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THE POPULATION STATUS OF THE  
FEDERALLY THREATENED PITCHER'S  
THISTLE (CIRSIIUM PITCHERI) IN THE  
GRAND SABLE DUNES AT PICTURED  
ROCKS NATIONAL LAKESHORE,  
MICHIGAN

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THE POPULATION STATUS OF THE FEDERALLY THREATENED  
PITCHER'S THISTLE (*CIRSIUM PITCHERI*) IN THE GRAND SABLE DUNES AT  
PICTURED ROCKS NATIONAL LAKESHORE, MICHIGAN

By

Kimberly Sue Danielson

THESIS

Submitted to  
Northern Michigan University  
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## ABSTRACT

### THE POPULATION STATUS OF THE FEDERALLY THREATENED PITCHER'S THISTLE (*CIRSIUM PITCHERI*) IN THE GRAND SABLE DUNES AT PICTURED ROCKS NATIONAL LAKESHORE, MICHIGAN

By

Kimberly Sue Danielson

Pitcher's thistle (*Cirsium pitcheri*), a federally threatened species, is a colonizing species endemic to the beaches and dunes of the western Great Lakes. The only occurrence of *C. pitcheri* on the south shore of Lake Superior is in the Grand Sable Dunes, a perched dunes system, at Pictured Rocks National Lakeshore, Michigan. This research focused on the population status, including the distribution, total population estimates, associated ecological communities, and conservation threats to *C. pitcheri* in the Grand Sable Dunes. I found that *C. pitcheri* was distributed throughout the dunes in a variety of habitats and the main populations of *C. pitcheri* occurred in distinct groups midway between the dune bluff and the forest. Total population size estimates indicate that the population may be one of the largest populations for the species. On a broad scale, *C. pitcheri* was associated with early to mid successional communities characterized by 50-70% bare sand cover. *Schizachyrium scoparium* can be considered an indicator species for *C. pitcheri*. Seedling densities were lowest in late successional communities. On a finer scale, *C. pitcheri* was associated with moderate (6-10°) windward west-facing slopes, reflecting sand movement patterns caused by prevailing W-NW winds. Areas where *C. pitcheri* co-occurs with the invasive species, *Centaurea stoebe*, should be a high priority for invasive species management. Dune stabilization due to recent climate change trends may fragment current *C. pitcheri* populations and reduced suitable habitat.

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## Introduction

The successful protection of a rare species depends on a thorough knowledge of the species' biology and the natural processes that maintain its habitat (Pavlik et al. 1993, Schemske et al. 1994), as well as an evaluation of its conservation threats (Lawler et al. 2002). My research focused on Pitcher's thistle (*Cirsium pitcheri*) [Torrey ex Eaton] T&G), a federally threatened plant (USFWS 1987) that is endemic to the beaches and dunes of the western Great Lakes, including lakes Michigan, Huron, and Superior. In 2002, the U.S. Fish and Wildlife Service approved a Pitcher's Thistle Recovery Plan, which required in-depth studies of all populations to create management plans to assist the goal of delisting the species (USFWS 2002). My research objectives were to determine the current population status (distribution, densities and demographics), associated ecological communities, and conservation threats (exotic invasive species and dune stabilization) of *C. pitcheri* in the Grand Sable Dunes (GSD) at Pictured Rocks National Lakeshore (PIRO), Michigan, U.S.A.

The 890-ha Grand Sable Dunes is a perched dune system, 40-90 m above lake-level, that harbors the only U.S. population of *Cirsium pitcheri* in the Lake Superior basin. Only 8% of *C. pitcheri* populations occur on perched dunes (USFWS 2002) and perched dunes respond differently to climatic and geological processes than lake-level beaches and dunes (Anderton and Loope 1995, Loope et al. 2004). Although few in number, populations of *C. pitcheri* on perched dunes may be many orders of magnitude larger than lake-level populations. The remoteness and protected status of the GSD also provides habitat with little anthropogenic disturbance, and the isolated location at the northern edge of the species distribution range provides a unique species assemblage and climatic patterns. With the exception of McEachern (1992), most studies of *C.*

*pitcheri* have been conducted on the lake-level beaches and dunes of Lakes Michigan and Huron at the southern part of its range.

*Cirsium pitcheri* is considered an early-successional species that colonizes beaches and open dunes and requires disturbance for establishment. It can persist as the plant community develops, but eventually it disappears from late successional communities (Bach 1978, McEachern 1992). It has many adaptive characteristics that favor its survival on xeric windswept beaches and dunes, including narrow, pinnatifid, densely tomentose leaves and a long taproot that provides escape from heat, access to moisture, and anchors the plant in shifting sandy habitats. It is a sexually reproducing monocarpic perennial that persists as a vegetative rosette for 3-10 years before flowering once and then dying. It has cream to light purple colored flowers that are borne in composite inflorescences and are pollinated by a variety of pollinators (Loveless 1984). In late summer, seeds are wind dispersed as individual achenes within 4 m of the parent plant, or sand may bury entire seed heads when the parent plant dies and falls over (Loveless 1984, McEachern 1992). Seedling establishment is critical for the species' long-term persistence (Hamze and Jolls 2000).

#### *Cirsium pitcheri* and the Dynamic Great Lakes

As an endemic species, the evolutionary history of *C. pitcheri* is intimately linked to the geological history of the Great Lakes region. Genetic studies show *C. pitcheri* is genetically depauperate and closely related to the western Platte thistle, *Cirsium canescens* (Loveless and Hamrick 1988, Gauthier et al. 2010). *C. pitcheri* most likely originated by rapid speciation from an isolated founder population of its suspected ancestor, *Cirsium canescens*, which established in the Great Lakes region in newly created glacial outwash habitat provided by the retreat of the

Wisconsin ice sheet roughly 10,000 years ago (Loveless and Hamrick 1988). Since then, *C. pitcheri* has evolved in a more restricted landscape, dependent on the cycles of dune building and erosion unique to the Great Lakes.

The current distribution and ecology of *C. pitcheri* has been influenced by the geological and climatic processes that drive dune formation and dune succession. In the Great Lakes region, the rate of dune formation is directly influenced by water levels (Arbogast and Loope 1999, Loope and Arbogast 2000, Arbogast et al. 2002). Water levels affect the impact of waves on the shore, which dictates how much sand is available to be blown inland. In perched dunes, like the GSD, high lake-levels cause dune building and development of sparsely vegetated communities due to destabilization of the bluff by wave erosion; whereas, low lake-levels cause dune quiescence and stabilization of dunes by vegetation due to stabilization of the bluff (Marsh and Marsh 1987, Anderton and Loope 1995, Loope et al. 2004). Since the end of the last glaciation (~10,000 years BP), the water levels in the Great Lakes has fluctuated greatly from their present level (Anderton and Loope 1995, Loope and Arbogast 2000). These lake level fluctuations have both expanded and contracted suitable habitat for *C. pitcheri* in the GSD and throughout the species range.

### Sand Movement and Dune Succession

Plant succession in sand dunes is distinguished from other primary successions because the major physical stresses are related to continuous windblown sand movement (Cowles 1901, Olson 1958, Doing 1985, Moreno-Casasola 1986, Litcher 1998, Maun and Perumal 1999, Martinez et al. 2001). Maun and Perumal (1999) showed the distribution of plant species in dunes was correlated with rates of sand deposition, and species were eliminated when burial

exceeded the tolerance limits for that species. In general, dune communities occur in linear zones that parallel the shoreline, and a succession gradient occurs from the shoreline to inland driven by decreasing frequency and intensity of sand movement (Cowles 1901, Olson 1958). However, this vegetation continuum shifts in time and space with long term changes in disturbance patterns influenced by lake-level fluctuations as suggested by McEachern (1992).

Near the shoreline, the frequency and intensity of disturbance by sand movement prevents succession from advancing, and only species that have special adaptations to overcome constant sand burial (e.g. *Ammophila brevigulata*) can survive (Disraeli 1984, Maun and Lapierre 1984, Maun 1998). Inland from the lake, the frequency and intensity of disturbance decreases allowing more species to colonize that are less tolerant of sand movement. In stabilized late-successional habitats, where sand movement is non-existent or limited to occasional dustings of finer material in suspension, tree species (e.g. *Pinus banksiana*) become established and eventually shade out dune plants (Olson 1958, Bach 1978, Litcher 1998).

However, the gradient of dune succession is not always linear from the lake inland to the forest. Dune succession is often interrupted inland by stochastic wind events, which cause localized patchy disturbances or ‘blowouts.’ In these localized disturbances, succession is reset to earlier stages, which facilitates the introduction of early successional species (Olson 1958). Additionally, fine-scale sand movement patterns on individual dunes can cause distinct species assemblage depending on topographic position. In general, sand is eroded from the windward side of a dune and deposited on the leeward side causing different microsites. The windward side is often sparsely vegetated, because most plants do not survive the desiccation of their root system caused by erosion of sand (Maun 1998), and the species on the leeward side must be tolerant to a high frequency and intensity of sand burial (Dech and Maun 2005).

Previous studies on *C. pitcheri* showed that burial by sand can be beneficial or detrimental depending on the rate of deposition and the life stage of the plant (seed, seedling, vegetative, or flowering). For example, *C. pitcheri* seeds require burial for successful germination, but as burial depths increase, both seed germination and seedling emergence decrease (Hamze and Jolls 2000, Chen and Maun 1999). In fact, Chen and Maun (1999) showed that seedling emergence occurred at a maximum depth of 8 cm, but most seedlings emerged from 2 cm depth. Multiple studies have found that partial burial of *C. pitcheri* seedlings and juveniles can stimulate growth, but extreme or complete burial can be detrimental to plants (Maun et al. 1996, Rowland and Maun 2001, Perumal and Maun 2006). Maun et al. (1996) showed that partial burial of juvenile plants up to 75% (15 cm) of their height was beneficial because it enhanced net photosynthetic rates, total chlorophyll content, chlorophyll a:b ratio, plant vigor and total plant biomass, but burial to 100% of their height (20 cm) killed all plants. Additionally, small amounts of repeated burial (1 cm for 4 days or 2 cm for 8 days) showed significantly greater stimulation of growth compared to a one-time burial (4 cm or 8 cm) (Maun et al. 1996). Given these tolerance limits, *C. pitcheri* should be most successful in habitats maintained by intermediate levels of disturbance.

#### Invasive species – *Centaurea Stoebe*

As a federally threatened species, it is important to understand the threats to the long-term viability of *C. pitcheri*. One of the most critical threats to the long-term viability of *C. pitcheri* in the Grand Sable Dunes is the relatively recent incursion of the exotic invasive spotted knapweed (*Centaurea stoebe* [formerly *Centaurea maculosa*]) (Marshall 2004). Sand dune systems are especially vulnerable to exotic species invasion because they are naturally disturbed



and there is limited competition by native plants for growing space and pollinators (Marshall 2004). *Centaurea stoebe* is a threat to *C. pitcheri* and other native dune vegetation because it is strongly allelopathic (Rindenour and Callaway 2001, Weir et al. 2003), it uses associations with mycorrhizal fungi to drain resources from other plants (Callaway et al. 2004), and rapid colonization leads to dune stabilization (Leege and Murphy 2001). Although sand dunes stabilize naturally as a result of native plant succession, rapid stabilization as a consequence of invasive species can exclude organisms adapted to disturbance by sand movement (Garcia-Mora et al. 2000). A current assessment of *C. stoebe* populations and identification of areas where both *C. stoebe* and *C. pitcheri* co-occur can determine areas where invasive species removal is a high priority.

