Grand Valley State University

ScholarWorks@GVSU

Masters Theses
Graduate Research and Creative Practice

12-2014

Predictive Modeling of Floral Species Richness in Michigan Prairie Fen Communities

Nichole R. Mason
Grand Valley State University

Follow this and additional works at: https://scholarworks.gvsu.edu/theses

Part of the Biology Commons

ScholarWorks Citation

Mason, Nichole R., "Predictive Modeling of Floral Species Richness in Michigan Prairie Fen Communities" (2014). *Masters Theses*. 745.
https://scholarworks.gvsu.edu/theses/745

This Thesis is brought to you for free and open access by the Graduate Research and Creative Practice at ScholarWorks@GVSU. It has been accepted for inclusion in Masters Theses by an authorized administrator of ScholarWorks@GVSU. For more information, please contact scholarworks@gvsu.edu.

PREDICTIVE MODELING OF FLORAL SPECIES RICHNESS IN MICHIGAN PRAIRIE FEN COMMUNITIES.

Nichole Rianne Mason

A Thesis Submitted to the Graduate Faculty of

GRAND VALLEY STATE UNIVERSITY

In

Partial Fulfillment of the Requirements

For the Degree of

Master of Science

Department of Biology

December 2014

DEDICATION

This thesis is dedicated to my friends and family, especially to my husband, who provided a constant source of love, encouragement, and support.

ACKNOWLEDGMENTS

I would like to thank my advisor, Dr. Gary Greer, for his guidance and endless patience through this process, and Drs. Shaily Menon and Robert Hollister, members of my committee, for their direction and assistance with this research. Without the assistance of Drs. Tim Evans, Dave Warners, and Garett Crow I would still be identifying plant specimens. I am eternally grateful for all of their guidance and instruction.

Thanks to Dr. Ali Locher, Alynn Martin, Josh Green, Echo Prafke-Marson, and Thomas Schmidt for their many hours of dedicated field, laboratory, and GIS assistance. Thank you to Dr. Neil MacDonald and to my graduate cohort including James Smit and Jake Doggett, among many others, for reviewing my manuscript. I would also like to thank the Michigan Nature Association, the Michigan Audubon, Ebersole Environmental Education Center, Pierce Cedar Creek Institute, City of Middleville, Calhoun County, the Michigan Army National Guard Fort Custer Training Facility, and the Michigan Department of Natural Resources for granting survey permission. Finally, I thank the Michigan Natural Features Inventory for the use of their prairie fen records and resources. Support for this research was provided by the Michigan Space Grant Consortium Graduate Fellowship Program and the Grand Valley State University Presidential Grant.

ABSTRACT

Prairie fens contain high levels of floral biodiversity, including 19 state threatened or endangered plant species, and are classified as rare and vulnerable communities by the Michigan Natural Features Inventory. The objective of this thesis was to develop multiple-regression (MR) models that reliably predict total, native, and invasive floral species richness for use by conservation organizations. Floral biodiversity surveys were conducted in eight southern Michigan prairie fens during the 2012 growing season. Simple linear regressions between fen size and biodiversity were used to optimize sampling strategy and effort (i.e., number of transects and plots per transect) in surveys conducted in 12 additional prairie fens in the 2013 season. Prairie fen characteristics including proximity to neighboring fens, size, shape, depth to water table, elevation, and land cover of the environmental matrix within a 250m buffer zone around each prairie fen were included as independent variables in the developed models. Nine sets of MR (MR families) were developed to predict total, native, and invasive floral species richness. The first MR family contained all normally distributed variables ($p \leq 0.05$) to optimize the independent variables (i.e., find the minimal set of independent variables to generate a robust MR). As these models were not significant, the subsequent MR families were developed using ordinated independent variables. Correspondence Analysis (CA) was performed for each latter model family to retain as much variation as possible. The loading scores of each significant CA axis were used as independent variables for the eight subsequent MR families. Multiple Regression Family 2, the simplest of the ordinated model families, produced significant models and was the most reliable with the highest R^2_{adj} and highest model fit compared to the other MR families. These models were most influenced by the land cover of the area immediately surrounding a prairie fen and, notably, did not include fen hydrology. We recommend managers consider the current land cover surrounding a fen, namely the presence of forested areas that negatively impacted diversity when developing management strategies.

TABLE OF CONTENTS

LIST OF TABLES

TABLE PAGE

LIST OF FIGURES

INTRODUCTION

Calcareous temperate-zone fen communities are naturally rare wetlands, distributionally limited throughout North America due to their climate and hydrologic requirements (Eggers and Reed 1997, Amon et al. 2002). Often found at the intersection of an outwash plain and a moraine (Ruhfel 2005) or along an ice contact ridge (Spieles et al. 1999), calcareous fens may develop under several conditions. Fens may occur when highly pressurized groundwater is forced through a break in an impermeable soil layer, resulting in discharged water becoming surface water (Amon et al. 2002, Bedford and Godwin 2003). Alternatively, when groundwater is forced to move laterally after being prevented from moving downward, and is discharged near a lake edge or on a hill slope (Ruhfel 2005) a fen may develop.

North American fens have become increasingly rare, isolated, and fragmented as a result of urbanization and agricultural development (Bedford and Godwin 2003, Bart et al. 2011). Several studies have shown substantial loss of fens in North American in the last century (Bedford and Godwin 2003). Miller and Crumpton (2012) concluded that only 3-4% of the original wetlands in the Des Moines Lobe are still present today, and Nekola (1994) found a staggering loss of 93% of fens in Iowa fens (Crancer 2011).

Prairie fens are a subgroup of calcareous temperate-zone fens, restricted to areas with limestone bedrock or other calcareous glacial till close to the surface (Landis et al. 2012). This - in addition to human-caused disturbance and fragmentation (Wheeler 1988) - limits prairie fen distribution to northeastern and central United States (Amon et al. 2002, Bart et al. 2011). These regions possess the necessary underlying bedrock for maintaining an environment with a constant source of calcareous groundwater (Kost and Hyde 2009). In Michigan, prairie fens are found within the Kalamazoo-Battle Creek and Jackson interlobates, which occur where the Michigan, Saginaw and Huron-Erie glaciers met (Landis et al. 2012). Due to the combination of limestone bedrock and the high water table, prairie fens are calcareous from the internal flow of calcium and magnesium bicarbonate rich groundwater (Spieles et al. 1999, Bowles et al. 2005). This influx of minerals buffers the groundwater resulting in a circumneutral pH, typically ranging from 6.8-8.2 (Kost and Hyde 2009, Landis et al. 2012).

Prairie fens are supplied by a rarely fluctuating (Ruhfel 2005) source of groundwater (Wassen et al. 1996), differentiating them from precipitation fed bogs and stream fed swamps (Bedford and Goodwin 2003). Generally dominated floristically by non-emergent graminoids (Ruhfel 2005), prairie fens routinely possess a high diversity of forbs as well (Crancer 2011). These communities provide habitat for approximately 40% of state protected faunal and floral species (Kost and Hyde 2009) including the eastern massasauga, (*Sistrurus c. catenatus, state threatened, federal candidate species),* Mitchell's satyr butterfly (*Neonympha mitchellii mitchellii*, state endangered), shooting star (*Dodecatheon meadia*, state endangered), and wild sweet William (*Phlox maculate*, state threatened; Spieles et al. 1999, Landis et al. 2012).

There are approximately 140 prairie fens in Michigan, totaling 4,800 acres, all of which are found within the lower third of the Lower Peninsula (Spieles et al. 1999). Michigan prairie fens exhibit a wide range in size, from <1 - 320 acres, but most are less than 12 acres (Amon et al. 2002). Roughly 8% of these fens are believed to be "high quality", while 10% have been classified as "low quality" (Landis et a. 2012). Considering their limited distribution, average small community size, and high floral and faunal biodiversity (Meyer et al. 2003, Ruhfel 2005), the Michigan Natural Features Inventory (MNFI) has classified prairie fens as GS/S3 communities (Kost and Hyde 2009). A G3/S3 classification defines prairie fens as vulnerable communities with few occurrences at the state and local level (Spieles et al. 1999), designating them as communities of high conservation concern.

Prairie fens may develop three (Kost and Hyde 2009) to five (Spieles et al. 1999) different vegetation zones. These zones form as a result of environmental gradients in groundwater flow, pH, conductivity, and mineral and nutrient availability (Bowles et al. 2005). Species richness and species composition within a prairie fen can change substantially from zone to zone. The outer-most vegetation zone that may form is the wooded fen zone located along prairie fen margins. Compared to other prairie fen zones, the wooded zone is dryer and has more upland characteristics (Spieles et al. 1999). Dominated by shrubs and trees, this zone is greater in prairie fens with a lack of disturbance such as the absence of flooding from beaver dams and fire suppression (Michigan Nature Association 2010). Woody species such as tamarack (*Larix laricina*), poison sumac (*Toxicodendron vernix*), and *Cornus* spp. are commonly found in this zone. Herbaceous species such as Joe-pye weed (*Eupatorium maculatum*) and marsh violet (*Viola cucullata*), characteristic of a sedge-meadow (described below), may be found in the wooded fen zone as well (Kost and Hyde 2009). A sub-category of this zone, the wetter wooded zone, may also occur. This zone is similarly found along the outer margins of a fen, and may resemble a deciduous swamp based on the characteristic vegetation. Red maple (*Acer rubrum*) and meadowsweet (*Spiraea alba*), in addition to species found in the wooded fen, are common in the wetter wooded prairie fen zone (Spieles et al. 1999).

Located between the wooded zone and either the depression zone (described below) or boardering a body of water is the sedge-meadow zone, also referred to as the fen meadow (Kost and Hyde 2009). This zone is usually the largest, and has the highest level of grass, sedge, shrub, and forb diversity (Spieles et al. 1999). Plant species such as big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), shrubby cinquefoil (*Potentilla fruticosa*), and Ohio goldenrod (*Solidago ohioensis*) are characteristic of this zone (Kost and Hyde 2009). Several threatened and endangered species, such as white lady-slipper (*Cypripedium candidum*, state threatened), Prairie Indian plantain (*Cacalia plantaginea*, state threatened), and Queen-of-the-prairie (*Filipendula rubra,* state threatened) can be found in this zone as well. The sedge-meadow zone has no standing water but is saturated, and has the highest proportion of herbaceous cover compared to the other vegetation zones (Spieles et al. 1999).

Closest to the margins of lakes, rivers, springs, or ponds, is the depression zone. The depression zone is typically inundated, containing up to 12 inches of standing water during the spring or early summer (Kost and Hyde 2009). Characteristic plant species include spike-rush (*Eleocharis rostellata*) and three-square (*Schoenoplectus pungens*; Spieles et al. 1999), and the state threatened wild rice (*Zizania aquatic* var. *aquatic*) can also be found in the shallow waters of the depression zone.

The marl zone forms in areas of the prairie fen with calcareous groundwater seepage (Kost and Hyde 2009) found within any of the previously mentioned zones, and can cover large areas of the fen or occur as small patches. Marl zone is characterized by higher levels of standing water, greater magnesium and calcium carbonate ($CaCO_3$) accumulation, and a lower cation exchange capacity (Bowles et al. 2005). These environmental conditions result in lower nutrient availability relative to other prairie fen zones (Spieles et al. 1999). Due to these conditions, the marl zone is sparsely vegetated by a few well-adapted species (Kost and Hyde 2009). Plant species such as twig-rush (*Cladium mariscoides*), pitcher plant (*Sarracenia purpurea*), and horned bladderwort (*Utricularia cornuta*) are commonly found in this zone, and state special-concern English sundew (*Drosera anglica*) is also associated with the marl zone.

The above zones describe how individual prairie fens can vary widely in species richness and composition, influenced by environmental gradients. At a larger scale, species richness and community composition of prairie fens are likely influenced by regional processes. The theory of island biogeography proposes that the species richness of an island is determined by regional spatial dynamics that affect colonization and extinction (MacArthur and Wilson 1967, Mouquet and Loreau 2002), namely island size and isolation. Larger islands close to similar islands will have high levels of species richness due to an increase in available habitat and dispersal ability. Smaller, more isolated islands will contain fewer species in comparison (MacArthur and Wilson 1967). While originally describing literal islands separated by water, the theory has subsequently been applied to fragmented mainland habitats (Brose 2001). The current study applies this theory of regional processes influencing community species richness to the prairie fens within Michigan.

While the theory of island biogeography focuses on regional-level processes, metacommunity theory examines the importance of local events and processes on community species richness (Leibold et al 2004). Local dynamics such as dispersal ability, resource availability, and competition influence the species richness of a community (Mouquet and Loreau 2002, Kneitel and Miller 2003). A metacommunity is defined as a set of communities connected through the dispersal of potentially interacting species (Holyoak et al. 2005) which could apply to Michigan prairie fens. Based on variations in dispersal, community size, and community quality, a set of communities can be categorized as one of four model perspectives: patch dynamics, species sorting, mass effect, and neutral models (Table 1; Leibold et al. 2004, Holyoak et al. 2005).

Isolation can significantly influence the species richness and community composition of prairie fens. Isolated communities have limited seed dispersal due to increased edge effect, which can hinder the colonization of a species (Middleton et al. 2006). Brose (2001) found that approximately 20% of wetland plant species in eastern Germany were negatively influenced by isolation; the remaining 80% of species were able to successfully disperse utilizing seed banks and wind, water, and animal-mediated dispersal mechanisms.

The prairie fens in Michigan do not fit perfectly into any one of the four described metacommunity models (Table 1). Prairie fens have defining soil and flora characteristics identifying them as specific communities (Spieles et al. 1999), but exhibit a wide range in size, shape, environmental conditions (e.g., peat depth, fen elevation, and soil and groundwater pH) and surrounding land cover (Houlahan et al. 2006). These factors impact the presence and abundance of species present in a prairie fen (Bowles et al. 2005), as well as creating a limiting environment where only specialized species can survive and successfully colonize (Mitsch and Gosselinnk 2007). Noting these community characteristics, Michigan prairie fens fit closest with the species-sorting model. The species-sorting model states that habitat selection is a driving force behind community composition, which likely applies when the habitat maintains harsh living environments and requires adaptations of colonizing species (e.g., adventitious roots, nitrogen-fixing bacteria, aerenchyma; Keddy 2010).

To empirically determine that the prairie fen communities of Michigan meet the criteria to be classified as a metacommunity, dispersal rates of constituent species would need to be quantified between fens that are expected to be connected via seed dispersal. This study did not look at specific dispersal rates of individual species, as it falls outside the scope of this thesis. While I cannot state that the observed prairie fens are a metacommunity, it is reasonable to assume that dispersal does occur between these relatively small prairie fen patches (Brose 2001, Middleton et al. 2006), as several wetland-specific species were observed in prairie fens (e.g., *Angelica atropurpurea, Glyceria striata, Triadenum fraseri*; Reznicek et al. 2011). Michigan prairie fens serve as a potential meta-community in this study, assuming a significant relationship is present between the observed prairie fen species richness and both community size (acreage) and isolation. Two isolation metrics are used in this study; the distance to the closest fen (m) and the average distance to the nearest three prairie fens (m).

The purpose of the study reported here was to examine factors influencing species richness of prairie fens within southern Michigan and to develop the simplest multiple-regression models possible (Hawkins 2004) that reliably predict their total, native, and invasive components. The factors investigated include fen isolation and size, the composition of the surrounding environmental matrix, and fen hydrology. Several combinations of these independent variables within the models were considered, as many factors are likely to influence the species richness of a prairie fen.

METHODS

Species Richness Surveys

Floral species richness surveys of twenty-two prairie fens in southern Michigan were completed during the 2012 and 2013 field seasons (Fig. 1, Table 2), from which native and invasive components were determined. Eight fens were surveyed in 2012 and used to optimize sampling strategy for the remaining fourteen fens in 2013. Species richness surveys were conducted by subsampling quadrats along transects within each fen. All stems within each of the 20cm × 20cm (hereafter "plot") corners of a 1-m^2 quadrat, amounting to a total sampling area of 0.16-m^2, were recorded and a voucher specimen for each species observed was collected for later identification. Each voucher specimen was pressed and dried for at least 48 hours, and identification nomenclature follows Crow and Hellquist (2000a, 200b) and the University of Michigan's *Michigan Flora Online* (Reznicek et al. 2011). All voucher specimens are stored at Grand Valley State University's herbarium in accordance with MDNR permits PRD-SU-2012-041 and PRD-SU-2013-042.

