Plant Voucher Data
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Collection #	Family	Scientific Name	Date	Collection location
187	Juncaceae	*Juncus brachycephalus* (Engelm.) Buchenau	8/3/2009	Ref 3
64	Juncaceae	*Juncus dudleyi* Wiegand	6/3/2008	Ref 2
218	Cupressaceae	*Juniperus virginiana* L.	8/17/2009	Ref 2
183	Fabaceae	*Lathyrus palustris* L.	6/15/2009	Ref 2
206	Poaceae	*Leersia oryzoides* (L.) Sw.	8/6/2009	Block 2 cleared
237	Asteraceae	*Liatris spicata* (L.) Willd.	9/10/2009	Ref 3
208	Lauraceae	*Lindera benzoin* (L.) Blume	8/17/2009	Block 2 uncleared
219	Campanulaceae	*Lobelia kalmii* L.	8/17/2009	interlake fen
209	Campanulaceae	*Lobelia siphilitica* L.	8/17/2009	Block 3 uncleared
261	Caprifoliaceae	*Lonicera* L.	9/14/2009	Near Ref 1
3	Lamiaceae	*Lycopus americanus* Muhl. ex W. Bartram	9/9/2007	Ref 1
5	Lamiaceae	*Lycopus uniflorus* Michx.	9/9/2007	Ref 1
113	Primulaceae	*Lysimachia quadriflora* Sims	7/28/2008	Ref 3
165	Primulaceae	*Lysimachia thyrsiflora* L.	5/30/2009	Block 6 cleared
52A	Lythraceae	*Lythrum salicaria (L.)*	9/13/2007	Block 5
2	Lamiaceae	*Mentha arvensis* L.	9/9/2007	Ref 1
221	Scrophulariaceae	*Mimulus ringens* L.	8/24/2009	Block 1 cleared
28	Poaceae	*Muhlenbergia glomerata* (Willd.) Trin.	9/11/2007	Ref 1
243	Poaceae	*Muhlenbergia mexicana* (L.) Trin.	9/11/2009	Blocks 5-6
210	Dryopteridaceae	*Onoclea sensibilis* L.	8/17/2009	Block 2 uncleared
95	Apiaceae	*Osmorhiza claytonii* (Michx.) C.B. Clarke	6/5/2008	Block 2
217	Oxalidaceae	*Oxalis stricta* L.	8/17/2009	Block 6 cleared
126	Apiaceae	*Oxypolis rigidor* (L.) Raf.	7/25/2008	Block 2 uncleared
245	Poaceae	*Panicum capillare* L.	9/11/2009	Block 6 cleared
30	Poaceae	*Panicum dichotomiflorum* Michx.	9/11/2007	Ref 2
202	Vitaceae	*Parthenocissus quinquefolia* (L.) Planch.	8/6/2009	Block 2 cleared
229	Scrophulariaceae	*Pedicularis lanceolata* Michx.	8/24/2009	Ref 1
107	Crassulaceae	*Penthorum sedoides* L.	7/25/2008	Block 1 cleared
68	Poaceae	*Phalaris arundinacea* L.	6/4/2008	Ref 1
200	Phytolaccaceae	*Phytolacca americana* L.	8/6/2009	Block 2 cleared
204	Urticaceae	*Pilea pumila* (L.) A. Gray	8/6/2009	Block 2 cleared
199	Plantaginaceae	*Plantago major* (L.)	8/6/2009	Upland near Ref 1
71	Poaceae	*Poa pratensis* L.	6/4/2008	Ref 1
249	Polygonaceae	*Polygonum amphibium* L.	7/16/2009	interlake fen
130	Polygonaceae	*Polygonum hydropiperoides* Michx.	8/14/2008	Block 1 cleared
131	Polygonaceae	*Polygonum punctatum* Elliot	8/14/2008	Block 1 cleared
6	Polygonaceae	*Polygonum sagittatum* L.	9/9/2007	Ref 1
207	Polygonaceae	*Polygonum virginianum* L.	8/6/2009	Block 2 uncleared
129	Salicaceae	*Populus tremuloides* Michx.	8/14/2008	Block 3 cleared
234	Rosaceae	*Potentilla fruticosa* auct. non L.	8/24/2009	Ref 2
109	Lamiaceae	*Prunella vulgaris* L.	7/25/2008	Block 1 cleared
160	Rosaceae	*Prunus serotina* Ehrh.	5/19/2009	Block 2 uncleared
223	Fagaceae	*Quercus* sp.	8/24/2009	Block 5 uncleared
76	Ranunculaceae	*Ranunculus recurvatus* Poir.	6/4/2008	Block 1
230	Rhamnaceae	*Rhamnus cathartica* L.	8/24/2009	Block 3 uncl
33	Cyperaceae	*Rhynchospora alba* (L.) Vahl	9/11/2007	Ref 2