#### The Need for a Current Population Status

Most of the information about *C. pitcheri* populations throughout the species range is unknown or outdated and very few populations have been studied in enough detail to know the true status of the population. The known baseline information about most populations is very basic and includes the general location, dune type, the quality of the habitat, size class (based on area or linear extent and qualitative or quantitative estimates of abundance), date of last observation, and protection status (USFWS 2002). The baseline information on the population of *C. pitcheri* in the Grand Sable Dunes indicates it is in the largest size class (>10,000 plants) with populations locally common, and it is located in habitat of the highest quality with a protected status. Additionally, a survey of *C. pitcheri* in the GSD was conducted in 1988 (McEachern et al. 1989), but the entire dunes were not surveyed extensively and the mapping was not intended to provide an overall distribution and population size estimate. Therefore, digitally mapping the distribution, estimating population densities and total population size,

coupled with determining associated physiographic and community variables and assessing the threats to the population will help park managers create a management plan to protect the population, and allow for accurate long term monitoring.

### Research Objectives

The main goal of my research was to determine the population status of *Cirsium pitcheri* in the Grand Sable Dunes at Pictured Rocks National Lakeshore to assist the National Park Service in developing a management plan to further protect the species and assist in the goal of delisting the species. My research objectives were to 1) delineate and describe the distribution and total population size of *C. pitcheri* in the Grand Sable Dunes, 2) use a multivariate approach to determine which physiographic and biotic variables are associated with *Cirsium pitcheri* habitat, and 3) determine the distribution of the exotic invasive species, *Centaurea stoebe*, and identify areas where the long-term viability of *C. pitcheri* in the Grand Sable Dunes is threatened due to co-occurrence with *C. stoebe*.

## Methods

### Distribution of *Cirsium pitcheri*

To delineate the distribution of *Cirsium pitcheri* in the Grand Sables Dunes, the dunes were gridded off into 80 x 80-m cells ( $n = 853$ ), following methods similar to Pavlovic et al. (2005) in the Indiana Dunes National Lakeshore. In the field, the corners of the cells were located using a Garmin GPS Map 76Cx and flagged. In June and July of 2007, each cell was surveyed by two people (myself and a field assistant) by a systematic 5-10 minute search. Individual plants in all age classes (seedling, vegetative, and flowering) were tallied using a counter and categorized into five abundance classes: 0 = absent, “sparse” = 1-10, “low” = 11-30, “medium” = 31-100, “high” = 100+.

The distribution of the exotic invasive species, *Centaurea stoebe*, was mapped during the same survey to identify areas where *Cirsium pitcheri* and *Centaurea stoebe* co-occur. In each cell, % cover of *Centaurea stoebe* was visually estimated and categorized into cover classes: “0” = 0%, “1” = 1-10%, “2” = 10-25%, “3” = 25-50%, “4” = 50+%.

### Estimates of Population Densities and Total Population Size

*Cirsium pitcheri* population densities and total population size were estimated using two methods. First, a “double sampling” method (Cochran 1977) was used by combining the rapid distribution assessment (rank of abundance in the 80 x 80 m cells) with more precise sampling to estimate the mean density and variance for each ranked value. For each abundance class, 10 random 80 x 80-m cells were selected. A complete census of a whole 80 x 80-m cell was considered to be logistically impractical, so 25, 5-m radius ( $78.5 \text{ m}^2$ ) plots were randomly

sampled within each cell. The sample size (number of 5-m radius plots) was determined using formulas from (Zar 1999, p. 109). The precision was set for an estimate within 25% of the true mean and  $\alpha$  error level of 0.05.

In the field, the center of each 5-m radius plot was located using a Garmin GPS Map76Cx unit and the perimeter of the plot was flagged. The total number of *C. pitcheri* plants in each stage class; seedlings, vegetative, and flowering was counted. Each plant was assigned to a stage class based on morphology: *seedling*, if the cotyledons were still present, *vegetative*, if the plant was a non-flowering rosette, or *flowering*, if the plant had flowering heads. These data were summarized to determine the mean density (plants/0.1ha) and 95% confidence limits for each *C. pitcheri* abundance class assigned to the 80 x 80-m cells in the dune-wide distribution survey. Total population size was estimated by multiplying the number of cells in each abundance class by the mean density of that abundance class.

A second independent method was used to estimate the total population size by taking advantage of *C. pitcheri* counts that were made in 287, 7.5-m radius plots used in the associated ecological community portion of the study (see next section). These plots were established in a stratified random design and total population size, stratified means and variances were calculated following methods in Krebs (1989, p. 214).

#### Associated Ecological Communities

A multivariate approach was used to determine which physiographic and biotic variables were associated with *Cirsium pitcheri* in the Grand Sable Dunes. Using stratified random sampling, 300, 7.5-m radius plots were established throughout the dunes. Roughly equal

numbers of plots (50-75) were sampled within each *C. pitcheri* abundance class assigned to each 80 x 80-m cell in the initial dune-wide survey.

In each 7.5-m radius plot, *C. pitcheri* counts, biotic, and physiographic variables were measured. *C. pitcheri* counts were separated into life stage classes, seedling, vegetative, or adult, based on morphology. Percent cover of *C. pitcheri*, all other plant species, biotic lifeforms (trees, shrubs, herbaceous plants, grass, moss and lichen) and litter (defined as dead plant matter) were measured using a modified version of the Braun-Blanquet cover abundance categories: 1 = 0-1%, 2 = 1-3%, 3 = 3-7%, 4 = 7-15%, 5 = 15-25%, 6 = 25-50%, 7 > 50%. Because vegetation on the dunes was relatively sparse, cover class limits were set to preferentially differentiate among species with low cover.

Physiographic characteristics measured in each plot included: % bare sand cover, slope gradient (degrees), and aspect (degrees), and a visual assessment of the amount of sand movement. Slope was measured across the plot using a Suunto clinometer. Sand movement was subjectively categorized as no movement, low, medium and high deposition or deflation.

### Data Preparation and Analysis

#### *Wind Energy and Aspect/Slope Index*

Cumulative wind energy for 2006 through 2010 was calculated from wind direction and wind speed (kts) measurements collected in 10-minute intervals from the Great Lakes Observing System (GLOS) weather station (46°40'47" N 85°58'11" W) in Grand Marais, Michigan (NOAA 2011). To examine the directional distribution of wind energy, measurements were combined into 45° sectors (0-45°, 45-90°, etc.). The energy content per sector =  $T * v^3$ , where T is the cumulative time the wind blows in a sector, and v is the average velocity of wind in that sector.

The power generated (e.g. kWh) also requires the “swept area” in  $m^2$ , but the relative wind energy can be calculated without the area term.

Slope and aspect were transformed into an index of topographic “exposure”, similar to the moisture stress index used by Jenkins (1992). The predominant northwest wind off Lake Superior onto the Grand Sable Dunes results in different microclimates associated with topographic position. In general, sand is being eroded from the windward west facing slopes and being deposited on leeward east facing slopes. To capture this trend, aspect was converted into a continuous circular variable by adding  $90^\circ$  to the original angle and then taking the cosine of the new angle (in radians). This procedure results in west-facing aspects having positive values (approaching +1) and east-facing aspects having negative values (approaching -1). Slope can interact with aspect to increase or decrease microclimatic effects. For example, a steep west-facing slope may be more prone to erosion than one with a shallower gradient. For the purpose of this analysis, the slope gradient was ranked as follows: “0” =  $0-5^\circ$ , “1” =  $6-10^\circ$ , “2” =  $11-20^\circ$ , and “3” =  $20^+$ . These ranks were multiplied together with the cosine of the transformed aspects to construct an aspect/slope index (ASSL), which ranges from -3 (steep east-facing slope) to +3 (steep west-facing slope).

### *Defining Successional Stages*

Each 7.5-m radius plot was classified as early- (n=92), mid- (n=123), or late-successional (n=72) based criteria of Bach (1978) and McEachern (1992) including % bare sand cover, species composition and % cover, basic life-form % cover, and sand movement categories. I summarized the successional stages by calculating the mean % cover ( $\pm$ std), frequency of occurrence (%) and importance value (IV) ( $IV = ((\text{relative cover} + \text{relative frequency})/2) * 100$ )

for all the life forms and individual species found in the plots. *C. pitcheri* densities (per 0.1 ha) for each life stage class were compared among successional stages using Kruskal-Wallis and Tukey's Q post hoc analysis. A 3 x 3 chi-square contingency analysis was used to see if the frequencies of different life history stages (seedling, vegetative, flowering) of *C. pitcheri* varied depending on successional stage.

### *Cirsium pitcheri* Habitat Modeling

I used Canonical Correspondence Analysis (CCA) in PC-ORD 5.10 (McCune and Mefford 2006) to investigate dune-wide vegetation community patterns along several environmental gradients. Successional stage was used as a categorical variable. A Monte Carlo randomization test (99 simulations) was conducted to determine the statistical strength of the first axis. Eigenvalues and the % variation explained were also recorded for each analysis.

Nonparametric multiplicative regression (NPMR) was performed in HyperNiche 2.12 to model the response of *C. pitcheri* to multiple interacting environmental factors (McCune and Mefford 2009). Most other regression techniques cannot effectively deal with the non-linear responses of species along environmental gradients (McCune 2006). NPMR is useful because it models the interaction between predictors by multiplying them together creating a non-linear response which more closely resembles natural responses. Two kinds of models were generated: one where the dependent variable was *C. pitcheri* density and the other where the dependent variable was binomial, the presence or absence of *C. pitcheri*. Monte Carlo randomization tests were conducted to evaluate whether the model was stronger than expected by chance. A sensitivity analysis and single variable models were conducted to evaluate the relative importance of different predictors in a particular model.

## Results

### Distribution and Estimates of Total Population Size

The distribution of *Cirsium pitcheri* in the Grand Sable Dunes shows that the population exhibited high spatial connectivity rather than being distributed in isolated sub populations (Figure 1). *C. pitcheri* was present in 72% of the 80 x 80-m grid cells. Most of the cells lacking *C. pitcheri* were along the lakeside rim of the dunes, but even on the steep slopes adjacent to the lake occasional *C. pitcheri* individuals were found. *C. pitcheri* was abundant ( $\bar{x} = 121/0.1$  ha, 95% CI = 68 - 175) in 13% of the dunes and common ( $\bar{x} = 46/0.1$  ha, 95% CI = 30 - 62) in 17% of the dunes. These densities do not include seedlings because their numbers were considered too variable from year to year and even within growing season (McEachern 1992). The largest areas with high *C. pitcheri* densities were mainly 500 – 1000 m inland and were nested between *Pinus banksiana* stands, but linked together by areas of lower *C. pitcheri* densities.

The two methods used to calculate the total population size produced somewhat different estimates. The estimate based on the *C. pitcheri* abundance class densities in the 853 80 x 80-m cells was 152,000 plants and the estimate based on the 287 stratified random plots was 251,200 plants (95% CI = 187,200 - 315,300), rounded to the nearest 100 plants.

