A MULTISCALE SPATIAL ANALYSIS OF OAK OPENINGS PLANT DIVERSITY WITH IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

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ABSTRACT

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Oak savannas of the Midwestern U.S. are among the most imperiled North American plant communities. The 478-km^2 Oak Openings region of Northwestern Ohio is one of the few landscape-scale savanna systems remaining in the Midwest. Despite conversion of large portions of the Oak Openings for human land uses, the region still supports high levels of floristic diversity. However, regional patterns of Oak Openings plant diversity within the modern landscape are not well understood. My research objectives were 1) to determine the current extent and distribution of Oak Openings plant communities, 2) to quantify multiscale patterns of plant species richness within the context of the surrounding landscape, and 3) to build predictive species distribution models of rare plants to evaluate regional patterns in habitat suitability.

First, using multi-seasonal Landsat images, I determined that <3% of the Oak Openings remains covered by native savannas, prairies, and barrens, while three-fourths of the region has been converted for urban, residential, and agricultural uses. Second, using measures of spatial heterogeneity derived from field data and remote sensing, I develop models of native and exotic plant species richness at two spatial extents and at four ecological levels for the Oak Openings. These models consistently explained more variation in exotic richness (better explained at the larger spatial extent) than in native richness (better explained at the smaller spatial extent). At all ecological levels, percentage of human-modified land cover in the surrounding landscape (negatively correlated with native richness, positively correlated with exotic richness) was a strong predictor of species richness. Finally, I developed species distribution models for nine rare plant species within the Oak Openings region using the Maxent modeling algorithm. Proportional land cover surrounding species occurrences accounted for a large proportion of the predictive power of all models. As percentage of human development increased in the surrounding landscape, the relative habitat suitability for modeled species decreased. From these collective results, I conclude that human-caused disturbances exert a strong influence on Oak Openings species richness patterns. It is therefore important for resource managers to consider landscape context when implementing conservation actions for the Oak Openings region.

This work is dedicated to my sons Benjamin and Zachary;
and to my grandfather, Edward C. Schetter (1913 – 2010),
who’s hard work, perseverance, and dedication to family
saw him through 97 years of life on this Earth

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GENERAL INTRODUCTION

The Oak Openings region of northwestern Ohio is widely regarded as one of the most floristically diverse land areas in Ohio, despite long-term conversion of large portions of the region for agricultural and urban land uses. The region harbors examples of remnant oak savanna and prairie communities now considered globally imperiled, and numerous plant species now considered rare in Ohio. Since the early twentieth century, the Oak Openings has attracted the attention of researchers from numerous colleges and universities and has long been the focus of conservation efforts by state and regional conservation organizations including Metroparks of the Toledo Area, The Nature Conservancy, and Ohio Department of Natural Resources. However, to date there has not been an attempt to systematically evaluate plant diversity in the Oak Openings at a regional scale within the context of the modern, human-dominated landscape. The following work is intended to address this gap in knowledge for the Oak Openings region, and to inform conservation and management of temperate oak savanna ecosystems.

This dissertation is presented in three main research chapters followed by a chapter of summary conclusions. Each of the first three chapters was written as a stand-alone document. The purpose of the first chapter was to determine the current extent and distribution of plant communities across the Oak Openings region by developing a land cover map identifying native communities within the context of the surrounding landscape. This chapter was written with coauthor Karen V. Root for submission to *Natural Areas Journal* and was subsequently published in the April 2011 issue of this journal (Vol. 31, pgs. 118–130). The aim of the second chapter was to quantify regional patterns of native and exotic plant species richness for savanna, prairie and barrens communities at multiple spatial scales within the context of the surrounding landscape using a combination of field data, remotely sensed data, and landscape pattern metrics.

This chapter was written with coauthors Timothy L. Walters and Karen V. Root for submission to the journal, *Environmental Management*. The aim of the third chapter was to build predictive species distribution models for multiple rare Oak Openings plant species using readily available environmental data, and to combine these models into a single multispecies habitat suitability model for the selected species. This chapter was formatted as a report to be submitted to Metroparks of the Toledo Area with the intent that model results and the supporting GIS data will be used to assist the organization with implementing conservation planning and land management strategies. This chapter may subsequently be reformatted for submission to a peer-review scientific journal.

