Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION

RESEARCH ARTICLE

Aboveground and Belowground Impacts Following Removal of the Invasive Species Baby's Breath (*Gypsophila paniculata*) on Lake Michigan Sand Dunes

Sarah M. Emery,[1,2] Patrick J. Doran,[3] John T. Legge,[3] Matthew Kleitch,[3] and Shaun Howard[3]

Abstract

The removal of invasive species is often one of the first steps in restoring degraded habitats. However, studies evaluating effectiveness of invasive species removal are often limited in spatial and temporal scale, and lack evaluation of both aboveground and belowground effects on diversity and key processes. In this study, we present results of a large 3-year removal effort of the invasive species, *Gypsophila paniculata*, on sand dunes in northwest Michigan (USA). We measured *G. paniculata* abundance, plant species richness, plant community diversity, non-native plant cover, abundance of *Cirsium pitcheri* (a federally threatened species endemic to this habitat), sand movement, arbuscular mycorrhizal spore abundance, and soil nutrients in fifteen 1000 m^2 plots yearly from 2007 to 2010 in order to evaluate the effectiveness of manual removal of this species on dune restoration. *Gypsophila paniculata* cover was greatly reduced by management, but was not entirely eliminated from the area. Removal of *G. paniculata* shifted plant community composition to more closely resemble target reference plant communities but had no effect on total plant diversity, *C. pitcheri* abundance, or other non-native plant cover. Soil properties were generally unaffected by *G. paniculata* invasion or removal. The outlook is good for this restoration, as other non-native species do not appear to be staging a "secondary" invasion of this habitat. However, the successional nature of sand dunes means that they are already highly invasible, stressing the need for regular monitoring to ensure that restoration progresses.

Key words: CAP, diversity, manual control, mycorrhizae, sand, soils.

Introduction

The removal of invasive species is often one of the first steps in restoring degraded habitats (Hulme 2006). There is a general assumption that the removal of invasive species should lead to an increase in native diversity because of reduced competition from the invader (Hobbs & Huenneke 1992; Jager & Kowarik 2010). However, management-oriented control actions often evaluate only changes in invader densities (Buckley 2008; Kettenring & Adams 2011), at the expense of tracking other aboveground and belowground impacts of removing a dominant invasive species, especially in the long term (Blossey 1999; Zavaleta et al. 2001). "Surprise effects," where there is the rapid increase of prior unnoticed species following the removal of an invasive alien (Caut et al. 2009), as well as secondary invasions by a new invasive species (Masters & Sheley 2001), are possible outcomes of invasive species management. For example, the non-native species *Poa pratensis* quickly increased in abundance after *Coronilla varia*, another invader, had been removed from sand prairie habitat in Illinois (Symstad 2004).

Additionally, belowground responses to invasive species removal are poorly understood within a restoration context (Kardol & Wardle 2010). There are many documented examples of invasive species altering soil nutrient levels (Mack et al. 2001), erosion (Lacey et al. 2003), and soil biodiversity (Grman & Suding 2010). However, examples of monitoring belowground responses after invasive species removal in a restoration context are scarcer (though see examples in Yelenik et al. 2004; Marchante et al. 2008), and in some cases actually indicate short-term undesired consequences of restoration efforts, such as increased erosion (Vincent et al. 2009). An understanding of connections between desired plant community targets in a restoration and key belowground diversity and processes, such as the mutualistic role of mycorrhizal fungi, or nutrient cycling, will enhance our ability to both refine and achieve restoration goals (Kardol & Wardle 2010).

This study reports on both aboveground plant community and belowground soil conditions responses following the

[1]Department of Biology, University of Louisville, Louisville, KY 40292, U.S.A.
[2]Address correspondence to S. M. Emery, email sarah.emery@louisville.edu
[3]The Nature Conservancy in Michigan, Lansing, MI 48906, U.S.A.

doi: 10.1111/j.1526-100X.2012.00915.x

removal of an invasive species over a 4-year period in a restoration of lacustrine sand dune habitat. Baby's breath (*G. paniculata*) is an invader of sand dune systems in northwest Michigan. A native to Eurasia, *G. paniculata* was likely introduced to North America as an ornamental in the late 1800s (Darwent & Coupland 1966). From its introduction site near Point Betsie (44°41′08″N, 86°15′11″W) in the northwestern Lower Peninsula of Michigan, *G. paniculata* has been dispersed primarily to the northeast by prevailing winds to invade other open dune sites along a 260 km stretch of shoreline (Kleitch 2009, Fig. S1, Supporting Information). In some areas, *G. paniculata* now comprises 80% of all vegetation (Karamanski 2000). It is believed that *G. paniculata* creates problems for the dunes by over-stabilizing a typically wind-disturbance driven habitat, making it unsuitable for native species such as *Cirsium pitcheri*, and may be capable of out-competing native matrix species (e.g. *Schizachyrium scoparium* and *Ammophila breviligulata*) for resources due to its deep root system, which can reach up to 4 m in depth (Darwent & Coupland 1966; Karamanski 2000).

In response to this invasion, The Nature Conservancy (TNC) and the National Park Service at Sleeping Bear Dunes National Lakeshore (SBDNL) initiated a multi-year effort in 2007 to remove *G. paniculata* from their properties in northwest Michigan (U.S.A.), in attempts to restore native sand dune plant communities. The goal of this study is to evaluate the effects of this removal effort on aboveground plant communities and belowground processes. In particular, we ask (1) Do the results of the current management method indicate that eradication of *G. paniculata* is possible? (2) Do sites invaded by *G. paniculata* have lower plant species diversity (including smaller *C. pitcheri* populations), or altered belowground processes? (3) Does removal of *G. paniculata* restore plant communities and belowground processes?

