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Research Article

Spotted Knapweed Spread and Plant Community Changes in a Lacustrine Dune System

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ABSTRACT

Perched sand dunes are ecosystems vulnerable to anthropogenic influence along the Great Lakes, including Grand Sable Dunes in Pictured Rocks National Lakeshore along Lake Superior. Spotted knapweed (*Centaurea stoebe*) is a nonnative plant species that has colonized these dunes and spread into increasingly more areas of the ecosystem. I conducted plant surveys in areas with and without spotted knapweed in 2003, and then resurveyed those areas in 2018. Frequency of spotted knapweed increased in both areas surveyed. Additionally, dominance shifted with spotted knapweed becoming the most important species in the area originally invaded and third most important in the area originally uninvaded. There were approximately two-thirds of species shared between the two survey years, but many of the added species in 2018 were woody. Species richness increased between years, as did species diversity. Nonmetric multidimensional scaling ordination displayed community shifts as convergent succession. While the plant communities in the two areas were rather dissimilar in 2003, they converged as overlapping communities in 2018. Additionally, the shift between years in the area originally invaded was smaller compared to the shift between years in the area originally uninvaded. Due to the continuous evolution of plant communities within sand dune ecosystems, there is a need to monitor changes and quantify nonnative species spread patterns. Dominance by spotted knapweed may be facilitating dune stabilization and converging communities along a modified successional trajectory.

Index terms: Centaurea stoebe; Great Lakes; invasive species; sand dunes; succession

INTRODUCTION

Lacustrine sand dune ecosystems provide a unique opportunity to observe and measure plant community changes over relatively short periods of time (Lichter 1998). Those plant communities are composed of species adapted to exploit limiting resources and survive repeated disturbances (e.g., Carter 1991; Maun 1998; Maun and Perumal 1999; Bach 2001). Stabilization occurs through progression of succession, with increasing diversity as new species colonize, and retention of sand and soil crusts (Cowles 1899; Olson 1958; Lichter 1998). Additionally, there is an expectation (i.e., intermediate disturbance hypothesis) that this increasing diversity will eventually plateau and then decrease over time (Morrison and Yarranton 1973; Catford et al. 2012).

Spotted knapweed (*Centaurea stoebe* L. ssp. *micranthos* (Gugler) Hayek [syn *C. maculosa* Lam., *C. biebersteinii* DC], Asteraceae) is a nonnative plant species originally introduced to the west coast of North America in the late 1800s and has subsequently spread across much of the United States and Canada (Watson and Renney 1974; Harris and Cranston 1979). In addition to reducing wild and domestic grazer production, spotted knapweed alters native plant and insect communities (e.g., Harris and Cranston 1979; Tyser and Key 1988; Hansen et al. 2009). While biological, herbicide, and hand-pulling control have been pursued for decades, there is limited control of spotted knapweed over large geographic areas and an integrated management strategy may be necessary at more localized scales (Sheley et al. 1998).

Specifically within sand dune ecosystems, spotted knapweed has a major influence on plants, arthropods, and mammals. Latsch (2011) described plant community changes related to herbicide application to spotted knapweed, with increases in graminoids over the course of the study as spotted knapweed was controlled. Marshall and Storer (2007) demonstrated that absence of spotted knapweed increased the likelihood of a state threatened locust species; this was in combination with increases in typical food plants. In competition studies, spotted knapweed decreased seedling growth of a state threatened plant species and reduced juvenile survival in a federally threatened plant species (Marshall 2011; Rand et al. 2015). Small mammal communities respond with increased activity, especially mice, in areas invaded by spotted knapweed, which likely has further cascading influences on plant and arthropod communities due to predation (Malick et al. 2012).

Sand dune ecosystems are vulnerable along the Great Lakes, accounting for 3.4% of shoreline, with perched dunes identified as of critical concern (Marsh 1990). The Grand Sable Dunes in Pictured Rocks National Lakeshore is a perched dune system of concern along Lake Superior. Marshall et al. (2008) conducted plant community surveys in areas of Grand Sable Dunes colonized by spotted knapweed and areas without invasion. In that single year study, native species richness and diversity were greater in areas not invaded by spotted knapweed; conversely, nonnative richness and diversity were greater in areas with spotted knapweed (Marshall et al. 2008). Due to the continuous evolution of plant communities, especially in sand dune ecosystem with repeat disturbances, there is a need to monitor