CHAPTER I

ASSESSING AN IMPERILED OAK SAVANNA LANDSCAPE IN NORTHWESTERN OHIO USING LANDSAT DATA

ABSTRACT

Land cover change caused by humans represents a major threat to the long term viability of natural areas. It is important to accurately classify and map existing natural areas so that this threat can be fully assessed within a given landscape. Availability of free orthorectified Landsat images through the U.S. Geological Survey provides a potentially valuable tool to evaluate human impacts to natural landscapes. We performed a supervised classification of multi-seasonal Landsat images to test the limits of using these images for mapping mixed landscapes at regional to local scales and to assess land cover changes within the Oak Openings region of Northwestern Ohio. Overall accuracy of our 15-class land cover map was 60% and 69% using traditional and fuzzy set analysis respectively. Overall map accuracy improved to 72% and 79% for traditional and fuzzy set analysis respectively using a more broadly defined 7-class land cover map. Accuracy of individual classes varied considerably, although classes made up of larger patches typically achieved greater accuracy. Human-dominated land cover classes currently occupy 73% of the Oak Openings region while <3% of the region remains covered by native savannas, prairies and barrens. Currently 10% of the region is permanently protected, including nearly all remnant savannas and wet prairies >1 ha. Our findings highlight the utility of using Landsat images to evaluate mixed-use landscapes at regional scales but demonstrate the limitations of using these images at local scales.

INTRODUCTION

Land cover change caused by human land use increasingly threatens the long-term viability of natural areas across the globe (Foley et al. 2005). By the end of the 21st century, land use change is projected to have a larger global impact on the biodiversity contained within natural areas than any other factor (Chapin et al. 2000). In order to assess the impacts of land use / land cover change on natural systems, it is imperative that natural areas are accurately classified and mapped within the context of other existing land cover types at a scale usable by local land managers and conservation planners.

Satellite-based remotely sensed images are widely used as the basis for developing vegetation-based land cover maps (Fassnacht et al. 2006). Use of remote sensing technology for natural areas mapping offers several advantages over traditional field-based mapping techniques, such as greater efficiency and cost effectiveness per mapping unit, expanded spatial and temporal coverage, and the ability to frequently update existing maps (Xie et al. 2008). Additionally, multispectral sensors which detect electromagnetic radiation beyond visible wavelengths of light provide information on the composition of map features not available using conventional aerial photographs or field-based observations. However, the initial cost of obtaining remotely-sensed images along with the complexity of necessary image processing methods may deter potential end users from otherwise using this technology.

In late 2005, the United States Geological Survey (USGS) helped to address this issue when it began offering geodetically accurate, orthorectified Landsat images over the Internet at no charge (Tucker et al. 2004, NASA 2010). Landsat is the longest running satellite-based imagery program, providing multispectral data for much of the Earth’s surface every 16 days with a maximum image resolution of 30 meters. In recent years, Landsat data have been used to effectively assess and map a variety of natural community types at regional scales (Townsend and Walsh 2001, Wang and Moskovits 2001, McCarthy et al. 2005, Domaç and Süzen 2006, Stuart et al. 2006). However, we did not find any peer-reviewed studies evaluating the use of Landsat data at local scales (that could be used, for example to assess individual management units). The availability of free geodetically accurate Landsat data combined with relatively low-cost image processing software provides land managers and conservation planners with an opportunity to assess the status of many at-risk natural communities, such as Midwest oak savannas.

At the time of European settlement, oak savannas covered large portions of the north central United States (i.e., Midwest oak savannas). These fire-maintained communities persisted within a broad transition zone between the Great Plains and Eastern Deciduous Forest (Nuzzo 1986, Anderson 1998). Following settlement, Midwest oak savannas became heavily fragmented as a result of fire exclusion, agriculture, and urbanization (Nuzzo 1986, Grossmann and Mladenoff 2007). Today, Midwest oak savannas are considered critically endangered in the U.S. (Noss et al. 1995), as are temperate savannas worldwide (Hoekstra et al. 2005). Although high quality oak savannas currently comprise only ~0.02% of their historic extent throughout the Midwest (Nuzzo 1986), they continue to sustain high levels of biodiversity relative to other upland communities (Leach and Givnish 1999).

We conducted this study to map and assess the current status and distribution of remnant oak savanna communities across a human-dominated landscape in Northwestern Ohio known as the Oak Openings region. Our objectives were 1) to test the limits of using Landsat images for land cover classification and mapping at regional and local scales; and 2) to identify the current extent, distribution, and protection status of historic Oak Openings plant communities in relation to the surrounding matrix of human-dominated land cover types. It was our intention to use relatively simple classification and mapping protocols that could be easily replicated by other practitioners without the need for detailed vegetation surveys or more advanced image processing / GIS capabilities.