### Successional Stages and *Cirsium pitcheri*

Early successional plots (n = 92) were characterized by high % bare sand cover ( $\bar{x} = 90\%$ ), medium to high deposition and deflation and a low species richness (s = 27) (Table 1). Plots were dominated by *Ammophila breviligulata*, found in 83% of plots, but included *Salix interior*, *Salix cordata*, *Artemisia campestris*, *Arabis lyrata* and *Cirsium pitcheri*. *C. pitcheri*



was present in 45% of the early-successional plots and ranked as the second most important (IV) forb.

Mid-successional plots (n = 123) were characterized by moderate % bare sand cover ( $\bar{x}$  = 53%), low to medium sand deposition and a higher species richness (s = 56). Plots were dominated by a mixture of the three grasses, *Schizachyrium scoparium*, *Ammophila breviligulata*, and *Deschampsia flexuosa*. Other characteristic species included *Prunus pumila*, *Hieracium* spp., *Tanacetum huronense*, *Lathyrus japonicus*, *Solidago hispida*, *Lithospermum canescens*, and *Oenothera* spp. (*O. biennis*, *O. parviflora*). *C. pitcheri* reached its maximum cover ( $\bar{x}$  = 0.92%) and frequency (65%) in mid succession.

Late-successional plots (n = 72) were characterized by low bare sand cover ( $\bar{x}$  = 20%), no sand movement to low deposition, high moss cover ( $\bar{x}$  = 19%) and invading trees, especially *Pinus banksiana* ( $\bar{x}$  = 16%). Shrub cover ( $\bar{x}$  = 16%) reached its highest in late successional habitats, including *Arctostaphylos uva-ursi*, *Rosa blanda*, and *Juniper communis*. Grass cover was high ( $\bar{x}$  = 15%) with the same species as in other stages, but also *Poa* spp. ( $\bar{x}$  = 5%). Other characteristic species included *Smilacina stellata*, *Fragaria virginiana*, *Stellaria longipes*, *Equisetum hyemale*, *Rumex acetosella*, and the invasive species *Centaurea stoebe*, which was found in 25% of late successional plots. *Cirsium pitcheri* cover (0.12 %) and frequency (22%) was lowest in late-successional habitats.

The highest densities of *C. pitcheri* were found in mid-successional habitats ( $H = 39.6$ ,  $df = 2$ ,  $p < 0.001$ ) (Table 2). *C. pitcheri* densities in mid succession were roughly 3 times higher than in early succession and 11 times higher than in late succession. The proportion of flowering and vegetative (combined) versus seedling varied significantly among succession stages ( $\chi^2 =$

64.45,  $df = 2$ ,  $p < 0.001$ ). The largest effect was due to the much lower than expected densities of seedlings in late succession with seedlings nearly 50 times more abundant in mid compared to late succession (Table 2).

### Canonical Correlation Analysis

The CCA showed that the most important environmental variables influencing all species distribution in the Grand Sable Dunes were successional stage, % bare sand cover, and the slope steepness (Figure 2). These environmental variables are represented by a linear combination of orthogonal vectors that show correlation with species and the vector length is proportional to the strength of the correlation. On axis 1, early successional sites on the left side correlated with high % bare sand, whereas late successional sites on the right side correlated with low % bare sand and high % of vegetation cover. Similarly, axis 2 was defined by increasing slope steepness near the top and moss covered flat areas on the bottom. The eigenvalues for the first two axes were 0.376 and 0.222, respectively, and accounted for only 7.3% of the species environmental variation. The first axis was significant ( $p = 0.01$ ) using a Monte Carlo randomization test. *Cirsium pitcheri* was located on the left side of the CCA joint plot in association with high % bare sand cover, low to moderate slopes, and between early and mid succession. Ecologically similar species that were closely clustered with *C. pitcheri* included *Schizachyrium scoparium*, *Deschampsia flexuosa*, *Arabis lyrata*, *Solidago hispida*, *Lathyrus japonicus* and *Oenothera* spp.

The broad, dune-wide picture of the CCA obscures some of the trends within early, mid and late successional habitats. I ran separate Detrended Correspondence Analysis (DCA) for each successional stage (figures not shown) which demonstrated that *C. pitcheri* was associated with a very different suite of species in each stage. In early succession, *C. pitcheri* was

associated with *Ammophila breviligulata*, including *Oenothera* spp. and *Corispermum hyssopifolium*. Curiously, it was distanced from *Tanacetum huronense*, which is associated with high sand deposition, as well as species associated with high sand deflation (*Salix interior*, *Artemisia campestris* and *Arabis lyrata*). In mid succession, *C. pitcheri* was associated with the three grasses, *Schizachyrium scoparium*, *Deschampsia flexuosa*, *Ammophila breviligulata*, and a suite of common dune species, including *Hieracium* spp., *Lithospermum canescens*, *Arabis lyrata*, *Oenothera* spp. *Artemisia campestris*, and the exotic invasive *Centaurea stoebe*. In late succession, *C. pitcheri* was associated with the same suite of common dune species, but also increasing moss and lichen cover and *Pinus banksiana* in varying stages of colonization. Other species including *Arctostaphylos uva-ursi*, *Hudsonia tomentosa*, *Trifolium pratense*, *Asclepias syriaca*, *Stellaria longipes*, and the exotic invasive *Centaurea stoebe*.

#### *Cirsium pitcheri* Habitat Modeling

The prevailing wind in the GSD resulted in the strongest cumulative energy coming from the NW, but a secondary peak occurred from the SW (180°- 225°) (Figure 3). Sites with NW aspects had the highest densities of *C. pitcheri*, followed by SW, SE and NE (Kruskal-Wallis;  $p < 0.001$ ) (Figure 3). Also, there was a higher frequency of occurrence of *C. pitcheri* on west-facing slopes compared to east-facing slopes ( $\chi^2 = 3.83$ ,  $df = 1$ ,  $p = 0.03$ ). Interestingly, *C. pitcheri* is clearly associated, in a general way, with slopes exposed to higher wind energy; however, the highest densities were found on aspects adjacent to the sectors with the strongest wind energy (Figure 3). Sites with moderate 6 – 10° slopes had the highest densities of *C. pitcheri*, followed by 0 -5°, 11 – 20°, and 20°+ slopes (Kruskal-Wallis Test;  $p = 0.003$ ); however,

the highest frequencies of occurrence were on the shallowest slopes (0 -5°) and decreased with increasing slope steepness ( $\chi^2 = 17.1$ ,  $df = 3$ ,  $p = 0.001$ ).

The results of the nonparametric multiplicative regression (NPMR) in Hyperniche showed which variables were the most important for predicting the abundance and probability of occurrence of *C. pitcheri* in the Grand Sable Dunes (Table 3). The most important variable predicting the abundance of *C. pitcheri* was % *Schizachyrium scoparium* cover. The abundance of *C. pitcheri* increased as % *Schizachyrium scoparium* cover increased up to its maximum cover of 40% (Figure 4). The most important variable predicting the probability of occurrence of *C. pitcheri* was % bare sand cover. The highest probability of occurrence ( $P = 0.6 - 0.7$ ) of *C. pitcheri* was in habitats with 50-70% bare sand (Figure 5). Additionally, *C. pitcheri* was more likely to be present in areas with extremely high % bare sand cover compared to habitats with minimal % bare sand cover. The aspect/slope index (ASSL) was an important variable predicting both the abundance and probability of occurrence. The probability of occurrence of *C. pitcheri* was high for a broad range of topographic positions; however, densities of *C. pitcheri* peaked in habitats with moderate (6-10°) west facing slopes (Figure 6). Regardless of the aspect, extreme slopes had the lowest *C. pitcheri* densities and probability of occurrence.

#### Invasive species - *Centaurea stoebe*

*Centaurea stoebe* was present in 24% of the Grand Sable Dunes, but patchily distributed in small populations throughout the dunes (Figure 7). The main populations of *C. stoebe* were restricted inland, near tourist sites. The highest frequencies and % cover were in late successional habitats (Table 1). *Cirsium pitcheri* co-occurred with *C. stoebe* in 61% of the cells

scattered throughout the dunes (Figure 7). Two-thirds of the co-occurrences (43%) were in cells with high densities of *C. pitcheri* (abundance categories medium and high).

## Discussion

### Distribution and Estimates of Total Population Size

*Cirsium pitcheri* was distributed throughout the Grand Sable Dunes (GSD), in a variety of habitats, from the dune bluff inland to the forest. The largest areas with highest densities occurred in distinct groups located midway between the dune bluff and the forest edge and were spatially connected by areas with lower densities; however, it is unknown whether genetic exchange via pollinators occurs between these populations. Small patches with high densities of *C. pitcheri* were found in the deflation zone extending along the dune bluff, which may provide suitable habitat due to constant wind erosion compared to periodic catastrophic sand deposition in the foredunes slightly inland from the dune bluff (Marsh and Marsh 1987, McEachern 1992). Most of the areas with low densities or lacking *C. pitcheri* were in the most active areas along the edge of the dune bluff and in stabilized areas near the edge of the forest. My distribution results are consistent with the findings of McEachern et al.'s (1989) survey of *C. pitcheri* in the GSD.

The estimates of the total population size of *C. pitcheri* in the GSD indicate that this population may be one of the largest populations throughout the species range. The two population estimates of 152,000 and 251,200 (95% CI: 187,200 - 315,300) were somewhat different, but this was not unexpected given the patchy distribution of *C. pitcheri*. These initial estimates of population densities and total population size, coupled with a digitized distribution and associated physiographic and community variables, are useful for future comparison and creating management plans that protect suitable habitat and minimize the risk of extirpation of *C. pitcheri* in the GSD.

Comparisons of the total population size in the GSD to most populations of *C. pitcheri* throughout the species range are incongruous and incompatible due to large differences in population size and geomorphic dune types. The only other ‘mega-population’ in a perched dune system that would be appropriate for comparison occurs at Sleeping Bear Dunes National Lakeshore. In 2005, it was proposed to map the population of *C. pitcheri* at Sleeping Bear Dunes National Lakeshore over a period of years to provide park managers with a complete *C. pitcheri* abundance and distribution map (Pavlovic et al. 2005). Comparisons of the two similar populations will provide useful insights about *C. pitcheri* on large perched dune systems.

Standardization of methods and repeat surveys will be necessary to compare populations and update the status of *C. pitcheri*. A case in point, in 2005 the population status of *C. pitcheri* at Indiana Dunes National Lakeshore (INDU) was updated from the previous survey in 1992, which estimated a total population size of 2370 plants. Through detailed GPS mapping and counting of all plants (categorized by life history stage) in a population, as well as collecting associated physiographic and community variables, they found a total of 6536 plants in 205 separate populations in a variety of dune communities (Pavlovic et al. 2005). Population estimates were most likely drastically different due to different sampling methods. Additionally, several 1992 populations were not relocated, but many new populations were found and some patches had spread in size and increased in number. This comprehensive survey will allow park managers to observe changes in the *C. pitcheri* population distribution, size and demographics at INDU. However, the amount of accuracy achieved at INDU is impractical for the entirety of large populations, like in the GSD and at Sleeping Bear Dunes National Lakeshore. Establishment of long-term monitoring plots in a subset of these large populations could allow for detailed measurements of population change.