Methods

Sampling Design

In July 2007, we established fifteen 1000 m^2 (20 m × 50 m) plots within the TNC and SBDNL properties (Fig. 1). Five plots were invaded with *Gypsophila paniculata* that was removed by field crews in 2008, with follow-up treatment in 2009 and 2010 ("managed"). Four plots were invaded with *G. paniculata*, but not managed ("invaded"). Five plots had *G. paniculata* absent or in very low abundances, and so served as a target for restoration efforts ("reference"). One additional invaded plot had *G. paniculata* removed in 2008 only due to miscommunication with managers and so was recategorized as a managed plot. All 15 plots were located within the matrix of a larger dune system that was at least several hectares in size to avoid edge effects associated with the management, and land managers were careful to avoid leaving piles of dead plants in the sampling plots in 2008. Of the 15 plots, nine were located in Sleeping Bear Dunes National Lakeshore and six were located on TNC's Zetterberg Preserve at Point Betsie. Owing to differences in latitude (SBDNL is just north of TNC land, Fig. 1) and some differences in management history, we treated park location as a block factor for all analyses.

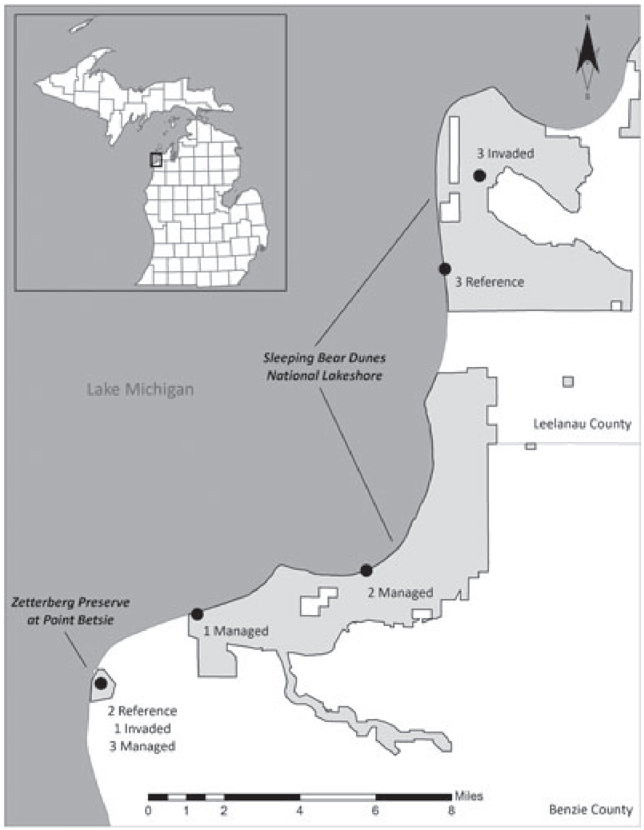

Figure 1. Map showing the location of plots in this experiment.

Land managers were particularly interested in plant community responses to management, and so every year in July, from 2007 to 2010, we measured *G. paniculata* abundance, plant species diversity, and *Cirsium pitcheri* abundance. *Cirsium pitcheri* is a federally threatened native species endemic to Great Lakes dune habitat and so we carefully monitored demographic responses of this species to management. Such species may serve as "indicator species" in restorations. Understanding various ecological processes, such as aboveground–belowground linkages, can also inform restoration targets, and so we measured sand movement and soil nutrients as examples of ecosystem processes, and arbuscular mycorrhizal fungi (AMF) abundance as a measure of belowground biota and status of mutualistic interactions.

Treatment Methods

Starting in May 2008, crews of 10–15 people manually removed individual *G. paniculata* plants from removal plots on SBDNL and TNC property. Using a square-nosed spade, crew members cut the taproot of plants as far below the ground surface as possible, with the goal of cutting below the caudex of the plant to prevent resprouting (McGowan-Stinski & Gostomski 2006). Cut plants were piled together in haphazardly placed mounds outside of sampling plots in 2008, and in following years dead plants were left in place after cutting. An experienced crew member could remove an average of 3–5 plants/minute using this method (McGowan-Stinski & Gostomski 2006). During the summers of 2008–2010, crews spent over 25,000 person hours treating 348 ha (Howard 2010). The plots that we monitored were initially treated in 2008 and re-treated in 2009 and 2010.

Aboveground Vegetation Sampling

Every year in July, from 2007 to 2010, beginning 1 year prior to removal efforts, we measured *G. paniculata* cover, plant species diversity, and *C. pitcheri* abundance in each of the 15 plots. To measure *G. paniculata* cover and species diversity in each plot, we estimated the cover of individual species, as well as bare sand, in ten 1 m^2 quadrats regularly located around the boundaries of the large plot (approximately 10 m apart along perimeter) using a modified Daubenmire scale (Daubenmire 1959). Species cover and plant species richness values from the quadrats were averaged to give cover values for each species in each of the 15 plots. We then walked the entire plot to identify any plant species that did not occur in the quadrats and assigned a cover value of 1% to these species for later calculations. We calculated Shannon diversity (H') (Begon et al. 2005) per plot based on the average species cover values for the whole plot. We also categorized plant species as native and non-native based on Voss (1985) to estimate cover of non-native species (excluding *G. paniculata*) in each plot.

We recorded the abundance of *C. pitcheri* in each plot by walking the entire plot and counted the total number of juvenile rosettes and adults. Seedlings were not counted due to the difficulty in visually locating these.