STUDY AREA

The 478 km^2 Oak Openings region of Northwestern Ohio (41^o 25' to 41^o 44' N; 83^o 34' to 84^o 2' W) features one of only a few landscape-scale oak savanna systems remaining in the Midwestern United States (Figure 1). The Oak Openings lies within the Lake Plains physiogeographic region of Ohio's western Lake Erie basin (Braun 1989). Topography is level to gently rolling, ranging from 180 to 220 meters elevation. Soils are post-glacial beach sand (depth of <1 m to >2 m) deposited over clay till; depth to bedrock (limestone and dolomite) is typically >6 m (Stone et al. 1980). Climate is humid continental; mean monthly temperatures range from -10 ^oC to 23 ^oC; mean annual precipitation is 81 cm (USDA-NRCS 2010). Historically, the region was characterized by a system of post-glacial beach ridges with oak savannas persisting on the ridge tops and wet prairies persisting within the lowland interdunal areas (Moseley 1928, Brewer and Vankat 2004). Following European settlement, the region's natural communities were systematically altered through drainage, agriculture, fire exclusion, and urban expansion from the Toledo metropolitan area (Mayfield 1976). As with other Midwest oak savanna remnants, the Oak Openings remains a local biodiversity hotspot harboring 143 state endangered, threatened, or potentially threatened plant species (ODNR Division of Natural Areas and Preserves 2008), 24 state endangered, threatened, or 'of concern' animal species (ODNR Division of Wildlife 2008), one federally endangered species (Karner blue butterfly, *Lycaeides melissa samuelis*), and five globally vulnerable or imperiled plant communities (alliances; Faber-Langendoen 2001) within an area that collectively represents <0.5% of Ohio's total land area.

METHODS

Classification system

We consulted with local plant ecologists and Ohio Natural Heritage Program staff to develop a hierarchical land cover classification system that 1) was consistent with U.S National Vegetation Classification standards (Comer et al. 2003, Jennings et al. 2009), and 2) could be feasibly mapped under the constraints of a 30m Landsat image pixel. The resulting classification system shown in Table 1 consisting of 11 natural / seminatural and four cultural classes is based largely on physiognomic characteristics rather than floristic composition, falling roughly within the mid level hierarchy described by Jennings et al. (2009). Based on field observations made during training site selection and map accuracy assessment, we were also able to describe predominant floristic and/or human features associated with each class (Table 1).

Landsat image selection

Using the USGS Global Visualization Viewer (USGS 2009), we selected three Landsat-5 TM scenes acquired on 12 November 2005, 3 March 2006, and 24 June 2006 for Path 20, Row 31 containing our entire study area. We selected Landsat-5 TM images over Landsat-7 ETM+ images to avoid additional image processing required to fully utilize ETM+ images after the loss of the on-board scan line corrector (SLC) in May 2003 (NASA 2010). We chose to evaluate multi-seasonal images (fall, spring, summer) for our map classification because previous research has shown that this improves classification accuracy for mapping both forests (Townsend and Walsh 2001) and grasslands (Peterson et al. 2002). We selected these three images over other available images because 1) they occurred within a relatively narrow 7-month timeframe, 2) featured 0% cloud cover for the entire study area, and 3) received Level 1 Terrain Corrected (L1T) image processing by USGS. All L1T images include radiometric, geometric, and precision correction (NASA 2010), which allowed us to avoid potentially time-consuming and costly image preprocessing prior to use. According to the Ground Control Points (GCP) Residual Report downloaded with each scene, average Root Mean Square (RMS) error among ground control points for all three scenes was < 4.8m (< 0.16 pixel). All images were downloaded in GeoTif image format projected to Universal Transverse Mercator coordinates (UTM Datum WGS84).

Supervised image classification

We performed a supervised classification of the multi-seasonal images of our study area using ER Mapper 6.4 (Earth Resources Mapping, Inc., San Diego, CA). We selected a maximum likelihood classification model with equal prior probability and general typicality to assign each 30-m image pixel to a single land cover class. Although atmospheric correction was not performed by USGS for the images obtained, we simulated atmospheric correction by applying dark object subtraction (i.e., subtraction of the smallest reflectance value in a given spectral band from all pixels in that band; Chang et al. 2008) to all images prior to classification. We performed the supervised classification using spectral bands 1-5, and 7 from each of the three selected TM scenes so that 18 total spectral bands were used for the classification, each with 30-m pixel resolution. This required a minimum of $n + 1$ (where n = number of spectral bands) or 19 total pixels (1.71 ha) of each training class (ER Mapper 6.4). The thermal infrared band (band 6) from each image was omitted from analysis due to its reduced 60-m pixel resolution. Training sites were delineated using ArcGIS 8.3 (ESRI, Redlands, CA) and imported into ER Mapper 6.4 prior to analysis.

Through preliminary analyses, we found that croplands were especially difficult to classify due to seasonal changes in type and phenology of planted crops. To bypass this problem, we did not use training sites for croplands while performing the supervised classification. Instead, after completing supervised classification of the image data into 14 classes without croplands, we overlaid a cropland "mask" to the 14-class image to produce the final 15-class image. This mask was developed from publicly available croplands data for the study area (USDA 2007), which we visually inspected and corrected using 0.3-m resolution orthophotos acquired in 2006 (OSIP 2009). After applying the croplands mask, the final 15-class image was clipped to an area representing the historic extent of the Oak Openings region (Brewer and Vankat 2004).