Appendix B
Plant Voucher Data
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Collection #	Family	Scientific Name	Date	Collection location
89	Grossulariaceae	*Ribes cynosbati* L.	6/5/2008	Block 2
106	Brassicaceae	*Rorippa palustris* (L.) Besser	7/25/2008	Block 1 cleared
227	Rosaceae	*Rosa multiflora* Thunb.	8/24/2009	near Ref 1
69	Rosaceae	*Rosa palustris* Marsh.	6/4/2008	Ref 1
253	Rosaceae	*Rubus pubescens* Raf.	7/16/2009	
67	Rosaceae	*Rubus strigosus* Michx.	6/3/2008	Ref 2
250	Asteraceae	*Rudbeckia hirta* L.	7/16/2009	Ref 2
92	Polygonaceae	*Rumex orbiculatus* A. Gray	6/5/2008	Block 2
9	Salicaceae	*Salix discolor* Muhl.	9/9/2007	Ref 1
99	Caprifoliaceae	*Sambucus canadensis L.*	6/5/2008	Block 3
205	Lauraceae	*Sassafras albidum* (Nutt.) Nees	8/6/2009	Block 1 uncleared
29	Poaceae	*Schizachyrium scoparium* (Michx.) Nash	9/11/2007	Ref 2
215	Cyperaceae	*Scirpus acutus* Muhl. ex Bigelow	8/17/2009	interlake fen
111	Cyperaceae	*Scirpus americanus* Pers.	7/28/2008	Ref 3
108	Cyperaceae	*Scirpus atrovirens* Willd.	7/25/2008	Block 1 cleared
17	Lamiaceae	*Scutellaria galericulata* L.(17)	9/9/2007	Ref 1
4	Lamiaceae	*Scutellaria lateriflora* L.	9/9/2007	Ref 1
138	Asteraceae	*Senecio aureus L.*	5/15/2008	Ref 1
180	Asteraceae	*Senecio pauperculus Michx.*	6/5/2009	Ref 2
79	Liliaceae	*Smilacina stellata* (L.) Desf.	6/4/2008	Block 1
47B	Smilacaceae	*Smilax tamnoides* L.	9/12/2008	Block 3
158	Solanaceae	*Solanum dulcamara* L.	5/27/2009	Block 1 cleared
220	Asteraceae	*Solidago altissima* L.	8/24/2009	Ref 1
59	Asteraceae	*Solidago gigantea* Aiton	6/2/2008	Ref 3
228	Asteraceae	*Solidago ohioensis* Frank ex Riddell	8/24/2009	Ref 2
241	Asteraceae	*Solidago patula* Muhl. ex Willd.	9/10/2009	Ref 1
240	Asteraceae	*Solidago ridellii* (Frank ex Riddell) Rydb.	9/10/2009	Ref 2
211	Asteraceae	*Solidago rugosa* Mill.	8/17/2009	Block 2 cleared
226	Poaceae	*Sorghastrum nutans* (L.) Nash	8/24/2009	Ref 2
121	Poaceae	*Sphenopholis intermedia* (Rydb.) Rydb.	7/30/2008	Block 3 cleared
238	Rosaceae	*Spiraea alba* Du Roi	9/10/2009	Ref 3
181	Araceae	*Symplocarpus foetidus* (L.) Salisb. ex Nutt.	6/5/2009	Block 1 uncleared
233	Asteraceae	*Taraxacum officinale* F.H. Wigg.	8/24/2009	Upland near ref 1
182	Ranunculaceae	*Thalictrum dasycarpum* Fisch. & Avé-Lall.	6/15/2009	Ref 2
232	Thelypteridaceae	*Thelypteris palustris* Schott	8/24/2009	near Ref 1
114	Clusiaceae	*Triadenum fraseri* (Spach) Gleason	7/28/2008	Ref 3
34B	Liliaceae	*Triantha glutinosa* (Michx.) Baker	9/11/2007	Ref 2
231	Typhaceae	*Typha* sp.	8/24/2009	Block 6 cleared
222	Ulmaceae	*Ulmus* sp.	8/24/2009	pines between block 5, Ref3
212	Urticaceae	*Urtica dioica* L.	8/17/2009	Block 2 cleared
184	Verbenaceae	*Verbena hastata* L.	7/31/2009	Block 1 cleared
147	Verbenaceae	*Verbena urticifolia* L.	9/7/2008	Block 2
139	Violaceae	*Viola nephrophylla* Greene	5/9/2008	Block 5
201	Vitaceae	*Vitis riparia* Michx.	8/6/2009	Block 2 cleared
192	Liliaceae	*Zigadenus elegans* Pursh ssp. *glaucus* (Nutt.) Hultén	8/6/2009	Ref 3