At least three transects were surveyed per fen, one facing north-south, another east-west, and the third and all subsequent transects placed strategically throughout the fen to observe the maximum amount of diversity. Transects alternated in their direction between center-to-edge and edge-to-center in order to sample both fen areas. Plots were placed 5m apart along each transect, and the number of plots per transect were divided as equally as possible.

As the eight prairie fens surveyed in 2012 varied widely in size (3.5 to 50.6 acres, Table 2), the number of plots and transects surveyed increased with an increase in size to maintain equal sampling effort. The number of plots surveyed increased proportionally with fen size, with a pragmatic limit of 200 plots. The number of transects surveyed per fen increased with acreage, loosely based on the following rules: the number of transects increased by one for every increase of five acres. When the fen reached 30 acres, one transect was added for an increase of 10 acres due to limitations of time and labor. Due to prairie fen vegetation zones and in attempt to observe the most species richness possible, additional transects were surveyed as necessary.

To optimize sampling effort as a function of fen size, species area curves were created for all eight fens surveyed in 2012. The minimum number of plots required to encounter all species in a given fen was used as an initial estimate of an optimal sampling effort. A Coleman rarefaction curve based on the optimal number of plots and number of species encountered for each fen was used to refine the estimate of optimal sampling effort; i.e., optimal number of plots per unit fen area. To determine the number of plots to survey per unit fen area in the 2013 survey, a simple linear regression between fen acreage and the rarefaction-refined estimate of optimal sampling effort was used: number of plots = 2.882 * fen acreage + 60.660 ($R^2_{adj} = 0.819$, p = 0.001; Fig. 2). Similarly, a simple linear regression between fen acreage and the number of transects: number of transects = 0.1533 * fen acreage + 2.73 ($R^2_{adj} = 0.759$, p = 0.003; Fig. 3).

Based on the above equations, 14 additional prairie fens distributed across eight counties in southern Michigan were surveyed during the 2013 field season (Table 2). Selection of fens for survey was based on ease of access and ability to obtain permission to survey.

Independent Model Variables

Prairie fen composition is likely to be determined in large part by fen size, isolation, the character of the surrounding environmental matrix (Houlahan et al. 2006), and hydrology. Consequently, all of these factors were considered when developing the predictive multiple regression models.

ArcMap® version 10 (ESRI 2011) was used to determine the total acreage of each prairie fen. The distance from each surveyed prairie fen to the closest neighboring fen (m) and the average distance from a surveyed fen to the nearest three fens (m) were also measured in ArcMap®; all distances were measured from polygon (prairie fen) center-to-center. Patch Analyst extension (Rempel et al. 2012) in ArcMap® was used to calculate the Mean Perimeter-Area Ratio (MPAR; Elkie et al. 1999) to determine the influence of fen shape and edge-effect on prairie fen species richness.

A buffer of 250m surrounding each fen (Goodwin and Baldwin 2003, Houlahan et al. 2006) was created in ArcMap® to determine the effect of the surrounding environmental matrix on floral community structure. Land cover was categorized using the most recent land cover layer obtained via MiGDL (2001) and contained 31 separate categories. Five of these were not present in any of the established 250m buffer zones and were disregarded. Most of the land cover categories occurred as small patches within few buffer zones (Table 3), and all categories were not present in every fen buffer. Each land cover category was quantified as total acreage within each fen buffer in Patch Analyst (Rempel et al. 2012). To control for varying fen acreage and hence differences in area values in the buffer zone, land cover quantities within the buffer zone were represented as percentages.

The "Michigan Digital Elevation Model", 90m x 90m resolution, obtained from the Michigan Geographic Data Library (MiGDL 1998) was used to calculate the difference in elevation (DE) between the fen and the 250m buffer zone immediately surrounding it. The Zonal Statistics tool in ArcMap® (ESRI 2011) was used to determine the average elevation of the fen and the average elevation of its buffer zone. The DE was calculated by subtracting the average fen elevation from the average buffer zone elevation. A negative elevation implies that the buffer was below the fen (e.g., the fen is located on a hill), while a positive value indicates that the buffer is at a higher average elevation than the enclosed fen (e.g., the fen is in a bowl). Prairie fens with a lower average elevation than its buffer are likely to receive runoff from the buffer.

The difference in the average depth to the water table (DWTD) was calculated between the fen and its buffer zone. DWTD was calculated from information in the MiGDL (2005) file "Water Table Contours - Montmorency County, Michigan", with a 30m x 30m grid resolution. The average DWTD was calculated using the Zonal Statistic tool, as for DE. Although the layer name is specific to one Michigan county, water table depth information for every county relevant to this study was available within the specified layer. A negative DWTD indicates that the fen was farther from the water table compared to its buffer. If DWTD was positive, the buffer was farther away from the water table than the fen. Assuming that the buffer is composed of similar geological features, fens with positive DWTD are likely to experience more upwelling.

Some negative values existed in the DWTD layer. These were likely error due to the differences in how the fen layer and water table depth layer values were calculated and extrapolated, and combining these layers likely compounded this error (Locher 2014). The cells with negative values were mostly located in areas very close to the water table (i.e., around lakes or within fens) and were very small. Therefore, all negative cells were assumed to be a layer calculation error and were replaced with zeros. Baker Audubon, McDonald Lake, and Hampton Creek were the only prairie fens without any negative DWTD in either the fen or buffer zone.

Use of Ordination

Multiple regression ranks variables according to their influence, but does not produce weights for each independent variable. If the scale of measurement varies widely between variables, as is the case in this study, the variables with greater absolute scales may have a disproportionate influence on the regression. Ordinating the original variables and using the resultant axes scores as synthetic variables within the multiple regressions removes the scaling issue. Ordination also simplified the development of the multiple regressions. Since every land cover category did not occur within each prairie fen buffer zone, each category could not be used as an independent variable within the multiple regression models due to the number of zeros present and their subsequent lack of normality. Instead of regrouping or reclassifying some of the land cover categories and transforming others to meet the multiple regression test assumptions, all categories were left untransformed and uncombined in the ordination, along with the other variables (fen acreage, isolation, and hydrology; Hovick et al. 2012). This created a simple approach that also allowed all variables (and therefore all variation) to be retained within the multiple regression models. Ordination axis scores and model residuals were tested for normality and homoscedasticity. Correspondence Analysis (CA) was chosen for ordination of the independent variables because it is a chi-squared analysis, enabling it to handle double-zeros (Borcard et al. 2011).

Multiple Regression Models

Nine multiple regression model families were developed and used to predict three diversity metrics: total species richness, native species richness, and invasive species richness. "Model Family" is defined as a set of three multiple regression models with the same independent variables, predicting the above diversity metrics. Model Family 1 was developed without the use of ordination and contained all variables that were normally distributed ($p = 0.05$). Twelve independent variables were retained (Table 5); however, one of these was a synthetic variable that included four land cover categories: Forage Crop, Non-vegetated Farmland, Orchard, and Row Crop in response to large numbers of zeros.

All independent variables within Model Families 2 - 8 were ordinated using CA (Hovick et al. 2012). Axis scores that captured at least 5% of the cumulative variation were included as variables within the multiple-regression models (Table 4). In all model families described below, with the exception of Model Family 5, the first three CA axes met this criterion. Model Family 5 had five CA axes included.

Model Family 2 was the simplest of the ordinated models, containing the fewest variables within the ordination. All 26 land cover variables, fen acreage, fen isolation, and MPAR (Table 5) were ordinated using CA; variables accounting for fen hydrology were notably absent. Model Family 3 contained all the variables from the previous model, with the addition of one variable - difference in elevation between the fen and its surrounding buffer (DE; Table 5). The DWTD between the surveyed fen and its buffer (Table 5), in addition to all variables within Model Family 2 were added to Model Family 4. Model Family 5 contained both hydrology variables, DWTD and DE, for the surveyed fens as well as all Model Family 2 variables (Table 5). The sixth model family included all the variables from Model Family 5, but used a different measure of fen isolation, average distance (measured center-to-center) to the three nearest fens, for comparative purposes. Model Family 7 included all the variables from the fourth model family as the distance to the nearest fen proved a stronger measure of isolation than the average distance to three fens. Additionally, Model Family 7 included the difference in elevation (DE) between the fen and its buffer zone for the fen nearest to each surveyed fen. Model Family 8 included all the variables from the fourth model, and included the difference in depth to the water table (DTWD) between the fen and its buffer zone for the nearest fen. The ninth and final model family included all the variables from the eighth model, and included the DE for the nearest fen.

Statistical Analysis

Pearson's Correlations were performed to indirectly test prairie fen metacommunity strength. Total, native, and invasive species richness were correlated with fen size (acreage) and both isolation metrics: distance to the nearest fen and average distance to three nearest fens. The same correlations were also performed for eastern and western fens to determine metacommunity strength at a more local scale. Acreage, distance to the nearest fen, and average distance to three nearest fens were Log_{10} transformed when necessary. Correlations were also performed between the diversity metrics to determine the relationship between total species richness and invasive species richness.

Holms-Bonferroni Method (Holms 1979) was applied to each model produced to correct for multiple comparisons error. Model Families was determined reliable based on model significance and R^2_{adj} values.

Regression assumes that observations are independent of one another; e.g., species richness and composition in fens in this study. To test that this assumption was not violated, spatial autocorrelation between surveyed prairie fens was examined in ArcMap® (ESRI 2011) using Moran's I (Moran 1950). The Euclidean distance measure was used, and the Conceptualization of Spatial Relationships was the Inverse Distance Squared. Moran's I was calculated for total species richness and for the invasive species richness : total species richness ratio for fens.

Three Nonmetric Multidimensional Scaling (NMDS) were performed using Bray-Curtis dissimilarity matrices to compare community composition (Clarke 1993) based on: (1) year surveyed (2012 vs. 2013), (2) geographical location (east vs. west side of Michigan), and (3) public vs. private ownership. Post-hoc comparisons between the two groups for each NMDS were made using multi-response permutation procedures (MRPP), which compares the within-group to between-group distances for the sample units (Murray et al. 2012).

All tests were calculated in R version 3.1.1 (R Core Development Team 2014) with packages MASS (Venables and Ripley 2002), UsingR (Verzani 2014), and Vegan version 2.0-10 (Oaksanen et al. 2013) while species area curves were created in Microsoft Excel (Microsoft 2010).

RESULTS

The total species richness of the prairie fens ranged from eleven to sixty-six species (Table 2, Fig. 4), with an average of 41 species (± 13.7) per fen. The majority of the species observed were native species (37.5 ± 12.9), ranging from 82.6% - 100% of species. In contrast, few invasive species were observed within fen communities (3.5 ± 1.4), ranging from 0% - 17% of species (Fig. 5). Total species richness was strongly, positively correlated with native species richness ($r^2 = 0.98$, $p < 0.001$; Fig. 6). Similarly, invasive species richness correlated significantly and positively with total richness ($r^2 = 0.40$, $p = 0.002$; Fig. 7).

Following the logic of island biogeography, relatively large prairie fens were expected to have greater species richness compared to smaller fens due to the increased habitat availability. Contrary to this expectation, no significant relationships between fen acreage and total species richness ($r^2 = 0.12$, $p = 0.12$; Fig. 8), native species richness ($r^2 = 0.12$, $p = 0.095$; Fig. 9), or invasive species richness of a fen ($r^2 = 0.002$, $p = 0.86$) were present when all 22 surveyed fens were considered. However, two fens consistently appeared as outliers, Pierce Cedar Creek Institute fen (PCCI) and Shaw Lake fen. When these two fens were omitted, Spearman's Rank Correlation revealed a significant, negative relationship between fen acreage and invasive species richness ($r^2 = -0.55$, $p > 0.001$; Fig. 10). Larger fens were more likely to have fewer invasive species compared to smaller fens, but no such pattern was present for total or native species richness.

A relationship between fen isolation and species richness was not detected. The distance to the nearest fen did not significantly correlate with total species richness ($r^2 = 0.02$, $p = 0.55$), native species richness ($r^2 = 0.02$, $p= 0.53$), or invasive species richness ($r^2 < 0.0001$, $p = 0.97$). However, when the outlying fen, PCCI, was removed, total species richness ($r^2 = 0.19$, $p = 0.05$; Fig. 11) and native species richness ($r^2 = 0.19$, $p = 0.05$; Fig. 12) did significantly, positively correlate with the distance to the nearest fen. In contrast, when outlying fens (PCCI and Shaw Lake) were removed from the analysis no significant relationship was detected between distance to the nearest fen and invasive species richness (Fig. 13). Thus, total and native species richness of a prairie fen, when outliers are excluded, increase with greater distances to similar communities, but invasive species richness has no such relationship. Detection of a relationship between fen isolation and floral diversity depended on the metric used. When using the average distance to the three nearest fens as a broader metric of fen isolation, no relationship was detected with total ($r^2 = 0.15$, $p = 0.08$; Fig. 14), native ($r^2 = 0.13$, $p = 0.09$; Fig. 15), or invasive species richness ($r^2 = 0.17$, $p = 0.06$; Fig. 16), even with the exclusion of outlying fen communities.

When fens were separated according to geographical location (eastern and western Michigan fens), only two significant relationships were detected. Average distance to three fens was significantly and positively correlated with total ($r^2=0.24$, $p=0.05$) and native species richness ($r^2=0.24$, $p=0.05$) for western Michigan fens. No significant relationships were detected for eastern Michigan fens between acreage and total ($r^2=0.02$, $p=0.84$), native ($r^2=0.04$, $p=0.76$), or invasive species richness (r^2=0.65, p=0.1). Similarly, western Michigan fens also failed to significantly correlate fen acreage with total (r^2=0.14, p=0.14), native (r^2=0.15, p=0.13), or invasive species richness (r^2=0.03, p=0.48). The distance to the nearest fen had no detectable relationship with total (r^2=0.59, p=0.13; r^2=0.02, p=0.6), native (r^2=0.65, p=0.1; r^2=0.02, p=0.59), or invasive species richness (r^2=0.33, p=0.31; r^2=0.003, p=0.85) for eastern or western Michigan fens, respectively. A relationship between the average distance to three fens and total (r^2=0.35, p=0.3), native (r^2=0.41, p=0.24), or invasive (r^2=0.5, p=0.19) species richness was not found in eastern Michigan fens, while only invasive species richness (r^2=0.16, p=0.12) failed to correlate with the average distance to three fens in western Michigan communities.

A linear relationship between either of these measures of fen isolation and total species richness would have supported the hypothesis that the fens surveyed constituted a metapopulation with varying degrees of connectivity. The absence of such a relationship at a state level is consistent with either the complete absence of connectivity or very high levels of connectivity. Given the wide range of distances among the fens surveyed (0.1 - 32 km for distance to the nearest fen, 2 - 36 km for the average distance to the three nearest fens), we suspect the latter. Likewise, the absence of a linear relationship between fen isolation and invasive species richness indicates that magnitude of invasion is not a function of fen connectivity.

Model Performance

The majority of model families retained three CA axes as independent variables, the exception being Model Family 5 with five axes. Model Family 2 and 3 explained 86% of the cumulative variation within their significant CA axes, slightly more than Model Family 4 at 85.9%. Model Family 5 CA axes explained the least cumulative variation, 84.3%, despite including the most axes. The CA axes used in Model Families 7 and 8 accounted for 85.7% of the cumulative ordination variation, marginally more than Model Families 6 and 9 with 85.6%.

All but two model families (Model Family 1 and Model Family 6) produced statistically significant models (Table 6). Substituting the average distance to the nearest three prairie fens for the distance to the nearest prairie fen did not increase the models predictive ability, as shown by Model Family 6. Ordinating the variables prior to the multiple regression proved necessary as Model Family 1 was not statistically significant for any of the diversity metrics (Table 6).

Prairie fen hydrology was measured as DE and DWTD, and at least one of these variables was included in all model families excluding Model Families 1 and 2. Unexpectedly, their inclusion in the model families did not improve the models ability to predict any of the three diversity metrics compared to Model Family 2. The simplest of the ordination based model families, Model Family 2, produced the highest adjusted-R^2 values for total species richness ($R^2_{adj} = 0.35$, p = 0.01, Fig. 17, Table 6) and native species richness ($R^2_{adj} = 0.33$, p = 0.02, Fig. 18). The invasive species richness model within Model Family 5 ($R^2_{adj}= 0.36$, p = 0.02) performed minutely better than the invasive species model of Model Family 2 ($R^2_{adj} = 0.33$, p = 0.02, Fig. 19). Model 2 predicted 54% of total and invasive richness, and 45% of native richness within one standard deviation. Within two standard deviations, Model 2 predicted 82% of the total and native richness and 86% of invasive richness. Hence, I conclude that Model Family 2 is the best method for predicting all metrics of prairie fen species richness.