Training site selection

In September 2007 we conducted field surveys throughout the study area to select representative training sites for the various natural / seminatural land cover classes. For each site visited, we took representative site photos, mapped their location using a handheld GPS receiver (Garmin GPS III+), and recorded qualitative site descriptions with information on canopy coverage and characteristic species for each vegetation stratum. We evaluated additional training sites using high-resolution (0.15 to 0.3 m) color orthophotos for classes that could be easily interpreted on the orthophotos such as Upland Coniferous Forests, Perennial Ponds, and the various cultural classes. For the final classification, we used 106 training sites for 14 classes totaling 356 ha (average of 8 training sites and 25 ha per class).

Accuracy assessment

We assessed the accuracy of the final land cover map by comparing a sample of individual map pixels of each land cover class to specific points on the ground to produce a traditional “crisp” classification where each point on the ground represents only a single land cover class (Foody 2002). We compiled the results into a standard confusion or error matrix to evaluate “producer’s accuracy” (corresponding to errors of omission) and “user’s accuracy” (corresponding to errors of commission) for the final map. Because traditional “crisp” accuracy assessment requires that each sample location is assigned to only a single class, areas of ambiguity such as ecotones between plant communities are not represented. Additionally, the magnitude of misclassification errors cannot be judged from the final confusion matrix (Gopal and Woodcock 1994). Therefore we also evaluated map accuracy using fuzzy set theory by applying the ‘linguistic scale’ of Gopal and Woodcock (1994) to each sample pixel on the ground for its agreement with each land cover class as follows:

1. *Absolutely Wrong*: The answer is unacceptable.
2. *Understandable but Wrong (Not Right)*: Not a good answer. There is something about the site that makes the answer understandable, but there is clearly a better answer. This answer would pose a problem for a user of the map.
3. *Reasonable or Acceptable Answer*: Maybe not the best possible answer but it is acceptable; this answer does not pose a problem to the user if it is seen on the map.
4. *Good Answer*: Would be satisfied to find this answer given on the map.
5. *Absolutely Right*: No doubt about the match.

Townsend and Walsh (2001) provide a more detailed description of this approach for classifying vegetation-based land cover maps.

We conducted a stratified random sampling of 25 map pixels for each land cover class (375 total pixels) using the individual 30m pixel as the sampling unit. To ensure a reasonable distribution of samples across the entire study area, we set the minimum distance between sample points to 150 meters (5 pixels). In order to boost sample size without increasing substantially the amount of work required for field validation, we chose to also evaluate the four neighboring pixels adjacent to each accessible sample pixel following Nusser and Klaas (2003). Pixels located within the training sites used for the supervised classification were excluded from selection. Prior to pixel validation, we assigned random identification numbers to each sample location to prevent prior knowledge from biasing the results.

We initially evaluated sample pixels using high resolution (0.3m) color orthophotos acquired in 2006 (OGRIP 2006). For samples that we could confidently identify using orthophotos (e.g. Croplands, Dense Urban, Residential / Mixed, Perennial Ponds, Upland Coniferous Forests) we conducted no ground validation. For all other samples, we visited each pixel cluster (i.e., the central pixel and its 4 neighbors) on the ground using a handheld GPS receiver and high resolution orthophoto maps. We conducted ground visits from September through December 2009 to evaluate structural vegetative characteristics. For each pixel cluster, we took representative site photos, recorded qualitative site descriptions with information on canopy coverage and characteristic species for each vegetation stratum, and assigned class membership using both “crisp” and “fuzzy” classes for each of the five pixels within the pixel cluster. We also noted any obvious changes on the ground compared to the 2006 orthophotos.

Regional assessment

To assess land cover changes in the Oak Openings region since European settlement, we compared the final land cover map with GIS data obtained from historic vegetation maps of the study area (Brewer and Vankat 2004). We evaluated the current protection status for each natural / seminatural land cover class using GIS shape files compiled for all permanently protected parks and preserves within the study area (Figure 1). We used ArcGIS 8.3 to compile per-class data on total area, number of discrete landscape patches, mean patch area, and related landscape characteristics.

RESULTS

Map accuracy assessment

The completed land cover map of the Oak Openings region is shown in Figure 2. Of the 1875 pixels selected to assess the map's accuracy, 1392 pixels (74%) were evaluated. A total of 710 pixels (38%) were evaluated on the ground, 682 pixels (36%) were evaluated from orthophotos, while 483 pixels (26%) were not evaluated because they could not be reliably classified from orthophotos and occurred on private properties where permission was not secured to inspect them on the ground.

Overall accuracy of the final 15-class map using a traditional "crisp" classification was 60% (Table 2). Kappa (a measure of agreement due to chance, from 0 – 1, where 0 indicates agreement entirely due to chance, while 1 indicates true agreement between mapped classes and reference points) was 0.56. Producer's accuracy ranged from 21% for sand barrens to 90% for upland savannas. User's accuracy ranged from 11% for sand barrens to 96% for perennial ponds. Overall map accuracy improved to 69% using the 'RIGHT' function of Gopal and Woodcock (1994), where fuzzy membership is based on the frequency that each mapped class is assigned a score of 3, 4, or 5 on the linguistic scale for a given field validation site. Accuracy of individual classes using the 'RIGHT' function ranged from 16% for sand barrens to 99% for perennial ponds.

