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RESEARCH ARTICLE

Ecological Assessment of Dune Restorations in the Great Lakes Region

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Abstract

Because of the economic and environmental importance of stabilizing fragile sand dune habitats, restoration of dunes has become a common practice. Restoration efforts in the Great Lakes and East Coast regions of North America often consist of planting monocultures of the dominant native grass species, *Ammophila breviligulata*. We evaluated 18 dune restoration projects in the Great Lakes region conducted over the past 25 years. We characterized attributes of diversity (plants and insects), vegetation structure (plant biomass and cover), and ecological processes (soil nutrients and mycorrhizal fungi abundance) in each restoration, and we compared these measures to geographically paired natural dune communities. Restoration sites were similar to reference sites in most measured variables. Differences between restorations and reference sites were mostly explained by differences in ages, with the younger sites supporting slightly lower plant diversity and mycorrhizal spore abundance than older sites. Plant community composition varied little between restored and reference sites, with only one native forb species, *Artemisia campestris*, occurring significantly more often in reference sites than restored sites. Although it remains unclear whether more diverse restoration plantings could accelerate convergence on the ecological conditions of reference dunes, in general, traditional restoration efforts involving monoculture plantings of *A. breviligulata* in Great Lakes sand dunes appear to achieve ecological conditions found in reference dunes.

Key words: ***Ammophila breviligulata*, diversity, indicator species analysis, insects, mycorrhizae.**

Introduction

Although often a common practice in the past, today monoculture plantings of a single, common species are generally discouraged for ecological restoration efforts because of the artificially high dominance by the planted species, slow colonization by subordinate species, and generally inferior community structure (Kanowski et al. 2003; Sheley & Half 2006). However, due to their more predictable colonization dynamics, primary successional habitats may be one exception where a simple approach to restoration can be an effective means of restoring entire plant communities. Sand dunes represent one such system. Sand dunes throughout the world are fragile systems that provide habitat for endemic plant species, shelter neighboring wetlands, and serve as tourist attractions. Native dune vegetation also protects human developments by stabilizing soil, and will be an important habitat in mediating the negative impacts of global climate change, including rising sea levels, severe storms, and greater erosion (Cochard et al. 2008). As such, dunes provide the physical substrate for maintaining ecosystem integrity along the aquatic–terrestrial border (Arun et al. 1999; Albert 2000).

However, these dynamic systems are subject to both natural and human-caused disturbances such as storm blowouts, mining efforts, pedestrian traffic, and invasive species. Because of the economic and environmental importance of stabilizing sand, restoration of dunes after disturbances has become a common practice. Restoration efforts in dune habitats often consist of planting dominant native grass species that function as dune builders due to extensive root systems and ability to grow under constant sand burial (Maun 1998). Since the 1950s, *Ammophila breviligulata* (hereafter referred to simply as *Ammophila*), a highly clonal, perennial, cool-season (C_3) grass and the dominant native pioneer plant species in temperate coastal and lacustrine dunes of North America (Gleason & Cronquist 1991), has been planted in monocultures for restoration purposes (Seneca & Cooper 1971; Maun 1984).

This strategy mimics natural dune succession in eastern and Great Lakes dunes of North America, which begins with colonization of a single plant species, *Ammophila*, in fairly sterile soil conditions (Cowles 1899; Webley et al. 1952). One main role of *Ammophila* is dune building through the stabilization of sand, contributing to a buildup of organic matter and allowing soil microbial communities to develop (Olson 1958; Lichter 2000). Thus, soil biota may play an important role in later dune community development. Specifically, mycorrhizal fungi may facilitate the establishment and survival of dune plants, as

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well as contribute to sand stabilization (Gemma et al. 1989). For example, arbuscular mycorrhizal fungi (AMF) can promote soil stability by cross-linking soil particles in extraradical hyphal networks (e.g., Clough & Sutton 1978; Koske & Polson 1984; Moreno-Espindola et al. 2007) and by producing the glycoprotein glomalin, which is associated with the formation of stable soil aggregates (reviewed by Rillig 2004; Rillig & Mummey 2006). Although restorations aim to mimic the natural development of dune communities, some restoration sites have reported extremely low mycorrhizal presence (Kurtboke et al. 2007). On the other hand, restoration activities can increase abundance or shift composition of mycorrhizal fungi unintentionally through contaminated nursery soil (Gemma & Koske 1997; Koske & Gemma 1997). These differences in soil biota may feedback to impact plant community development (Bever 1994), resulting in suboptimal restoration of plant diversity.