Two modifications were made to Model Family 2 in attempt to improve model fit. First, the two outlying fens (PCCI and Shaw Lake; see Figs. 17-19) were removed from the CA and subsequent multiple regression models. Second, the land cover categories were combined into five classifications, Agriculture, Forest, Shrubland, Wetland, and Developed (Table 3) for simplicity. Neither modification resulted in more predictive models compared to unaltered Model Family 2. Therefore, Model Family 2 remained the best set of predictive models.

Prairie fen acreage was the most influential variable in CA Axis 1 for all ordinations, along with two land cover categories within the buffer zone, Aspen and Lowland Mixed Forest. Neither of the isolation metrics or DWTD proved to be significant within the ordinations. The DE for the surveyed fen was only influential in axis 5 of Model Family 5 (Table 4). The majority of the land cover categories comprised a relatively small amount of the total buffer area surrounding each prairie fen (Table 3); however, three categories - Lowland Deciduous, Lowland Shrubland, and Mixed Upland Deciduous - dominated, accounting for 42.5% of buffer zone land cover. Likely as a function of their ubiquitous coverage, none of these variables were relevant in any of the CA axes (Table 4).

Moran's I revealed an absence of spatial autocorrelation between the surveyed fen communities for total species richness (I = 0.23, variance = 0.07, z score = 1.06, p = 0.29) or for the invasive species richness : total species richness ratio (I = 0.11, variance = 0.07, z score = 0.63, p = 0.53). Distance Threshold was calculated as 32,635.7m. Therefore, while fens within this threshold are more likely to be similar compared with fens found outside of the threshold, their species richness and invadedness are still independent of one another.

Prairie Fen Floral Composition

Nonmetric Multidimensional Scaling (NMDS; stress = 0.19, axes = 2) comparing floral community structure for publically versus privately owned fens did not detect significant differences (MRPP significance of delta = 0.466; Fig. 20). Likewise, an NMDS of fens surveyed in the 2012 and 2013 field seasons did not detect significant differences in community composition (MRPP significance of delta = 0.281; Fig. 21a). In contrast, NMDS detected significant differences in the floral composition of fens located on the western side versus the eastern side of Michigan (MRPP significance of delta = 0.007; Fig. 21b). No specific set of species were found exclusively on one side of the state.

DISCUSSION

Model Family 1 was the only family to contain non-ordinated independent variables and failed to produce significant models. A lack of ordination resulted in the transformation of some independent variables but not others, and resulted in exclusion of several variables due to failure to meet test assumptions. This resulted in a more complicated process than necessary, and is contradictory to the goal of this study.

The simplest of the ordinated model families was Model Family 2, which best fit the three metrics of species richness based on adjusted-R^2 values. Model 2 was the best at fitting both total and native richness, and was nearly identical with Model 5 at fitting invasive species richness (R^2_{adj} = 0.33 and 0.36, respectively). The use of ordination in model creation limits the direct application of Model Family 2 to the communities it was developed from, although the methodology is not fen specific. To appropriately apply these models to other communities, the independent variables need to be re-ordinated for the communities of interest.

The first CA axis within Model Family 2 was most influenced, negatively, by fen acreage, Aspen, and Lowland Mixed Forest. Therefore, smaller fens were more likely to have greater species richness compared to larger fens. Fens with Aspen and Lowland Mixed Forest land cover categories within their surrounding buffer zones were likely to have fewer species compared to fens with aspen and lowland mixed forest comprising smaller portions of their buffer zone. The presence of forested land surrounding a fen is likely detrimental to species richness due to loss of open habitat (Kost and Hyde 2009) and encroachment by woody species. Prairie fens were historically exposed to wildfires, hindering shrub and tree domination and increasing ground exposure to light (Kost and Hyde 2009).

Although Model Family 2 contained the best model fit, less than 40% of variation was explained by any model. In attempt to improve the model fit, the two outlying fens were removed and the land cover categories were combined into broader classifications. However, the resultant models were as-predictive or less so than Model Family 2. Therefore, the extra effort did not yield better predictive models (Hawkins 2004). The combination of potentially inaccurate measures of hydrology, not accounting for historic land cover or directly quantifying levels of community disturbance (Pollock et al. 1998), and stochastic community assembly patterns are all factors that could account for the model variation. Fen quality and diversity is widely understood to be highly influenced by its hydrology (Kost and Hyde 2009, Keddy 2010) which was not directly measured in this study. Using readily available GIS layers for DE and DWTD calculations in lieu of directly quantifying fen hydrology could have resulted in inaccuracy, as error in data extrapolation for each layer could compound when combined. Alternatively, as all fens have similar hydrology, the lack of variation could result in hydrology being a non-influential predictor variable.

Land cover immediately surrounding a wetland is understood to have an impact on floral diversity (Houlahan and Findlay 2004, Houlahan et al. 2006). The surrounding land cover was shown to be an influential factor in our models as well, as shown by the influence of several categories in each CA axis. While the current land cover was accounted for in all model variations, historic land cover was ignored, which may also contribute to the model's residuals. Urbanization and agricultural development have resulted in highly fragmented wetlands, altering wetland species ability to disperse (Middleton et al. 2006) and highlighting the importance of accounting for past and present surrounding land cover. A fen located next to a historic agricultural site that has since been abandoned, or the clear cutting of a nearby forest that has since developed into a young/early successional forest or herbaceous openland area can have an influence on current fen diversity. Soil conditions (Turner and Friese 1998), groundwater chemistry (Vitt and Chee 1990, Jeglum and He 1995), and herbivore (Paige and Whitham 1987, Parker and Hays 2005, Parker et al. 2006) or pollinator behavior (Jules and Shahani 2003, Muñoz and Cavieres 2008) may change or be impacted by the historic land cover (Foster et al. 2003). Significant changes may have been made to the landscape since the layer's creation in 2001, resulting in greater prediction variation. The historic presence of agricultural fields (Dupouey et al. 2002) could significantly impact the diversity of fens.

None of the model variations included a separate variable specific to fen disturbance. Some of the prairie fens are surrounded by trails, encouraging hiking and cycling, while others are managed with periodic burning (Michigan Nature Association 2010). Several fens are surrounded by residential buildings, agricultural fields, or bordering a lake used for recreation. Flooding from beavers had occurred in at least one of the surveyed fens. Failure to account for these factors may contribute to the residual of Model Family 2. Quantifying the immediate surrounding land cover should eliminate most of this bias as roads, urban areas, and agriculture were directly measured with the land cover layer. However, quantification of the disturbance to each fen was not directly measured and included in any developed model.

Another likely reason for the low explanatory power may be a highly stochastic nature of community assembly (Tilman 2004), for the fens studied. While traditional community assembly theories favor competition (Kelt et al. 1995), and niche differentiation, stochastic events can be highly influential (Hubbell 2001). Community assembly is not dictated solely by environmental factors (Chase 2007), as measured in the current study, but is also influenced by stochastic dispersal, colonization, and extinction events, which may result in unpredictable patterns of community composition. The potentially stochastic process of community assembly could be the driving force behind the lack of explanatory power from the models.

In accordance with the theory of island biogeography (MacArthur and Wilson 1967) and metacommunity theory (Leibold et al. 2004), both isolation and size of a fen were expected to heavily influence diversity (Bedford and Godwin 2003). While fen size was influential, isolation was not a major influence on any CA axis in any model family. Based on principles of island biogeography, prairie fens that were closer to other fens were expected to have a higher biodiversity compared to fens that were more isolated. Similarly, larger fens were expected to have higher biodiversity compared to smaller fens (Bedford and Godwin 2003). Yet, a significant relationship between either of the isolation metrics used in this study (the distance to the nearest similar community and average distance to the nearest three similar communities) and any of the diversity metrics was not detected for all surveyed fens. Upon removal of outlying fens, positive relationships between total and native species richness and isolation were revealed. As fens become more isolated, total and native species richness increased. This unexpected pattern may be the result of fens relying primarily on seed banks (Jensen 2004) and less on seed dispersal due to the uniqueness of both the fen communities and wetland plants and the difficulty of long distance seed dispersal (Cain et al. 2000). However, many studies have highlighted the importance of seed dispersal to maintain high diversity in wetland communities (van der Valk and Verhoeven 1988, Rossell and Wells 1999, Van den Broek and Beltman 2006), but is not strongly supported by these results.

Spatial autocorrelation for total and invasive species richness : total species richness was not detected. Thus, the species richness of a prairie fen is not influenced by surrounding species rich or poor fens. Similarly, fens surrounded by heavily invaded fen communities are no more likely to contain invasive species than a fen surrounded by communities with no invasive species present. Since there was no spatial autocorrelation detected, and neither isolation metric was not influential within the CA axes, it is assumed that isolation does not have a large influence in fen diversity when all fens are considered. Prairie fens in southern Michigan consequently appear to have limited dependence on dispersal from surrounding similar communities, instead relying on the presence of a seed bank or on the dispersal from the immediately surrounding area for species colonization**.** Yet fens at a more local level likely do function as a metacommunity, supported by significant, positive relationships detected between average distance to three fens with total and native richness for western Michigan fens. The large geographic area surveyed, with considerable gaps between western and eastern fens, is expected to hinder detection of a stronger, state-wide metacommunity link.

Prairie fen size (acreage) did not have a detectable relationship with total or native richness at a state or local level, but had a negative association with invasive species richness. Acreage was also an influential variable in the first axes all of CAs. Thus, I conclude that fen size is influential to the overall diversity of a prairie fen, but is not the driving factor of species richness.

High native richness of fens had no observable negative impact on the presence of invasive species, contradictory to the theory of Biotic Resistance (Elton 1958, Fargione et al. 2003, Tilman 2004). The results of the current study are better explained by the Invasion Paradox described by Fridley et al. (2007) where, at a broad scale, the native - exotic richness relationship is widely observed to be positive (Rout and Callaway 2009). Specifically, neutral processes with variance in colonization and immigration rates (Fridley et al. 2007) are likely contributing to the high invasive species richness in native-rich fens. Many other studies have found that the number of invasive species in a community increase with high levels of diversity (Planty-Tabacchi et al. 1996, Stohlgren et al. 2006) and that established communities may not be able to fully resist invasion (Levine et al. 2002).

Another plausible explanation for the observed increase in invasive species richness with higher native richness could be community stability. Communities with high levels of diversity can have high levels of species turnover and are less stable as a result, where stability is defined as resistant to invasion and the ability of native species to persist (May 1973, Stohlgren et al. 1999). However, this assumes that light and nutrients are not limiting factors, which conflicts with the physical conditions of prairie fen communities (Kost and Hyde 2009). Although prairie fens are classified as "rich fens" due to their calcium-heavy groundwater (Amon et al. 2002), the species found in these communities still have to adapt to stressful and limiting wetland conditions such as inundation and low cation exchange capacity (Mitsch and Gosselink 2007).

Community Assembly

NMDS results indicate that the fens located in eastern Michigan are significantly different in community composition than fens in western Michigan. This could be attributed to the fens spanning a large geographical area, limiting the likelihood of dispersal between fens (Cain et al. 2000), as well as the large difference in number of fens sampled on each side of the state.

In addition to fewer fens in southeastern Michigan surveyed compared to the western side of the state, it is important to note that biodiversity surveys were done via transect (Buckland et al. 2007) and quadrat (Bowles et al. 2005) sampling. As a result, it is possible that all species present in a community were not encountered. This would alter the perceived community composition of each fen. Species-area curves were produced for each fen surveyed in the 2012 field season to ensure that sampling continued past the inflection point, ensuring the majority of species were encountered. The results of these species-area curves determined how many plots and transects were to be surveyed during the 2013 field season. While it would be ideal to survey the entirety of each fen, that method was not reasonably feasible. Therefore, while the NMDS revealed a significant grouping of prairie fens based on their geographical location, it is possible that this is a product of small sample size and incomplete community composition surveys.

CONCLUSION

While it is impossible to replace insights gained by field surveys, they are resource-intensive and not always feasible. The goal of this study was to develop a model that could be used to predict the total, native, and invasive species richness of a prairie fen, aiding in the prioritization of communities and guiding the distribution of limited resources (time, energy, personnel, and money). The CA developed for Model Family 2, the models with the best fit, was most influenced by fen size and the presence of several land cover categories in the surrounding buffer. Larger prairie fens with greater proportions of Aspen and Lowland Mixed Forest within their surrounding buffer were more likely to have fewer species compared to smaller fens with limited Aspen and Lowland Mixed

Forest in the surrounding area. This is likely due to encroachment of woody species on the prairie fen, resulting in loss of suitable open habitat. Larger fens with substantial Aspen and Lowland Mixed Forest within the surrounding buffer should be prioritized for monitoring and management, while smaller, open fens should be less of a management concern. Fen isolation and disturbance had no apparent influence on diversity, and should not be considered primary threats to the communities.

FUTURE WORK

Based on wetland ecology and literature recommendations, model families incorporated prairie fen hydrology, size and shape, isolation, and the surrounding land cover. Future studies should conduct direct groundwater sampling to quantify water table depth and groundwater chemistry, measure peat depth, and account for historical land cover, which could result in models with less variation. All model families developed in this study measured disturbance levels indirectly, as a result of the current land cover surrounding the fen. Disturbance levels should be directly quantified and included as a separate variable, which may result in better model fitting.

LITERATURE CITED

Amon, J.P., C.A. Thompson, Q.J. Carpenter, and J. Miner. 2002. Temperate zone fens of the glaciated Midwestern USA. Wetlands 22: 301 – 317.

Bart, D., M. Simon, Q. Carpenter, and S. Graham. 2011. Historical land use and plant-community variability in a Wisconsin calcareous fen. Rhodora 954: 160-186.

Bedford, B. L. and K. S. Godwin. 2003. Fens of the United States: distribution, characteristics, and scientific connection versus legal isolation. Wetlands 23: 608-629.

Borcard, D., F. Gillet, and P. Legendre. 2011. Numerical Ecology with R. Springer. New York, New York. Pages 115-152.

Bowles, M.J., P.D. Kelsey, and J.L. McBride. 2005. Relationships among environmental factors, vegetation zones, and species richness in a North American calcareous prairie fen. Wetlands 25: 685-697.

Brose, U. 2001. Relative importance of isolation, area and habitat heterogeneity for vascular plant species richness of temporary wetlands in east-German farmland. Ecography 24: 722-730.

Buckland, S.T., D.L. Borchers, A. Johnston, P.A. Henrys, and T.A. Marques. 2007. Line transect methods for plant surveys. Biometrics 63: 989-998.

Cain, M.L., B.G. Milligan, and A.E. Strand. 2000. Long-distance seed dispersal in plant populations. American Journal of Botany 87: 1217-1227.

Clarke, K.R. 1993. Non-parametric multivariate analysis of changes in community structure. Australian Journal of Ecology 18: 117-143.

Crancer, C.J. 2011. Restoration and vegetation response in Kirk Fen, a prairie fen in Ann Arbor, Michigan. University of Michigan, unpublished Master's Thesis, pp. 225.

Crow, G.E. and C.B. Hellquist. 2000a. Aquatic and Wetland Plants of Northeastern North America. Vol. 1. Pteridophytes, Gymnosperms, and Angiosperms: Dicotyledons. University of Wisconsin Press. Madison, Wisconsin. 536 pp.

Crow, G.E. and C.B. Hellquist. 2000b. Aquatic and Wetland Plants of Northeastern North America. Vol. 2. Angiosperms: Monocotyledons. University of Wisconsin Press. Madison, Wisconsin. 456 pp.

Elkie, P.C., R.S. Rempel, and A.P. Carr (1999) Patch Analyst user's manual: a tool for quantifying landscape structure. NWST Technical Manual TM-002

Elton, C.S. 1958. The ecology of invasions by animals and plants. Methuen, London, UK.

Environmental Systems Research Institute; ESRI. 2011. ArcGIS Desktop: Release 10. Redlands, CA.

Farigone, J., C.S. Brown, and D. Tilman. 2003. Community assembly and invasion: An experimental test of neutral versus niche processes. Proceedings of the National Academy of Sciences 101: 8916-8920.