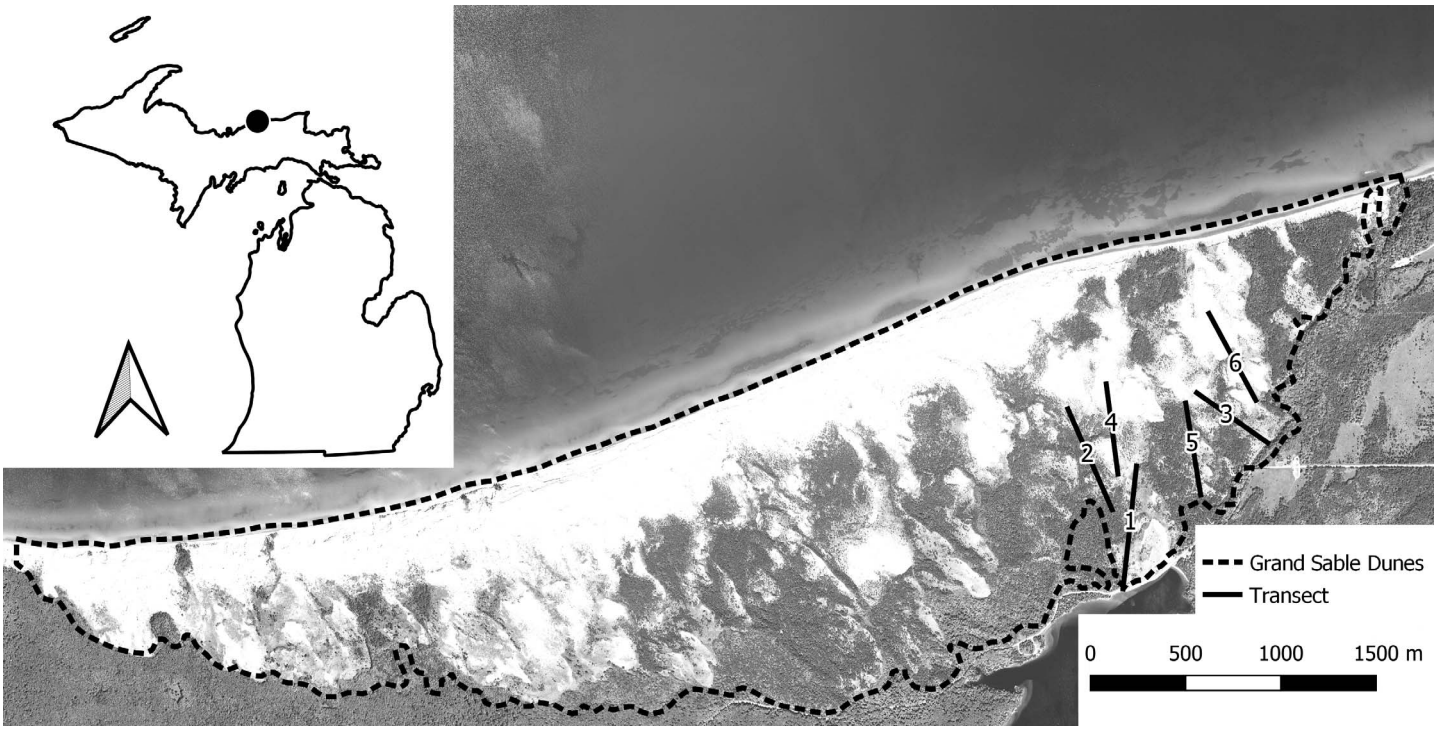

Figure 1.—Transect arrangement in Grand Sable Dunes, Pictured Rocks National Lakeshore, Michigan (closed circle, inset). Transects 1, 2, 3 were in areas originally invaded by spotted knapweed. Transects 4, 5, 6 were originally not invaded. (2016 USDA-FSA-APFO National Agriculture Imagery Program orthoimage)

over time how communities change and quantify patterns of nonnative species spread. The objectives of this study were to compare and contrast the plant community structure and composition between areas historically with and without spotted knapweed colonization.

METHODS

Study Site

The study site was located in the Grand Sable Dunes, Pictured Rocks National Lakeshore, Michigan (46°39′27″N, 86°1′56″W). Grand Sable Dunes is a perched dune system maintained through sand movement from shoreline bluffs and deposits from Lake Superior. Spotted knapweed has transitioned at the site from rare in the early 1970s (Read 1975) to common in the early 2000s (Marshall et al. 2008).

Plant Survey

Surveys were initiated in July 2003 and the methods were originally presented by Marshall et al. (2008). In summary, the three largest patches of spotted knapweed (10.7, 6.3, and 4.8 ha) were selected and 500–600 m long transects were established along the long axes of the patches (Figure 1). Three adjacent areas were selected without spotted knapweed invasion and 500 m long transects were established. Each transect was divided into 20 m segments and a 1 m^2 quadrat was randomly located along each segment. All plants within each quadrat were identified to species (except *Rubus* spp.) and percent cover for each species was estimated. A second plant survey was conducted during June 2018 along the same transects originally surveyed. Quadrat locations were established on 20 m spacing along each transect (not necessarily the same location as 2003), cover was estimated, and species were identified as before. Species richness (count) and species diversity (Shannon index) were calculated for each quadrat for all species, native species, and nonnative species. Since spotted knapweed presence and absence defined the invaded and non-invaded categories, it was omitted from the nonnative species richness and diversity measures. However, it was included in calculations of Sørensen similarity and overall species richness and diversity.

Analysis

For analysis, areas were categorized as originally invaded and non-invaded in 2003. Frequency of spotted knapweed (percent of quadrats with the species) was compared with a two-way analysis of variance (ANOVA) with transects as the survey units ($n = 6$) and invaded/non-invaded categories and years as factors. A Pearson's correlation was used to relate mean percent bare ground in 2003 to percent cover of spotted knapweed in 2018 at the transect level. Species richness and species diversity were compared with a two-way ANOVA with quadrats as the survey units and invaded/non-invaded categories and years as factors. Tukey's HSD was used as a post hoc test for ANOVA tests.