Appendix B

Plant Voucher Data

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Collection #	Family	Scientific Name	Date	Collection location
88	Cyperaceae	*Eleocharis rostellata* (Torr.) Torr.	6/4/2008	Grand River Fen
81	Cyperaceae	*Eriophorum viridicarinatum* (Engelm.) Fernald	6/4/2008	Grand River Fen
85	Poaceae	*Hierochloe odorata* (L.) P. Beauv.	6/4/2008	Grand River Fen
87	Poaceae	*Muhlenbergia richardsonis* (Trin.) Rydb.	6/4/2008	Grand River Fen
136	Saxifragaceae	*Parnassia glauca*	8/14/2008	Grand River Fen
84	Rosaceae	*Physocarpus opulifolius* (L.) Maxim., orth. cons.	6/4/2008	Grand River Fen
255	Lamiaceae	*Pycnanthemum virginianum* (L.) T. Dur. & B.D. Jacks. ex B.L. Rob. & Fernald	7/16/2009	Grand River Fen
256	Rhamnaceae	*Rhamnus alnifolia* L'Hér.	7/16/2009	Grand River Fen
82	Valerianaceae	*Valeriana uliginosa* (Torr. & A. Gray) Rydb.	6/4/2008	Grand River Fen

All specimens on pages 1-4 collected: USA Michigan, Jackson County, Clarklake, MacCready Reserve. 42° 7’37N 84° 23’30W. Elevation 300m, in prairie fen wetland. Collection date noted above.

All specimens on page 5 collected: USA Michigan, Jackson County, Liberty, Grand River Fen. 42° 5’02N 84° 27’38W. Elevation 300m, in prairie fen wetland. Collection date noted above.

Investigator's Name:
Anna K. Fiedler

Date: 24 August, 2010

Received the above listed specimens for deposit in the Michigan State University Herbarium.

24 Aug 2010

Curator Date

Appendix C.1 Record of Deposition of Insect Voucher Specimens*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa, which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: 2010-04

Title of thesis or dissertation (or other research projects):

RESTORATION OF PRAIRIE FEN PLANTS, INSECTS, AND ABIOTIC PROCESSES

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums:

Investigator's Name(s) (typed)
Anna Katherine Fiedler

Date 24 August 2010

*Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America.
Bull. Entomol. Soc. Amer. 24: 141-42.