Belowground Sampling

From 2008 to 2010, we measured sand movement in plots as a measure of dune stability. Soil stability is an important component of dune habitats (Marshall & Storer 2008), with many native species dependent on active sand movement (Maun & Lapierre 1984). From 2008 to 2009, we measured the yearly change in sand surface levels by placing two PVC posts in the middle of each plot. Sand surface levels were marked on the post, and changes in surface level from year to year were recorded. In 2010, we measured short-term sand movement by placing two "sand traps" modified from Leatherman (1978) in each plot. Sand was collected in each trap for 2 weeks, and then measured by volume to quantify short-term sand movement through saltation.

From 2007 to 2009, we measured AMF spore abundance in the soil as a measure of soil biota responses to management. To measure AMF spore abundance for each plot, we collected and combined twenty-five 15 cm deep × 1.9 cm diameter soil cores, haphazardly chosen within the plot, in years 2007, 2008, and 2009 (2010 sampling was dropped due to lack of differences among treatments in the earlier samplings) in order to have one composite soil sample per plot per year. We used wet-sieving and sucrose density gradient centrifugation (Walker et al. 1982) on 50 mL of sand from each plot to isolate spores. We then counted spores and identified them to "morpho-types" under a microscope in the laboratory.

In 2010, nutrients (P, K, Ca, Mg, NO_3, and NH_4) and percent organic matter analyses were conducted on a subset of the composited soil from each plot by the University of Kentucky Soil Testing Laboratory (Lexington, KY, U.S.A.). These served as rough measures of ecosystem processes of nutrient cycling and decomposition.

Data Analysis

We conducted ANOVAs on data from the 15 plots to compare the effectiveness of management in reducing *G. paniculata* abundance, and changing plant species richness, plant community diversity, non-native plant cover, *C. pitcheri* abundance, sand movement, AMF spore abundance, and soil nutrients. Park site was used as a block factor. We were not explicitly interested in variation between park sites, and so these block effects are not discussed in the results (though are presented in data tables). All these analyses were performed using Systat v. 12 (SYSTAT Software Inc 2007).

To compare plant composition among treatments over time, we used PERMANOVA (Anderson 2001), which is a non-parametric analog to MANOVA that can account for unbalanced, multi-factor designs. Species data were square-root transformed, and we used a Bray–Curtis distance measure with 999 permutations to test for model significance.

To visualize how plant communities shifted over time with management, we used a canonical analysis of principal coordinates (CAP). CAP is a constrained ordination technique that is appropriate for community composition data (Anderson & Willis 2003). This ordination technique is useful in that it constrains an ordination to show only the variability due to a chosen factor, while ignoring other irrelevant factors (such as blocks). We overlaid species vectors (biplots) onto the ordination to show species associated with each treatment over time (any $r > 0.5$ with CAP axes). We performed the CAP on square-root transformed species data and used a Bray–Curtis distance measure with 999 permutations to test for significance. The software package PERMANOVA+ for PRIMER (Anderson et al. 2008) was used to conduct the PERMANOVAs and CAPs.

Results

Gypsophila paniculata Control

Our invaded plots had approximately 50% *G. paniculata* cover, while reference plots had very little *G. paniculata* (<5% cover). In plots where *G. paniculata* was removed, the cover dropped to 20% in the first year, and eventually to 5% by 2010. In managed plots, cover of *G. paniculata* was significantly lower in 2008–2010 compared to the pre-treatment year 2007, while *G. paniculata* cover did not change significantly from year to year in the reference and unmanaged plots (Table 1, Fig. 2).

Table 1. Results of separate ANOVAs for the effects of treatment, year, and interaction between treatment and year on measured community and ecosystem responses.

Source	*df*	Gypsophila paniculata *cover* *F*	*p*	*Plant Species Richness* *F*	*p*	*H′* *F*	*p*	*Non-native Plant Cover* *F*	*p*	*Native Plant Cover* *F*	*p*	Cirsium pitcheri *Abundance* *F*	*p*	*Bare Ground* *F*	*p*	*Mycorrhizal Spore Abundance* *F*	*p*	*Mycorrhizal Morpho-species Richness* *F*	*p*
Treatment	2	54.1	<0.001***	3.27	0.047**	0.08	0.92	27.85	<0.001***	86.84	<0.001***	26.5	<0.001***	20.4	<0.001***	1.00	0.38	1.44	0.25
Year	3	4.83	0.005***	0.51	0.53	0.44	0.72	0.91	0.44	2.51	0.07*	1.67	0.19	1.35	0.27	2.47	0.10	9.38	0.001***
Treatment × Year	6	4.28	0.002***	0.30	0.93	1.16	0.34	0.28	0.94	2.64	0.028**	1.51	0.20	0.80	0.58	0.09	0.99	0.87	0.45
Block	1	0.03	0.86	23.9	<0.001***	8.49	0.005***	9.78	0.003***	5.20	0.03**	3.79	0.06*	12.52	0.001***	n/a		n/a	

Statistically significant results are indicated by an asterisk (*$p < 0.10$, **$p < 0.05$, ***$p < 0.01$).

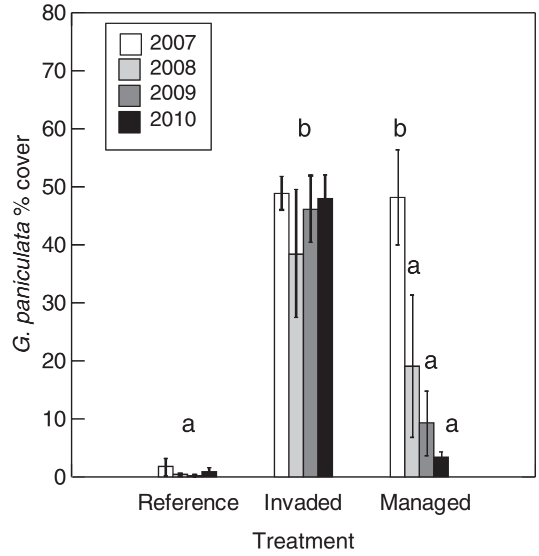

Figure 2. Effects of removal efforts on *Gypsophila paniculata* cover (2007 are pre-treatment data). Different letters represent significant differences at $p < 0.05$ using post hoc Tukey comparisons. Error bars represent 1 SE.