A modified importance value was calculated for each species in each year and area surveyed (invaded and non-invaded). Importance values were calculated as the sum of relative frequency and relative dominance divided by two. Relative frequency was calculated as frequency for a species divided by the sum of all frequencies, where frequency was the number of quadrats in which a species occurred divided by the total

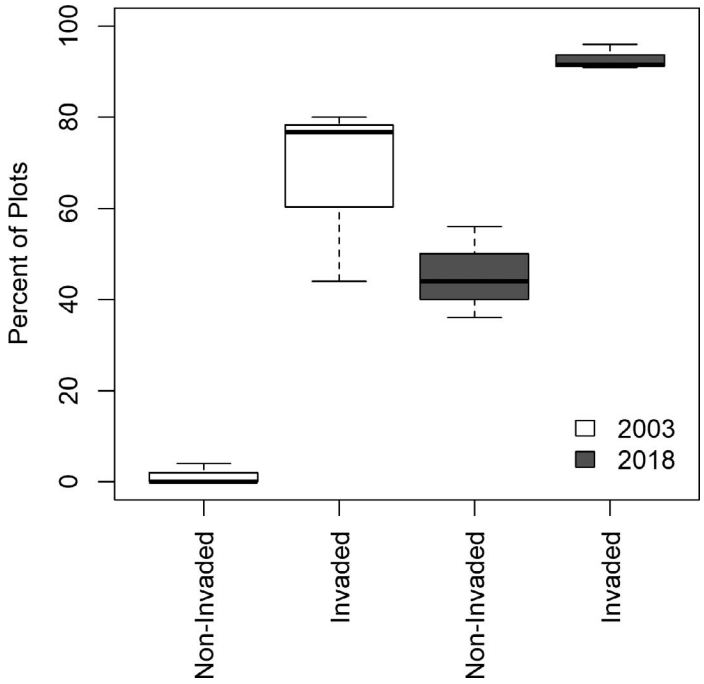

Figure 2.—Percent of quadrats with spotted knapweed presence in areas originally invaded and uninvaded in 2003 and 2018.

number of quadrats. Relative dominance was calculated as sum of percent cover for a species divided by sum of all percent cover. Typically, relative density is included in importance values; however, as I did not count individual stems, this component of the value was omitted. Species were ranked based on importance values.

Sørensen similarity index was calculated to qualitatively compare overall species lists between years and within areas originally invaded and non-invaded. Nonmetric multidimensional scaling (NMDS) was used to visualize plant communities at the transect level with an alternative Gower distance, which omits double-zeros from distance calculations (Anderson et al. 2006). Data analysis was conducted using R 3.6.1 base and *vegan* packages (Oksanen et al. 2019; R Core Team 2019).

RESULTS

In 2003, 160 quadrats along the six transects were surveyed, resulting in 29 species in 19 families. Returning to the transects in 2018, 146 quadrats were surveyed, resulting in 51 species in 28 families. Transects 3 through 6 were 500 m long in both surveys and included 25 quadrats each. In 2003, transects 1 and 2 were 600 m long but were shortened to 500 m in the 2018 survey, with transect 1 having 21 quadrats (four omitted quadrats due to excessive abundance of *Toxicodendron radicans* [L.] Kuntze [Anacardiaceae]) and transect 2 having 25 quadrats. The reductions in quadrats for transects 1 and 2 in 2018 compared to 2003 account for the overall reduction of 14 quadrats.

In 2003, the two areas were categorized as being invaded and not by spotted knapweed. At the north end of transect 5 (Figure 1), a single quadrat did have spotted knapweed in 2003, even though the transect was categorized as non-invaded. Along transects where spotted knapweed was originally absent, it became far more common, increasing over the 15 y to nearly 50% of quadrats (Figure 2). Along transects originally invaded by spotted knapweed, the percent of quadrats with occurrences of spotted knapweed also increased (Figure 2). While invaded/non-invaded categories included presence/absence of spotted knapweed in the definition, it was included in the two-way ANOVA to quantify the change in colonization over the study period. As expected, there was a significant difference in percent of quadrats between areas originally categorized as invaded and non-invaded ($F = 70.59$, df = 1,8, $P < 0.001$). Additionally, there was a significant increase in percent of quadrats with spotted knapweed from 2003 to 2018 ($F = 26.32$, df = 1,8, $P < 0.001$; Figure 2). However, there was not a significant interaction between these factors. Mean percent bare ground in 2003 and mean percent spotted knapweed in 2018 were negatively related ($r = -0.83$, $P = 0.038$).

Table 1.—Top five ranked species in areas originally not invaded by spotted knapweed (*Centaurea stoebe* L. ssp. *micranthos* [Gugler] Hayek) and areas invaded during surveys conducted in 2003 and 2018 within Grand Sable Dunes, Pictured Rocks National Lakeshore. Ranking based on importance values calculated from relative frequency and relative dominance.