Hawkins, D.M. 2004. Perspective - The problem of overfitting. Journal of Chemical Information and Computer Sciences 44: 1-12.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics 6: 65-72.

Holyoak, M., M.A. Liebold, N. Mouquet, R.D. Holt, and M.F. Hoopes. Metacommunities: a framework for large-scale community ecology. Pages 1-27 *in* Holyoak, M., M.A. Leibold, and R.D. Holt, editors. Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago, IL, USA.

Houlahan, J.E. and C.S. Findlay. 2004. Effect of invasive plant species on temperate wetland plant diversity. Conservation Biology 18: 1132-1138

Houlahan, J., P. Keddy, K. Makkey, and C.S. Findlay. 2006. The effects of adjacent land-use on wetland plant species richness and community composition. Wetlands 26: 79–96

Hovick, S.M., C.J. Peterson, and W.P. Carson. 2012. Predicting invasiveness and range size in wetland plants using biological traits: a multivariate experimental approach. Journal of Ecology 100: 1373-1382.

Jensen, K. 2004. Dormancy patterns, germination ecology, and seed-bank types of twenty temperate fen grassland species. Wetlands 24: 152-166.

Jules, E.S. and P. Shahani. 2003. A broader ecological context to habitat fragmentation: Why matric habitat is more important than we thought. Journal of Vegetation Science 14: 459-464

Keddy, P.A. 2010. Wetland Ecology: principles and conservation. Cambridge, United Kingdom.

Kost, M.A. and D.A. Hyde (2009) Exploring the Prairie Fen Wetlands of Michigan.106pp.

Landis, D.A., A.K. Fiedler, C.A. Hamm, D.L. Cuthrell, E.H. Schools, D.R. Pearsall, M.E. Herbert, P.J. Doran. 2012. Insect conservation in Michigan prairie fen: addressing the challenge of global change. Journal of Insect Conservation 16: 131-142.

Leibold, M.A., M. Holyoak, N. Mouquet, P. Amarasekare, J.M. Chase, M.F. Hoopes, R.D. Holt, J.B. Shurin, R.Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecological Letters 7: 601-613.

Levine, J.M., T. Kennedy, and S. Naeem. 2002. Neighborhood scale effects of species diversity on biological invasions and their relationship to community patterns. In: Biodiversity and Ecosystem Functioning (eds Loreau, M., Naeem, S. & Inchausti, P.). Oxford University Press, Oxford, UK, pp. 114–124.

Locher, Alexandra 2014. Personal Communication.

MacArthur, R.H. and E.O. Wilson. 1967. The theory of island biogeography. Monographs Population Biology. Princeton University Press.

May, R.M. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, New Jersey, USA.

Meyer J.L., L.A. Kaplan, D. Newbold, D.L. Strayer, C.J. Woltermade, J.B. Zedler. 2003. Where Rivers Are Born: The Scientific Imperative for Protecting Small Streams and Wetlands. Washington (DC): American Rivers and Sierra Club.

Michigan Geographic Data Library (1998). Michigan Digital Elevation Model.

Michigan Geographic Data Library (2001). IFMAP/GAP Lower Peninsula Land Cover. MDNR, Forest, Mineral and Fire Management Division.

Michigan Geographic Data Library (2005). Water Table Contours - Montmorency County, Michigan. Groundwater Inventory and Mapping Project.

Michigan Nature Association. 2010. Big city meets prairie fen. http://michigannature.wordpress.com/2010/08/02/big-city-meets-prairie-fen/

Microsoft. 2010. Microsoft Excel computer software. Redmond, Washington: Microsoft

Middleton, B., R. van Diggelen, and K. Jensen. 2006. Seed dispersal in fens. Applied Vegetation Science 9: 279-284.

Miller, B.A. and W.G. Crumpton. 2012. Wetland hydrology class change from prior to European settlement to present on the Des Moines Lobes, Iowa. Wetlands Ecological Management. 20: 1-8.

Mitsch, W.J. and J.G. Gosselink. 2007. Wetlands. Fourth Edition. John Wiley & Sons, Hoboken, New Jersey. pp. 582.

Moran, P.A. 1950. Notes on Continuous Stochastic Phenomena. Biometrika 37: 17-23.

Muñoz, A.A. and L.A. Cavieres. 2008. The presence of a showy invasive plant disrupts pollinator service and reproductive output in native alpine species only at high densities. Journal of Ecology 96: 459-467.

Murray, B.D, S.A. Holmes, C.R. Webster, and J.C. Witt. 2012. Post-disturbance plant community dynamics following a rare natural-origin fire in a *Tsuga canadensis* forest. PLOS One DOI: 10.1371/journal.pone.0043867.

Nekola, J. 1994. The environment and vascular flora of Northeastern Iowa fen. Rhodora. 96: 121-169.

Oaksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P.R. Minchin, R.B. O'Hara, G.L. Simpson, P.Solymos, M.H.H. Stevens, and H.Wagner. 2013. Vegan: Community Ecology Package. R package version 2.0-5. http://CRAN.R-project.org/package=vegan.

Paige, K.N. and T.G. Whitham. 1987. Overcompensation in response to mammalian herbivory: The advantage to being eaten. The American Naturalist 129: 407-416.

Parker, J.D. and M.E. Hays. 2005. Biotic resistance to plant invasions? Native herbivores prefer non-native plants. Ecology Letters 8: 959-967.

Parker, J.D., D.E. Burkepile, and M.E. Hays. 2006. Opposing effects of native and exotic herbivores on plant invasions. Science 311: 1459-1461.

Planty-Tabacchi, A., E. Tabacchi, R.J. Naiman, C.DeFerrari, and H.Décamps. 1996. Invasibility of species-rich communities in riparian zones. Conservation Biology 10: 598-607.

Pollock, M.M., R.J. Naiman, and T.A. Hanley. 1998. Plant species richness in riparian wetlands – a test of biodiversity theory. Ecology 79: 94 – 105.

R Development Core Team (2014) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/

Rempel, R.S., D. Kaukinen., and A.P. Carr. 2012. Patch Analyst and Patch Grid. Ontario Ministry of Natural Resources. Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario.

Reznicek, A.A., E.G. Voss and B.S. Walters. 2011. *Michigan Flora Online*. University of Michigan. Web, http://michiganflora.net\home.aspx.

Rossell, I.M. and C.L. Wells. 1999. The seed banks of a southern Appalachian fen and an adjacent degraded wetland. Wetlands 19: 365-371.

Rout, M.E. and R.M. Callaway. 2009. An invasive plant paradox. Science 324: 734-735.

Ruhfel, B. 2005. Fen restoration and management at Matthaei Botanical Gardens. University of Michigan, unpublished Master's Thesis, pp. 158.

Spieles, J.B., P.J. Comer, D.A. Albert, and M.A. Kost. 1999. Natural community abstract for prairie fen. Michigan Natural Features Inventory, Lansing, MI. 5 pp. (Updated 2010)

Stohlgren, T.J., D. Binkley, G.W. Chong, M.A. Kalkhan, L.D. Schell, K.A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs 69: 25-46.

Stohlegren, T.J., D. Barnett, C. Fllather, P. Fuller, B. Peterjohn, J. Kartesz, and L.L. Master. 2006. Species richness and patterns of invasion in plants, birds, and fishes in the United States. Biological Invasions 8: 427-447.

Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. Proceedings of the National Academy of Sciences 101: 10854-10861.

Turner, S.D. and C.F. Friese. 1998. Plant-mycorrhizal community dynamics associated with a moisture gradient within a rehabilitated prairie fen. Restoration Ecology 6: 44-51.

Van den Broek, T. and B. Beltman. 2006. Germination and seedling survival in fens undergoing succession. Plant Ecology 185: 221-237.

van der Valk, A.G. and J.T.A. Verhoeven. 1988. Potential role of seed banks and understory species in restoring quaking fens from floating forests. Vegetatio 76: 3-13.

Venables, W.N. and B.D.Ripley. 2002. Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0.

Verzani, J. 2014. UsingR: Data sets for the text "Using R for Introductory Statistics". R package version 0.1-18. http://CRAN.R-project.org/package=UsingR.

Wassen, M.J., R. van Diggelen, L. Wolejko, and J.T.A. Verhoeven. 1996. A comparison of fens in natural and artificial landscapes. Vegetatio 126: 5-26.

Wheeler, B.D. and M.C.F. Proctor. 2000. Ecological gradients, subdivisions and terminology of north-west European mires. Journal of Ecology 88: 187-203.

TABLES AND FIGURES

Table 1. Summary of the four metacommunity perspectives (see Holyoak et al. 2005 for more detailed description).

Patch Dynamics	Based on Island Biogeography theory from MacArthur and Wilson (1967). Assumes similar patches, low inter-patch movement, and that the system is not at equilibrium. Species available for colonization based on Mainland species diversity.
Species Sorting	Communities change over environmental gradients, and the impact of abiotic and species interaction are considered. Assumes dissimilar patches, and the system is at equilibrium between colonization of a species and the next disturbance event.
Mass Effect (Source-Sink)	Communities are assumed dissimilar with high inter-patch movement, driven by changes in total mass. The system is not at equilibrium, it is possible to reach equilibrium.
Neutral Model	Based on Neutral Theory (Hubble 2001). Predicts gradual loss of competitive species due to ecological drift among similar patches, with localized inter-patch movement.

Table 2. Observed total, native, and invasive species richness, acreage, and year field survey was conducted for each of the 22 Michigan prairie fens surveyed.

Prairie Fen Site	Species Richness			Acreage	Year Surveyed
	Total	Native	Invasive		
Baker Audubon*	45	40	5	5.9	2013
Bowens Mill Fen	30	27	3	11.5	2012
Butternut Creek*	61	57	4	10.9	2013
Hall Lake Fen	26	23	3	9.6	2012
Hall Lake Fen*	41	39	2	14.7	2013
Hampton Creek*	39	34	5	3.9	2013
Helmer Brook	60	54	6	12.8	2013
Hill Creek (Great Fen)	43	41	2	50.6	2012
Jackson Lake Fen*	34	30	4	11.9	2012
Jephtha Lake Fen*	35	33	2	16.2	2013
Kern Road	28	24	4	3.7	2013
McDonald Lake	50	47	3	1.6	2013
Middleville Fen (Spring Park)*	23	19	4	6.2	2012
Pierce Cedar Creek Institute Fen*	66	60	6	148	2013
Pickerel Lake	58	54	4	12.8	2013
Shaw Lake	11	11	0	3.5	2012
Tiplady Fen	50	47	3	17.7	2013
Trout Lake	46	41	5	2.5	2013
Turner Creek Wetlands	26	24	2	17.1	2012
Waterloo Long Lake Fen	41	38	3	36.2	2013
Whiteman Lake*	48	44	4	13.4	2013
Yankee Springs	41	38	3	34.2	2012

*privately owned prairie fen

Table 3. The mean and standard deviation for each of the 26 land cover categories contained within 250m of each fen buffer (as a percentage of the buffer). Refer to MiGDL (2001) for detailed description of each category.

Land Cover Category	Mean	Standard Deviation
Aspen[1]	0.6	0.73
Emergent Wetland[2]	2.0	1.7
Floating Aquatic[2]	1.2	0.97
Forage Crop[3]	5.0	9.2
Herbaceous Openland[4]	8.3	5.4
High Intensity Urban[5]	0.88	2.5
Low Intensity Urban[5]	1.8	3.4
Lowland Coniferous[1]	1.1	2.2
Lowland Deciduous[1]	13.0	8.4
Lowland Mixed Forest[1]	0.03	0.10
Lowland Shrubland[4]	15.8	10.7
Mixed Non-forested Wetland[2]	1.7	1.3
Mixed Upland Deciduous[1]	13.7	9.8
Non-vegetated Farmland[3]	0.18	0.61
Northern Hardwood Association[1]	8.7	8.4
Oak Association[1]	4.5	3.9
Orchard[3]	0.27	1.04
Pine Association[1]	7.5	9.5
Road[5]	2.2	3.9
Row Crop[3]	2.1	3.5
Sparsely Vegetated[5]	0.02	0.07
Upland Coniferous[1]	0.24	0.39
Upland Deciduous[1]	1.2	2.1
Upland Mixed Forest[1]	2.2	1.9
Upland Shrubland[4]	1.08	0.74
Water[2]	4.5	6.1

[1]: Forested land cover categories
[2]: Wetland land cover categories
[3]: Agriculture land cover categories
[4]: Shrubland land cover categories
[5]: Urban/human - developed land cover categories

Table 4. The three most influential variables and their loading scores for axes explaining at least 5% of the cumulative variation within each Correspondence Analysis. Axes explaining at least 5% of cumulative variation were used as independent variables in multiple regression Model Families 2-9.

	CA Axis 1		CA Axis 2		CA Axis 3	
Model Family 2	Fen Acreage	-14.16	Sparsely Vegetated	-44.06	Lowland Mixed Forest	11.12
	Aspen	-5.93	Non-vegetated Farmland	-42.15	Northern Hardwood	-10.03
	Lowland Mixed Forest	-5.19	High-intensity Urban	-38.32	High-intensity Urban	10.01
Model Family 3	Fen Acreage	-5.91	Sparsely Vegetated	-10.14	Lowland Coniferous Forest	-2.36
	Aspen	-2.48	Lowland Mixed Forest	-9.84	Lowland Mixed Forest	1.73
	Lowland Mixed Forest	-2.18	Non-vegetated Farmland	-9.71	Northern Hardwood	-1.57
Model Family 4	Fen Acreage	-5.9	Sparsely Vegetated	-10.1	Lowland Coniferous Forest	-2.32
	Aspen	-2.48	Lowland Mixed Forest	-9.8	Lowland Mixed Forest	1.82
	Lowland Mixed Forest	-2.21	Non-vegetated Farmland	-9.67	High-intensity Urban	1.64
Model Family 5	Fen Acreage	-14.03	Sparsely Vegetated	-43.65	Lowland Coniferous Forest	-14.39
	Aspen	-5.91	Lowland Mixed Forest	-42.28	Lowland Mixed Forest	12.34
	Lowland Mixed Forest	-5.34	Non-vegetated Farmland	-41.79	High-intensity Urban	11.1

Table 4 Continued

	CA Axis 1		CA Axis 2		CA Axis 3	
Model Family 6	Fen Acreage	-14.03	Sparsely Vegetated	-43.65	Lowland Coniferous Forest	-14.39
	Aspen	-5.91	Lowland Mixed Forest	-42.28	Lowland Mixed Forest	12.34
	Lowland Mixed Forest	-5.34	Non-vegetated Farmland	-41.79	High-intensity Urban	11.1
Model Family 7	Fen Acreage	-5.87	Sparsely Vegetated	-10.08	Lowland Coniferous Forest	-2.30
	Aspen	-2.47	Lowland Mixed Forest	-9.78	Lowland Mixed Forest	1.87
	Lowland Mixed Forest	-2.22	Non-vegetated Farmland	-9.66	High-intensity Urban	1.68
Model Family 8	Fen Acreage	-14.03	Sparsely Vegetated	-43.65	Lowland Coniferous Forest	-14.39
	Aspen	-5.91	Lowland Mixed Forest	-42.28	Lowland Mixed Forest	12.34
	Lowland Mixed Forest	-5.34	Non-vegetated Farmland	-41.79	High-intensity Urban	11.1
Model Family 9	Fen Acreage	-14.03	Sparsely Vegetated	-43.65	Lowland Coniferous Forest	-14.39
	Aspen	-5.91	Lowland Mixed Forest	-42.28	Lowland Mixed Forest	12.34
	Lowland Mixed Forest	-5.34	Non-vegetated Farmland	-41.79	High-intensity Urban	11.1

Table 4 Continued

	CA Axis 4		CA Axis 5	
Model Family 2	-	-	-	-
Model Family 3	-	-	-	-
Model Family 4	-	-	-	-
Model Family 5	Lowland Mixed Forest	24.65	Lowland Coniferous Forest	-14.2
	Forage Crops	-20.53	DE for Surveyed Fen	12.6
	Sparsely Vegetated	17.95	Water	12.58
Model Family 6	-	-	-	-
Model Family 7	-	-	-	-
Model Family 8	-	-	-	-
Model Family 9	-	-	-	-