In this study, we evaluate ecological attributes of 18 restoration projects in the Great Lakes region conducted over the past 25 years. Although restorations are often evaluated based solely on the return of native plant species, recently there has been a call for a broader approach, measuring effects of the restoration efforts on diversity in other trophic groups (Young 2000; Woodcock et al. 2008). Organisms such as insects and soil biota are known to form feedback relationships with plant communities, as well as contribute to ecosystem functioning (Bever 1994; Young 2000). Often these other trophic levels have different dynamics than the plant communities. Ideally, a "successful" restoration is one that satisfies multiple targets, such as restoring species diversity, key population abundances (such as endangered or dominant species), and evidence of restored ecosystem function (Zedler 2007). To measure the progress of dune restorations, we characterized (1) attributes of diversity, specifically plants and insects; (2) vegetation structure, specifically abundance of an ecosystem engineer species, plant biomass, and cover; and (3) belowground ecological processes, specifically soil nutrients and mycorrhizal abundance (Ruiz-Jaen & Aide 2005) in each restoration, and compared these measures to paired reference dune communities which served as target conditions for the restorations.

Methods

Site Selection

Great Lakes sand dunes represent the most extensive freshwater dunes in the world, covering over 1,000 km^2 in Michigan alone (Albert 2000). Extensive restoration efforts, usually involving monoculture plantings of *Ammophila breviligulata*, have taken place in the region. In summer 2006, we identified 18 dune restoration sites where *Ammophila* had been planted within the past 25 years (Fig. 1). Restorations ranged in size, but were at least 900 m^2. All sites were located on public lands, including national lakeshores, state and roadside parks, and city parks in Michigan and Indiana. In most cases, goals

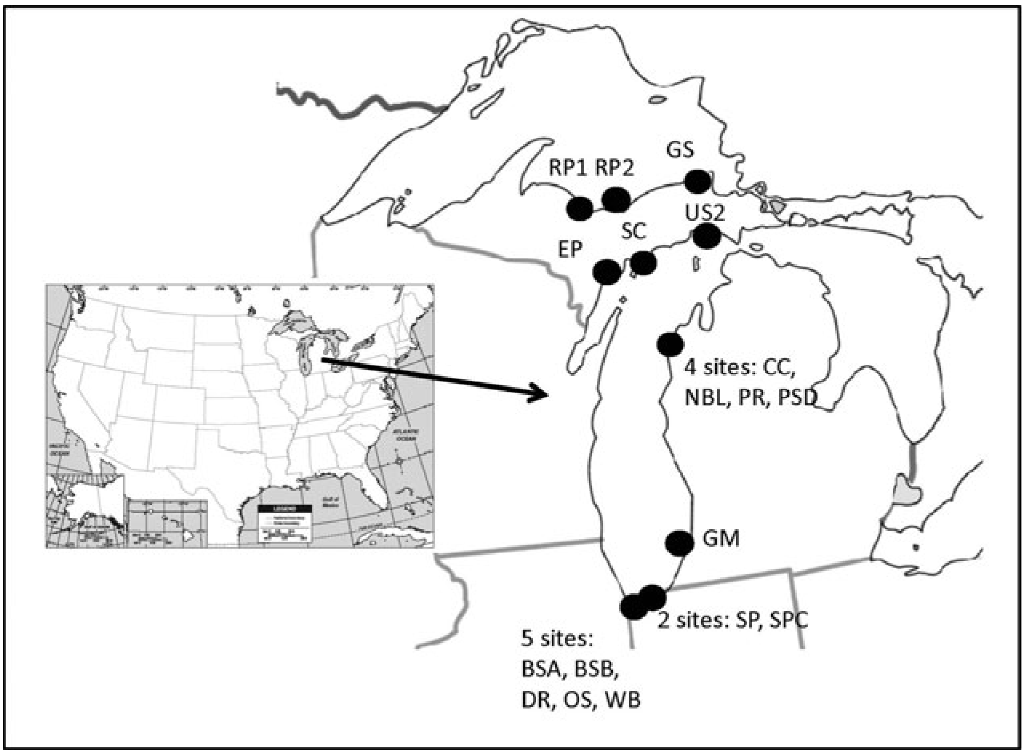

Figure 1. Map of sites for survey of sand dune restorations using *Ammophila breviligulata* plantings. Each site included paired restored and natural dune communities. For most analyses, GM and SP were excluded because of different restoration methods compared to other sites.

for restorations included both stabilizing sand and increasing native dune plant diversity (see Appendix). Histories of these sites were based on personal communication with park staff as well as park records. Two sites (SP and GM) had a suite of native species planted as part of restoration efforts (Palmgren 2000; M. Mycroft 2006, Indiana Dunes State Park, personal communication), whereas all other sites involved planting of *Ammophila* only. Details of restorations, such as the exact year of planting, were often difficult to determine based on incomplete agency records; so, we broadly classified them as either very young (2 years old), young (approximately 5 years old), or mature (approximately 20 years old). For each restoration site, we also located a geographically paired natural dune site, usually within 100 m of the *Ammophila* planting, which we used as a reference system for comparison. Two broad types of reference dunes were used depending on the age of the restoration: young foredunes (approximately 10 years old) and older backdunes (at least 30 years old). Although the extended history, including age, of reference sites is unknown, locations of reference dunes were determined based on discussions with land managers who were familiar with recent site histories. All of our sites were dominated by *Ammophila*, and so were appropriate reference communities.