	Non-Invaded		Invaded	
Species	2003	2018	2003	2018
Ammophila breviligulata Fernald	1	1	1	2
Artemisia campestris L.	3			
Carex eburnea Boott	4	4		5
Carex umbellata Schkuhr ex Willd.	5	5		4
Centaurea stoebe L. ssp. *micranthos* (Gugler) Hayek		3	2	1
Fragaria virginiana Duchesne			5	
Hieracium caespitosum Dumort.		2	3	3
Lathyrus japonicus Willd.	2			
Pinus banksiana Lamb.			4	

In 2003, spotted knapweed was the second most important species in the area invaded, behind *Ammophila breviligulata* Fernald (Poaceae); in 2018, spotted knapweed shifted to be the most important (Table 1). As a definition to the category, spotted knapweed was not abundant in the non-invaded area in 2003, but became the third most important species in 2018, behind *A. breviligulata* and *Hieracium caespitosum* Dumort (Table 1). Incidentally, *H. caespitosum* is also a nonnative species. In the non-invaded area, two sedges (*Carex eburnaea* Boott and *C. umbellata* Schkuhr ex Willd) were relatively important and remained so between the survey years. Interestingly, those sedges moved into the top five for the invaded area (Table 1).

Other species of interest within the dunes also experienced changes in abundance. *Pinus banksiana* Lamb. (Pinaceae) defines early successional forests establishing in the dunes. In the area originally invaded by spotted knapweed, *P. banksiana* did not dramatically change between years, occurring in 16% of quadrats in 2003 and 15% in 2018, although its importance value ranking did reduce from 4th to 13th (Table 1). However, in the area originally non-invaded, *P. banksiana* increased from occurring in 3% of quadrats to 19%, which did not change its importance value ranking. *Tanacetum bipinnatum* (L.) Sch. Bip. (Asteraceae) is a Michigan state threatened species and decreased in

abundance in areas originally invaded from occurring in 10% of quadrats in 2003 to 4% in 2018, declining in importance value from 14th to 20th. However, *T. bipinnatum* nearly doubled occurrences in the area originally non-invaded from 9% of quadrats in 2003 to 17% in 2018. However, with the increase in species in the non-invaded area, *T. bipinnatum* importance value ranking declined from 8th to 11th. *Stellaria longipes* Goldie (Caryophyllaceae) is a Michigan state species of concern and increased in number of quadrats in both the originally invaded areas (2003 = 1% to 2018 = 7%) and originally non-invaded areas (2003 = 0% to 2018 = 12%). Finally, the number of quadrats that contained zero plant cover had minimal change, with two quadrats bare in the originally invaded area in 2003 and zero in 2018, and with one quadrat bare in the originally non-invaded area in 2003 and one in 2018 (occurring along different transects between years).

Overall, Sørensen similarity index was 0.65 between years, suggesting nearly two-thirds of species were shared between 2003 and 2018. For areas originally invaded by spotted knapweed, the Sørensen similarity was 0.67 between the two years; seven species occurred in 2003 but were not encountered in 2018 and 14 species were added in 2018. Half of the added species were woody shrubs and trees. For areas originally non-invaded, the Sørensen similarity was 0.53 between years; three species did not occur in 2018 that were encountered in 2003 and 29 species were added. Twelve of the added species were woody shrubs or trees. Of the species added in 2018, nine were shared between the areas non-invaded and invaded (Sørensen = 0.42), five of which were woody species including four members of Rosaceae (*Amelanchier arborea* [Michx. f.] Fernald, *Prunus pumila* L., *P. virginiana* L., *Rosa blanda* Aiton) and a member of Sapindaceae (*Acer saccharum* Marshall).

Total richness was not significantly different between areas originally invaded and non-invaded. However, there was a significant difference between years where 2018 had increased richness values ($F_{1,302} = 51.56$, $P < 0.001$; Figure 3A). Separating plant species into native and nonnative categories resulted in differences in invaded and non-invaded for native species richness, with areas originally non-invaded having greater richness than those invaded ($F_{1,302} = 17.31$, $P < 0.001$; Figure 3B). Similar to total richness, native richness was greater in 2018 compared to 2003 ($F_{1,302} = 31.00$, $P < 0.001$) and there was no significant interaction between invasion category and year. Areas originally invaded had greater nonnative richness ($F_{1,302} = 21.73$, $P < 0.001$; Figure 3C). However, there was no difference between years or an interaction.

Total diversity had similar patterns as total richness, with no difference between areas originally invaded and non-invaded and greater values in 2018 ($F_{1,298} = 60.17$, $P < 0.001$; Figure 3D). Native species diversity was significantly greater in areas non-invaded than invaded ($F_{1,295} = 28.93$, $P < 0.001$) and in 2018 than 2003 ($F_{1,295} = 45.28$, $P < 0.001$), with no significant interaction between these two factors (Figure 3E). There were no significant differences between areas originally invaded and non-invaded, 2003 and 2018, or the interaction of the two for nonnative species diversity (Figure 3F).

Nonmetric multidimensional scaling (NMDS) ordination using alternative Gower distance between transects and years based on species percent covers resulted in a stress of 0.11 (Figure 4). In 2003, non-invaded transects were much more variable in their distances compared to other transects, resulting in relatively large error bars around the mean (open circles, Figure 4). Additionally, mean distances between the non-invaded and invaded were relatively far apart (open symbols, Figure 4). However, in 2018, the non-invaded and invaded mean distances were much closer together compared to 2003, suggesting less dissimilarity between transects (closed symbols, Figure 4). While transects appear to converge, the shift for invaded transects from 2003 to 2018 was considerably less than those transects originally not invaded by spotted knapweed.