Table 5. Independent variables included for each multiple regression model family. Model Families 2-9 were ordinated, and their axes scores used as independent variables within the multiple regressions. Model Family 1 was not ordinated; all variables were normally distributed or normal after a Log_{10} transformation (p=0.05)

	Model Family								
	1	2	3	4	5	6	7	8	9
Acreage	X‡	X	X	X	X	X	X	X	X
MPAR	X‡	X	X	X	X	X	X	X	X
Distance to Nearest Fen	X‡	X	X	X	X		X	X	X
Average Distance to Three Fens						X			
DE for Surveyed Fen			X		X	X	X	X	X
DWTD for Surveyed Fen				X	X	X	X	X	X
DE for Nearest Fen							X		X
DWTD for Nearest Fen	X							X	X
Aspen Association		X	X	X	X	X	X	X	X
Emergent Wetland		X	X	X	X	X	X	X	X
Floating Aquatic	X‡	X	X	X	X	X	X	X	X
Forage Crop	X*‡	X	X	X	X	X	X	X	X
Herbaceous Openland		X	X	X	X	X	X	X	X
High-Intensity Urban		X	X	X	X	X	X	X	X
Low-Intensity Urban		X	X	X	X	X	X	X	X
Lowland Coniferous Forest	X‡	X	X	X	X	X	X	X	X
Lowland Deciduous Forest		X	X	X	X	X	X	X	X
Lowland Mixed Forest		X	X	X	X	X	X	X	X
Lowland Shrubland	X‡	X	X	X	X	X	X	X	X
Mixed Upland Deciduous Forest	X	X	X	X	X	X	X	X	X
Non-vegetated Farmland	X*‡	X	X	X	X	X	X	X	X

[*] indicates variables combined into synthetic "Agriculture" variable

[‡] indicates Log10 transformation applied

Table 5 Continued

	Model Family								
	1	2	3	4	5	6	7	8	9
Northern Hardwood Association	X[‡]	X	X	X	X	X	X	X	X
Oak Association		X	X	X	X	X	X	X	X
Pine Association	X[‡]	X	X	X	X	X	X	X	X
Road		X	X	X	X	X	X	X	X
Row Crop	X[*‡]	X	X	X	X	X	X	X	X
Sparsely Vegetated		X	X	X	X	X	X	X	X
Upland Coniferous Forest		X	X	X	X	X	X	X	X
Upland Deciduous Forest		X	X	X	X	X	X	X	X
Upland Mixed Forest		X	X	X	X	X	X	X	X
Upland Shrubland		X	X	X	X	X	X	X	X
Water	X[‡]	X	X	X	X	X	X	X	X

[*] indicates variables combined into synthetic "Agriculture" variable

[‡] indicates Log10 transformation applied

Table 6. Results from multiple regression models. Each model was used to predict each of three dependent variables: (1) fen total species richness, (2) native species richness, and (3) invasive species richness. The variables within Model Families 2-9 were ordinated in separate Correspondence Analysis to standardize them, while the variables in Model Family 1 were not.

	Total Species Richness	Native Species Richness	Invasive Species Richness
Model Family 1	$p = 0.2034$ Adj. $R^2 = 0.3$	$p = 0.2$ Adj. $R^2 = 0.31$	$p = 0.48$ Adj. $R^2 = 0.033$
Model Family 2	$p = 0.01$* Adj. $R^2 = 0.35$ $y = 43.651 - 1.085CA1 + 12.048CA2 + 9.937CA3$	$p = 0.02$* Adj. $R^2 = 0.33$ $y = 40.1522 - 0.8285\ CA1 + 10.9292\ CA2 + 10.3806\ CA3$	$p = 0.02$* Adj. $R^2 = 0.33$ $y = 3.4989 - 0.2562CA1 + 1.119CA2 - 0.4432CA3$
Model Family 3	$p = 0.01$* Adj. $R^2 = 0.34$ $y = 43.5568 - 0.4732CA1 + 2.763CA2 + 1.4633CA3$	$p = 0.02$* Adj. $R^2 = 0.31$ $y = 40.0557 - 0.3663CA1 + 2.5051CA2 + 1.5306CA3$	$p = 0.02$* Adj. $R^2 = 0.33$ $y = 3.50116 - 0.10692CA1 + 0.25793CA2 - 0.06727CA3$
Model Family 4	Adj. $R^2 = 0.34$ $p = 0.01$* $y = 43.453 - 0.4854CA1 + 2.7695CA2 + 1.3615CA3$	Adj. $R^2 = 0.30$ $p = 0.02$* $y = 39.9516 - 0.3794CA1 + 2.5108CA2 + 1.4319CA3$	Adj. $R^2 = 0.33$ $p = 0.02$* $y = 3.50168 - 0.10603CA1 + 0.25871CA2 - 0.07044CA3$

*indicates model significance after correcting for multiple comparisons with the Holms-Bonferroni Method.

Table 6 Continued

	Total Species Richness	Native Species Richness	Invasive Species Richness
Model Family 5	Adj. $R^2 = 0.32$ $p = 0.03$* y = 43.647 - 1.185CA1 + 9.943CA3 + 9.344CA3 - 7.642CA4	Adj. $R^2 = 0.27$ $p = 0.45$ y = 40.1297 - 0.9171CA1 + 9.0557CA2 + 8.383CA3 - 8.3503CA4	Adj. $R^2 = 0.36$ $p = 0.02$* y = 3.5174 - 0.2679CA1 + 0.8878CA2 - 0.9606CA3 + 0.708CA4
Model Family 6	Adj. $R^2 = 0.24$ $p = 0.08$	Adj. $R^2 = 0.21$ $p = 0.11$	Adj. $R^2 = 0.28$ $p = 0.06$
Model Family 7	Adj. $R^2 = 0.21$ $p = 0.07$	Adj. $R^2 = 0.18$ $p = 0.09$	Adj. $R^2 = 0.25$ $p = 0.04$* y = 3.38307 - 0.18906CA1 - 0.23213CA2 - 0.04264CA3
Model Family 8	Adj. $R^2 = 0.34$ $p = 0.02$* y = 43.353 - 1.18CA1 + 12.069CA2 + 7.931CA3	Adj. $R^2 = 0.3$ $p = 0.02$* y = 39.8478 - 0.9284CA1 + 10.9421CA2 + 8.3797CA3	Adj. $R^2 = 0.33$ $p = 0.02$* y = 3.505 - 0.2518CA1 + 1.1272CA2 - 0.4485CA3
Model Family 9	Adj. $R^2 = 0.34$ $p = 0.02$* y = 43.353 - 1.18CA1 + 12.069CA2 + 7.931CA3	Adj. $R^2 = 0.3$ $p = 0.02$* y = 39.8478 - 0.9284CA1 + 10.9421CA2 + 8.3797CA3	Adj. $R^2 = 0.33$ $p = 0.02$* y = 3.505 - 0.2518CA1 + 1.1272CA2 - 0.4485CA3

*indicates model significance after correcting for multiple comparisons with the Holms-Bonferroni Method.

Table 7. Observed and predicted total, native, and invasive species richness for all surveyed prairie fens. Predicted values were derived from Model Family 2 multiple regressions.

Prairie Fen Site	Species Richness		Native Richness		Invasive Richness	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
Baker Audubon*	45	44.6	40	41.1	5	3.5
Bowens Mill Fen	30	36.9	27	33.6	3	3.3
Butternut Creek*	61	44.8	57	41.3	4	3.5
Hall Lake Fen	26	40.7	23	37	3	3.7
Hall Lake Fen*	41	44.2	39	40.7	2	3.5
Hampton Creek*	39	39.8	34	36.2	5	3.5
Helmer Brook	60	43.4	54	39.9	6	3.4
Hill Creek (Great Fen)	43	43.1	41	39.4	2	3.7
Jackson Lake Fen*	34	43.9	30	40.4	4	3.4
Jephtha Lake Fen*	35	44.8	33	41.3	2	3.5
Kern Road	28	37.3	24	33.6	4	3.7
Middleville Fen (Spring Park)*	23	42.7	19	39.1	4	3.6
Pierce Cedar Creek Institute Fen (PCCI)*	66	65.3	60	59.6	6	5.7
Pickerel Lake	58	41.5	54	37.9	4	3.5
Shaw Lake	11	9.2	11	9.3	0	-0.12
Tiplady Fen	50	41.6	47	38	3	3.6
Trout Lake	46	37.1	41	33.3	5	3.8
Turner Creek Wetlands	26	37.7	24	34.4	2	3.3
Waterloo Long Lake Fen	41	42.7	38	39	3	3.7
Whiteman Lake*	48	37.9	44	34	4	3.9
Yankee Springs	41	42.1	38	38.4	3	3.7

*indicates privately owned prairie fens

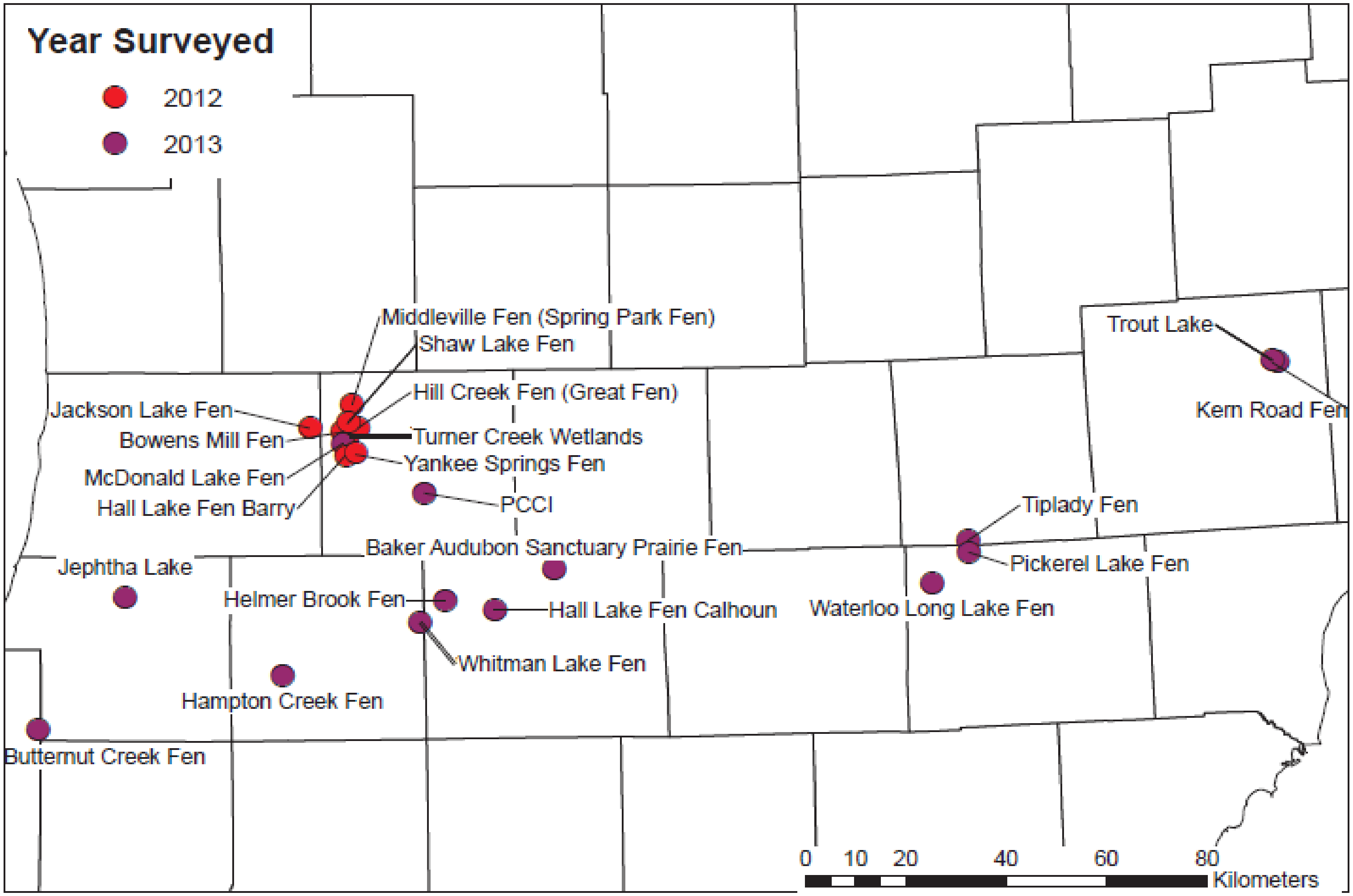

Figure 1. Map of surveyed prairie fen communities.

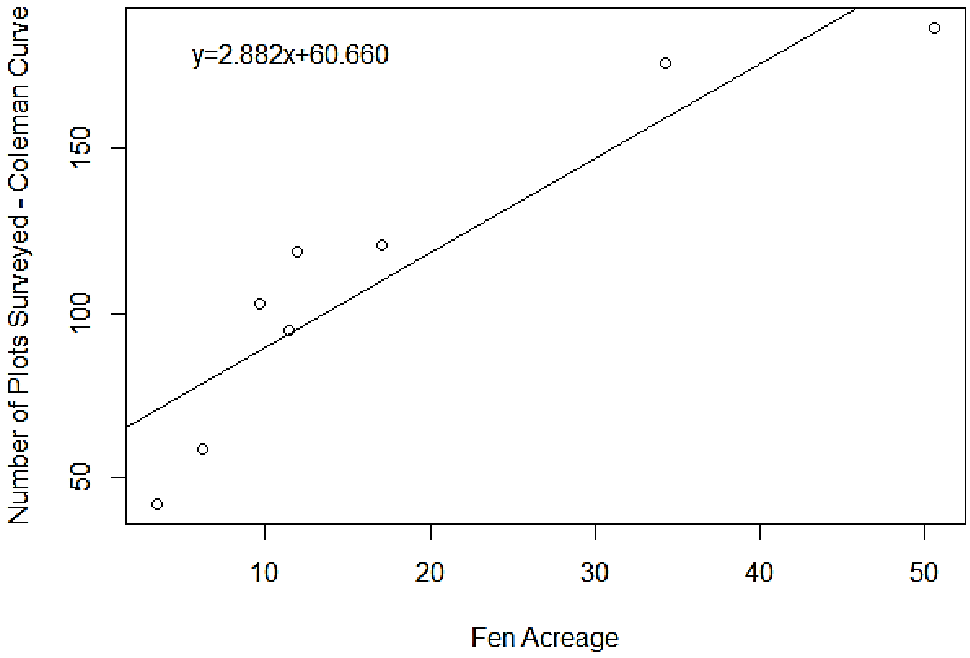

Figure 2. Linear regression between fen acreage and optimal sampling effort (i.e., number of plots that captured all species encountered) based on 2012 field surveys (R^2_{adj}= 0.82, p = 0.001). This equation was used to determine optimal sampling effort (i.e., total number of plots to survey per fen acreage) during the 2013 field season.

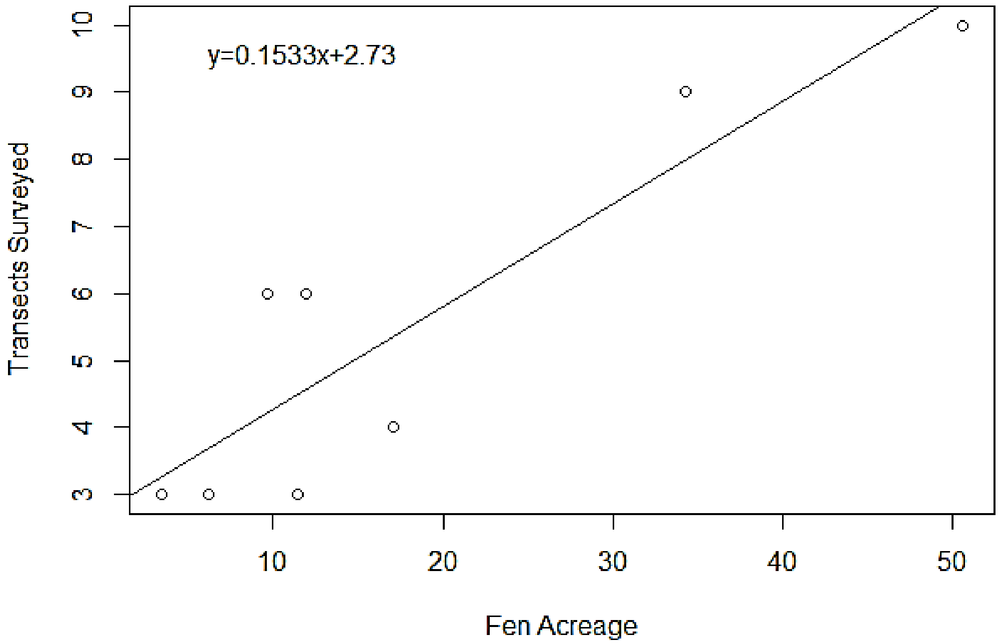

Figure 3. Linear regression based on eight prairie fens surveyed during the 2012 field season (R^2_{adj}= 0.76, p = 0.003). The resultant equation was used to determine the number of transects to be surveyed in each prairie fen during the 2013 field season.