Deposit as follows:
Original: Include as Appendix 1 in ribbon copy of thesis or dissertation.

Copies: Include as Appendix 1 in copies of thesis or dissertation.
Museum(s) files.
Research project files.

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

Appendix C

Insect Voucher Specimen Data

Page 1 of 6 Pages

		Number of:		
Species or other taxon	Date collected	Larvae	Nymphs	Adults
Hemiptera				
Pentatomidae *Acrostemum hilare*	27 July 2009, food web#66			1
Reduviidae *Zelus luridus* (Stal)	19 August 2009, food web #235			1
Miridae *Neurocolpus nubilus* (Say)	6 July 2009, food web #26, #34			2
Phymatidae *Phymata pennsylvanica* (Handlirsch)	27 July 2009, food web #64			1
Phymatidae *Phymata pennsylvanica* (Handlirsch)	19 August 2009, food web #187			1
Thyreocoridae *Corimelaena pulicaria*	19 August 2009, food web #213			1
Thyreocoridae *Corimelaena pulicaria*	27 July 2009, food web #80			1
Hymenoptera				
Vespidae *Dolichovespula arenaria* (Fabricius)	1 September 2009, food web #296, #268			2
Vespidae *Vespula vidua*	1 September 2009, food web #313, #299			2
Vespidae *Dolichovespula maculata*	19 August 2009, food web #189			1
Vespidae *Dolichovespula maculata*	1 Septemeber 2009, food web			1
Vespidae *Polistes fuscatus* (Fabricius)	1 September 2009, food web #275			1
Braconidae	19 August 2009, food web #143, #168, #209			3
Ichneumonidae	1 September 2009, food web #320, #328			2
Crabrionidae *Ectemnius trifasciatus* (Say)	15 July 2008			1
Crabrionidae *Ectemnius continuus* (Fabricius)	27 July 2009, food web #77			1
Crabrionidae *Tachytes aurulentus* (Fabricius)	20 July 2009			1
Sierolomorphidae	15 July 2008			1
Tiphiidae *Myznum* sp.	19 August 2009, food web #190			1
Vespidae *Ancistrocerus antilope antilope* (Panzer)	19 August 2009, food web #141			1
Vespidae *Ancistrocerus* sp.	19 August 2009, food web #222, #150			2
Vespidae *Eumenes fratemus* (Say)	19 August 2009, food web #132			1
Vespidae *Ancistrocerus catskil albophaleralus (Saussure)*	19 August 2009, food web #140			1
Vespidae *Euodynerus foraminotum* (Panzer)	1 September 2009, food web #252			1
Vespidae *Stenodynerus* sp.	19 August 2009, food web #158			1

*All specimens collected: USA Michigan, Jackson County, Clarklake, MacCready Reserve. 42° 7'37N 84° 23'30W. Elevation 300m, in prairie fen wetland. Date noted above.