## The Influence of Sand Movement

In sand dunes worldwide, the frequency and intensity of disturbance by sand movement is one of the major factors influencing plant zonation and succession (Cowles 1901, Olson 1958, Doing 1985, Moreno-Casasola 1986, Litcher 1998, Maun and Perumal 1999, Martinez et al. 2001). In the Grand Sable Dunes, *Cirsium pitcheri* was found in a wide range of habitats including the most dynamic, windswept early-successional habitats on the lakeshore rim and in inland blowouts. At the other end of the spectrum, *C. pitcheri* was well represented in stabilized late-successional areas inland near the forest edge. Although, *C. pitcheri* was not strictly associated with one type of dune community, the distribution and closely associated variables of *C. pitcheri* in the GSD suggest that it was most abundant in mid-successional communities maintained by intermediate levels of sand movement disturbance. My results are consistent with previous studies of *C. pitcheri* throughout the species range (Loveless, 1984, Keddy and Keddy 1984, McEachern 1992, Bowles et al. 1993).

However, the mosaic-like distribution of *C. pitcheri* in the GSD reflects sand movement patterns on multiple scales. On a broad scale, *C. pitcheri* was associated with early to mid successional communities characterized by 50-70% bare sand cover. Bare areas are created when sand movement (burial and erosion) exceeds the tolerance limits of the species in an area (Maun and Perumal 1999, Maun 1998); therefore, % bare sand cover is a basic broad-scale indicator of the frequency and intensity of disturbance by sand movement. Similarly, McEachern (1992) found that throughout the species range, *C. pitcheri* densities were highest in habitats characterized by 75-85% bare sand cover. Considering just the extremes, *C. pitcheri* had a higher probability of occurrence for habitats with extremely high % bare sand cover



compared to habitats with little % bare sand cover. This suggests that *C. pitcheri* is able to tolerate intermediate levels of disturbance by sand movement, but the frequency and intensity of disturbance in extremely dynamic areas, and the lack of disturbance in stabilized areas, may be unsuitable for the long-term survival and persistence of *C. pitcheri*.

On a finer scale, *C. pitcheri* was topographically associated with moderate (6-10°) windward west-facing slopes. This reflects sand movement patterns caused by prevailing W-NW winds off Lake Superior where sand is eroded from windward west-facing slopes and deposited sand on leeward east-facing slopes. Dech and Maun (2005) showed that high levels of sand deposition on leeward slopes can cause zonation of vegetation along a burial gradient, with shifts in species dominance from species dependent on sand burial to species intolerant to sand burial. Previous sand burial studies have shown that *C. pitcheri* is intolerant of high sand deposition (Maun et al. 1996, Chen and Maun 1999, Hamze and Jolls 2000, Rowland and Maun 2001, Perumal and Maun 2006). Therefore, my results suggest that environmental conditions on the windward side of a dune are more suitable for the survival and reproduction of *C. pitcheri* compared to the leeward side.

Furthermore, *C. pitcheri* densities appear to be higher in areas with aspects adjacent to the strongest cumulative wind energy (Figure 3). In a typical blowout, the bare areas are bordered by the dune stabilizer *Ammophila breviligulata*. Sand-laden winds lose speed as they blow through stands of *A. breviligulata* causing the sand to be deposited (Salsbury 1952). Curiously, I observed that *C. pitcheri* is also found on the very edge of the bare areas in blowouts intermixed with *A. breviligulata*. Perhaps *C. pitcheri* is present in this type of habitat because its seeds are carried by the wind and deposited as wind velocities start to decrease at the edge of *A.*

*breviligulata* stands. Germination of *C. pitcheri* seeds is facilitated when the seed coat is scarified (Chen and Maun 1998); therefore, higher germination may occur in windswept deflation areas where the seeds are blown around with the sand. However, seedling mortality is probably very high in these dynamic habitats (McEachern 1992). Additionally, surviving individuals may be stimulated by low levels of sand deposition (Maun et al. 1996).

### Succession and *Cirsium pitcheri*

Peak *C. pitcheri* densities were found in mid successional communities, followed by 3 times lower densities in early- and 11 times lower densities in late-successional communities. Studies of other Great Lakes dune habitats have shown similar unimodal patterns of species abundance, where a species enters the succession in low abundance, increases to a peak and later decreases to local extinction or remains a component of the forest (Olson 1958, Litcher 1998). Fundamentally, the “boundaries” of successional stages are dictated by species’ tolerance limits to disturbance by sand movement (Maun and Perumal 1999).

Why does *C. pitcheri* peak in mid successional communities? Mid successional communities represent areas that are, most likely, maintained by intermediate levels of disturbance by sand movement. In the GSD, mid successional communities were characterized by approximately 50% bare sand and dominated by a mixture of the three grasses, *Schizachyrium scoparium*, *Ammophila breviligulata*, and *Deschampsia flexuosa*. The NPMR models showed that % *Schizachyrium scoparium* cover was the best predictors of *C. pitcheri* abundance in the GSD. *S. scoparium* reaches its peak abundance in mid-successional communities and is intolerant of high amounts of sand deposition, but seedlings and established clumps can overcome some burial by sand through internodal elongation (Olson 1958). It is likely that *C.*

*pitcheri* and *S. scoparium* have similar disturbance optima, where the frequency and intensity of sand movement is favorable for the growth and reproduction of both species. Furthermore, McEachern (1992) found that throughout the species range, the highest *C. pitcheri* densities were found in mid-successional habitats characterized by the co-dominance of *Ammophila breviligulata* and *Calamovilfa longifolia*. However, *C. longifolia*'s range does not extend into the GSD (Voss 2011); therefore, my results suggest that *S. scoparium* replaces *C. longifolia* as a key indicator of *C. pitcheri* in the northern part of its range.

Lower *C. pitcheri* abundance in early- and late-successional habitats suggest that there are environmental constraints at both ends of the successional gradient that exceed the tolerance limits for *C. pitcheri*; however, the constraints in early- and late-successional habitats are very different but equally linked to rates of sand movement. *C. pitcheri* was one of the few herbaceous plants that consistently inhabited early successional habitats in the GSD. These populations are vulnerable to extreme environmental conditions including high frequency and intensity of sand movement (deposition and erosion), xeric conditions, and limited nutrients (Olson 1958, Bach 1978, Litcher 1998). In a four-year demographic study of *C. pitcheri*, McEachern (1992) observed that extreme sand deposition in early-successional habitats had catastrophic effects on *C. pitcheri* populations. In some areas, sand burial depths, up to 24 cm, eliminated nearly all *C. pitcheri* individuals and decreased the size of surviving individuals. However, plots that experienced only a few centimeters of sand accumulation had an increase in recruitment of *C. pitcheri* seedlings and increased small juvenile survival. McEachern (1992) concluded the frequency and intensity of disturbance can have varying effects on each population throughout the landscape.

*C. pitcheri* in late successional habitats represents somewhat of a paradox. Is it an integral part of late successional communities being maintained in limited microsites and/or do these populations represent historical legacies of larger more frequent disturbances? My results suggest both. Late successional habitats were quite variable, but *C. pitcheri* was consistently abundant in habitats with high % moss cover. These moss covered microsites may provide suitable germination conditions and allow for the persistence of *C. pitcheri* in stabilized late successional habitats. Additionally, McEachern (1992) suggested that populations of *C. pitcheri* in the GSD occurring in sites dominated by high % moss cover, *Schizachyrium scoparium*, and *Hudsonia tomentosa* may represent the most late successional habitats that *C. pitcheri* occurs in throughout the species range.

*C. pitcheri* populations in late-succession may also represent historical legacies of larger more frequent disturbances that formerly maintained viable populations in these locales. The lowest densities of *C. pitcheri* were found in late successional with 50 times fewer seedlings than in mid-successional communities. However, seedling densities vary from year to year depending on environmental conditions and population demographics (McEachern 1992); therefore, my results from one growing season may not provide an accurate description of the long-term trends of *C. pitcheri* in late successional habitats, especially considering the monocarpic perennial life history of the species. Regardless, the potential lack of seedling recruitment in late successional habitats in the GSD needs long term monitoring to determine the long term persistence of *C. pitcheri* populations in these habitats.

Possible explanations of low densities of *C. pitcheri* in late successional communities include increased resource competition, reduced germination success and increased seed

predation. Diminished sand movement in late successional sites allows for an increase in vegetation and a higher diversity of species including those that are not tolerant to sand movement (e.g. *Pinus banksiana*) (Litcher 2000). Tilman (1985) theorized that early successional species adapted to survive conditions with low soil nutrients and high availability of light are often replaced by superior competitors as soil nutrient and light availability conditions change. Additionally, Loveless (1984) found that germination was higher for buried *C. pitcheri* seeds than for exposed seeds and Hamze and Jolls (2000) found that germination was suppressed by light and increased by burial. Unburied seeds are also at a higher risk of seed predation. *C. pitcheri* seeds are preyed upon by birds, goldfinches, sparrows and other ground feeding birds, ground squirrels and small mammals (Loveless 1984). Also, seed predation may be higher in habitats with the exotic invasive *Centaurea stoebe*, which appear to attract a greater abundance of mice, compared to habitats with native vegetation (Malick 2011). However, little is known about seed loss due to post-dispersal predation.

#### Invasive species - *Centaurea stoebe*

The invasion of the exotic species, *Centaurea stoebe*, is one of the most critical threats to *Cirsium pitcheri* and other dune endemics in the Grand Sable Dunes. My results show that populations of *C. stoebe* are scattered across the dunes and overlaps with main populations of *C. pitcheri*. Populations of *C. stoebe* appear to be restricted to mid- and late-successional habitats, although it is unclear whether highly disturbed early-successional habitats are unsuitable or whether *C. stoebe* is just slow in colonizing these areas. *C. stoebe* seeds usually land within 0.9-1.2 m of the parent plant and may not disperse lakeside against the prevailing wind. The alleopathic affect of *C. stoebe* (Rindenour and Callaway 2001, Weir et al. 2003) coupled with

rapid dune stabilization (Leege and Murphy 2001) could lead to decreased recruitment of *C. pitcheri* seedlings and degradation of suitable *C. pitcheri* habitat.

### Dune Stabilization and Climate Change

Historically, suitable habitat for *Cirsium pitcheri* has most likely expanded and contracted depending on the rates of dune formation, which is intimately linked to fluctuations of the water level of Lake Superior (Anderton and Loope 1995, Loope and Arbogast 2000) The current distribution of *C. pitcheri* in the Grand Sable Dunes is not static, but is constantly changing and it reflects the dynamic environment of the dunes. The influence of historical lake-level fluctuations on dune formation helps explain the current distribution and the potential changes that may result from recent lake warming and lower lake-levels.

In the GSD, evidence of historical quiescence has been suggested through the presence of buried soils throughout the dunes (Anderton and Loope 1995). Radiocarbon dating of these buried soils showed that there have been at least 5 and perhaps as many as 11 soil burial episodes in the past 5500 years. The presence of buried soils and exhumed ghost forests in the dunes implies that there have been historic lake-level fluctuations causing dramatic shifts in the sand supply along the bluff edge. In the past, periods of bluff stability due to lower lake-level allowed vegetation to invade the dunes. It is unclear and unlikely that each buried soil represents a complete forestation of the dunes, but the presence of charcoal in several soil profiles suggests that occasionally forests were large enough to carry a fire (Anderton and Loope 1995). Loope and McEachern (1998) suggested that during times of dune quiescence and stabilization, *C. pitcheri* populations would have been reduced and isolated to disturbed habitats along the bluff

edge and fragmented populations in inland blowouts. In contrast, when lake-levels increased dune building buried these soils, thus, increasing the habitat availability for *C. pitcheri*.