By moving up one level in the land cover classification hierarchy (seven total classes), overall map accuracy improved to 72% with a kappa of 0.65 (Table 3). Producer's accuracy ranged from 56% for shrublands to 90% for savannas while user's accuracy ranged from 45% for savannas to 96% for water. Overall map accuracy using the 'RIGHT' function increased to 79% with individual class accuracy ranging from 47% for savannas to 99% for water.

Status of Oak Openings region

According to the final land cover map, since European settlement 73% of the Oak Openings region has been converted to human-dominated land uses while only 27% of the region remains classified as natural or seminatural (Figure 2, Table 4). Nearly 40% of the region has become built-up for urban / residential uses concentrated in the northeastern portion of the region (closest to the city of Toledo's urban core). Cultivated croplands (primarily row-crops of corn and soybeans) make up 27% of the region, concentrated in the southwestern portion of the region. Three-fourths of the Oak Openings' 13000 ha of remaining natural / seminatural lands, concentrated in the central portion of the region, were classified as forests and woodlands.

Savannas, wet prairies, upland prairies, and sand barrens, which are of greatest interest to local conservation organizations, have faced severe declines since European settlement (Table 4). According to the final land cover map, these areas collectively represent <3% (1400 ha) of the region's land area. Wet prairies appear to have faced the sharpest declines. Once occupying over one-quarter of the region (Brewer and Vankat 2004), wet prairies now represent <0.1% (40 ha) of the Oak Openings' land area. Based on our field observations, many of the nearly 200 ha of wet shrublands identified on the land cover map are likely former wet prairies now dominated by dense stands of the invasive shrub glossy buckthorn (*Rhamnus frangula* L.).

Currently 10% (4608 ha) of the Oak Openings region's land area has been permanently protected as parks and preserves (Figure 1, Table 4). Seventy one percent (3283 ha) of all parks and preserves were classified as forests / woodlands, including 627 ha of non-native coniferous forests planted on public lands in the mid twentieth century for soil stabilization. An additional 16% (725 ha) of all parks and preserves were classified as cultural land cover types of little or no conservation interest. Although parks and preserves currently contain 39% of all areas classified as savannas, two thirds of all wet prairies, and 17% of all upland prairies and barrens, these classes collectively represent just 7% of all conservation lands in the region. When evaluating the status of larger patches on the landscape ($\geq$ 1 ha), nearly all areas classified as oak savannas or wet prairies are contained in parks and preserves, while the majority of areas classified as upland prairies or sand barrens remain unprotected (Table 4).

DISCUSSION

Map Evaluation

We developed a working land cover map of the Oak Openings region with two primary objectives in mind. First, we wanted to test the limitations of our relatively simple classification and mapping procedure to evaluate regional- to local-scale mixed-use landscapes using widely available Landsat data. The Oak Openings provided an ideal test case to assess mapping accuracy at both regional and local scales because it consists of a heterogeneous mix of human dominated, forested and grassland communities. Our detailed 15-class map of the Oak Openings achieved an overall map accuracy of 60% using traditional "crisp" classification and 69% using fuzzy classification. Overall accuracy of the map improved to 72% (crisp) and 79% (fuzzy) when we considered the next higher level in the classification hierarchy. Although overall classification accuracy would likely have improved by including ancillary data (e.g. soils, topography, geology) into our model (Domaç and Süzen 2006), we wanted to keep our methods as simple as possible so that they could be applied by other practitioners with limited remote sensing or modeling capabilities.

There are currently no universally accepted standards for evaluating map accuracy (Xie et al. 2008). A target of 80% overall map accuracy is often used as an acceptable standard for vegetation-based land cover maps (Smith et al. 1999). However, evaluating a map's accuracy is not a clear-cut process because it depends largely on the intended use of the map (Crist and Deitner 2007). The error matrix provides important information for end users to assess whether the map meets their intended purpose. In the case of the Oak Openings land cover map, higher levels of accuracy were achieved when evaluating forests and woodlands (86% producer's accuracy and 81% user's accuracy; Table 3) compared to prairies and meadows (60% producer's accuracy and 56% user's accuracy; Table 3). This disparity in map accuracy may be attributed at least in part to patch size. Mean patch size of forests and woodlands was 3.7 ha compared to a mean patch size of 0.5 ha for grasslands and meadows (derived from Table 4). Smaller patches are especially susceptible to map pixel misregistration and field validation / GPS errors.