Investigator: Anna K. Fiedler

Date 24-Aug-10

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

8/24/2010

Curator Date

Voucher number 2010-04

Appendix C

Insect Voucher Specimen Data

Page 2 of 6 Pages

		Number of:		
Species or other taxon	Date collected	Larvae	Nymphs	Adults
Hymenoptera cont.				
Formicidae*Dolichoderus pustulatus* (Mayr)	15 June 2009, food web #22			1
Formicidae*Dolichoderus pustulatus* (Mayr)	19 August 2009, food web #230			1
Formicidae *Camponotus novaeboracensis*	17 July 2008			1
Formicidae*Camponotus novaeboracensis*	14 July 2008			1
Formicidae*Camponotus caryae* (Fitch)	17 July 2008			1
Formicidae*Camponotus caryae* (Fitch)	24 July 2009			1
Formicidae*Formica fusca* (Linneaus)	24 July 2009			1
Formicidae *Formica glacialis* (Wheeler)	19 August 2009, food web #215			1
Formicidae *Formica glacialis* (Wheeler)	27 July 2009, food web #98			1
Apidae *Xylocopa virginica* (Linneaus)	31 August 2009			1
Anthophoridae *Melissodes ur. illata*	19 August 2009, food web #160			1
Halictidae *Lasioglossum tegulare* (Robt.)	6 July 2009, food web #52			1
Halictidae *Lasioglossum nelumbonis* (Robertson)	6 June 2008			1
Halictidae *Lasioglossum nymphaearum* (Robt.	5 August 2009			1
Halictidae *Lasioglossum paradmirandum* (K. & At.)	8 August 2008			1
Halictidae *Lasioglossum coriaceum* (Smith)	31 August 2009			2
Halictidae *Lasioglossum cressonii* (Robertson	3 July 2009			2
Halictidae *Lasioglossum (Lasioglossum) leucozonium* (Schrank)	12 June 2008			1
Halictidae *Lasioglossum (Lasioglossum) leucozonium* (Schrank)	6 September 2008			1
Halictidae *Lasioglossum lineatulum* (Crawford	19 August 2009, food web #229			1
Halictidae *Lasioglossum lineatulum* (Crawford	1 September 2009, food web #298			1
Halictidae *Lasioglossum pectorale* (Smith)	4 June 2009			1
Halictidae *Lasioglossum pectorale* (Smith)	3 July 2009			1
Halictidae *Lasioglossum pilosum* (Sm.)	31 August 2009			2
Halictidae *Lasioglossum (Dialictus) rohweri*	6 September 2008			3
Halictidae *Lasioglossum versans* (Crawford)	6 September 2008			2
Halictidae *Lasioglossum (Dialictus)* sp. 2	4 June 2009			1
Halictidae *Lasioglossum* sp. 2	4 June 2009			2
Halictidae *Lasioglossum (Dialictus)* sp. 1	8 August 2008			1
Halictidae *Lasioglossum (Dialictus)* sp. 1	6 September 2008			1
Halictidae *Lasioglossum (Dialictus)* sp. 4	3 July 2009			1
Halictidae *Lasioglossum (Dialictus)* sp. 5	5 August 2009			1
Halictidae *Lasioglossum (Dialictus)* sp. 6	4 June 2009			1
Halictidae *Lasioglossum (Dialictus)* sp. 7	4 June 2009			1
Halictidae *Lasioglossum (Dialictus)* sp. 8	5 August 2009			1
Halictidae *Lasioglossum (Dialictus)* sp. 9	5 August 2009			1

*All specimens collected: USA Michigan, Jackson County, Clarklake, MacCready Reserve. 42° 7'37N 84° 23'30W. Elevation 300m, in prairie fen wetland. Date noted above.
Anna K. Fiedler. Voucher number 2010-04