Aboveground Vegetation

All plots had approximately the same plant species richness (15 species per 20 m × 50 m plot, though invaded plots had slightly higher richness than reference plots, Fig. 3a), and the same community diversity (H' approximately 1.75). Removing *G. paniculata* from treatment plots had no significant effect on plant species richness (Table 1, Fig. 3a) or on community diversity (Table 1, data not shown). The managed plots initially had non-native (excluding *G. paniculata*) plant cover intermediate between the invaded and reference sites (10% cover versus 20% cover in the invaded plots and close to 0% cover in the reference plots), and there was no effect of the management on non-native plant (excluding *G. paniculata*) cover in the managed plots (Table 1, Fig. 3b).

Cirsium pitcheri abundance was much greater in the reference plots compared to the invaded and managed plots (Fig. 4), and there was no effect of *G. paniculata* removal on *C. pitcheri* abundance (Table 1).

The PERMANOVA analysis indicated significant differences in plant community composition between all treatments in 2007 ($p < 0.10$ for all comparisons; Table 2, Fig. 5). In 2008, the first year of management, managed plots were not significantly different from reference plots, while invaded plots were significantly different from both the reference plots and the managed plots (Table 2, Fig. 5). In 2009, after 2 years of management, the same pattern held with managed plots not significantly different from reference plots, and invaded plots significantly different from both the reference plots and the managed plots. By 2010, with 3 years of management, the same general pattern held with managed plots not significantly different from reference plots. Invaded plots still differed from reference plots and managed plots ($p < 0.10$, Table 2, Fig. 5).

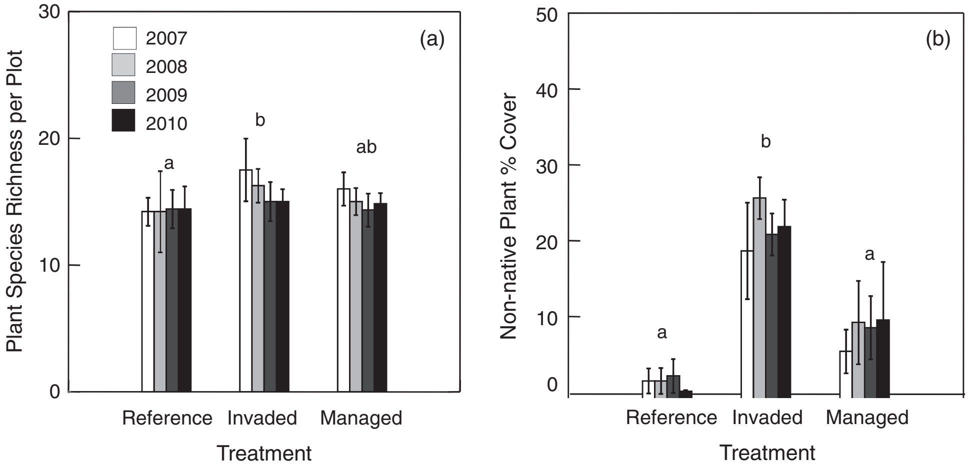

Figure 3. Effects of removal efforts on (a) total plant species richness, and (b) non-native plant cover. Different letters represent significant differences at $p < 0.05$ using post hoc Tukey comparisons. Error bars represent 1 SE.

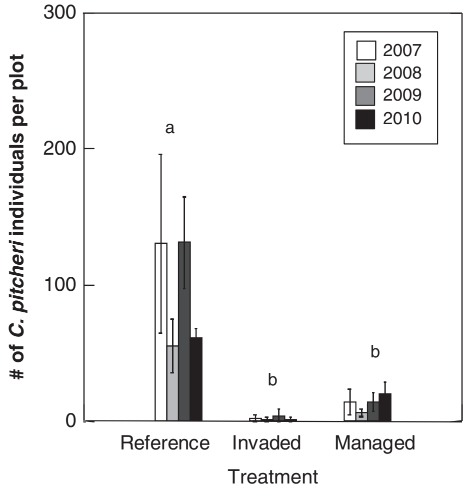

Figure 4. Effects of removal efforts on *Cirsium pitcheri* abundance. Different letters represent significant differences at $p < 0.05$ using post hoc Tukey comparisons. Error bars represent 1 SE.

The CAP analyses illustrated the shifts in community composition of the managed plots through time (Fig. 5, detailed CAP statistics reported in legend). In 2007, each type of plot was characterized by different species. The biplot correlation analysis showed that invaded sites were associated with several other non-native species, including *Silene latifolia*, *Poa compressa*, and *Centaurea maculosa*. Reference plots were associated with native species such as *Prunus pumila*, *Lithospermum canescens*, and *Koeleria macrantha*. To-be managed sites had their own unique composition characterized by both native and non-native species such as *Artemisia campestris*, *Solidago racimosa*, *Ammophila breviligulata*, and *Agropyron cristatum*. Similar species associations characterized the treatments through 2010, though the differences between the managed and reference plots were not significant in later years (Fig. 5).