Recent warming trends in Lake Superior water temperature, declining ice cover and increased evaporation have been linked to lower water levels (Assel et al. 2003, Assel et al. 2004, Assel 2005). A sustained decrease in lake level could cause dune quiescence in the GSD and would inevitably lead to shrinking open dune habitat and more fragmented *C. pitcheri* populations. Similarly, the currently forested Nodaway dune field, a perched dune system located 150 km east of the GSD on Lake Superior, is thought to have gradually stabilized after lake levels dropped at the end of the Nipissing high stand (~6000-4000 yrs B.P.) (Arbogast 2000). In the GSD, aerial photographs have revealed that *Pinus banksiana* dominated forests have increased five-fold on the dunes since the 1930's (Loope and McEachern 1998). Similar *P. banksiana* expansions have been reported in the Sleeping Bear Dunes, a perched dune field along the east coast of Lake Michigan (Synder 1985, Businski 1992). I have noted four small *C. pitcheri* populations that have become completely isolated by *P. banksiana* expansion in the GSD and many of the large areas with high densities of *C. pitcheri* are sandwiched between *P. banksiana* expansions and risk becoming separated from each other if recent trends of dune stabilization continue.

Localized dune stabilization is also possible due to sand accumulation behind the breakwater that protects the Grand Marais harbor 3500 m east of the GSD. Since its construction over a century ago, a wedge of sand has been accumulating, resulting in widened beaches extending 2,500 - 3,000 m toward the east end of the GSD (Marsh 1990). If the wedge of sand reaches the dunes, localized dune stabilization is likely due to decreased bluff erosion.

## Summary and Conclusions

A systematic survey of 853 80 x 80-m cells in the Grand Sable Dunes showed that *C. pitcheri* was distributed throughout the dunes in a variety of habitats and that main populations of *C. pitcheri* occurred in distinct groups midway between the dune bluff and the forest. Through two independent methods, total population size estimates of 152,000 and 251,200 (95% CI: 187,200 - 315,300) indicate that the population of *C. pitcheri* in the Grand Sable Dunes may be one of the largest populations for the species.

The closely associated ecological communities of *C. pitcheri* reflect sand movement patterns on multiple scales. On a broad scale, *C. pitcheri* was associated with early to mid successional communities characterized by 50-70% bare sand cover. Peak densities occurred in mid-successional habitats dominated by *Schizachyrium scoparium*, which can be considered an indicator species for *C. pitcheri* in the Grand Sable Dunes. Low seedling densities in late-successional habitats needs further investigation to determine if it is an artifact of a single season and, if not, why recruitment is lower in late-successional habitats. On a finer scale, *C. pitcheri* was associated with moderate (6-10°) windward west-facing slopes, reflecting sand movement patterns caused by prevailing W-NW winds.

The distribution of the exotic invasive, *Centaurea stoebe*, covers 25% of the dunes and co-occurs with main populations of *C. pitcheri*. Areas where the two species co-occur should be a high priority for invasive species management. Dune stabilization and expanding *Pinus banksiana* stands due to recent climate change trends may fragment current populations and reduce suitable habitat for *C. pitcheri* in the GSD. Ironically, the speciation of *C. pitcheri* was probably driven by climate change, but now it represents a serious threat to its existence.



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Table 1. Importance value, mean cover (%) and frequency of occurrence for species (%) that occurred in the successional stages, early, mid, and late successional, in the Grand Sable Dunes at Pictured Rocks National Lakeshore, Michigan, USA, 2008.

Successional Stage		Early (n=92)				Mid (n=123)				Late (n=72)			
species	spp code	IV	% cover	±std	Freq	IV	% cover	±std	Freq	IV	% cover	±std	Freq
<b>Early Successional</b>													
<i>Ammophila breviligulata</i>	ammbre	<b>23.9</b>	<b>2.31</b>	<b>±2.17</b>	<b>0.83</b>	11.2	5.08	±9.86	0.99	8.64	7.22	±18.3	0.86
<i>Salix interior</i>	salint	<b>17.1</b>	<b>1.70</b>	<b>±2.74</b>	<b>0.55</b>	3.44	1.24	±2.48	0.44	1.05	0.41	±1.48	0.22
<i>Salix cordata</i>	salcor	<b>13.7</b>	<b>1.59</b>	<b>±3.98</b>	<b>0.30</b>	2.87	1.31	±4.51	0.24	0.96	0.35	±0.97	0.21
<i>Artemisia campestris</i>	artcam	<b>9.69</b>	<b>0.40</b>	<b>±0.71</b>	<b>0.67</b>	3.88	0.31	±0.43	0.97	2.32	0.14	±0.27	0.68
* <i>Cirsium pitcheri</i>	cirpit	<b>6.10</b>	<b>0.22</b>	<b>±0.50</b>	<b>0.45</b>	3.70	0.92	±2.44	0.65	0.82	0.12	±0.41	0.22
<i>Arabis lyrata</i>	aralyr	<b>3.18</b>	<b>0.04</b>	<b>±0.08</b>	<b>0.28</b>	2.82	0.11	±0.12	0.76	1.43	0.05	±0.07	0.43
<b>Mid Successional</b>													
<i>Schizachyrium scoparium</i>	schsco	4.45	0.23	±0.57	0.28	<b>14.6</b>	<b>7.34</b>	<b>±8.82</b>	<b>0.96</b>	4.07	2.41	±3.56	0.65
<i>Prunus pumila</i>	prupum	4.05	0.35	±1.03	0.16	<b>6.44</b>	<b>2.76</b>	<b>±6.11</b>	<b>0.63</b>	4.04	2.33	±3.99	0.67
<i>Hudsonia tomentosa</i>	hudtom	1.27	0.09	±0.56	0.07	<b>5.05</b>	<b>2.56</b>	<b>±9.32</b>	<b>0.32</b>	3.52	2.96	±8.89	0.35
<i>Deschampsia flexuosa</i>	desfle	2.48	0.10	±0.37	0.17	<b>4.94</b>	<b>1.30</b>	<b>±2.36</b>	<b>0.84</b>	1.70	0.32	±0.59	0.44
<i>Hieracium</i> spp.	hiespp	0.60	0.01	±0.02	0.05	<b>4.55</b>	<b>1.18</b>	<b>±2.15</b>	<b>0.78</b>	4.45	2.22	±3.97	0.82
<i>Tanacetum huronense</i>	tanhur	2.42	0.16	±1.16	0.13	<b>3.85</b>	<b>1.34</b>	<b>±6.12</b>	<b>0.51</b>	2.09	0.30	±0.76	0.57
<i>Lathyrus japonicus</i>	latjap	3.03	0.20	±1.19	0.16	<b>3.85</b>	<b>0.78</b>	<b>±3.44</b>	<b>0.76</b>	2.08	0.29	±0.55	0.57
* <i>Cirsium pitcheri</i>	cirpit	6.10	0.22	±0.50	0.45	<b>3.70</b>	<b>0.92</b>	<b>±2.44</b>	<b>0.65</b>	0.82	0.12	±0.41	0.22
<i>Solidago hispida</i>	solhis	3.47	0.06	±0.23	0.29	<b>3.50</b>	<b>0.26</b>	<b>±0.40</b>	<b>0.89</b>	2.06	0.10	±0.14	0.61
<i>Lithospermum canescens</i>	litcam	2.70	0.03	±0.08	0.24	<b>2.09</b>	<b>0.08</b>	<b>±0.12</b>	<b>0.56</b>	1.46	0.09	±0.15	0.43
<i>Oenothera</i> spp.	oenspp	1.80	0.02	±0.04	0.16	<b>1.89</b>	<b>0.06</b>	<b>±0.08</b>	<b>0.51</b>	0.37	0.01	±0.03	0.11
<b>Late Successional</b>													
<i>Pinus banksiana</i>	pinban		--			2.42	0.87	±2.41	0.31	<b>15.0</b>	<b>16.1</b>	<b>±23.1</b>	<b>0.60</b>
<i>Arctostaphylos uva-ursi</i>	arcuva		--			4.57	2.34	±10.5	0.28	<b>7.26</b>	<b>6.74</b>	<b>±15.2</b>	<b>0.56</b>
<i>Poa</i> spp.	poaspp		--			1.04	0.23	±0.78	0.20	<b>6.03</b>	<b>4.78</b>	<b>±9.19</b>	<b>0.67</b>
<i>Smilacina stellata</i>	smiste		--			2.31	0.87	±4.03	0.28	<b>4.71</b>	<b>3.48</b>	<b>±9.12</b>	<b>0.58</b>
<i>Populus balsamifera</i>	popbal		--			0.88	0.28	±1.03	0.13	<b>3.54</b>	<b>3.15</b>	<b>±10.9</b>	<b>0.31</b>
<i>Fragaria virginiana</i>	fravir		--			2.27	0.20	±0.38	0.56	<b>3.24</b>	<b>0.34</b>	<b>±0.69</b>	<b>0.92</b>