DISCUSSION

Since the early years of ecological science, lacustrine sand dunes have represented key systems to understand successional processes (e.g., Cowles 1899). Unfortunately, such active dune systems also are prime candidates for invasion by nonnative species that can subsequently alter those successional pathways, disturbance regimes, and community structure (Castillo and Moreno-Casasola 1996; Mack and D'Antonio 1998; Leege and Murphy 2001). The shift of spotted knapweed from rare to common in Pictured Rocks National Lakeshore raises a concern regarding plant, insect, and mammal communities within the Grand Sable Dunes (Read 1975; Marshall and Storer 2007; Marshall et al. 2008; Marshall 2011; Malick et al. 2012).

Spotted knapweed has continued to spread into new areas within the Grand Sable Dunes, becoming more common, colonizing portions of the dunes not originally invaded by this species. Not only is this species now occurring in new areas, community dominance has begun to shift away from the expected most important species (i.e., *A. breviligulata*) toward spotted knapweed (both increases in frequency of occurrence and percent cover). In these Great Lakes sand dune systems, *A. breviligulata* is a common, early succession community defining species, and occurs throughout active foredunes (Maun 1984; Voss 2001). While *A. breviligulata* frequency increased, its cover in the invaded areas of the dunes substantially decreased. This shift away from *A. brevilgulata* dominance toward spotted knapweed dominance may be an indication of successional aging of the dunes (Lichter 2000) and potential stabilization associated with spotted knapweed colonization. The correlation between bare ground in 2003 and spotted knapweed cover in 2018 suggested that spotted knapweed was not necessarily only colonizing areas with elevated bare ground (i.e., open space). Additionally, the new species added to both areas over the 15 y between surveys suggests more native species, especially woody species, have been able to colonize the dunes as they age.

One federally threatened species commonly found in Grand Sable Dunes did not occur in any of the survey quadrats—*Cirsium pitcheri* (Torr. ex Eaton) Torr. & A. Gray. The survey transects were farther back in the dunes (approximately 0.5 km from Lake Superior). The lack of *C. pitcheri* was likely related to its affinity for more active portions of the Grand Sable Dunes, closer to Lake Superior (Marshall 2014). Additionally, there are elevation differences in this portion of the Grand Sable Dunes, compared to other parts of the same dune system, that add to