Evaluating Species Diversity

We quantified plant and insect composition in all restored and natural sites. We assessed plant community composition (including all native and exotic plant species) along transects through the native and restored dune communities. At each of the 36 sites (18 restorations paired with 18 natural areas), we set up five parallel 25-m transects, each 5 m apart. We estimated relative cover of individual species, as well as bare sand, in a 1-m^2 quadrat at five points along each 25-m transect using a modified Daubenmire scale (Daubenmire 1959). Species cover and plant species richness were relativized (so total plant cover equaled 100%) and averaged for each site. This allowed us to calculate both plant species richness and Shannon diversity (H') (Begon et al. 2005) per square meter, as well as total plant species richness in each 25 $\times$ 25–m plot. We also categorized plant species as native and non-native to estimate relative cover of non-native species in each site. We also specifically recorded relative abundance of one federally threatened species, *Cirsium pitcheri*, which occurred in some sites. This species often grows in open dunes between *Ammophila* and other dune grasses (D'ulisse & Maun 1996), and is of conservation interest to many land managers. However, very little is known about whether planted *Ammophila* impedes or facilitates *C. pitcheri* survival.

To assess insect diversity, we took one sweep net sample (30.5-cm diameter mesh net with a 0.91-m handle) along each of the five 25-m transects, and later identified all individuals to family and morpho-species in the lab. All insect sampling was conducted in dry vegetation on sunny days to take advantage of maximum insect abundance. The paired-plot sampling design further helped control for daily variation in weather which could affect insect activity. Over 3,600 insects representing 321 morpho-species and 72 families were collected and identified. Common insect families included Cercopidae, Chironomidae, Cicadellidae, Delphacidae, Formicidae, and Sarcophagidae (see Appendix).

Evaluating Vegetation Structure

We harvested two 25 $\times$ 25-cm areas of vegetation in each site. Biomass was clipped at ground level and separated into aboveground biomass and litter. Samples were dried (48 hours at 60°C) and weighed, then averaged for each site.

Evaluating Ecosystem Processes

As *Ammophila* is a key species capable of ecosystem engineering in this habitat (Cheplick 2005), we considered estimates of *Ammophila* cover to serve as one measure of ecosystem processes. We also measured soil nutrients and mycorrhizal spore abundance for each site. We collected twenty-five 15-cm deep $\times$ 1.9-cm diameter soil cores from each site (five cores spaced 5 m apart along each transect described above), combining them to measure nutrient levels and mycorrhizal spore abundance. Nutrients (P, K, Ca, Mg, NO_3, NH_4) and percent organic matter analyses were conducted by the Michigan State University Soil and Plant Nutrient Laboratory (East Lansing, MI, U.S.A.). To quantify mycorrhizal spore abundance, we used wet-sieving and sucrose density gradient centrifugation (Walker et al. 1982) on 50 mL of sand from each site. We then counted and identified spore morpho-species under a microscope in the lab.

Statistical Analyses

We examined differences in plant and insect abundance and species richness, bare sand cover, *Ammophila* abundance, non-native plant abundance, *C. pitcheri* abundance, plant biomass, litter, nutrients, and mycorrhizal abundance and diversity between the restored sites and natural reference sites using paired *t* tests. For this analysis, we excluded the two restoration sites which planted multiple species in their restoration efforts (SP and GM). We used a liberal interpretation of significance for these tests in order to maximize our likelihood to detect any possible differences in sites, and so did not correct *p* values for multiple comparisons. For response variables that significantly differed between the two types of sites, we followed up with an analysis of covariance (ANCOVA), using the estimated age of all sites as a covariate. We also examined whether plant diversity was correlated with diversity in the other trophic groups (mycorrhizal spores and insects), as well as with *Ammophila* abundance, for each type of site using simple Pearson correlations, where site was the unit of replication. Data were square-root transformed as necessary to satisfy normality assumptions.

To compare plant composition between restored and natural sites, we used two approaches: multi-response permutation procedures (MRPP) with a Bray-Curtis distance measure (Zimmerman et al. 1985), and Euclidean distance (ED) measures (e.g., Collins et al. 2000). MRPP is similar to multivariate analysis of variance (MANOVA) but does not depend on assumptions of normality, which is rare in community data such as these. Although not a statistical analysis, ED measures allow quantitative comparisons between individual pairs of sites based on species relative cover data, and so can serve as a measure of site similarity. Larger EDs indicated greater differences in composition between pairs of sites.