Belowground Processes

There were no effects of treatment on sand stability. Bare ground did not increase when management was implemented (Table 1, data not shown). When we measured sand movement directly, we found no differences in yearly sand surface movement (Treatment: $F_{[2,12]} = 0.58$, $p = 0.58$; Block: $F_{[2,12]} = 0.03$, $p = 0.86$) or short-term sand movement (Treatment: $F_{[2,14]} = 1.21$, $p = 0.34$; Block: $F_{[2,12]} = 1.01$, $p = 0.34$).

Also, there were no effects of treatment on AMF spore abundance or morpho-species richness (Table 1). All plots had spore abundances of approximately 150 spores/50 mL sand in all sampling years. Spore diversity increased slightly across years, perhaps due to increased skill in identification of morphotypes in the laboratory, but did not differ across treatments (data not shown).

Soil phosphorus, potassium, and calcium showed differences among treatments in 2010, while magnesium, zinc, total nitrogen, soil organic matter, and pH were not different (Table 3). Reference plots had lower phosphorus and higher calcium in the soil than the invaded and managed plots. Invaded plots had higher potassium than the reference and managed plots. Unfortunately, with only 1 year of soil data, we cannot determine whether there have been any changes over time in these nutrients.

Discussion

This study is one of only a few large-scale, multi-year studies of plant community and soil responses to an invasive species removal as part of a habitat restoration effort (though see Heleno et al. 2010). Explicit goals for this restoration project included reducing or eliminating *Gypsophila paniculata* populations, increasing native plant diversity, and increasing *Cirsium pitcheri* abundance and habitat quality. Three years after the management of *G. paniculata*, some, but not all, of these goals have been reached.

Table 2. Results of PERMANOVAs for each year of the experiment.

	2007		2008		2009		2010	
Model Term	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Treatment	3.023	0.004***	2.84	0.007***	2.68	0.014**	2.59	0.021**
Block	2.59	0.034**	1.54	0.178	2.43	0.038**	2.56	0.038**
Pairwise Comparisons	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Invaded vs. Reference	2.25	0.011**	2.11	0.014**	2.17	0.012**	2.29	0.014**
Invaded vs. Managed	1.53	0.081*	1.89	0.028**	1.56	0.068*	1.63	0.060*
Managed vs. Reference	1.50	0.068*	1.12	0.284	1.15	0.298	1.02	0.384

Pseudo-F and pseudo-t statistics are reported, with p values based on Monte-Carlo randomization tests using 999 permutations. Statistically significant results are indicated by an asterisk (*$p < 0.10$, **$p < 0.05$, ***$p < 0.01$).