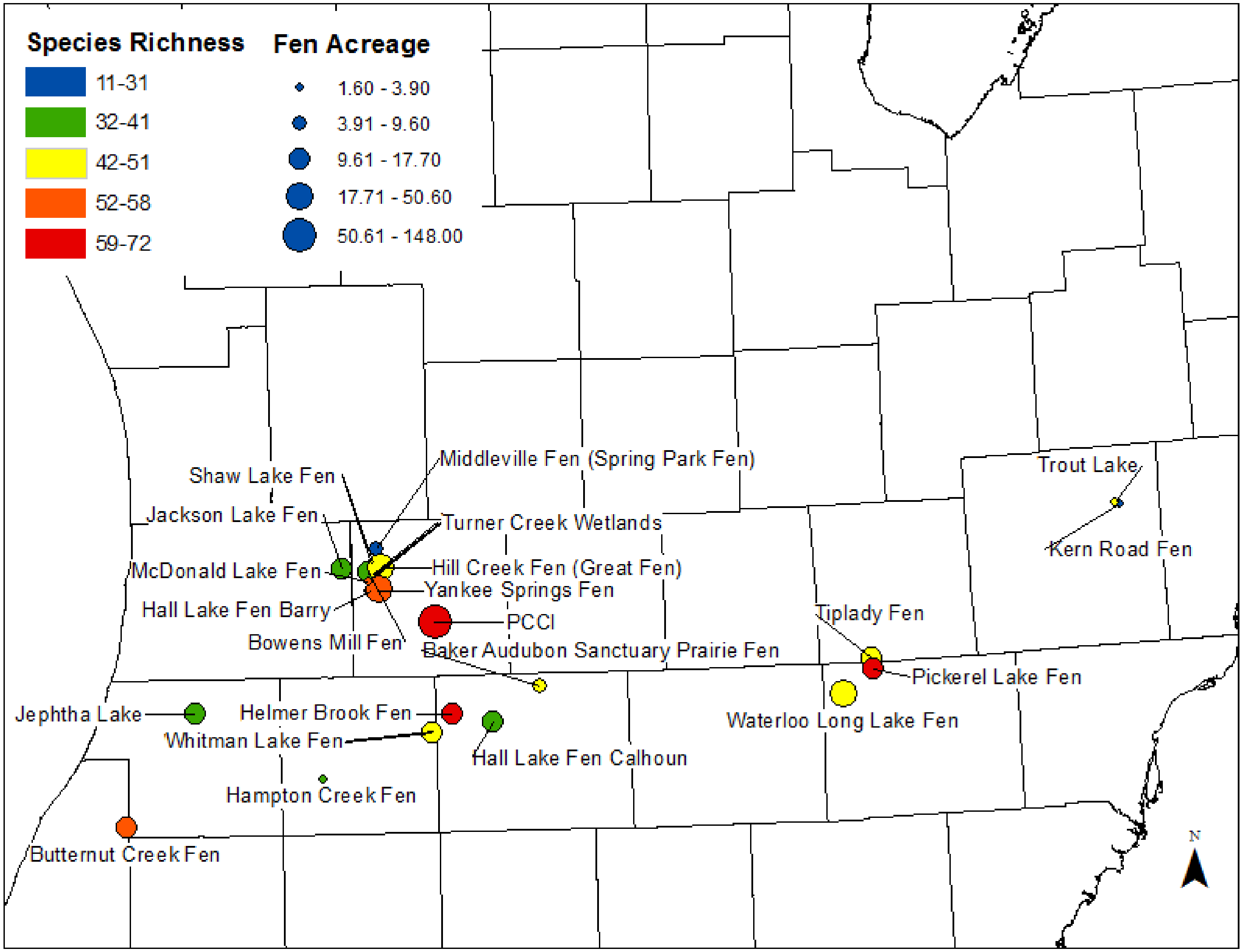

Figure 4. Floral species richness among surveyed prairie fens.

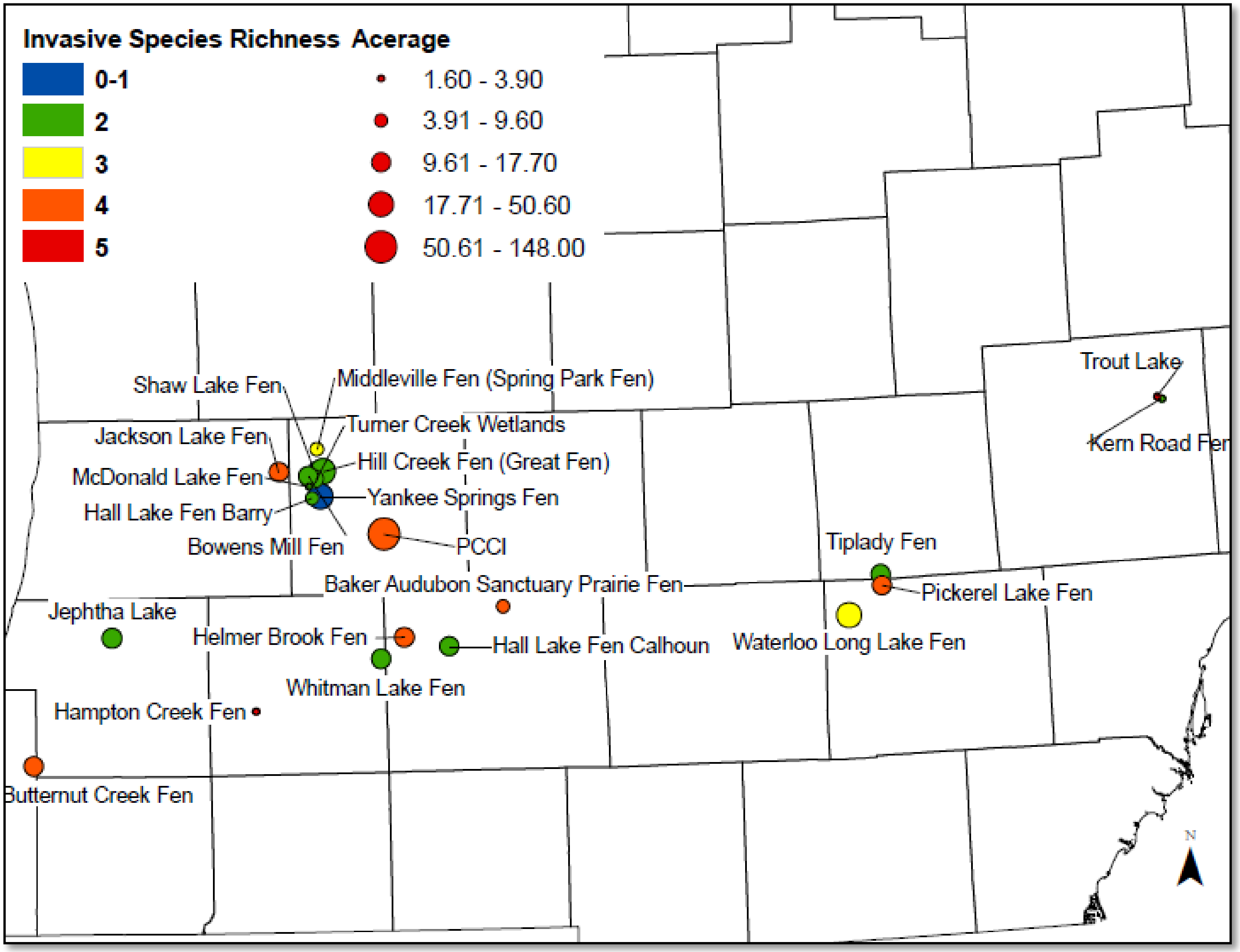

Figure 5. Number of invasive plant species among surveyed prairie fens.

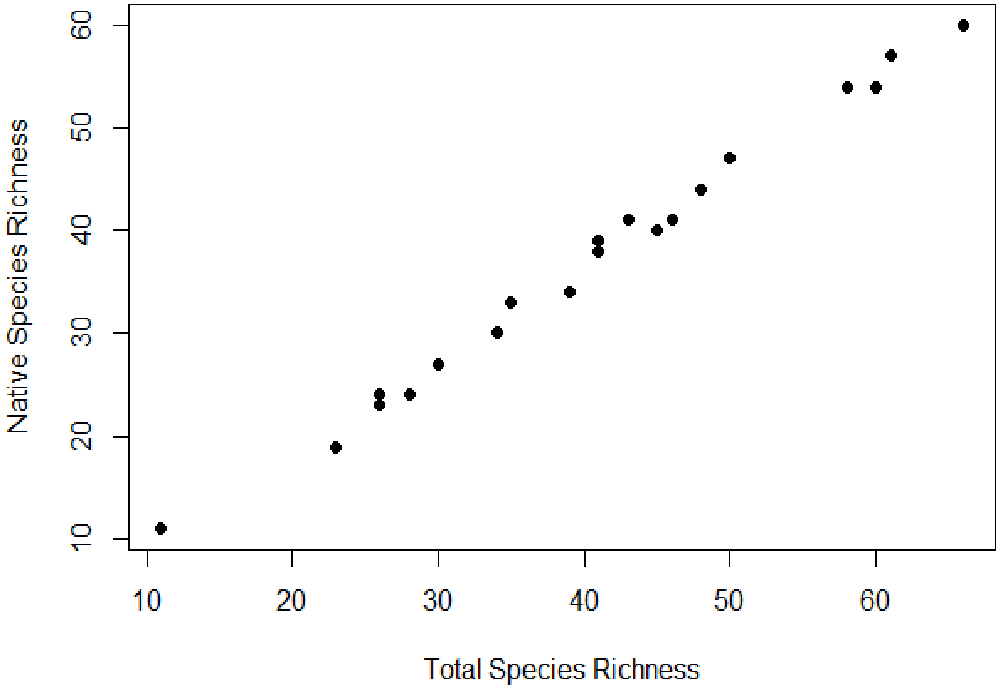

Figure 6. Pearson correlation between the total species richness and native richness for all surveyed prairie fens ($r^2 = 0.98$, $p < 0.001$). The majority of species found in each prairie fen were native species, an average of 37.5 (± 12.9) species per fen of the 41 (± 13.7) total species observed.

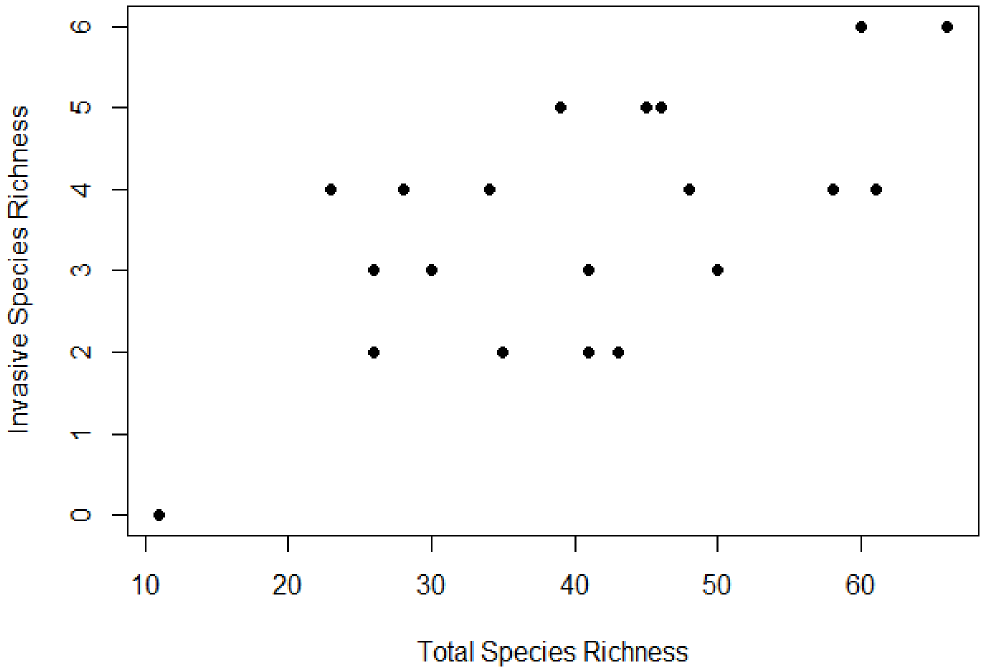

Figure 7. Pearson correlation between the total species richness and invasive species richness for all surveyed prairie fens ($r^2 = 0.40$, $p = 0.002$). Few invasive species (3.5 ± 1.4) were found in the prairie fens compared to the total number of species observed (41 ± 13.7).

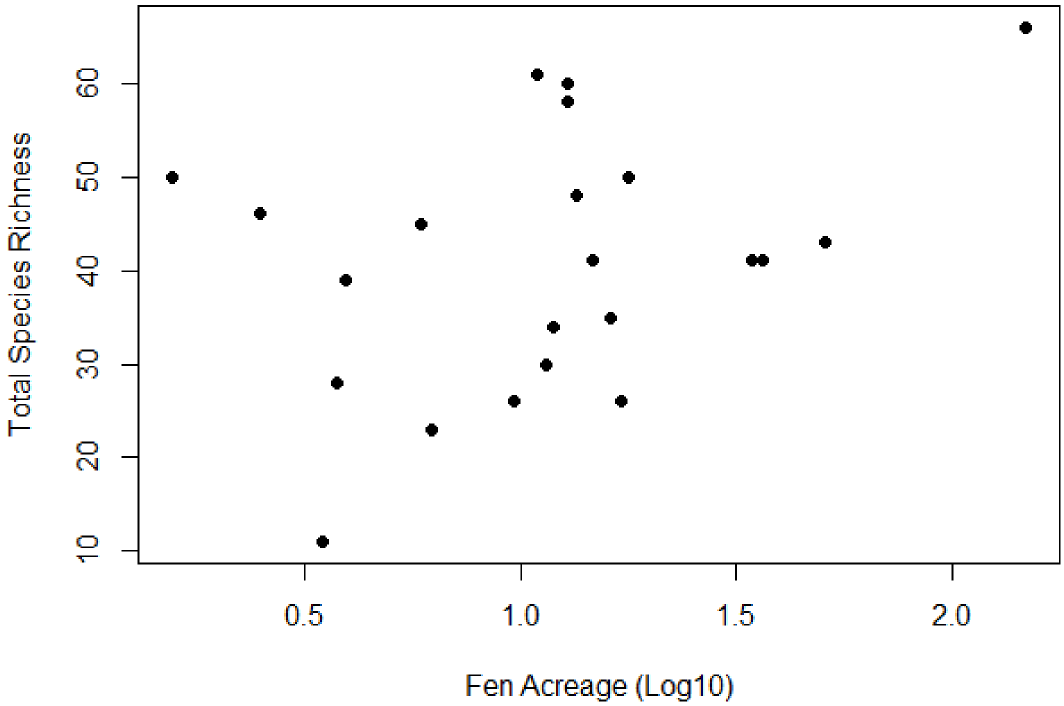

Figure 8. Pearson's correlation between total species richness and acreage of surveyed fens ($r^2 = 0.12$, $p = 0.12$). Lack of a significant relationship indicates species richness is not heavily influenced by fen size.