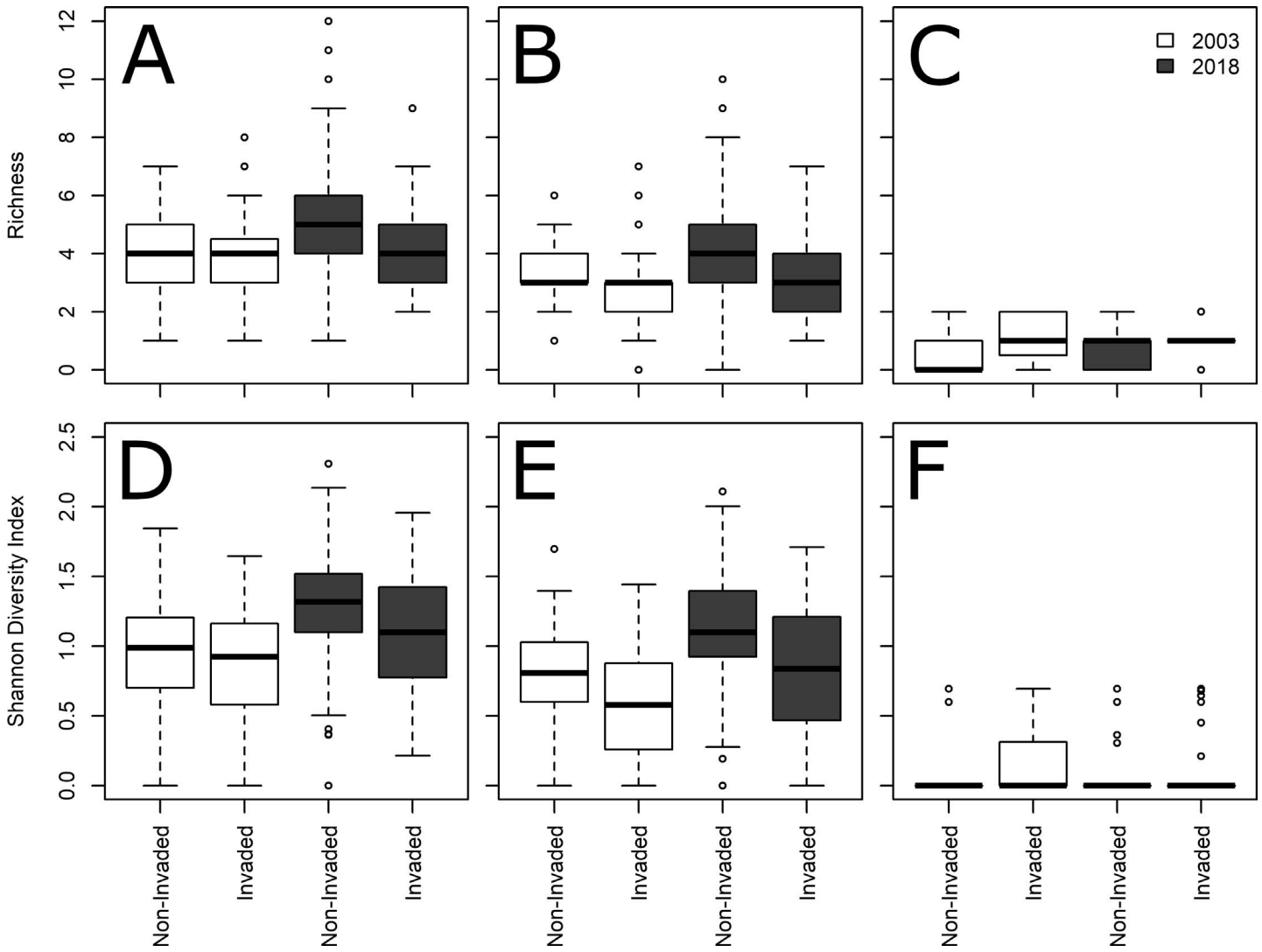

Figure 3.—Mean richness and Shannon's diversity index for transects originally invaded and uninvaded in 2003 (white) and in 2018 (shaded): (A) total richness, (B) native species richness, (C) nonnative species richness, (D) total diversity, (E) native species diversity, (F) nonnative species diversity.

the limited habitat availability for *C. pitcheri*. A single individual of a state threatened *Botrychium* sp. was observed in area originally invaded, although it was along a portion of the transect with relatively low spotted knapweed percent cover. Changes in *T. bipinnatum* (state threatened) and *S. longipes* (state species of concern) importance values followed expected patterns based on previous research in the Grand Sable Dunes (Marshall 2014). With increasing overall plant density, *T. bipinnatum* has been observed decreasing in abundance while *S. longipes* increases (Marshall 2014). While proportion of quadrats with *T. bipinnatum* in the area originally invaded by spotted knapweed followed this pattern, the opposite was observed here in the area originally not invaded by spotted knapweed.

In addition to the plant communities in Grand Sable Dunes, Marshall et al. (2008) noted differences in ground-dwelling arthropod communities between the two areas with and without spotted knapweed. For arthropod families like Formicidae, there were indications of dune stabilization in areas with spotted knapweed (Marshall et al. 2008). Over the 15 y between surveys, there has been further progression in succession and stabilization of the dunes—spotted knapweed colonizing substantially more areas and the occurrence of additional woody species. However, it is difficult to tease apart the cause and effect of this correlation. It is unclear if other species were stabilizing the dunes, facilitating spotted knapweed colonization, or if spotted knapweed stabilized the dunes, facilitating woody species colonization. Latsch (2011) also argued that spotted knapweed may be stabilizing the dunes and interrupting natural succession; increases in spotted knapweed percent cover resulted in both decreases in native dune species percent cover and increases in nonnative species percent cover. Native plant species may have very weak influence on spotted knapweed growth, while this species may be exerting substantial influence on the native species (Maron and Marler 2008; Marshall 2011). Even in high-diversity areas, spotted knapweed becomes abundant (Maron and Marler 2007). The unequal competitive interaction, along

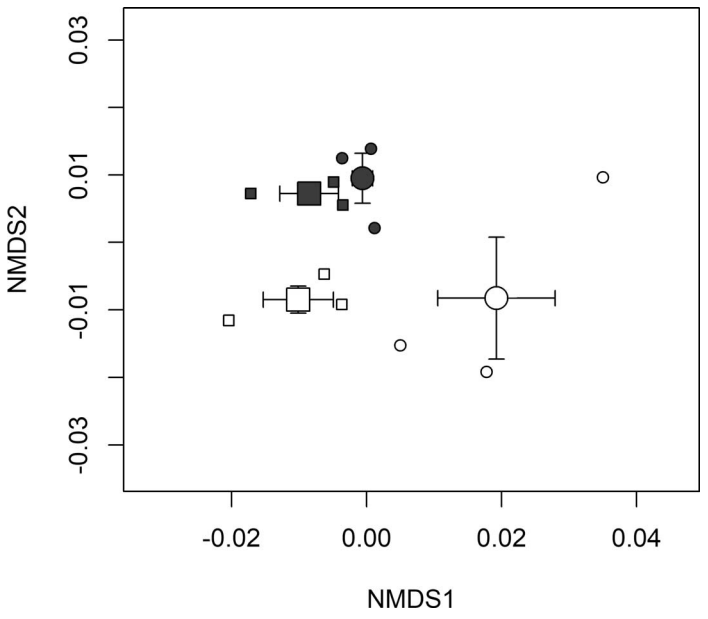

Figure 4.—Nonmetric multidimensional scaling (NMDS) ordination of transects in areas originally not invaded (circles) and invaded by spotted knapweed (squares) in 2003 (open symbols) and 2018 (shaded symbols). Ordination based on alternative Gower distance of relative species cover. Larger symbols represent mean values with standard error bars.

with the ability of spotted knapweed to colonize larger and larger portions of the Grand Sable Dunes, may lead to altered successional pathways. This has been demonstrated in grasslands with spotted knapweed invasion and likely applies here (Tyser and Key 1988).