We also used indicator species analysis (Dufrene & Legendre 1997; Mccune et al. 2002) to examine whether individual species were more or less associated with restored or natural sites. Indicator species analysis involves calculating a metric (indicator value, IV) that summarizes both the relative abundance and frequency of each species in each treatment such that:

$$IV_{kj} = RA_{kj} \times RF_{kj} \times 100$$

where RA is the relative abundance of a given species j in a given group k (i.e., natural or restored sites) and RF_{kj} is the proportional frequency of species j in group k (i.e., the proportion of sites in each category that contain species j). Values range from 0 to 100 (perfect indication). A perfect indication score means that a given species occurred only in a given site type and was always in that site type. The observed IV is compared to an expected IV calculated using Monte-Carlo randomizations of the data. For the MRPP, ED, and indicator species analyses, all extremely rare species (<5% total cover among all sites) were excluded, as by definition, these species could never be strong indicators (Mccune et al. 2002). We also excluded *Ammophila* from the MRPP and indicator species analysis, as the extreme dominance of this species swamped all differences in composition due to other species, and because we examined the response of this dominant species in a separate analysis. Finally, we included several species which we could identify confidently only to the genus level due to lack of flowers. It is possible that these represent more than one true species. The MRPP and indicator species analyses were performed in PC-ORD (Mccune & Mefford. 1999). All other analyses were performed in SYSTAT v.11 (Systat Software Inc. 2004)

Results

Diversity and Vegetation Structure

Restored sites had 14% lower total plant species richness per square meter than natural reference sites, but sites did not differ in total plant species richness, suggesting that species accumulation curves differed (Tables 1 & 2). Most of this pattern is explained by differences in age between sites, as the site type effect became non-significant when age was included as a covariate (Fig. 2a; ANCOVA age: $p = 0.025$, site type: $p = 0.244$), where younger sites had three times lower plant species richness per square meter than older sites. Restored and natural sites did not differ significantly in non-native plant abundance, *Cirsium pitcheri* abundance, insect abundance, or insect morpho-species richness (Table 1). Across all sites, there was no significant correlation between total plant species richness and mycorrhizal morpho-species richness per plot, although there was a stronger trend for restored sites (natural sites: $r = -0.19$, $p = 0.46$; restored sites: $r = 0.44$, $p = 0.07$). Correlations between total plant species richness and insect morpho-species richness per plot were also non-significant (natural sites: $r = 0.24$, $p = 0.34$; restored sites: $r = 0.34$, $p = 0.17$). Plant species richness was negatively related to *Ammophila* abundance in natural reference sites, but not restored sites (Fig. 3).

The MRPP analysis indicated no significant difference in plant community composition between restored and natural sites ($t = 0.11$, $p = 0.41$). Among 26 total species used in the indicator species analysis, only one had significant indication for a site type (Table 3). *Artemisia campestris*, a native, perennial forb, was significantly more associated with natural reference sites ($IV = 57.9$, $p = 0.021$). ED measures indicated that many restorations were compositionally similar to their reference community (Table 1). The average ED for all possible pairs of plots was 5.140, with two-thirds of all pairs of restored and reference plots having ED values below this mean. This indicated that restored sites were more similar to their reference site than reference sites were to other reference sites. Sites that showed the biggest differences in composition between restored and reference communities included GM, GS, SP, and WB. Restored sites did not differ from natural sites in total vegetation cover (percent bare sand cover), *Ammophila* cover, aboveground plant biomass, or litter biomass (Table 2).

Ecological Processes

Restored and natural sites were not different in nutrient availability, pH, or soil organic matter (Table 2). Restored sites had lower total mycorrhizal spore abundance, but again, this was due mostly to differences in age, as site type became non-significant when age was included as a covariate (Fig. 2b; ANCOVA age: $p = 0.073$, site type : $p = 0.661$). There were no differences between restored and natural areas in the richness of mycorrhizal morpho-species (Table 2).

Discussion

With this study we characterized dune restorations with reference to plant and insect diversity, vegetation structure, and ecosystem processes. Generally, restoration sites were similar to reference sites in most measured variables. Differences between restorations and reference sites were mostly explained by differences in ages, with the younger sites supporting slightly lower plant diversity and lower abundances of mycorrhizal spores. Older restoration sites were very similar to the older reference sites. The role that *Ammophila* plays in regulating diversity seems to differ in restored and natural systems, with plant diversity generally lower in natural sites with high *Ammophila* dominance, but no similar relationship

Table 1. Summary of measures of diversity and ecosystem processes for each pair of sites.