Appendix C

Insect Voucher Specimen Data

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Species or other taxon	Date collected	Number of: Larvae	Number of: Nymphs	Number of: Adults
Hymenoptera cont.				
Megachilidae *Heriades carinatus* (Cresson)	5 August 2009			2
Megachilidae *Heriades leavitti* (Crawford)	19 August 2009, food web #149			1
Megachilidae *Heriades variolosus* (Cresson)	5 August 2009			1
Megachilidae *Hoplitis pruducta* (Cresson)	4 June 2009			1
Megachilidae *Hoplitis spoliata* (Provancher)	4 June 2009			1
Megachilidae *Megachile campanulae* (Robertson)	3 July 2009			1
Megachilidae *Megachile inermis* (Provancher)	31 August 2009			1
Megachilidae *Megachile montivaga* (Cresson)	4 June 2009			1
Megachilidae *Megachile pugnata* (Say)	8 August 2008			1
Megachilidae *Megachile relativa* (Cresson)	3 July 2009			1
Megachilidae *Osmia georgica* (Cresson)	4 June 2009			2
Megachilidae *Osmia michiganensis* (Mitchell)	4 June 2009			1
Megachilidae *Osmia pumila* (Cresson)	12 June 2008			2
Megachilidae *Osmia simillima* (Smith)	12 June 2009			1
Megachilidae *Coelioxys modesta* (Smith)	27 July 2009, food web #58			1
Andrenidae *Andrena alleghaniensis* (Viereck)	4 June 2009			1
Andrenidae *Andrena carlini* (Cockerell)	4 June 2009			1
Andrenidae *Andrena cressonii* (Robt.)	4 June 2009			1
Andrenidae *Andrena nasonii* (Robertson)	4 June 2009			1
Andrenidae *Andrena (Tylandrena) perplexa* (Sm.)	12 June 2008			1
Andrenidae *Andrena placata* (Mitchell)	5 August 2009			1
Andrenidae *Andrena (Trachandrena) virginiana* (Mitchell)	5 August 2009			1
Andrenidae *Andrena (Cnemiandrena) hirticincta* (Prov.)	19 August 2009, food web #136			1
Apidae *Anthophora terminalis* (Cresson)	4 June 2009			1
Apidae *Anthophora terminalis* (Cr.)	6 July 2009, food web #36			1
Apidae *Anthophora ursina* (Cresson)	5 August 2009			1
Apidae *Apis mellifera* L.	31 August 2009			2
Apidae *Bombus impatiens* (Chandler)	31 August 2009			2
Apidae *Bombus citrinus* (Smith)	5 August 2009			1
Apidae *Bombus bimaculatus* (Psithyrus)	3 July 2009			1
Apidae *Bombus fevidus* (Fabricius)	19 August 2009, food web #180			1
Apidae *Ceratina calcarata/dupla* (Robertson)	3 July 2009			2
Apidae *Ceratina dupla*	4 June 2009			1
Apidae *Ceratina calcarata* (Robertson)	31 August 2009			1
Apidae *Ceratina strenua* (Smith)	6 September 2008			2
Colletidae *Hylaeus affinis* (Smith)	4 June 2009			1
Colletidae *Hylaeus* sp. 1	31 August 2009			2
Colletidae *Hylaeus* sp. 3	3 July 2009			1