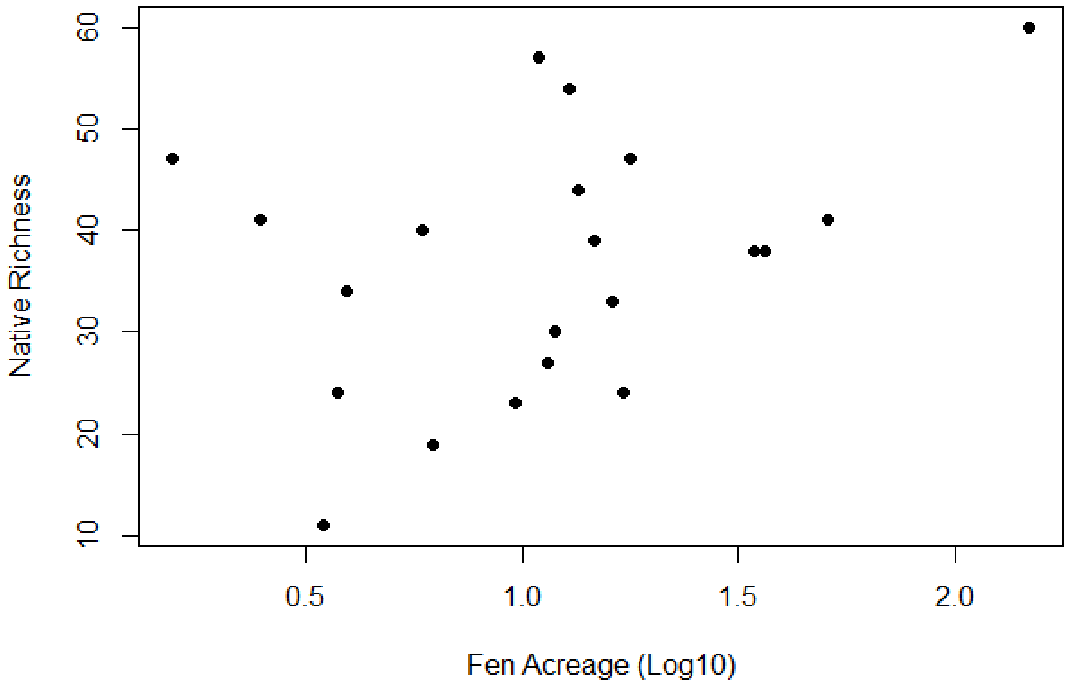

Figure 9. Pearson's correlation between the observed native species richness and acreage of surveyed fens ($r^2 = 0.12$, $p = 0.095$). No significant relationship was detected, indicating that the native richness of a fen is not dependent upon size.

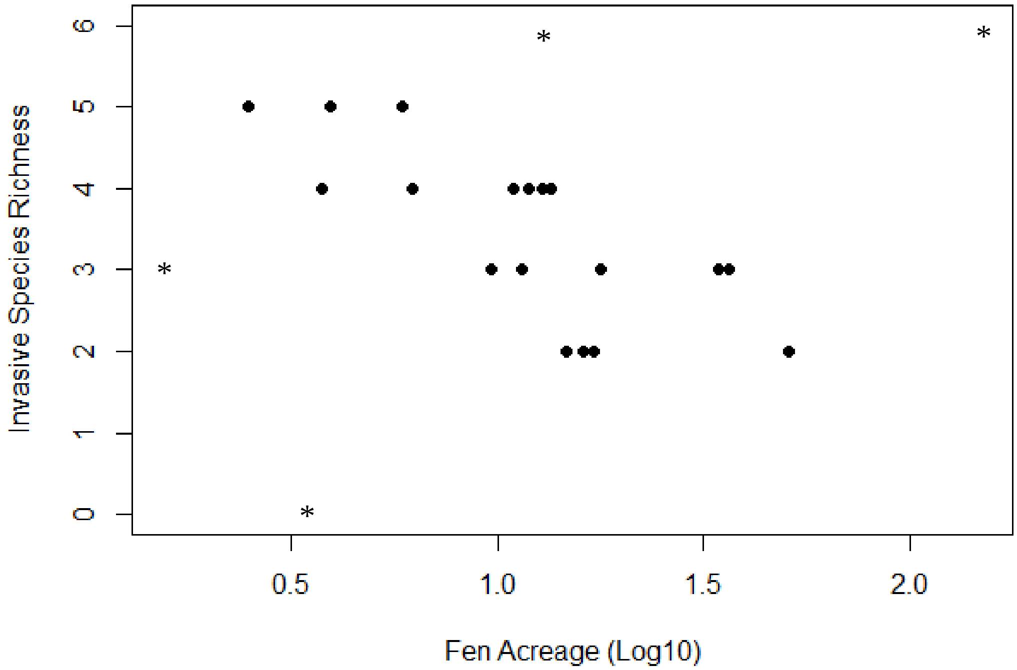

Figure 10. Pearson's correlation between invasive species richness and acreage ($r^2 = 0.55$, $p > 0.001$).

*indicates fens removed for analysis

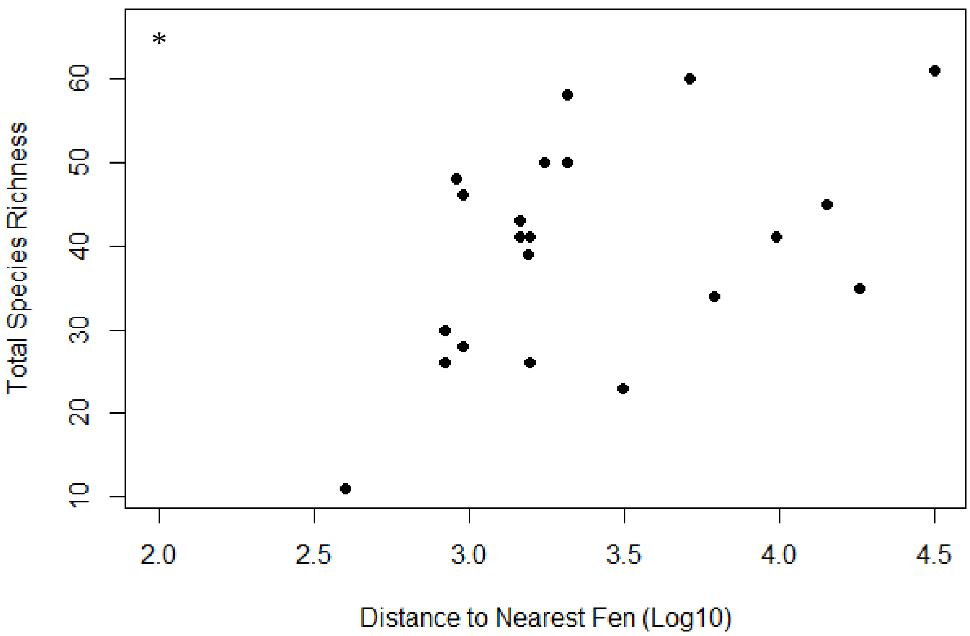

Figure 11. Pearson's correlation between total species richness of the surveyed fens and distance to the nearest fen ($r^2 = 0.19$, $p = 0.05$).

* indicates fen removed from analysis

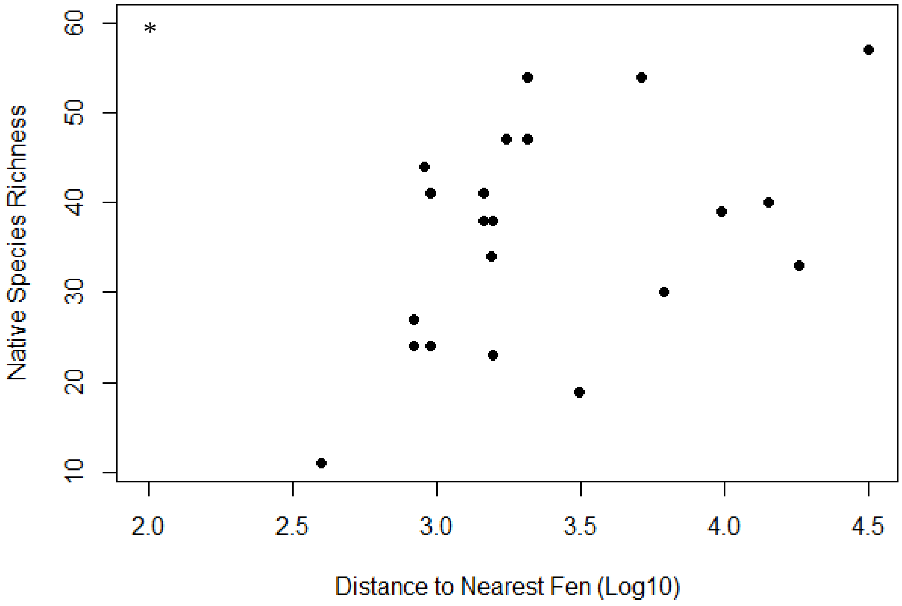

Figure 12. Pearson's correlation between native species richness of the surveyed fens and distance to the nearest fen ($r^2 = 0.19$, $p = 0.05$).

*indicates fen removed from analysis

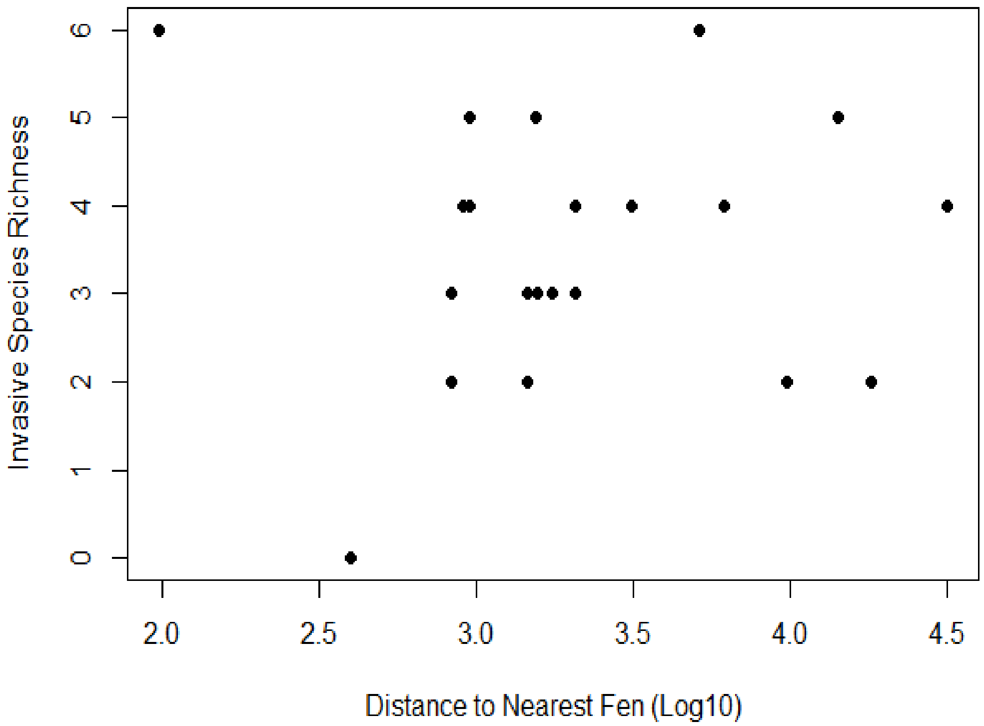

Figure 13. Spearman's Rank Correlation between the number of invasive species observed in the surveyed prairie fens and the distance to the nearest fen ($r^2 = 0.014$, $p = 0.62$).

*indicates outliers removed for analysis

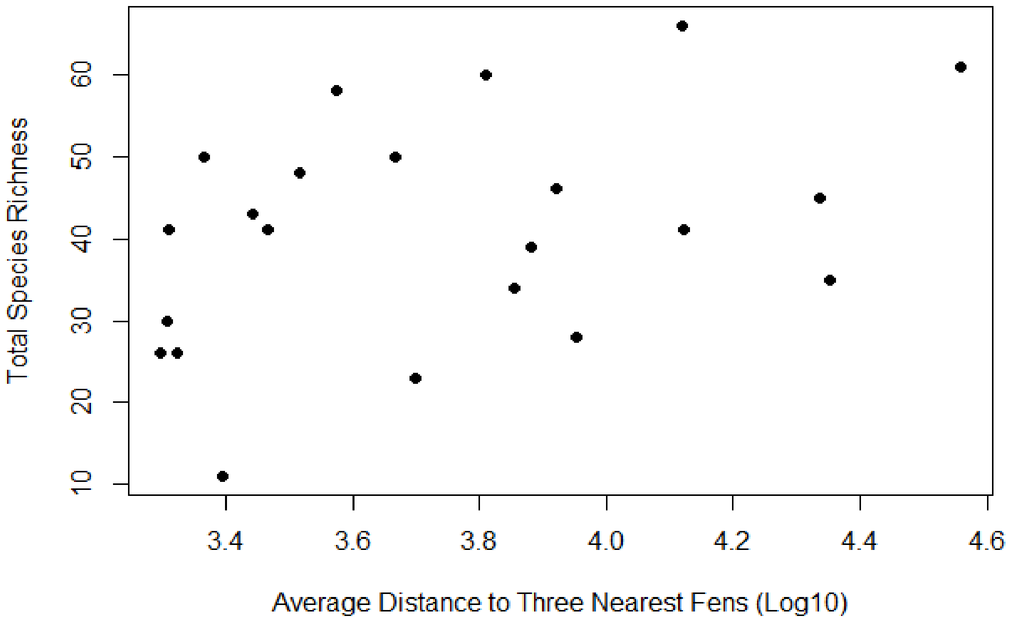

Figure 14. Pearson's correlation between total species richness of surveyed fens and the average distance to the three nearest prairie fens ($r^2 = 0.15$, $p = 0.08$).

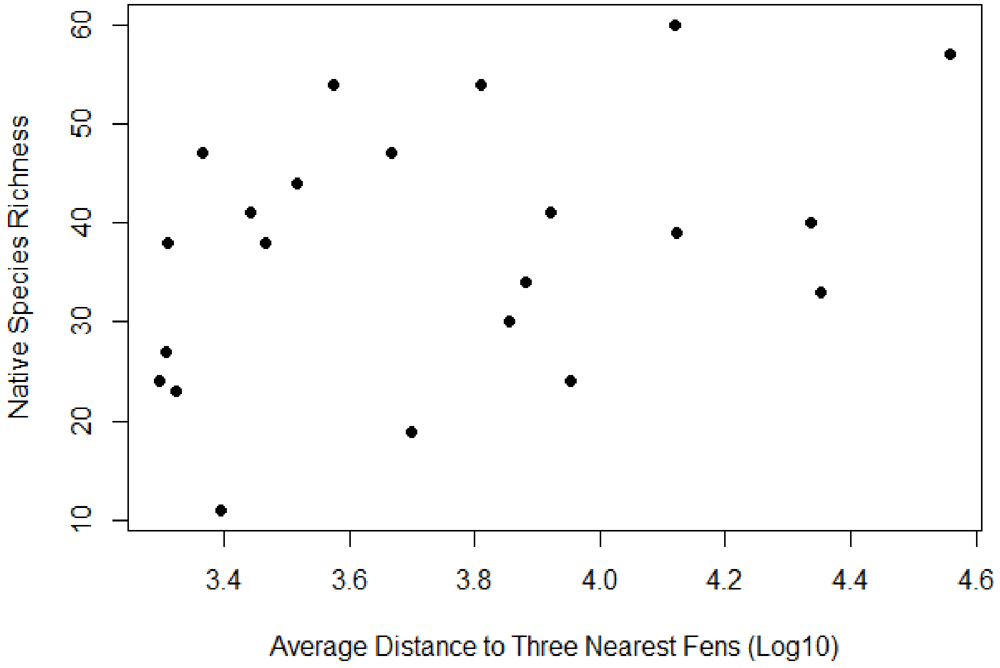

Figure 15. Pearson's correlation between native species richness in prairie fens and the average distance to three nearest fens (Log_{10}) ($r^2 = 0.13$, $p = 0.09$).