Successional Stage	Early (n=92)				Mid (n=123)				Late (n=72)				
	species	IV	% cover	±std	Freq	IV	% cover	±std	Freq	IV	% cover	±std	Freq
<b>Late Successional- Continued</b>													
<i>*Centaurea stoebe</i>	censto	--				1.21	0.47 ±3.44	0.14		<b>2.77</b>	<b>2.43 ±8.18</b>	<b>0.25</b>	
<i>Betula papyrifera</i>	betpap	--				0.43	0.12 ±0.57	0.07		<b>2.04</b>	<b>1.52 ±4.01</b>	<b>0.25</b>	
<i>Stellaria longipes</i>	stelon	--				1.69	0.06 ±0.10	0.46		<b>1.72</b>	<b>0.07 ±0.10</b>	<b>0.51</b>	
<i>Equisetum hyemale</i>	equhye	--				0.83	0.06 ±0.26	0.21		<b>1.33</b>	<b>0.31 ±1.34</b>	<b>0.33</b>	
<i>Rosa blanda</i>	rosbla	--					--			<b>1.03</b>	<b>0.55 ±2.50</b>	<b>0.18</b>	
<i>Acer saccharum</i>	acesac	--					--			<b>0.98</b>	<b>0.55 ±4.42</b>	<b>0.17</b>	
<i>Juniper communis</i>	juncom	--				0.75	0.10 ±0.37	0.17		<b>0.93</b>	<b>0.38 ±1.55</b>	<b>0.19</b>	
<i>Rumex acetosella</i>	rumace	--				0.83	0.15 ±0.58	0.17		<b>0.89</b>	<b>0.16 ±0.47</b>	<b>0.24</b>	
<i>Pinus strobus</i>	pinstr	--					--			<b>0.85</b>	<b>0.78 ±4.62</b>	<b>0.07</b>	
<i>Asclepias syriaca</i>	ascsy	--				0.46	0.06 ±0.46	0.11		<b>0.84</b>	<b>0.15 ±0.51</b>	<b>0.22</b>	
<i>Taraxacum officinale</i>	taroff	--				0.21	0.01 ±0.02	0.06		<b>0.83</b>	<b>0.03 ±0.07</b>	<b>0.25</b>	
<i>*Cirsium pitcheri</i>	cirpit	6.10	0.22 ±0.50	0.45		3.70	0.92 ±2.44	0.65		<b>0.82</b>	<b>0.12 ±0.41</b>	<b>0.22</b>	
<i>Amelanchier spp.</i>	almssp	--					--			<b>0.75</b>	<b>0.15 ±0.67</b>	<b>0.19</b>	
<i>Achillea millefolia</i>	achmil	--				0.33	0.01 ±0.03	0.09		<b>0.65</b>	<b>0.03 ±0.07</b>	<b>0.19</b>	
<i>Trifolium pratense</i>	tripra	--				0.35	0.08 ±0.52	0.07		<b>0.59</b>	<b>0.12 ±0.63</b>	<b>0.15</b>	
<i>Prunus virginiana</i>	pruvir	--					--			<b>0.48</b>	<b>0.14 ±0.67</b>	<b>0.11</b>	
<i>Pyrola spp.</i>	pyrspp	--					--			<b>0.47</b>	<b>0.08 ±0.34</b>	<b>0.13</b>	
<i>Picea glauca</i>	picgla	--					--			<b>0.43</b>	<b>0.15 ±0.51</b>	<b>0.10</b>	
<i>Toxicodendron radicans</i>	toxrad	--					--			<b>0.37</b>	<b>0.13 ±0.67</b>	<b>0.08</b>	
<i>Goodyera oblongifolia</i>	gooobl	--					--			<b>0.33</b>	<b>0.02 ±0.06</b>	<b>0.10</b>	
Lichen	lichen	--					--			<b>0.23</b>	<b>0.01 ±0.06</b>	<b>0.07</b>	
<i>Abies balsamea</i>	abibal	--					--			<b>0.21</b>	<b>0.04 ±0.25</b>	<b>0.06</b>	

Table 2. Mean density ( $\pm$  SE) of *Cirsium pitcheri* in three successional habitats, early, mid and late. Kruskal-Wallis results showing the Chi<sup>2</sup>, degrees of freedom, and p-value. Tukey's Q post hoc analysis showing p-values.

	Early <sup>1</sup> (n=92)	Mid <sup>2</sup> (n=123)	Late <sup>3</sup> (n=72)	Kruskal-Wallis			Tukey's Q – p-value		
	Mean Density (#/0.1 ha) ( $\pm$ SE)	Mean Density (#/0.1 ha) ( $\pm$ SE)	Mean Density (#/0.1 ha) ( $\pm$ SE)	Chi <sup>2</sup>	df	p-value	1v2	1v3	2v3
Total	59.3 ( $\pm$ 13)	191 ( $\pm$ 38)	18.1 ( $\pm$ 6.9)	39.6	2	<0.001	0.002	0.01	<0.001
Seedlings	14.6 ( $\pm$ 4.1)	56.5 ( $\pm$ 15)	1.18 ( $\pm$ 0.59)	29.1	2	<0.001	0.005	0.08	<0.001
Juveniles	43.4 ( $\pm$ 9.9)	125 ( $\pm$ 23)	15.6 ( $\pm$ 5.8)	35.1	2	<0.001	0.002	0.05	<0.001
Adults	1.60 ( $\pm$ 0.4)	9.25 ( $\pm$ 1.9)	1.34 ( $\pm$ 0.77)	26.7	2	<0.001	<0.001	>0.5	<0.001

Table 3. The best models predicting the abundance and probability of occurrence of *Cirsium pitcheri* determined by nonparametric multiplicative regression in Hyperniche. Including  $xR^2$  values for the best overall model and for each variable in a single variable model. Species codes are the first 3 letters of the genus and the first 3 letters of the species epithet; codes and full scientific names are given in Table 1. ASSL = aspect/slope index. SAND (C) = categorical sand movement variable including no movement and low, medium and high deposition or deflation.

\* Denotes the most important variable.

<b><u>Quantitative</u></b>						
	<u>All Plants</u>		<u>Seedlings</u>		<u>Vegetative + Flowering</u>	
	<u>Sensitivity</u>	<u><math>xR^2</math></u>	<u>Sensitivity</u>	<u><math>xR^2</math></u>	<u>Sensitivity</u>	<u><math>xR^2</math></u>
ASSL	0.039	0.006	0.049	-0.014	--	--
SCHSCO	0.035	0.158*	0.040	0.120*	0.077	0.125*
DEFLE	0.108	0.037	0.091	0.010	0.193	0.046
OENSPP	0.041	0.017	0.004	0.006	0.007	0.019
FRAVIR	0.118	0.013	--	--	--	--
SOLHIS	--	--	--	--	--	--
Model $xR^2$	0.62		0.71		0.41	
Monte Carlo	p<0.05		p<0.05		p<0.05	
<b><u>Presence/Absence</u></b>						
	<u>All Plants</u>		<u>Seedlings</u>		<u>Vegetative + Flowering</u>	
	<u>Sensitivity</u>	<u>logB</u>	<u>Sensitivity</u>	<u>logB</u>	<u>Sensitivity</u>	<u>logB</u>
ASSL	0.209	2.376	--	--	0.153	1.939
% SAND	0.277	6.273*	--	--	0.364	6.232*
SCHSCO	0.081	3.226	0.203	4.279*	0.082	3.615
OENSPP	0.289	3.779	0.024	2.075	0.274	4.071
SALCOR	0.170	-0.239	--	--	0.142	-0.272
TOTVEG	--	--	0.100	2.176	--	--
LITTER	0.186	5.120	--	--	0.198	4.907
SAND (C)	--	--	N/A	10.36	--	--
Model logB	12.8		17.4		12.5	
Monte Carlo	p<0.05		p<0.05		p<0.05	

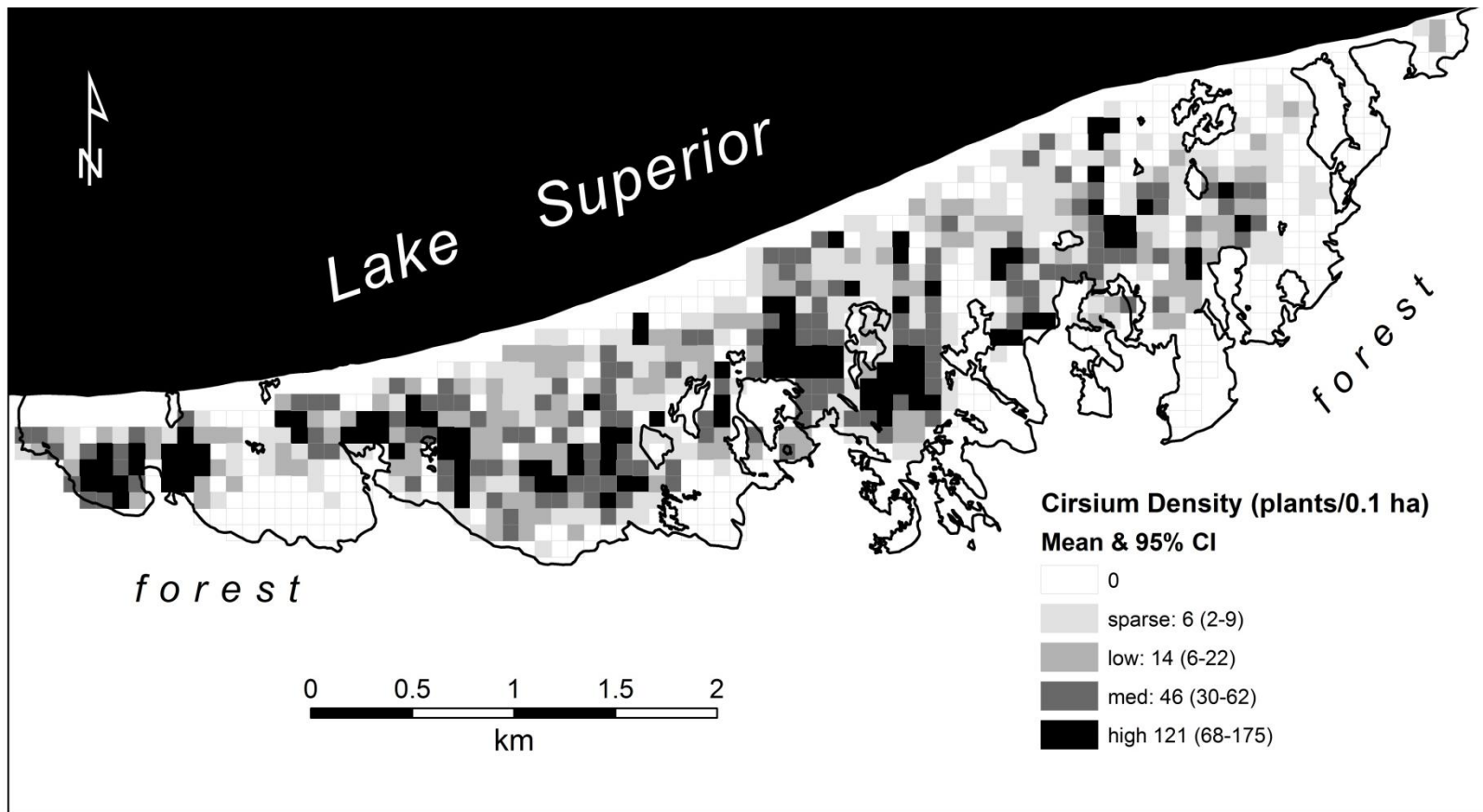


Figure 1. The distribution of *Cirsium pitcheri* in the Grand Sable Dunes at Pictured Rocks National Lakeshore, Michigan, USA, 2008. Individual *C. pitcheri* plants were tallied during a systematic survey in each 80 x 80-m grid cell. Counts were categorized into abundance categories. Abundance class mean densities were determined from *C. pitcheri* counts in 25 randomly located 5-m radius in 10 random 80 x 80-m cells for each abundance class.