We were particularly interested in evaluating the accuracy of the final Oak Openings land cover map in relation to classes of specific conservation interest to likely map users. For savannas, 27 out of 30 field validation sites were correctly classified (90% producer's accuracy, Table 2). However, 33 field validation sites that were not savannas were incorrectly classified as savannas resulting in a user's accuracy of 45% (Table 2). This suggests that map users will likely find most existing savannas within areas shown as savannas on the map but that many areas shown as savannas on the map are also likely to include other unrelated classes. An appropriate use of the map in this case would be to select areas for more targeted ground surveys to find potential restoration sites or previously unidentified savanna remnants.

The map generally performed poorly for discriminating among upland prairies and sand barrens, (Table 2). Again, patch size relative to the minimum mapping unit (i.e., a 30-m Landsat pixel) was a major contributing factor. Mean patch size of upland prairies and sand barrens was roughly the area of two map pixels (0.18 ha). The map was much better at classifying wet prairies where the mean patch area was equivalent to roughly 4 map pixels (0.36 ha). Perhaps another explanation for the map's inability to accurately classify native prairie types is that many native prairies may be too degraded from invasion of exotic cool-season species and are therefore spectrally too similar to other human-influenced cover types. For example, only one out of 23 upland prairie field validation sites and none of the 28 sand barren sites where assigned a fuzzy class membership score of 5 (absolutely right) compared to 18 out of 57 (31%) of wet prairies. The appearance of large clusters of Eurasian meadow pixels located in close proximity to upland prairie and sand barren classes, especially in the central portion of the region, lends some support to this hypothesis.

Our findings generally suggest that classification of multi-seasonal Landsat images provides a useful assessment tool for evaluating mixed-use landscapes at regional scales, especially those characterized by medium to large patches. However, Landsat data is probably unsuitable for evaluating local scale areas such as individual management units, especially when these areas are dominated by small patches (< 0.2 ha). Although use of fuzzy classification techniques improved overall map accuracy, our results highlight the challenge of using discrete classes for mapping vegetation occurring along a continuum of community types. It is worth noting that high-resolution (<4 meter) satellite imagery (e.g. QuickBird, IKONOS) is commercially available which could improve map accuracy, especially for troublesome vegetation types and small patches on the landscape (*refer to* Xie et al. 2008). However, these images are likely cost prohibitive to many practitioners, especially for use at regional scales. We believe that our simple approach to evaluating Landsat data offers an inexpensive option for assessing areas where detailed land cover maps are lacking provided that the limitations of the 30-m Landsat pixel are considered.

Implications for Midwest Oak Savannas

Our second major objective in completing this study was to assess the current status and distribution of historic plant communities in the Oak Openings region. Even taking into account various sources of map error, our results clearly demonstrate the large magnitude and extent of loss faced by native savannas, prairies and barrens. Using a pre-settlement map of the region (Brewer and Vankat 2004), we estimate that collectively these communities have declined 96% since European settlement of the region. In contrast, the extent of native forest communities (i.e., swamp forests, floodplain forests, and upland deciduous forests) across the region has declined by only an estimated 20% when compared to the historic extent of oak woodlands and floodplain forests at the time of European settlement (Brewer and Vankat 2004). This phenomenon is almost certainly due to the loss of natural fire regimes since European settlement, allowing historic savanna and prairie communities to revert to woodlands and forests through natural succession.

In recent years, local conservation organizations have focused much of their funding on acquisition of unprotected natural areas (Abella et al. 2007). Currently, 10% of the region’s land area has been secured as parks and preserves. While additional protection of natural areas within the region is certainly encouraged, the final land cover map shows that there are essentially no large remnant savannas, sand barrens or wet prairies remaining on unprotected lands. Although the majority of existing upland prairies remain unprotected in the region, further examination shows that the only large patches of unprotected upland prairie occur within the bounds of Toledo Express Airport. Based on the known extent of pre-settlement Oak Openings communities (Brewer and Vankat 2004), there likely remain numerous opportunities to restore prairies and savannas within areas now classified as forests. Our findings clearly reinforce the need for continued ecological restoration and management throughout the Oak Openings, especially within existing parks and preserves. It is our intent that the final land cover map is used by local land managers and conservation planners as a decision making tool to assist with development of a collaborative conservation and restoration plan for the Oak Openings region.

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Table 1. Oak Openings region land cover classification. Class descriptions are based on field observations by the authors in September 2007 and September - December 2009.