*All specimens collected: USA Michigan, Jackson County, Clarklake, MacCready Reserve. 42° 7'37N 84° 23'30W. Elevation 300m, in prairie fen wetland. Date noted above.
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		Number of:		
Species or other taxon	Date collected	Larvae	Nymphs	Adults
Hymenoptera cont.				
Colletidae *Hylaeus* sp. 2	5 August 2009			1
Halictidae *Agapostemon sericeus* (Forster)	4 June 2009			1
Halictidae *Agapostemon sericeus* (Forster)	5 August 2009			1
Halictidae *Agapostemon virescens* (Fabricius)	6 September 2008			1
Halictidae *Agochlora pura* (Say)	31 August 2009			2
Halictidae *Augochlorella aurata* (Smith)	4 June 2009			2
Halictidae *Augochloropsis metallica* (Fabricius	4 June 2009			2
Halictidae *Halictus confusus* (Smith)	5 August 2009			2
Halictidae *Halictus ligatus*	4 June 2009			2
Halictidae *Halictus parallelus* (Say)	6 June 2008			1
Halictidae *Halictus rubicundus*	19 August 2009, food web #177			1
Halictidae *Lassioglossum atlanticum* (Mitchell)	6 September 2008			2
Halictidae *Lassioglossum bruneri* (Crawford)	31 August 2009			1
Halictidae *Lassioglossum coeruleum* (Robt.)	15 June 2009, food web #5			1
Halictidae *Lassioglossum divergens* (Lovell)	12 June 2008			1
Halictidae *Lassioglossum illinoense* (Robt.)	31 August 2009			1
Halictidae *Lassioglossum macovpinense*	4 June 2009			1
Lepidoptera				
Hesperiidae *Euphyes conspicuus* (W.H.	10 July 2008			1
Hesperiidae Euphyes conspicuus (W.H.	17 July 2008			1
Hesperiidae *Polites mystic* (W.H. Edwards)	19 August 2009, food web #165			1
Nymphalidae *Phyciodes tharos* (Drury)	4 June 2009			2
Lycaenidae *Lycaena helloides* (Boisduval)	12 June 2008			1
Hesperiidae *Atrytone logan* (W.H. Edwards)	3 July 2009			2
Yponomeutidae *Atteva punctellan* (Cramer)	19 August 2009, food web #174			1
Nymphalidae *Polygonia progne* (Cramer)	6 September 2008			1
Hesperiidae Euphyes *origenes* (Fabricius)	4 June 2009			1
Hesperiidae Euphyes *conspicuus* (W.H.	10 July 2009			1
Hesperiidae Euphyes *vestis metacomet* (Harri	5 August 2009			1
Hesperiidae Euphyes *vestis metacomet* (Harri	14 July 2008			1
Hesperiidae *Poanes Massasoit* (Scudder)	3 July 2009			2
Pieridae *Pieris rapae* (Linnaeus)	8 August 2008			1
Pieridae *Pieris rapae* (Linnaeus)	6 September 2008			1
Satyridae *Megisto cymela* (Cramer)	4 June 2009			1
Papilionidae *Papilio troilus* (Linnaeus)	31 August 2009			1
Hesperiidae *Ancyloxypha numitor* (Fabricius)	12 June 2008			1
Hesperiidae *Ancyloxypha numitor* (Fabricius)	15 June 2009, food web #7			1
Hesperiidae *Epargyreus Clarus* (Cramer)	31 August 2009			1
Nymphalidae *Boloria bellona* (Fabricius)	5 August 2009			1
Nymphalidae *Boloria selene* (Fabricius)	6 September 2008			1
Nymphalidae *Speyeria cybele cybele* (Fabriciu	2 July 2008			1

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42° 7'37N 84° 23'30W. Elevation 300m, in prairie fen wetland. Date noted above.
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		Number of:		
Species or other taxon	Date collected	Larvae	Nymphs	Adults
Coleoptera				
Mordellidae *Mordella marginata* (Melsheimer)	27 July 2009, food web #79, #91			2
Falsomordellistena pubescens (Fabricius)	24 July 2009			2
Mordellidae *Mordella atrata* (Melsheimer)	6 July 2009, food web #27, #28			2
Scarabaeidae T*richiotinus affinus*	15 July 2008			1
Cerambycidae *Euderces picipes* (Fabricius)	17 July 2008			1
Cerambycidae *Euderces picipes* (Fabricius)	15 June 2009, food web #1			1
Cerambycidae *Typocerus velutinus* (Olivier)	14 July 2008			1
Coccinellidae *Harmonia axyridis* (Pallas)	19 August 2009, food web #183			1
Chrysomelidae *Ophraella notata*	27 July 2009, food web #81			1
Chrysomelidae *Diabrotica undecimpunctata* (Barber)	1 September 2009, food web #319			1
Lampyridae *Pyropyga* sp.	15 June 2009, food web #14			1
Lampyridae *Pyropyga* sp.	16 July 2009			1
Cantharidae *Chauliguathus marginatus*	17 July 2008			1
Diptera				
Syrphidae *Eristalis transversa* (Wiedemann)	19 August 2009, food web #129			1
Syrphidae *Eristalis flavipes* (Walker)	19 August 2009, food web #139			1
Syrphidae *Sericomyia chrysotoxoides*	19 August 2009, food web #172			1
Syrphidae *Helophilus fasciatus* (Macquart)	19 August 2009, food web #228			1
Syrphidae *Pipiza femorata* (Loew)	20 July 2009			1
Syrphidae *Tropodia quadrata* (Say)	17 July 2008			1
Syrphidae *Neoascia metallica* (Williston)	27 July 2009, food web #93			1
Syrphidae *Syrphus ribesii* (Linnaeus)	19 August 2009, food web #128,			2
Syrphidae *Syrphus rectus* (Osten Sacken)	19 August 2009, food web #173,			2
Syrphidae *Melanostoma mellinum* (Linnaeus)	1 September 2009, food web #323			1
Syrphidae *Syrphus vitripennis* (Meigen)	1 September 2009, food web #266			1
Syrphidae *Toxomarginatus*	14 July 2008			1
Syrphidae *Toxomarginatus*	17 July 2008			1
Syrphidae *Toxomarginatus germinatus*	19 August 2009, food web #126			1
Syrphidae *Sphaerophoria contigua* (Macquart)	1 September 2009, food web #330			1
Stratiomyidae *Odontomyia virgo*	15 June 2009, food web #13			1
Anthromyiidae *Hylemya platura* (Meigen)	1 September 2009, food web #322			1
Muscidae	24 July 2009			1
Tachinidae G*enea texensis* (Townsend)	1 September 2009, food web #287			1
Tachinidae *Gymnosoma occidua* (Walker)	19 August 2009, food web #175			1
Tachinidae *Jurinopsis adjusta* (Van der Wulp)	19 August 2009, food web #186			1
Bombyliidae *Anthrax Pluto*	24 July 2009			1
Bombyliidae *Villa* sp.	19 August 2009, food web #223			1
Stratiomyidae *Nemotelus* sp.	15 June 2009, food web #15, #16			2
Tachinidae *Gymnosoma occidua* (Walker)	1 September 2009, food web #312			1