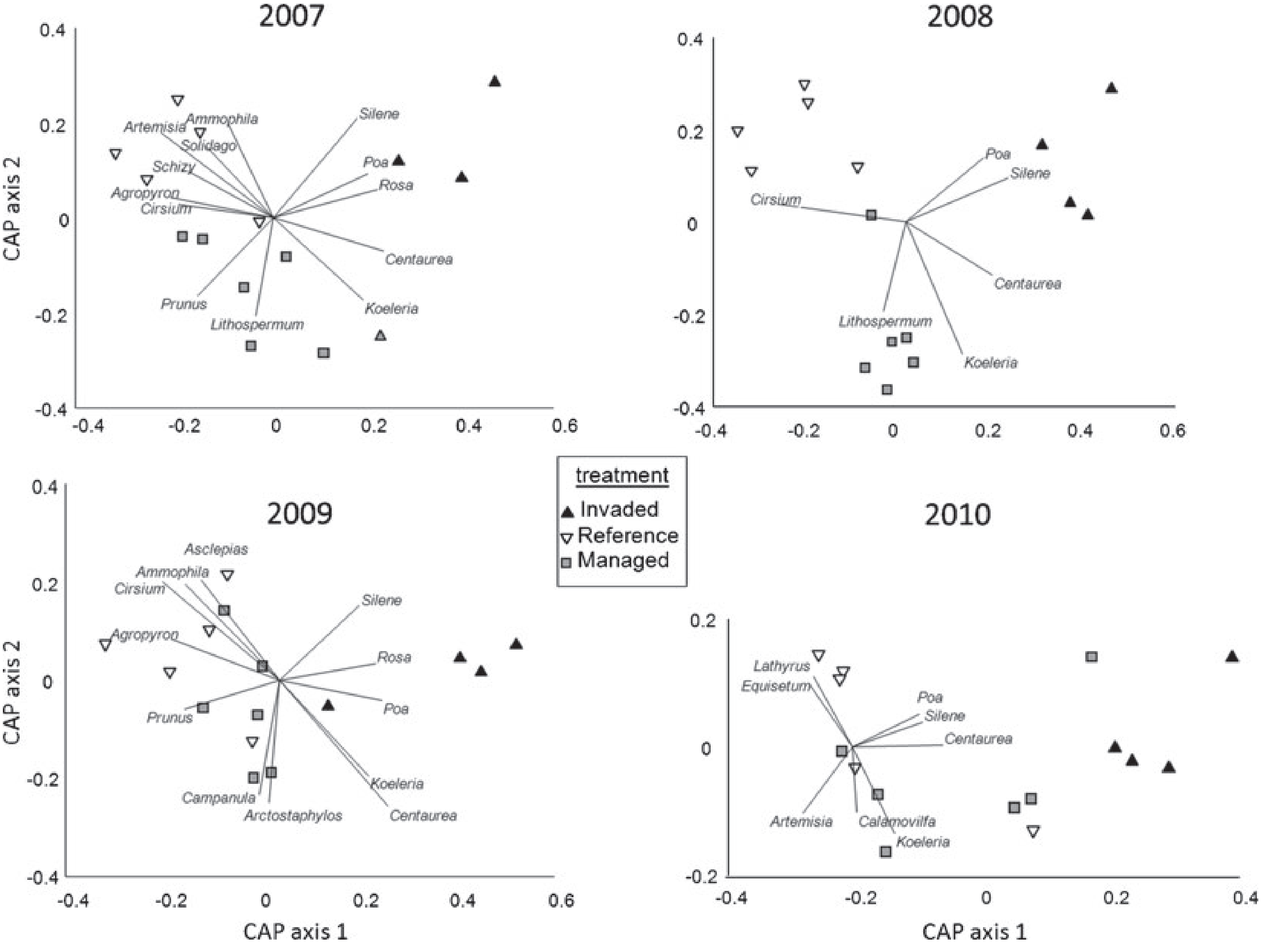

Figure 5. Results of CAP analyses for each year. The 2007 analysis was based on $m = 4$, and explained 77.9% of the variation in the data with a misclassification of 26.7%. The trace statistic for 2007 had $p < 0.001$ with 999 permutations. For the 2008 analysis, the CAP was based on $m = 8$, with 99.5% of the variation in the data explained and 26.7% of data misclassified. The trace statistic for 2008 had $p = 0.003$ with 999 permutations. For 2009, $m = 4$, explained 78.7% of the variation in the data with a misclassification of 26.7% and had trace statistic with $p = 0.05$. For 2010, $m = 3$, and explained 68.0% of the data variation with a misclassification of 33.3% and a trace statistic with $p = 0.043$.

Gypsophila paniculata cover has been greatly reduced by the management strategy of manual removal, but the species has not been eliminated from the area. Alternative management options, such as broadcast herbicide application, may be necessary to efficiently control dense populations of *G. paniculata*. Along these lines, spot treatment with herbicide (glyphosate) was incorporated into the control strategy starting in 2009 (Kleitch 2009). Additionally, regular monitoring and management will be needed to keep *G. paniculata* from re-establishing large populations in these areas due to nearby

Table 3. Effects of removal efforts on soil nutrients and properties (mean ± SE).

Treatment	Phosphorus (kg/ha)	Potassium (kg/ha)	Calcium (kg/ha)	Magnesium (kg/ha)	Zinc (kg/ha)	Nitrogen (% total)	% Organic Matter	pH
Invaded	17.1 b (±0.66)	71.54 a (±5.86)	985.3 a (±72.0)	214.32 (±9.34)	2.51 (±0.46)	0.052 (±0.036)	0.57 (±0.08)	8.17 (±0.10)
Reference	7.52 a (±0.77)	28.04 b (±2.18)	2600.3 b (±460.9)	190.61 (±11.08)	1.25 (±0.14)	0.005 (±0.000)	0.66 (±0.06)	8.48 (±0.09)
Managed	14.06 b (±2.54)	38.95 b (±4.76)	1234.4 a (±240.3)	178.03 (±12.54)	2.91 (±0.70)	0.012 (±0.003)	0.54 (±0.02)	8.18 (±0.13)

Letters indicate statistically significant differences among treatments ($p < 0.05$) after accounting for differences among blocks (ANOVA details not shown).

population sources on unmanaged private lands. However, such maintenance efforts should require fewer resources than the initial removal efforts (Kleitch 2009).

Gypsophila paniculata invasion was associated with a reduction in *C. pitcheri* abundance, and with the presence of other non-native species. However, invaded plots did not have lower total plant species richness or community diversity. Plots invaded by *G. paniculata* also did not differ in many belowground measures compared with reference plots (i.e. soil AMF abundance and diversity, soil organic matter, and many soil nutrients). *Gypsophila paniculata* presence was associated with increased soil phosphorus and potassium, and decreased soil calcium. The association with soil nutrients may be more of an indicator of habitat that *G. paniculata* prefers rather than any direct effect of *G. paniculata* on soil characteristics.

Removal of *G. paniculata* had no effect on total plant species richness, *C. pitcheri* abundance, or non-native (excluding *G. paniculata*) plant cover. When considering the role that plant diversity plays in ecosystem function, total richness is often important (Loreau et al. 2001). However, the relative abundance and identity of species in the community can also be important (Crawley et al. 1999; Emery & Gross 2006), and management efforts did shift plant community composition to more closely resemble reference plant communities. Reference communities were associated with several native plant species, while invaded communities were associated with several non-native plant species. Removal crews began controlling the invasive species *Centaurea maculosa* along with *G. paniculata* in 2009, which may explain some of this shift in plant community composition (Kleitch 2009). However, other non-native invasive species present in these sites, such as *Silene latifolia* and *Poa compressa*, appear to not take advantage of the disturbance caused by *G. paniculata* removal.

This community response is encouraging, as it seems that secondary invasion and surprise effects are not occurring. The lack of change in total plant species richness may be explained by the extremely seed-limited conditions of dune habitats (Lichter 2000; French et al. 2011), where seed banks are rare (Leicht-Young et al. 2009). Once native species are lost from these systems, it may be difficult for them to re-colonize due to distance from source populations. However, native species already present in the system apparently do not suffer from the disturbance caused by removal of *G. paniculata*.

This seed limitation probably explains the lack of increase of *C. pitcheri* populations in managed areas. Other studies have reported a lack of seedbank for this species (Rowland & Maun 2001). *Cirsium pitcheri* is a short-distance seed dispersed species (Keddy & Keddy 1984; USFWS 2002), and the lack of source populations in invaded areas may restrict spread of *C. pitcheri* in managed areas. Introduction of seeds or juvenile plants into these managed areas may be necessary to "jumpstart" recovery of these populations (D'Antonio & Meyerson 2002; Kettenring & Adams 2011).