Location	*Natural or Restored*	*Estimated Site Age (yr)*	*%Percent Bare Sand Cover*	*Ammophila Cover*	*Non-native Plant Percent Cover*	*Cirsium pitcheri Percent Cover*	*Plant Species Richness/ m^2*	*Plant Species Richness/ Site*	*Plant Diversity $(H')/m^2$*	*Aboveground Plant Biomass (g/m^2)*	*Total Insects/ Site*	*Insect Morpho-SR*	*AMF Spores/ 50 mL Soil*	*AMF Morpho-SR*	*Euclidean Distance Measure*
BSA	N	30	63.88	51.25	18.09	0	3.73	23	1.29	21.42	74	5.4	1,822.8	4	2.395
BSA	R	5	62.36	59.70	30.03	0	4.12	30	1.28	65.50	95	8.6	1,029	4	
BSB	N	30	39.24	59.93	4.60	0	5.23	30	1.65	68.32	98	8.2	3,371.2	6	1.814
BSB	R	5	54.80	63.03	7.45	0	4.04	31	1.36	78.19	117	9.8	641.9	6	
CC	N	30	69.96	70.48	1.90	0.21	2.62	11	0.49	21.08	43	6	3, 116.4	5	3.520
CC	R	20	35.92	82.96	2.00	0	1.73	4	0.37	140.40	17	2.6	1,376.9	3	
DR	N	30	44.12	34.05	28.65	0	5.27	21	1.91	77.04	172	16.8	2,552.9	4	5.965
DR	R	5	45.92	73.75	4.91	0	3.65	16	0.96	29.12	107	6.4	1,793.4	5	
EP	N	30	49.16	95.37	0.00	0.57	1.46	6	0.09	102.86	52	6.2	4,860.8	5	0.550
EP	R	5	46.48	96.82	0.11	0	1.23	4	0.10	69.02	44	2.4	2,332.4	6	
GM	N	30	49.28	29.41	4.00	0	4.23	14	1.24	126.92	103	8.2	2,175.6	6	7.956
GM	R	5	71.04	72.56	2.25	0	2.35	16	0.55	146.93	90	8.2	2,499	5	
GS	N	30	50.84	20.96	33.35	0	5.15	15	1.58	37.79	143	11.6	2,355.8	3	7.177
GS	R	20	51.48	58.23	8.33	0	5.48	11	1.19	49.29	37	5	2,548	6	
NBL	N	10	66.96	56.67	1.00	0	2.08	6	0.53	80.17	42	2.4	2,998.8	3	6.780
NBL	R	3	87.20	92.00	0.00	0	0.96	3	0.00	11.96	144	6.2	2,185.4	5	
OS	N	30	45.88	84.79	1.49	0	2.46	17	0.50	66.69	46	4	3,802.4	5	1.218
OS	R	5	81.16	85.02	2.78	0	2.00	15	0.43	18.89	109	8.6	465.5	4	
PR	N	30	68.52	49.70	9.43	0	3.73	19	1.28	38.88	192	15	4,615.8	5	4.663
PR	R	20	47.72	30.01	35.24	0	5.12	26	1.90	30.46	39	6	4,478.6	6	
PSD	N	30	27.44	27.97	3.39	0	7.31	24	2.25	122.32	111	6	1,283.8	5	4.044
PSD	R	20	33.88	35.49	7.20	0	6.42	22	1.98	76.49	82	8.6	1,048.6	4	
RP1	N	10	57.56	69.34	2.34	0	2.46	14	0.66	39.79	59	6.4	1,955.1	5	3.671
RP1	R	2	75.00	93.91	1.23	0	1.42	8	0.11	17.93	49	7	548.8	4	
RP2	N	10	61.48	78.05	0.00	0	2.48	7	0.45	30.20	68	6.2	842.8	6	1.284
RP2	R	2	89.32	76.00	1.60	0	1.15	8	0.05	6.53	8	1.4	499.8	3	
SC	N	30	67.16	71.33	17.44	2.14	2.28	10	0.79	20.46	47	4	1,323	6	4.836
SC	R	2	88.72	41.33	0.00	0	1.50	8	0.82	5.08	107	6.2	543.9	3	
SP	N	30	79.76	48.65	0.99	0	2.32	6	0.97	5.30	63	4.2	2,508.8	6	8.005
SP	R	2	87.28	25.03	2.12	0	2.50	17	0.94	4.44	56	5.6	828.1	4	
SPC	N	30	25.24	89.09	1.49	0	1.80	10	0.45	66.28	58	7.6	1,504.3	6	1.336
SPC	R	2	76.04	98.67	1.00	0	1.35	10	0.02	37.68	47	5.6	240.1	3	
US2	N	30	70.16	98.08	0.00	0.1	1.19	4	0.03	17.18	286	11.6	2,195.2	5	0.278
US2	R	5	72.24	99.16	1.33	0	1.31	9	0.03	20.50	180	7.2	2,944.9	4	
WB	N	30	44.48	94.30	0.00	0	1.24	3	0.23	203.69	145	11.4	656.6	5	7.122
WB	R	20	56.84	52.08	0.00	0	2.08	4	0.91	93.95	554	13.8	1,087.8	5	

Table 2. Paired t tests comparing restored and natural sites.