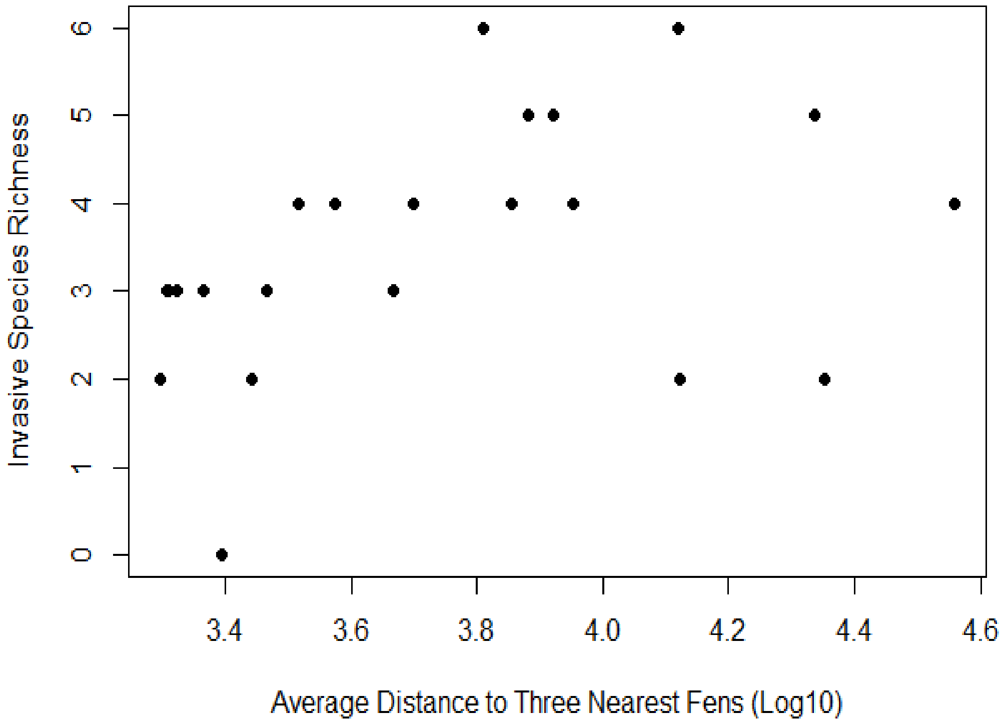

Figure 16. Pearson's correlation between the number of invasive species of surveyed fens and average distance to the three nearest fens (Log_{10}) ($r^2 = 0.17$, $p = 0.06$).

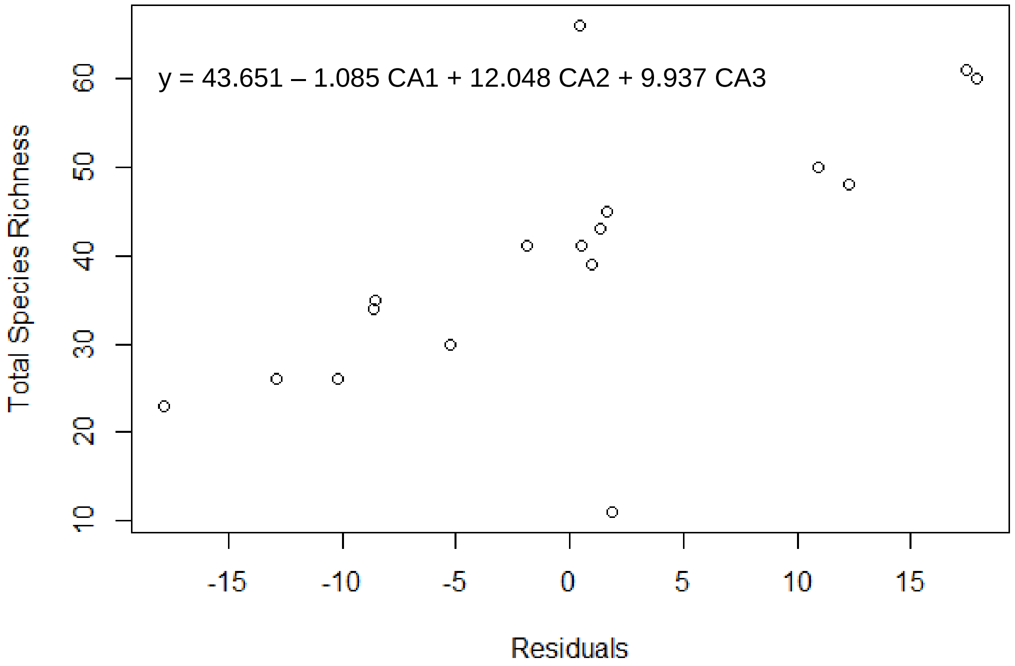

Figure 17. Model 2 total species richness residual plot ($R^2_{adj} = 0.35$, $p = 0.03$*). The model was least able to accurately predict total species richness at either extreme. Two outliers were observed, PCCI with high species richness and Shaw Lake with low species richness.

*Holms-Bonferroni correction for multiple comparisons applied

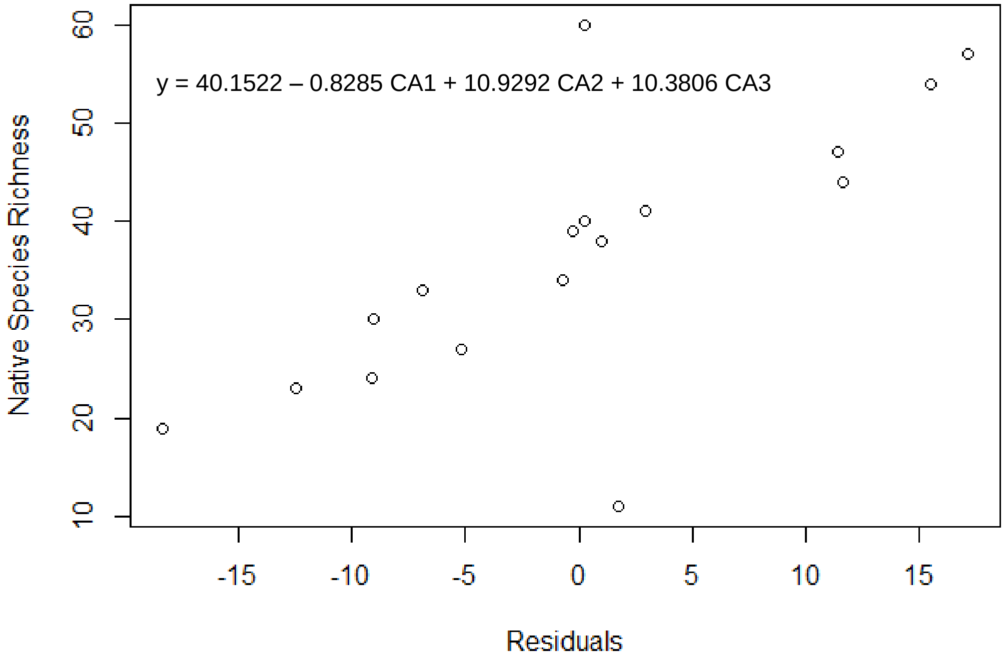

Figure 18. Model 2 native species richness residual plot ($R^2_{adj} = 0.33$, $p = 0.03$*). The model was least able to accurately predict native species richness at either extreme. Two outliers were observed, PCCI with high species richness and Shaw Lake with low species richness.

*Holms-Bonferroni correction for multiple comparisons applied

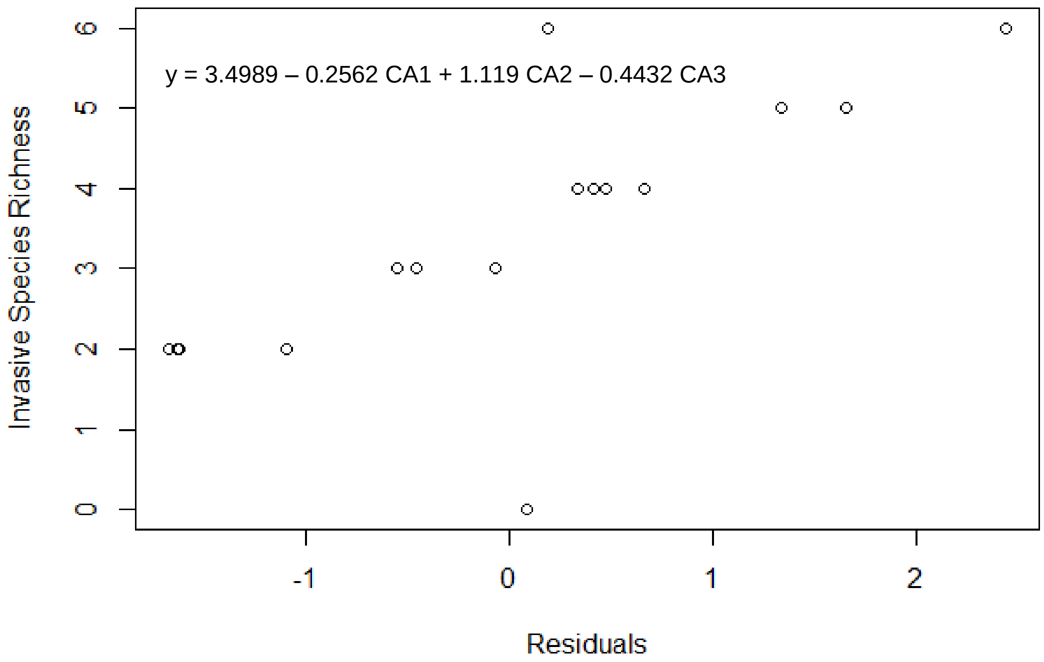

Figure 19. Model 2 invasive species richness residual plot (R^2_{adj} = 0.4, p = 0.03*). The model was least able to accurately predict invasive species richness at either extreme. Two outliers were observed, PCCI with high species richness and Shaw Lake with low species richness.

*Holms-Bonferroni correction for multiple comparisons applied

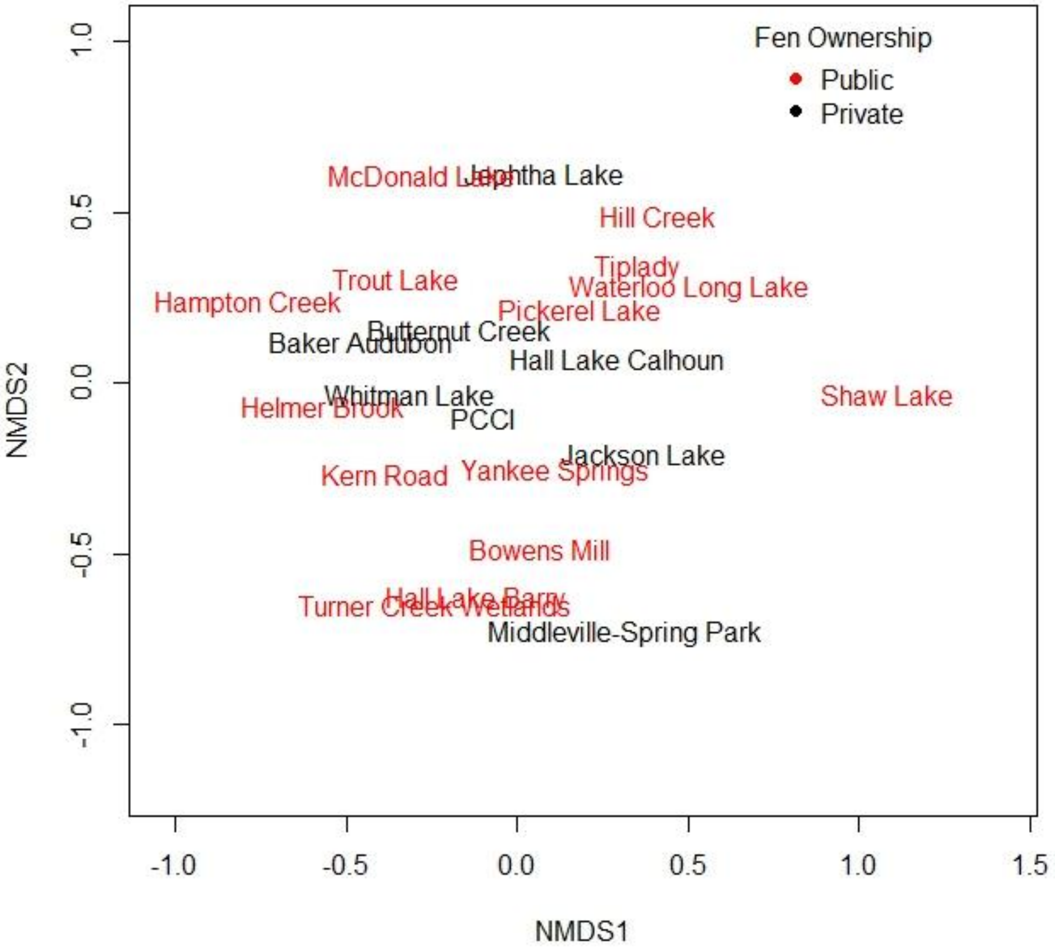

Figure 20. Nonmetric Multidimensional Scaling (NMDS) biplot comparing prairie fen community structure based on public vs. private ownership. NMDS revealed no significant groupings (MRPP significance of delta = 0.466), indicating that prairie fen community structure for publically owned fens are indistinguishable from privately owned fens.

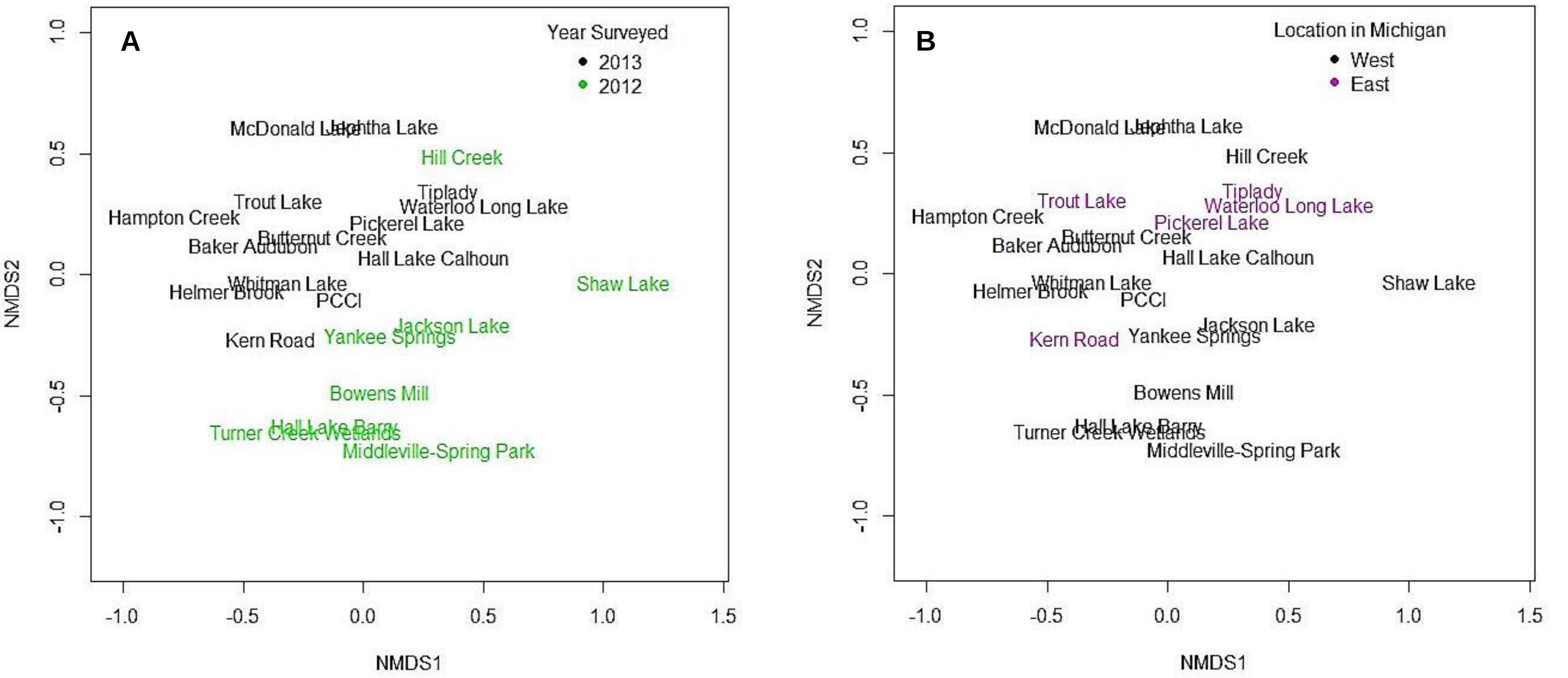

Figure 21. Nonmetric Multidimensional Scaling (NMDS) biplots comparing A) prairie fen community structure based on the year surveyed and B) prairie fen community structure based on the geographical location of the fen. There were no significant groupings present based on the year the fen was surveyed (MRPP significance of delta=0.281). However, there were significant groupings based on the geographical location of the surveyed prairie fens, indicating that community structure of prairie fens in western Michigan are significantly different than prairie fens in eastern Michigan (MRPP significance of delta=0.007).