Belowground processes, as measured by soil organic matter, soil nutrients, and AMF communities, were not affected by *G. paniculata* management, though our plot-level analyses may have masked plant–soil relationships at smaller scales (Landis et al. 2004). Sand movement, often cited as a key function of healthy dune systems (Lichter 2000), was also unaffected by management. However, we were limited in our measures of this, and did not have any pre-management data. Bare ground can serve as a surrogate measure of sand movement, and this tended to increase after management efforts (though not significantly). This holds promise for native plants, such as *Ammophila breviligulata*, which depend on sand movement to stimulate growth (Maun & Lapierre 1984).

From a biological perspective, the lack of effect of *G. paniculata*, presence or absence, on soil attributes may be attributed to the relatively stressful conditions of sand dunes compared to more stable and organic-matter-rich soil environments (Koske & Gemma 1997). Invasive species in other systems are known to affect soil conditions, even after removal of the invader (D'Antonio & Meyerson 2002). For example, nitrogen-fixing invaders such as *Myrica faya* and *Acacia* spp. have increased soil nitrogen, and *Mesembryanthemum crystallinum* invasion increased soil salinity (D'Antonio & Meyerson 2002). While the *G. paniculata* invasion has been established for at least 30 years, and roots of this plant reach depths of 3 m or more, the transient and high-stress nature of dune soils may mean abiotic factors rather than *G. paniculata* has the strongest effect on soil conditions. Only one soil nutrient, potassium, seemed affected at all by *G. paniculata* management. Further investigations of the consequences of this change, including studies that vary in spatial scale, are warranted.

Evaluations of weed-removal projects can be useful to land managers as they decide whether additional treatments are necessary after removal of an invasive species (Reid et al.

2009). In this case, 3 years after initial treatment, plant communities are slowly approaching those of the reference conditions, though mostly due to increases in abundance of native species already present in the community, rather than colonization of new species. These dune habitats may be one of the few where simple removal of an invasive species can restore the system. The outlook is good for the return of native plants if maintenance removal is continued, as other non-native species do not appear to be staging a "secondary" invasion of this habitat.

Implications for Practice

- Manual removal of *Gypsophila paniculata*, involving use of a square-nosed spade to cut the taproot of plants as far below the ground surface as possible, was effective at reducing cover of species from 50% to <5% on sand dune habitat in northwest Michigan. Approximately 25,000 person hours were spent to treat 348 ha from 2007 to 2010.
- Management has not resulted in a "secondary" invasion of other non-native plants and community composition in managed plots is now similar to reference plots.
- Because of the small regional species pool and lack of seed banks in this habitat, revegetation with desired species will most likely be necessary to increase total community richness. High-value species, such as *Cirsium pitcheri*, which are in low abundances, may also need targeted planting to establish healthy populations in these managed areas.

Acknowledgments

Thanks to Steve Yancho (SBDNL) for access to field sites and general support of this research. Thanks to David Griffith, Catherine Fargen, Allie Moehlman, Jane Bocchini, Emily Moehlman, Joy Uwimbabazi, Keera Lowe, Caitlin Rhodes, Alex Bryant, Maulik Vaishnav, John Land, and Brad Kimbrough for field and lab assistance. A special thanks to Jack McGowan-Stinski who originally initiated dune restoration efforts and evaluations of their success on TNC's preserve. This manuscript was improved by comments from Layla Cole, Jon Fisher, Luke Flory, Jensen Montambalt, Dan Salzer, Matt Herbert, and two anonymous reviewers. This research was made possible through the *National Parks Ecological Research Fellowship Program*, a partnership between the National Park Service, the Ecological Society of America and the National Park Foundation, and from the University of Louisville. Funding for *G. paniculata* management was provided by the Meijer Foundation.

LITERATURE CITED

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology **26:**32–46.

Anderson, M. J., and T. J. Willis 2003. Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology **84:**511–525.

Anderson, M. L., R. N. Gorley, and K. R. Clarke. 2008. PERMANOVA+ for PRIMER, Plymouth, UK.

Begon, M., C. Townsend, and J. L. Harper. 2005. Ecology: from individuals to ecosystems. Blackwell, Oxford, UK.

Blossey, B. 1999. Before, during and after: the need for long-term monitoring in invasive plant species management. Biological Invasions **1:**301–311.

Buckley, Y. M. 2008. The role of research for integrated management of invasive species, invaded landscapes and communities. Journal of Applied Ecology **45:**397–402.

Caut, S., E. Angulo, and F. Courchamp. 2009. Avoiding surprise effects on Surprise Island: alien species control in a multitrophic level perspective. Biological Invasions **11:**1689–1703.

Crawley, M. J., S. L. Brown, M. S. Heard, and G. R. Edwards. 1999. Invasion-resistance in experimental grassland communities: species richness or species identity? Ecology Letters **2:**140–148.

D'Antonio, C., and L. A. Meyerson. 2002. Exotic plant species as problems and solutions in ecological restoration: a synthesis. Restoration Ecology **10:**703–713.

Darwent, A. L., and R. T. Coupland. 1966. Life history of *Gypsophila paniculata*. Weeds **14:**313–318.

Daubenmire, R. 1959. A canopy coverage method of vegetation analysis. Northwest Science **33:**43–64.

Emery, S. M., and K. L. Gross. 2006. Dominant species identity regulates invasibility of old-field plant communities. Oikos **115:**549–558.

French, K., T. J. Mason, and N. Sullivan 2011. Recruitment limitation of native species in invaded coastal dune communities. Plant Ecology **212:**601–609.