Response Variable	*t*	*p*	*Natural Sites Grand Means*	*Restored Sites Grand Means*
Plant species richness (/m^2)	**2.06**	**0.057**	3.188	2.795
Plant species richness (whole plot)	0.65	0.526	13.500	13.500
Plant diversity (H')	1.62	0.126	0.885	0.718
Percent bare sand cover	1.86	0.083	53.26	62.82
Non-native plant cover	0.40	0.693	7.666	6.520
Ammophila cover	0.95	0.357	63.182	66.533
Cirsium pitcheri cover	1.40	0.183	0.183	0.000
Insect abundance	0.24	0.810	102.563	109.063
Insect richness	0.98	0.340	7.837	6.587
Plant biomass (g/m^2)	1.16	0.265	59.573	44.857
Litter (g/m^2)	0.26	0.795	70.930	63.227
Soil pH	1.40	0.180	7.419	7.575
Phosphorus (ppm)	0.00	1.000	2.938	2.938
Potassium (ppm)	1.58	0.135	9.563	10.937
Calcium (ppm)	1.43	0.174	174.250	231.000
Magnesium (ppm)	0.80	0.434	13.375	16.250
Nitrate (ppm)	0.95	0.355	0.500	0.400
Ammonium (ppm)	1.50	0.154	1.137	0.925
Percent organic matter	0.59	0.564	0.238	0.213
Mycorrhizal spore abundance	**3.41**	**0.003**	2516.386	1522.063
Mycorrhizal spore richness	0.88	0.390	4.875	4.500

in restored sites. This is interesting, as *Ammophila* has been shown to suppress plant diversity in other systems (e.g., Cheplick 2005). However, our survey indicates that other native species can establish in restoration sites, even at high abundances of *Ammophila*, perhaps because of the relatively high availability of space as measured by bare sand (50–60% of total cover) in these sites.

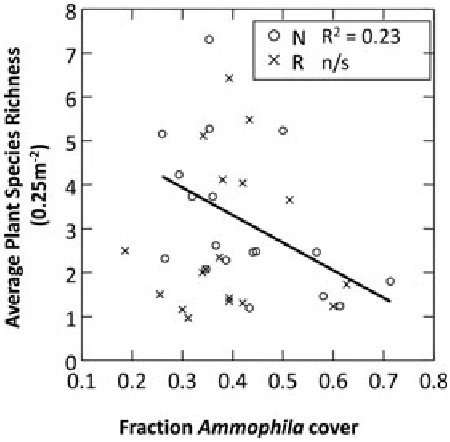

Figure 3. Relationship between *Ammophila* abundance and plant species richness for both natural (N) and restored (R) sites. Circles indicate native reference plots and x's indicate restoration plots.

Community composition varied little between restored and reference sites, with only one native species, *Artemisia campestris*, occurring more often in reference sites than restored sites. This is a threatened species in several states, but is fairly common in Michigan and Indiana (U.S.D.A. 2009). On the other hand, *Cirsium pitcheri* abundance, often a main concern for dune managers in this region, was very low across all sites and did not differ significantly between restored and reference sites, although the only four sites where it was found were reference sites. This potentially indicates that *C. pitcheri* will not colonize new dune restorations naturally, despite apparent suitable habitat created by these restorations (Keddy & Keddy 1984; Bowles et al. 1993). Surprisingly, the two sites that utilized alternative restoration techniques, planting many native species rather than just *Ammophila* (SP and GM), showed quite large differences in plant composition (measured

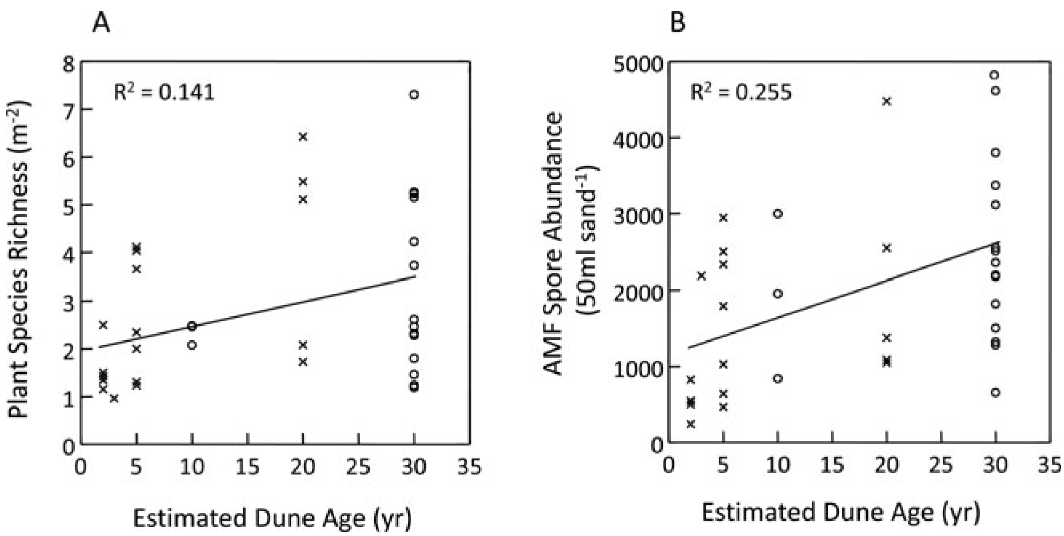

Figure 2. Significant relationships between dune age and (a) plant species richness, and (b) AMF spore abundance. Circles indicate native reference plots and x's indicate restoration plots. R^2 values are reported for a simple linear regression between dune age and the corresponding response variable.