In both areas, originally non-invaded and invaded, species richness and diversity increased between survey years. This is an expected result with dune succession described by Cowles (1899), increasing levels of stability and plant community composition from beach to stationary dunes and finally forest as seral stages of succession representing time. Diversity as a single measure may not be useful for making conservation decisions of the ecosystem and functional group redundancy (i.e., diversity within functional groups) may be more useful for management (García-Mora et al. 2000). However, in this case, species diversity further illustrates the patterns of change also displayed in Sørensen similarity and the NMDS ordination, which was based on dissimilarity. The ordination results aid in visualizing the structural changes within the Grand Sable Dune plant community. In 2003, the plant community composition and dominance were relatively different, with the non-invaded portion of the dunes having greater internal variability (i.e., large error bars around mean). Convergent succession has led to more similar plant communities in areas originally invaded and non-invaded. As noted, the convergence in 2018 between the invaded and non-invaded transects was the result of a small shift in distance for the originally invaded transects and a rather larger shift for transects without spotted knapweed in 2003 along axis 1. This partially includes the significant increase in spotted knapweed frequency in both areas surveyed. As this convergence was measured at the coarse-unit scale (i.e., transect), it was evident. However, at a finer scale (i.e., quadrat), such a pattern may not have been seen (Li et al. 2016).

In the past, the National Park Service has used herbicide application and hand-pulling as management techniques for spotted knapweed in the Grand Sable Dunes (Latsch 2011). Additionally, Latsch (2011) and Grzesiak (2013) demonstrated that National Park Service "spot-spray" guidelines (i.e., spray wand tip as close to the target plant as possible while spraying as much vegetative growth) significantly reduced spotted knapweed density when that species was targeted, while most other species displayed nonsignificant changes in density. Incidentally, graminoid species had significantly greater density as the study progressed with annual herbicide applications (Latsch 2011). The issue with this technique is the volume of time and herbicide needed to manage spotted knapweed in the Grand Sable Dunes. This dune complex is nearly 900 ha of critical dune habitat; 3.5% was colonized by spotted knapweed in 2003 (Marshall et al. 2008) and 9% was colonized in 2011 (Latsch 2011). Such large areas are difficult to manage with a spot-spray technique that must be applied annually—Grzesiak (2013) reported recovery by spotted knapweed over 2 y with cessation of herbicide application.

Management strategies that aim to simply kill spotted knapweed are not likely appropriate, but an integrated strategy may be more successful (Sheley et al. 1998). Promoting and planting native species, like *A. breviligulata*, may have positive influence on dune plant communities and negative influence on spotted knapweed (Emery and Rudgers 2012). Continuous monitoring of the Grand Sable Dunes to understand the influence spotted knapweed has on dune stabilization and plant community structure is important. However, climate factors may have greater influence on stabilization patterns, dune building, and subsequent plant communities (Marsh 1990; Loope et al. 2004; Emery and Rudgers 2014).

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LITERATURE CITED

Anderson, M.J., K.E. Ellingsen, and B.H. McArdle. 2006. Multivariate dispersion as a measure of beta diversity. Ecology Letters 9:683-693.

Bach, C.E. 2001. Long-term effects of insect herbivory and sand accretion on plant succession on sand dunes. Ecology 82:1401-1416.

Carter, R.W.G. 1991. Near future sea level impacts on coastal dune landscapes. Landscape Ecology 6:29-39.

Castillo, S.A., and P. Moreno-Casasola. 1996. Coastal sand dune vegetation: An extreme case of species invasion. Journal of Coastal Conservation 2:13-22.

Catford, J.A., C.C. Daehler, H.T. Murphy, A.W. Sheppard, B.D. Hardesty, D.A. Westcott, M. Rejmánek, P.J. Bellingham, J. Pergl, C.C. Horvitz, and P.E. Hulme. 2012. The intermediate disturbance hypothesis and plant invasions: Implications for species richness and management. Perspectives in Plant Ecology, Evolution and Systematics 14:231-241.

Cowles, H.C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. Botanical Gazette 27:95-117, 167-202, 281-308, 361-391.

Emery, S.M., and J.A. Rudgers. 2012. Impact of competition and mycorrhizal fungi on growth of *Centaurea stoebe*, an invasive plant of sand dunes. American Midland Naturalist 167:213-222.

Emery, S.M., and J.A. Rudgers. 2014. Biotic and abiotic predictors of ecosystem engineering traits of the dune building grass, *Ammophila breviligulata*. Ecosphere 5:87.

García-Mora, M.R., J.B. Galego-Fernández, and F. García-Novo. 2000. Plant diversity as a suitable tool for coastal dune vulnerability assessment. Journal of Coastal Research 16:990-995.

Grzesiak, K.E. 2013. Long-term effects of herbicide treatments on spotted knapweed and non-target plants in the Grand Sable Dunes. Master's thesis, University of Michigan, Ann Arbor.