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Species or other taxon	Date collected	Number of: Larvae	Number of: Nymphs	Number of: Adults
Hemiptera				
Lygaeidae *Lygaeus kalmii* (Stal)	14 July 2008			1
Miridae *Plagiognathus*	27 July 2009, food web #116, #117			2
Miridae *Plagiognathus*	19 August 2009, food web #233			1
Hymenoptera				
Vespidae *Polistes fuscatus* (Fabricius)	1 September 2009, food web #355			1
Formica ulkei (Emery)	1 September 2009, food web #348, #358			2
Formica fusca (Linneaus)	17 July 2008			1
Halictidae *Duforea marginata* (Cresson)	5 August 2009			1
Megachilidae *Megachile relativa* (Cresson)	31 August 2009			1
Andrenidae *Andrena (Callandrena) runcinatae* Ckrll.	31 August 2009			1
Andrenidae *Perdita octomaculata* (Say)	31 August 2009			2
Andrenidae *Pseudopanurgus nubruscensis* (Crawford)	1 September 2009, food web #338			1
Apidae *Bombus griseocollis* (DeGeer)	14 August 2008			1
Lepidoptera				
Hesperiidae *Polites mystic* (W.H. Edwards)	5 August 2009			1
Hesperiidae *Euphyes dion* (W.H. Edwards)	14 July 2008			1
Coleoptera				
Cantharidae *Polemius laticornis* (Say)	19 August 2009, food web #237			1
Cantharidae *Polemius canadensis* (Brown)	19 August 2009, food web #240			1
Rhagonycha luteicollis (Germar)	16 July 2009			1
Rhagonycha luteicollis (Germar)	24 July 2009			1
Diptera				
Syrphidae *Sphaerophoria* sp.	15 June 2009, food web #23			1
Tachinidae	24 July 2009			1
Stratiomyidae *Odontomyia* sp.	10 July 2008			1
Calliphoridae	17 July 2008			1
Tachinidae	24 July 2009			1
Tachinidae	17 July 2008			1
Tephritidae	15 June 2009, food web #24			1

***All specimens collected: USA Michigan, Jackson County, Liberty, Grand River Fen. 42° 5'02N 84° 27'38W. Elevation 300m, in prairie fen wetland. Date noted above.**

Anna K. Fiedler. Voucher number 2010-04