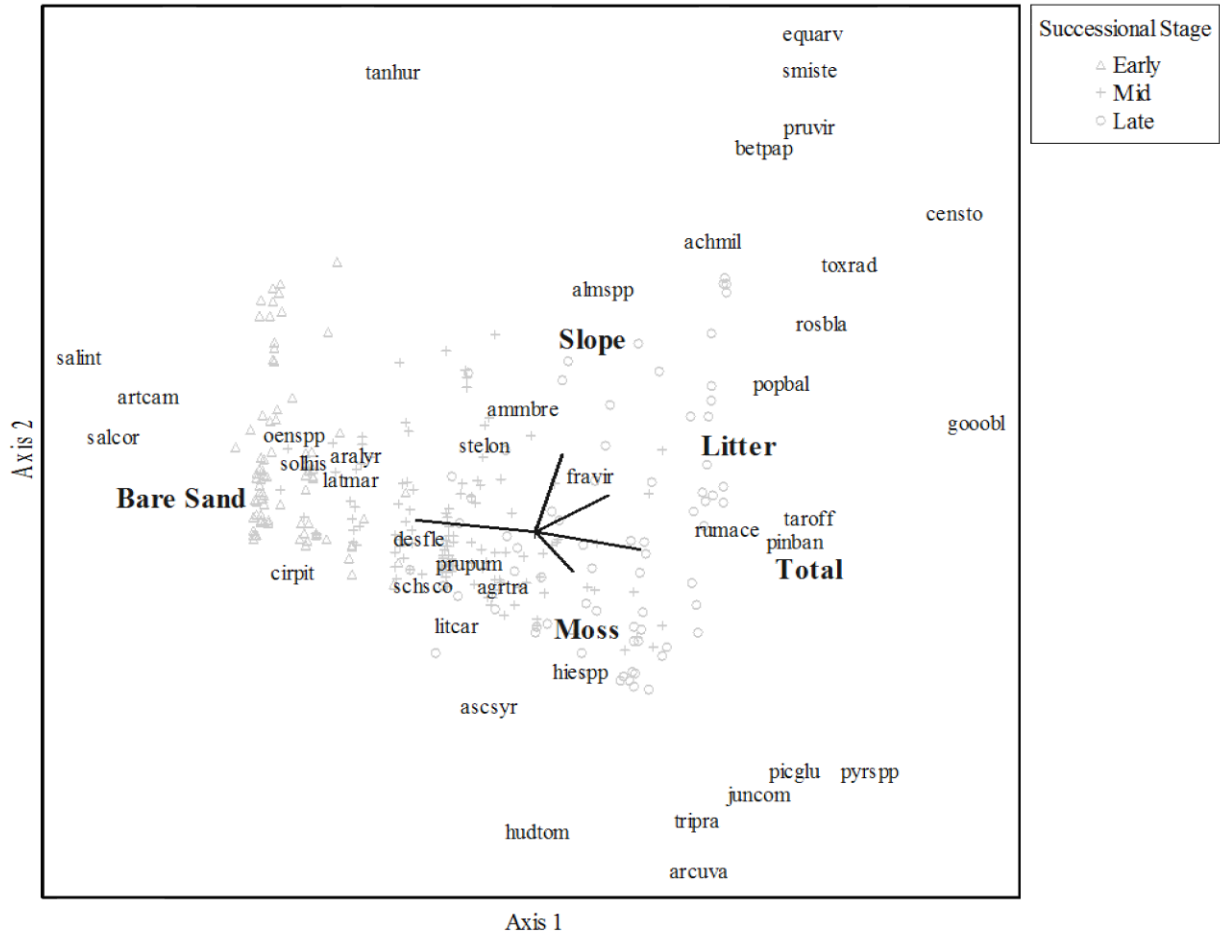


Figure 2. CCA joint plot showing categorical successional stages; early, mid, and late. The eigenvalues for the first two axes were 0.376 and 0.222, respectively, and accounted for 7.3% of the species environmental variation. The first axis was significant ( $p = 0.01$ ) using a Monte Carlo randomization test. Species codes are the first 3 letters of the genus and the first 3 letters of the species epithet; codes and full scientific names are given in Table 1.

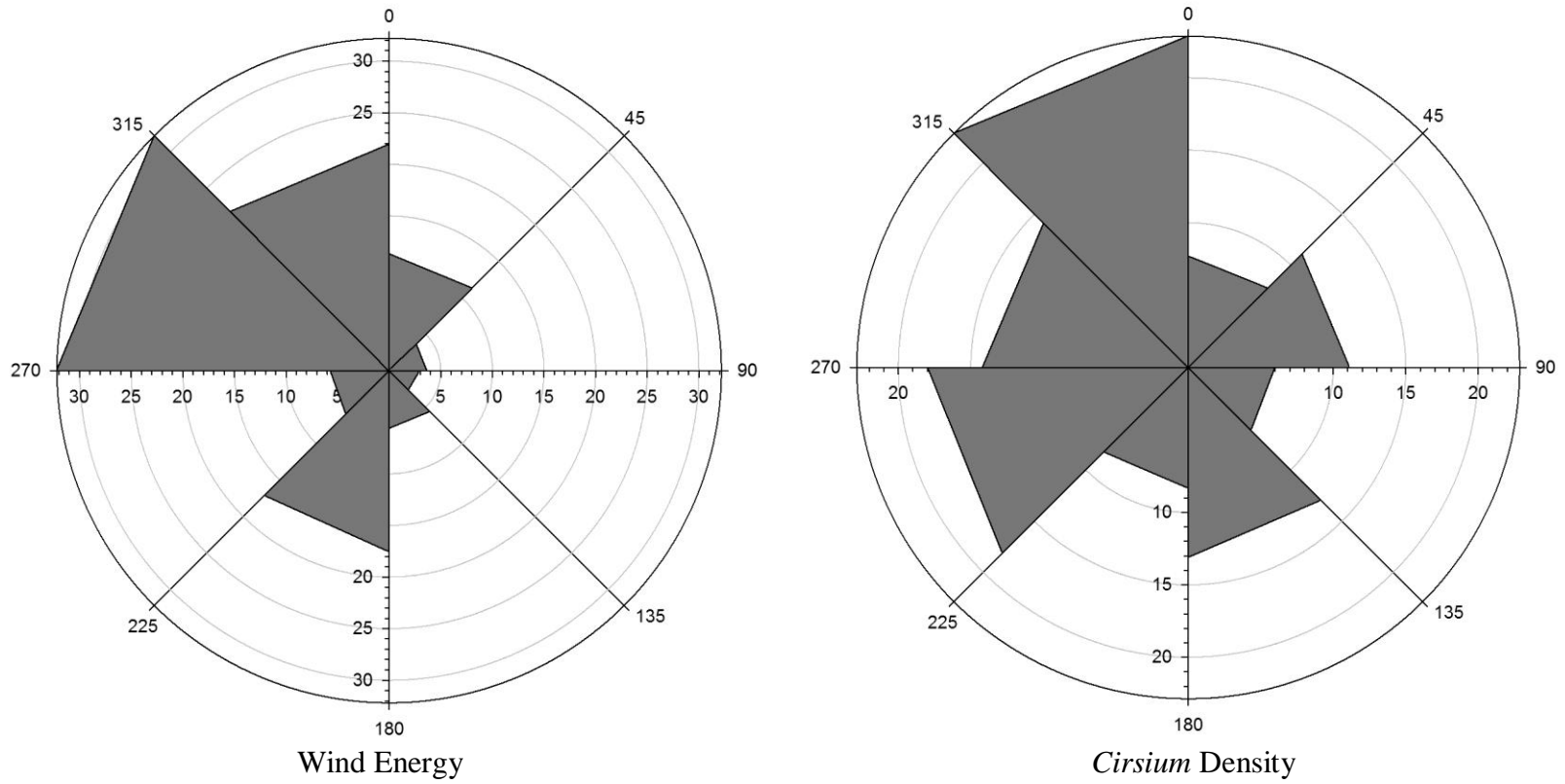


Figure 3. Rose diagrams comparing the directional distribution of cumulative (2006-2010) wind energy (time x velocity<sup>3</sup>) (relative %) and densities of *Cirsium pitcheri* (relative %) in the Grand Sable Dunes at Pictured Rocks National Lakeshore, Michigan USA, 2008.

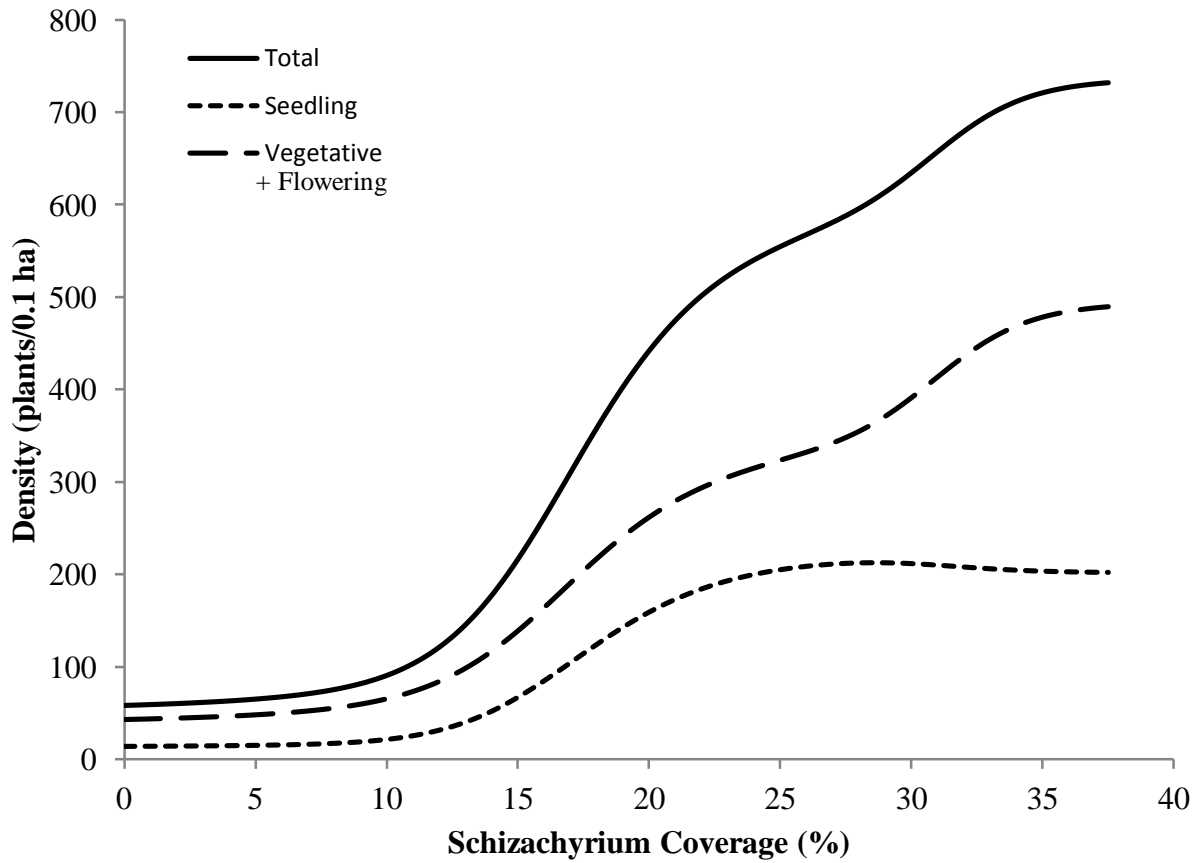


Figure 4. *Cirsium pitcheri* densities, by life history stage, as a function of % *Schizachyrium scoparium* cover, Grand Sable Dunes at Pictured Rocks National Lakeshore, Michigan USA, 2008. NPMR response curves generated using local mean Gaussian models in Hyperniche 2.12.