Class type (7)	Land Cover Class (15)	Class Description
NATURAL / SEMINATURAL		
Forests / Woodlands	Swamp Forests	Semi-permanent to seasonally-inundated closed canopy deciduous swamps and flatwoods on poorly drained soils; typically dominated by *Quercus palustris* Muench and/or *Quercus bicolor* Willd. *with Acer rubrum* L. common in the subcanopy.
	Floodplain Forests	Closed to open canopy deciduous forests on poorly to moderately well drained soils within floodplains (often broad and poorly defined due to flat topography); near stream channels or ditched waterways, characterized by large *Populus deltoides* Marsh., *Platanus occidentalis* L., and dead / dying *Fraxinus* sp. Broader floodplains often characterized by young even-aged stands of *Acer saccharinum* L., *Populus* sp., *Fraxinus* sp., and *Quercus* sp.
	Upland Deciduous Forests	Closed canopy mesic to dry forests (also a few open canopy woodlands) on moderately to well drained soils on slopes and ridges; typically dominated by *Quercus velutina* Lam., *Quercus alba* L. and/or *Quercus rubra* L.; understory characterized by *Sassafras albidum* (Nutt.) Nees*, Prunus serotina* Ehrh.*, Acer rubrum* and low growing *Vaccinium* sp.; herbaceous layer often characterized by continuous cover of *Carex pensylvanica* Lam.
	Upland Coniferous Forests	Mostly monospecific plantations of *Pinus* sp. with few adventive examples. Did not occur in the Oak Openings prior to European settlement (Moseley 1928).
Savannas	Upland Savannas	Open canopy stands of *Quercus velutina* and/or *Quercus alba* (with some *Quercus palustris* Muenchh. and *Quercus coccinea* Muenchh.) on well drained soils with a well developed shrub and/or herbaceous layer typically dominated by warm-season grasses (primarily *Andropogon gerardii* Vitm. and *Sorghastrum nutans* (L.)Nash.) and forbs.
Shrublands	Wet Shrublands	Semi-permanent to seasonally-inundated shrublands on poorly drained soils. Most observed sites were dominated by dense monospecific stands of *Rhamnus frangula* L. A few sites featured a more open shrub layer characterized by *Salix* sp., *Cornus* sp., *Cephalanthus occidentalis* L.*,* and *Physocarpus opulifolius* (L.) Maxim. and a well developed herbaceous layer characterized by *Carex* sp.

continued

Table 1. Continued.

Prairies & Meadows	Wet Prairies	Semi-permanent to seasonally-inundated prairies on poorly drained soils. Trees nearly to entirely absent, shrubs typically sparse or absent, herbaceous layer dominated by *Carex* sp., and/or *Calamagrostis* sp.
	Upland Prairies	Mesic to dry sand prairies characterized by warm-season grasses (typically Andropogon gerardii, Sorghastrum nutans, and Schizachyrium scoparium (Michx.) Nash) and forbs. Trees nearly or entirely absent, shrub layer typically sparse or absent.
	Sand Barrens	Early successional herbaceous communities on sand blowouts and recently-disturbed well drained soils; bare sand typically exceeds 50% of total ground cover. Characterized by *Schizachrium scoparium, Andropogon virginicus* L*.,* *Aristida* sp., annual forbs and drought tolerant species. Trees nearly or entirely absent. Shrub layer (characterized by *Rubus* sp. when present) typically sparse or absent. Many sites are also heavily influenced by Eurasian species.
	Eurasian Meadows	Mesic to dry cool-season grasslands and oldfields dominated by Eurasian species such as *Festuca* sp., *Poa* sp., and *Bromus* sp. Unmanaged sites often characterized by invasive shrubs such as *Rosa multiflora* Thunb. and *Eleaegnus umbellata* Thunb.
Water	Perennial Ponds	Permanent excavated ponds, impoundments, and former sand mines; not associated with natural surface water drainage; did not occur prior to European settlement.
CULTURAL		
Built-Up	Dense Urban	Areas dominated by large tracts of asphalt, parking lots, flat rooftops and other impermeable surfaces.
	Residential / Mixed	Areas of closely associated residential structures, mowed lawns and shade trees (typically all found within a 30-m map pixel); also includes roadways and maintained ditches where trees are absent.
Vacant	Turf / Pasture	Large areas of frequently mowed turf grasses such as cemeteries, athletic fields and golf courses; livestock pastures.
	Croplands	Characterized by large fields of row crops, primarily corn and soybeans.

Table 2. Error matrix and accuracy for the 15-class Oak Openings region land cover map. The RIGHT function evaluates whether the mapped class is acceptable for a given reference site using the linguistic scale of Gopal and Woodcock (1994).