Table 3. Indicator species analysis.

Species	*Indicator Group (p value)*
Ammophila breviligulata	None (0.450)
Artemisia campestris	Natural (**0.021**)
Asclepias syriaca	None (0.160)
Bromus sp.	None (1.00)
Calamovilfa longifolia	None (0.430)
Carex sp.	None (0.881)
Centaurea maculosa	None (0.556)
Chasmanthium latifolium	None (1.00)
Elymus canadensis	None (0.675)
E. hystrix	None (1.00)
Equisetum sp.	None (0.224)
Festuca sp.	None (1.00)
Hieracium sp.	None (0.738)
Lathyrus japonicus	None (0.495)
Monarda punctata	None (0.542)
Poa compressa	None (0.798)
Po. pratensis	None (0.717)
Pteridium aquilinum	None (0.599)
Rumex sp.	None (0.708)
Saponaria officinalis	None (0.776)
Schizachyrium scoparium	None (0.169)
Smilacina racemosa	None (1.00)
Solidago nemoralis	None (0.676)
Solidago sp.	None (0.945)
Toxicodendron radicans	None (0.289)
Vitis sp.	None (0.759)

Numbers in parentheses are p values calculated based on 1,000 randomizations in a Monte-Carlo simulation. Significant differences are bolded.

by ED) compared to their reference sites, with up to three times higher plant species richness (SP) or *Ammophila* cover (GM) than the nearby reference sites. The other two sites with very high ED values (GS and WB) had reference sites that were heavily invaded by exotic species such as *Centaurea maculosa* (GS) or had very high *Ammophila* dominance (WB). In general, though, traditional restoration efforts in Great Lakes sand dunes (i.e., monocultures of *Ammophila breviligulata*) appear to achieve normal restoration goals in terms of diversity and ecosystem properties.

Other studies in dune systems have found similar relationships between age of restoration and plant diversity. For example, Li et al. (2007) reported that vegetation cover and plant biomass increased continually with dune age in a Chinese system, whereas plant diversity increased during the first 30 years, then leveled off. In another Asian dune system, an 11-year-old dune restoration had lower organic carbon, nitrogen, and plant diversity than a 20-year-old dune restoration (Zuo et al. 2008). Because sand dunes rarely have persistent seed banks, plant diversity is regulated by plants' abilities to directly colonize sites (Lichter 2000). Therefore, it is not surprising that it may take 20–30 years for dune restorations to reach references levels of diversity and plant cover. Due to very small regional seed pools, rare species such as *C. pitcheri* may never be able to colonize without explicit help from land managers (Rowland & Maun 2001), despite available space for colonization within sites.

In many restorations, other trophic guilds such as animals are often slow to respond to restoration efforts, in part because individuals must immigrate to sites whereas plants are often directly and artificially introduced to sites (Longcore 2003). However, the data from our survey indicate that dune restorations and natural dunes have similar insect and mycorrhizal communities. What is surprising is the lack of relationship between plant diversity and diversity at these other trophic levels. Niche theory predicts, and many studies have shown, that plant diversity is positively correlated with diversity in other guilds (e.g., Knops et al. 1999). However, this lack of relationship may indicate that each level of diversity is responding to unique species in other communities rather than diversity per se (Loreau et al. 2001), or may be controlled by different abiotic factors or has different timescales for change (Hooper et al. 2000). For example, although bare sand beaches have very low abundance of mycorrhizal fungi, a study by Koske and Gemma (1997) found that mycorrhizal diversity reached mature dune levels within 5 years of restoration initiation, much faster than the development of plant communities on dunes. It may also be that late summer sampling did not adequately capture complete AMF spore diversity, as many AMF species sporulate during the fall (Gemma & Koske 1988). Although the extent of this survey did not allow us to sample during multiple seasons, further work would clarify the belowground biota of this system.

It is unexpected that most of these dune restorations and reference sites are fairly equal in diversity and ecological processes. In many restorations, the development of alternative stable states can be a problem (Woodcock et al. 2008). For example, grassland restoration often varies with changes in climatic variables from year to year (Macdougall et al. 2008). Fagan et al. (2008) found that environmental variables and restoration strategies altered the relative performance of grassland restorations in England, and that some sites were not meeting restoration goals even 60 years after initiation. It may be that dune restorations are more predictable because of the overriding effect of disturbance (e.g., sand movement) on successional trajectories. As dune restorations closely mimic natural dune primary succession with initial colonization by *A. breviligulata* (Cowles 1899) and a natural buildup of soil organic matter and biota, they may be more predictable than restoration efforts in other more complex or densely vegetated ecosystems (e.g., Van Aarde et al. 1998).

Implications for Practice

- Monoculture plantings of *Ammophila breviligulata* in dune habitats of the Great Lakes region have slightly lower plant diversity and lower mycorrhizal spore abundance than comparable reference sites, so addition of native mycorrhizal fungi to dune plantings may benefit some restorations in this area.
- Two native forb species, *Artemisia campestris* and *Cirsium pitcheri*, were rarely found in restored dune sites.