Grman, E., and K. N. Suding. 2010. Within-year soil legacies contribute to strong priority effects of exotics on native California grassland communities. Restoration Ecology **18:**664–670.

Heleno, R., I. Lacerda, J. A. Ramos, and J. Memmott. 2010. Evaluation of restoration effectiveness: community response to the removal of alien plants. Ecological Applications **20:**1191–1203.

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology **6:**324–337.

Howard, S. 2010. Lake Michigan dune restoration project: 2010 field season report. The Nature Conservancy, Lansing, Michigan.

Hulme, P. E. 2006. Beyond control: wider implications for the management of biological invasions. Journal of Applied Ecology **43:**835–847.

Jager, H., and I. Kowarik. 2010. Resilience of native plant community following manual control of invasive *Cinchona pubescens* in Galapagos. Restoration Ecology **18:**103–112.

Karamanski, T. J. 2000. Nationalized lakeshore: the creation and administration of sleeping bear dunes national lakeshore. National Park Service, Department of the Interior, Washington, DC.

Kardol, P., and D. A. Wardle. 2010. How understanding aboveground-belowground linkages can assist restoration ecology. Trends in Ecology & Evolution **25:**670–679.

Keddy, C., and P. Keddy. 1984. Reproductive biology and habitat of *Cirsium pitcheri*. Michigan Botanist **23:**57–67.

Kettenring, K. M., and C. R. Adams. 2011. Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. Journal of Applied Ecology **48:**970–979.

Kleitch, M. 2009. Lake Michigan dune restoration project summary-2009 field season report. The Nature Conservancy, Lansing, Michigan.

Koske, R. E., and J. N. Gemma. 1997. Mycorrhizae and succession in plantings of beachgrass in sand dunes. American Journal of Botany **84:**118–130.

Lacey, E. P., D. A. Roach, D. Herr, S. Kincaid, and R. Perrott. 2003. Multigenerational effects of flowering and fruiting phenology in *Plantago lanceolata*. Ecology **84:**2462–2475.

Landis, F. C., A. Gargas, and T. J. Givnish. 2004. Relationships among arbuscular mycorrhizal fungi, vascular plants and environmental conditions in oak savannas. New Phytologist **164:**493–504.

Leatherman, S. P. 1978. New aeolian sand trap design. Sedimentology **25:**303–306.

Leicht-Young, S., N. B. Pavlovic, R. Grundel, and K. J. Frohnapple. 2009. A comparison of seed banks across a sand dune successional gradient at Lake Michigan dunes (Indiana, USA). Plant Ecology **202:**299–308.

Lichter, J. 2000. Colonization constraints during primary succession on coastal Lake Michigan sand dunes. Journal of Ecology **88:**825–839.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, et al. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science **294:**804–808.

Mack, M. C., C. M. D'Antonio, and R. E. Ley 2001. Alteration of ecosystem nitrogen dynamics by exotic plants: a case study of C-4 grasses in Hawaii. Ecological Applications **11:**1323–1335.

Marchante, E., A. Kjoller, S. Struwe, and H. Freitas. 2008. Short- and long-term impacts of *Acacia longifolia* invasion on the belowground processes of a Mediterranean coastal dune ecosystem. Applied Soil Ecology **40:**210–217.

Marshall, J. M., and A. J. Storer. 2008. Comparative analysis of plant and ground dwelling arthropod communities in lacustrine dune areas with and without *Centaurea biebersteinii* (Asteraceae). American Midland Naturalist **159:**261–274.

Masters, R. A., and R. L. Sheley. 2001. Principles and practices for managing rangeland invasive plants. Journal of Range Management **54:**502–517.

Maun, M. A., and J. Lapierre. 1984. The effects of burial by sand on *Ammophila breviligulata*. Journal of Ecology **72:**827–839.

Mcgowan-Stinski, J., and T. Gostomski. 2006. Recommended removal methods for baby's breath (*Gypsophila paniculata*). The Nature Conservancy, Lansing, Michigan.

Reid, A. M., L. Morin, P. O. Downey, K. French, and J. G. Virtue. 2009. Does invasive plant management aid the restoration of natural ecosystems? Biological Conservation **142:**2342–2349.

Rowland, J., and M. A. Maun. 2001. Restoration ecology of an endangered plant species: Establishment of new populations of *Cirsium pitcheri*. Restoration Ecology **9:**60–70.

Symstad, A. J. 2004. Secondary invasion following the reduction of *Coronilla varia* (Crownvetch) in sand prairie. American Midland Naturalist **152:**183–189.

SYSTAT Software Inc. 2007. SYSTAT v. 12, Chicago, Illinois.

USFWS 2002. Pitcher's thistle (*Cirsium pitcheri*) recovery plan. U.S. Fish and Wildlife Service, Fort Snelling, Minnesota.

Vincent, K. R., J. M. Friedman, and E. R. Griffin. 2009. Erosional consequence of saltcedar control. Environmental Management **44:**218–227.

Voss, E. G. 1985. Michigan flora. University of Michigan Herbarium, Ann Arbor.

Walker, C., C. W. Mize, and H. S. Mcnabb. 1982. Populations of endogonaceous fungi at two locations in central Iowa. Canadian Journal of Botany **60:**2518–2529.

Yelenik, S. G., W. D. Stock, and D. M. Richardson. 2004. Ecosystem level impacts of invasive *Acacia saligna* in the South African fynbos. Restoration Ecology **12:**44–51.

Zavaleta, E. S., R. J. Hobbs, and H. A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology & Evolution **16:**454–459.

Supporting Information

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

Figure S1. Distribution of *G. paniculata* along Lake Michigan shoreline in the upper Lower Peninsula of Michigan.