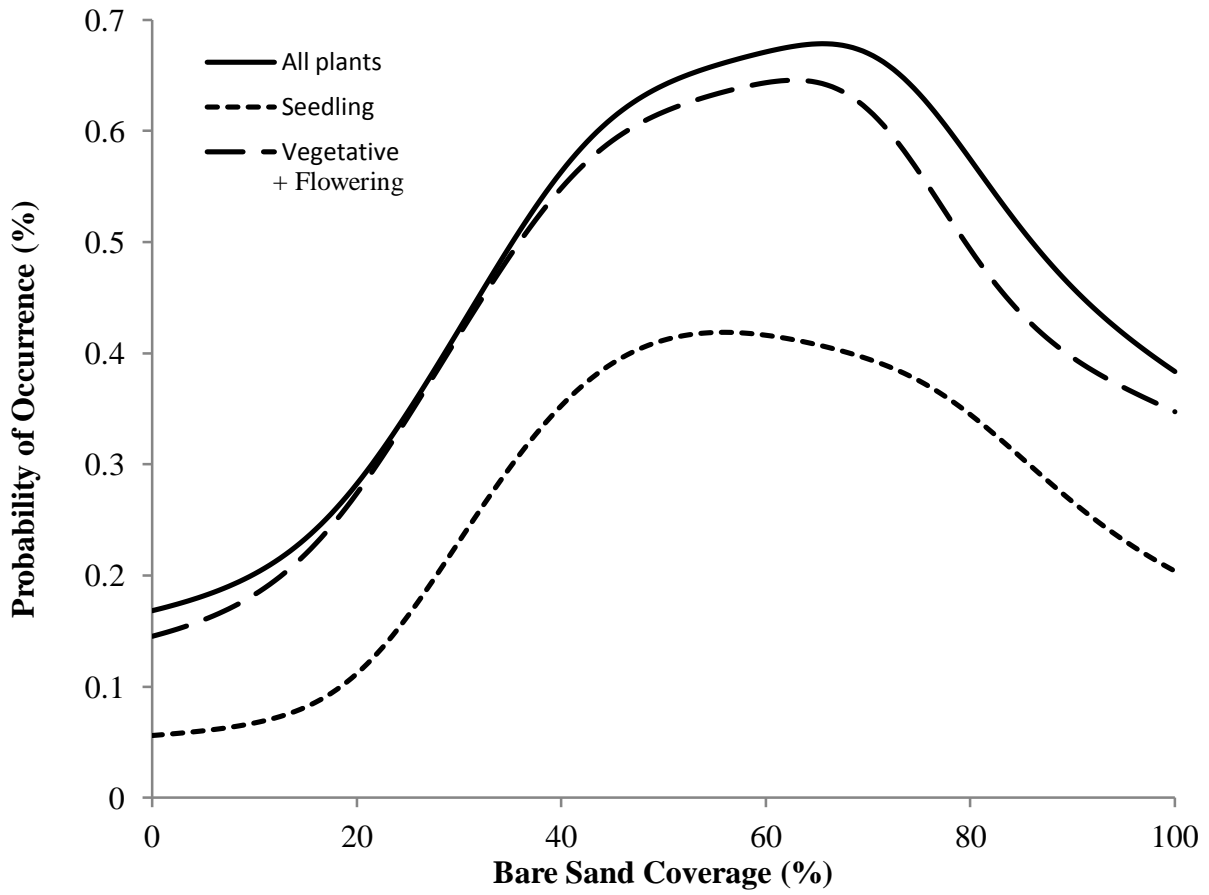


Figure 5. *Cirsium pitcheri* probability of occurrence, by life history stage, as a function of % bare sand cover, Grand Sable Dunes at Pictured Rocks National Lakeshore, Michigan USA, 2008. NPMR response curves generated using local mean Gaussian models in Hyperniche 2.12.

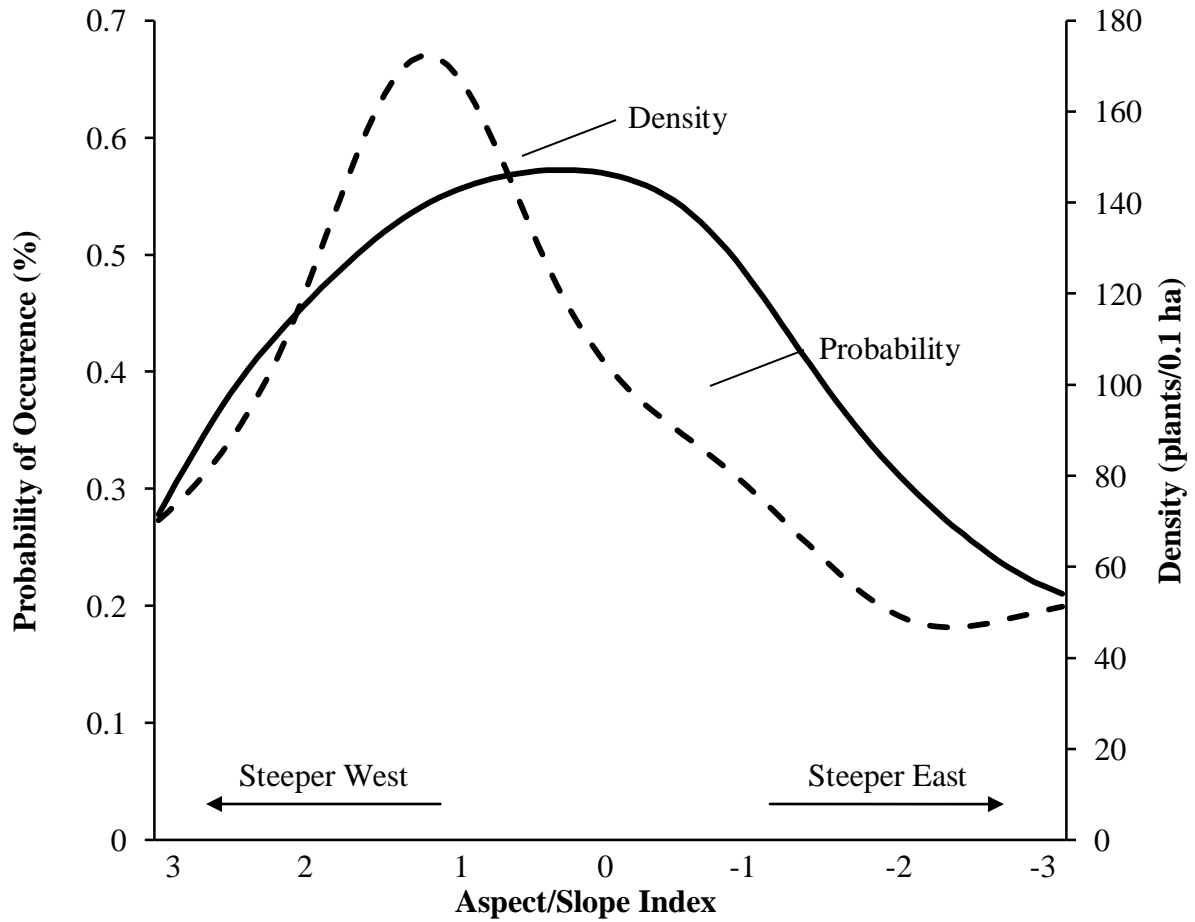


Figure 6. *Cirsium pitcheri* densities and probability of occurrence as a function of the aspect/slope index, a combination of aspect and slope, Grand Sable Dunes at Pictured Rocks National Lakeshore, Michigan USA, 2008. NPMR response curves generated using local mean Gaussian models in Hyperniche 2.12.

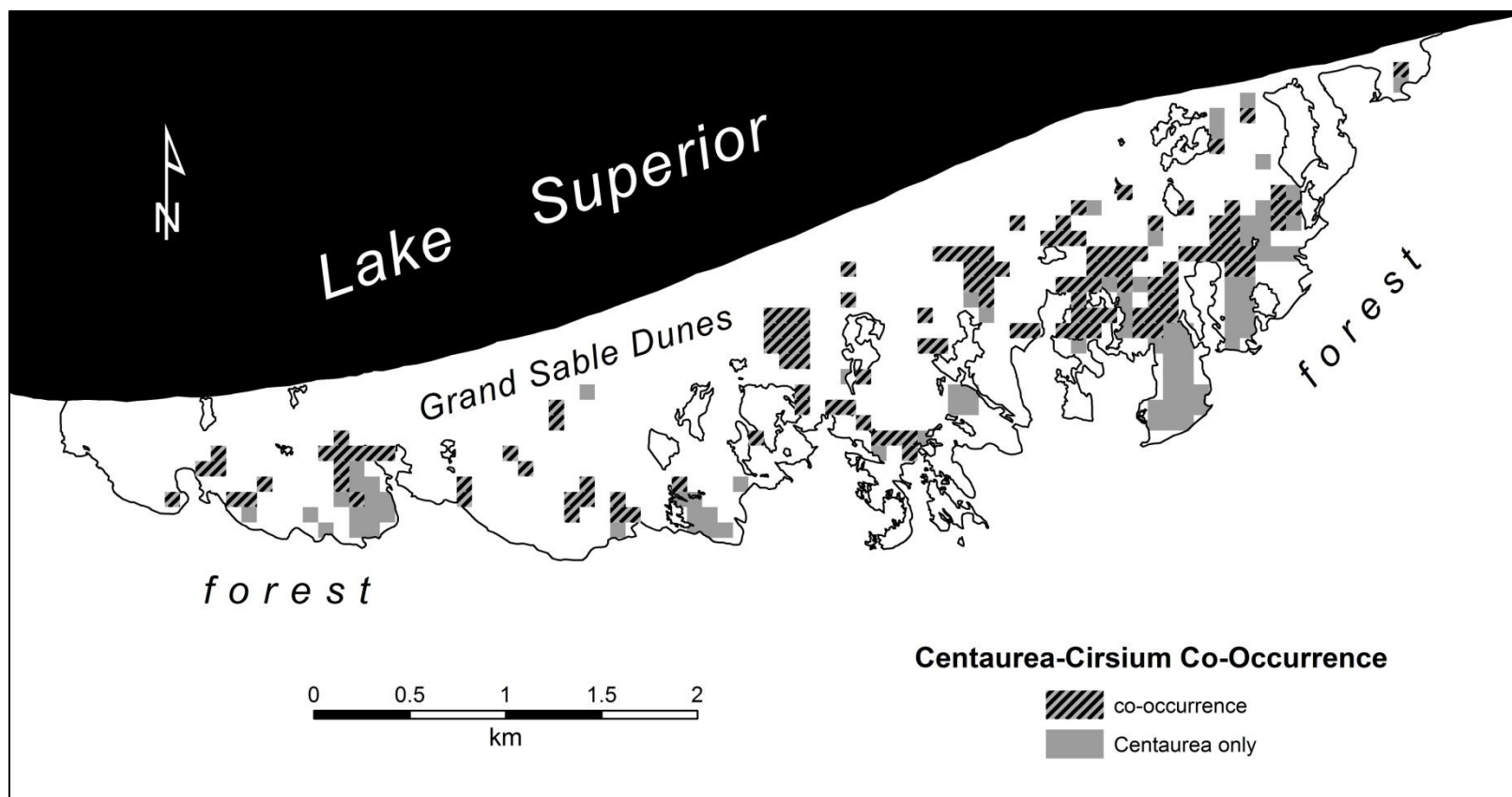


Figure 7. Map showing the distribution of the exotic invasive, *Centaurea stoebe*, and its co-occurrence with *Cirsium pitcheri* in the Grand Sable Dunes at Pictured Rocks National Lakeshore, Michigan, USA, 2008. Distribution was determined through a systematic survey of 853 80 x 80-m grid cells.