Planting seedlings in restorations may be the only way to build populations of these species.

- As Great Lakes dune restorations age, they become more similar to reference sites. In the Great Lakes region, traditional dune restoration efforts involving monoculture plantings of *A. breviligulata* (American beach grass) restore many measures of diversity and ecosystem processes during a 20–30 year time frame.

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Appendix A. Original intent of restoration, and common plants and insect families in survey sites.

Site Code	Natural or Restored	Site Agency	Intent of Restoration	Common Plants	Common Insect Families
BSA	N	Indiana Dunes National Lakeshore	Sand stabilization, native diversity	*Poa compressa, Schizachyrium scoparium*	Cercopidae
BSA	R			*Po. compressa, Po. pratensis*	Pachygronthidae, Scutelleridae
BSB	N	Indiana Dunes National Lakeshore	Sand stabilization, native diversity	*Calamovilfa longifolia, Po. pratensis, Toxicodendron* radius	
BSB	R			*Elymus canadensis, Schizachyrium scoparium*	Cercopidae
CC	N	Sleeping Bear Dunes National Lakeshore	Sand stabilization, native diversity	*Artemisia campestris*	Cicadellidae
CC	R			*Lathyrus japonicus*	Cercopidae
DR	N	Indiana Dunes National Lakeshore	Sand stabilization, native diversity	*Bromus inermis, Ca. longifolia, S. scoparium, T. radicans*	Cicadellidae, Formicidae
DR	R			*Monarda punctata, Po. compressa, S. scoparium,*	Pachygronthidae
EP	N	City of Escanaba, MI, U.S.A.	Sand stabilization	None	Cercopidae, Cicadellidae
EP	R			None	Formicidae
GM	N	Grand Mere State Park (Michigan DNR)	Sand stabilization, native diversity, mine restoration	*Equisetum sp., S. scoparium*	Cercopidae, Cicadellidae
GM	R			None	Chloropidae, Formicidae
GS	N	Pictured Rocks National Lakeshore	Sand stabilization, native diversity	*Centaurea maculosa, Equisetum sp., Hieracium sp., Rumex acetosella, Saponaria officinalis, S. scoparium*	Cicadellidae, Delphacidae, Rhyparochromidae, Ulidiidae
GS	R			*Ar. campestris, L. japonicus, R. acetosella, Solidago sp.*	Delphacidae
NBL	N	Sleeping Bear Dunes National Lakeshore	Sand stabilization, native diversity	*L. japonicus*	Sarcophagidae
NBL	R			None	Chironomidae
OS	N	Indiana Dunes National Lakeshore	Sand stabilization, native diversity	*Ar. campestris*	Cicadellidae
OS	R			*E. canadensis*	Chironomidae
PR	N	Sleeping Bear Dunes National Lakeshore	Sand stabilization, native diversity	Ce. maculosa	Cicadellidae, Formicidae, Reduviidae
PR	R			*Po. compressa, Solidago* nemoralis	Chironomidae, Pachygronthidae
PSD	N	Sleeping Bear Dunes National Lakeshore	Sand stabilization, native diversity	*Carex sp., So. nemoralis, Vitis sp.*	Cicadellidae, Delphacidae
PSD	R			*Smilacina racemosa*	Cicadellidae
RP1	N	Michigan Department of Transportation	Sand stabilization	None	Cercopidae
RP1	R			None	Cercopidae
RP2	N	Roadside Park: Michiga Department of Transportation	Sand stabilization	*Ar. campestris*	Cicadellidae, Formicidae
RP2	R			None	Cicadellidae
SC	N	Michigan Department of Transportation	Sand stabilization	*Po. compressa*	Formicidae
SC	R			*Ca. longifolia, Pteridium aquilinum*	Aphididae, Formicidae
SP	N	Indiana Dunes State Park (Indiana DNR)	Sand stabilization, native diversity	*Asclepias syriaca, S. scoparium*	Melyridae
SP	R			*Chasmanthium latifolium, E. histrix*	Coccinellidae, Delphacidae

Appendix A. Continued.

Site Code	Natural or Restored	Site Agency	Intent of Restoration	Common Plants	Common Insect Families
SPC	N	Indiana Dunes State Park (Indiana DNR)	Sand stabilization	*Vitus riparia*	Cercopidae, Chironomidae
SPC	R			None	Aphididae, Cicadellidae
US2	N	Roadside Park: Michigan Department of Transportation	Sand stabilization, native diversity	None	Chironomidae, Cicadellidae, Formicidae
US2	R			None	Chironomidae, Cicadellidae
WB	N	Indiana Dunes National Lakeshore	Sand stabilization, native diversity	None	Cicadellidae
WB	R			*V. riparia*, *Ca. longifolia*	Cicadellidae, Sarcophagidae