Hansen, A.K., Y.K. Ortega, and D.L. Six. 2009. Comparison of ground beetle (Coleoptera: Carabidae) assemblages in Rocky Mountain savannas invaded and un-invaded by an exotic forb, spotted knapweed. Northwest Science 83:348-360.

Harris, P., and R. Cranston. 1979. An economic evaluation of control methods for diffuse and spotted knapweed in Western Canada. Canadian Journal of Plant Science 59:375-382.

Latsch, M.E. 2011. Effects of management on native and exotic plant communities in Pictured Rocks National Lakeshore in the Upper Peninsula of Michigan. Doctoral dissertation, Michigan Technological University, Houghton.

Leege, L.M., and P.G. Murphy. 2001. Ecological effects of the non-native *Pinus nigra* on sand dune communities. Canadian Journal of Botany 79:429-437.

Li, S., M.W. Cadotte, S.J. Meiners, Z. Pu, T. Fukami, and L. Jiang. 2016. Convergence and divergence in a long-term old-field succession: The importance of spatial scale and species abundance. Ecology Letters 19:1101-1109.

Lichter, J. 1998. Primary succession and forest development on coastal Lake Michigan sand dunes. Ecological Monographs 68:487-510.

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

Loope, W.L., T.G. Fisher, H.M. Jol, J.B. Anderton, and W.L. Blewett. 2004. A Holocene history of dune-mediated landscape change along the southeastern shore of Lake Superior. Geomorphology 61:303-322.

Mack, M.C., and C.M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. Trends in Ecology & Evolution 13:195-198.

Malick, S.L., J.L. Belant, and J.G. Bruggink. 2012. Influence of spotted knapweed on diversity and abundance of small mammals in Grand Sable Dunes, Michigan, USA. Natural Areas Journal 32:398-402.

Maron, J.L., and M. Marler. 2007. Native plant diversity resists invasion at both low and high resource levels. Ecology 88:2651-2661.

Maron, J.L., and M. Marler. 2008. Field-based competitive impacts between invaders and natives at varying resource supply. Journal of Ecology 96:1187-1197.

Marsh, W.M. 1990. Nourishment of perched sand dunes and the issue of erosion control in the Great Lakes. Environmental Geology and Water Sciences 16:155-164.

Marshall, J.M. 2011. *Tanacetum bipinnatum* germination and competitive interaction with *Centaurea stoebe* seedlings. Michigan Botanist 50:139-145.

Marshall, J.M. 2014. Influence of topography, bare sand, and soil pH on the occurrence and distribution of plant species in a lacustrine dune ecosystem. Journal of the Torrey Botanical Society 141:29-38.

Marshall, J.M, and A.J. Storer. 2007. Presence of the "Threatened" *Trimerotropis huroniana* (Orthoptera: Acrididae) in relation to the occurrence of native dune plant species and the exotic *Centaurea biebersteinii*. Great Lakes Entomologist 40:17-22.

Marshall, J.M., A.J. Storer, and B. Leutscher. 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.

Maun, M.A. 1984. Colonizing ability of *Ammophila breviligulata* through vegetative regeneration. Journal of Ecology 72:565-574.

Maun, M.A. 1998. Primary succession and forest development on coastal Lake Michigan sand dunes. Ecological Monographs 68:487-510.

Maun, M.A., and J. Perumal. 1999. Zonation of vegetation on lacustrine coastal dunes: Effects of burial by sand. Ecology Letters 2:14-18.

Morrison, R.G., and G.A. Yarranton. 1973. Diversity, richness, and evenness during a primary sand dune succession at Grand Bend, Ontario. Canadian Journal of Botany 51:2401-2411.

Oksanen, J., F.G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P.R. Minchin, R.B. O'Hara, G.L. Simpson, P. Solymos, et al. 2019. vegan: Community ecology package. R package version 2.5-5. Accessed February 2020 from <https://CRAN.R-project.org/package=vegan>.

Olson, J.S. 1958. Rates of succession and soil changes on southern Lake Michigan sand dunes. Botanical Gazette 119:125-170.

Rand T.A., S.M. Louda, K.M. Bradley, and K.K. Crider. 2015. Effects of invasive knapweed (*Centaurea stoebe* subsp. *micranthos*) on a threatened native thistle (*Cirsium pitcheri*) vary with environment and life stage. Botany 93:543-558.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Accessed February 2020 from <https://www.R-project.org>.

Read, R.H. 1975. Vascular plants of Pictured Rocks National Lakeshore, Alger County, Michigan. Michigan Botanist 14:3-43.

Sheley, R.L., J.S. Jacobs, and M.F. Carpinelli. 1998. Distribution, biology, and management of diffuse knapweed (*Centaurea diffusa*) and spotted knapweed (*Centaurea maculosa*). Weed Technology 12:353-362.

Tyser, R.W., and C.H. Key. 1988. Spotted knapweed in natural area fescue grasslands: An ecological assessment. Northwest Science 62:151-160.

Voss, E.G. 2001. Michigan Flora. Part I. Gymnosperms and Monocots. Bulletin 55. Cranbrook Institute of Science, Bloomfield Hills, MI.

Watson, A.K., and A.J. Renney. 1974. The biology of Canadian weeds. 6. *Centaurea diffusa* and *C. maculosa*. Canadian Journal of Plant Science 54:687-701.