		Actual Land Cover (from reference sites)																
	Class	SF	FF	UD	UC	US	WS	WP	UP	SB	EM	PP	DU	RM	TP	CR	Row Total	User's Accuracy (%)	RIGHT (%)
	SF	**28**	10	16		1	6	1						1			63	44	59
	FF	4	**38**	28	1		14	5		1	9	4		9	1		114	33	40
	UD	7	4	**66**		1		3			1			5			87	76	83
	UC	5	7	5	**56**						1			3			77	73	78
	US		2	8		**27**	1		6	3	11				2		60	45	47
	WS	2	2			1	**43**	4						6			58	74	83
Classified Land Cover (from map)	WP						5	**36**			8	2		3			54	67	72
	UP		3	3			1		**7**	7	13			4	4	1	43	16	23
	SB								1	**6**	4		3	16	11	16	57	11	16
	EM			1	1		2	1	5	1	**39**			10	13	1	74	53	59
	PP		1									**79**		2			82	96	99
	DU									7		17	**61**	19	1	6	111	55	68
	RM	1	3	7	9		5			2	6	4	17	**175**	26	12	267	66	79
	TP			1				6	4	1	3			32	**41**	10	98	42	64
	CR							1			9			5	3	**129**	147	88	91
Column Total		47	70	135	67	30	77	57	23	28	104	106	81	290	102	175	**1392**	**Overall**	
Producer's Accuracy (%)		60	54	49	84	90	56	63	30	21	38	75	75	60	40	74		**60%**	**69%**
Kappa = 0.56																			

SF=Swamp Forests	US = Upland Savannas	SB=Sand Barrens	RM=Residential/Mixed
FF=Floodplain Forsts	WS=Wet Shrublands	EM=Eurasian Meadows	TP=Turf/Pasture
UD=Upland Deciduous Forests	WP=Wet Prairies	PP=Perennial Ponds	CR=Croplands
UC=Upland Coniferous Forests	UP=Upland Prairies	DU=Dense Urban	

Table 3. Error matrix and accuracy for the Oak Openings region land cover map using seven classes. The RIGHT function evaluates whether the mapped class is acceptable for a given reference site using the linguistic scale of Gopal and Woodcock (1994).

		Actual Land Cover (from reference sites)								User's	
									Row	Accuracy	
	Class	For	Sav	Shr	Pra	Wat	Bui	Vac	Total	(%)	RIGHT (%)
Classified Land Cover (from map)	For	**275**	2	20	21	4	18	1	341	81	87
	Sav	10	**27**	1	20			2	60	45	47
	Shr	4	1	**43**	4		6		58	74	83
	Pra	8		8	**128**	2	36	46	228	56	58
	Wat	1				**79**	2		82	96	99
	Bui	20		5	15	21	**272**	45	378	72	80
	Vac	1			24		37	**183**	245	75	87
Column Total		319	30	77	212	106	371	277	**1392**	**Overall**	
Producer's Accuracy (%)		86	90	56	60	75	73	66		**72%**	**79%**
Kappa = 0.65											

For=Forests & Woodlands
Sav=Savannas
Shr=Shrublands
Pra=Prairies & Meadows
Wat=Water
Bui=Built-up
Vac=Vacant

Table 4. Summary of land cover map results for the entire Oak Openings region and lands permanently protected as parks and preserves.

	Entire Region						
	Total			Patches >1 ha		Patches >5 ha	
Class	% area	# patches	Area (ha)	#	Area (ha)	#	Area (ha)
Natural / Seminatural	27.2	5219	12989	683	12107	252	11107
Forests and Woodlands	20.4	3488	9735	662	9122	256	8184
Swamp Forests	3.1	5100	1496	206	656	29	297
Floodplain Forests	8.9	9406	4259	804	2457	90	991
Upland Deciduous Forests	6.4	4336	3073	450	2303	111	1559
Upland Coniferous Forests	1.9	1289	907	116	709	41	544
Savannas (Upland Savannas)	0.8	1956	370	22	80	4	49
Shrublands (Wet Shrublands)	0.4	846	193	17	78	4	46
Prairies & Meadows	5.1	6242	2438	432	1340	53	559
Wet Prairies	0.1	116	40	4	22	2	15
Upland Prairies	1.3	3327	610	57	122	3	32
Sand Barrens	0.8	2152	359	27	48	-	-
Eurasian Meadows	3	4798	1429	220	589	16	184
Water (Perennial Ponds)	0.5	309	253	48	201	12	109
Cultural							
Built-up	39.2	6617	18749	642	17488	153	16414
Dense Urban	3.8	1957	1833	240	1434	60	1043
Residential / Mixed	35.4	7573	16915	679	15469	155	14331
Vacant	33.6	7236	16042	582	14252	157	13380
Turf / Pasture	6.6	9278	3141	545	1397	38	415
Croplands	27	305	12901	245	12863	134	12560
Total mapped	100		47779				

Table 4. Continued.

	Parks and Preserves						
	Total under protection			Patches >1 ha		Patches >5 ha	
Class	% area	# patches	Area (ha)	#	Area (ha)	#	Area (ha)
Natural / Seminatural	30	219	3883	83	3842	52	3773
Forests and Woodlands	34	370	3283	113	3214	49	3072
Swamp Forests	42	1619	631	93	336	18	195
Floodplain Forests	22	1984	931	141	549	16	313
Upland Deciduous Forests	36	1015	1094	134	904	44	716
Upland Coniferous Forests	69	279	627	78	579	33	472
Savannas (Upland Savannas)	39	409	142	13	61	4	48
Shrublands (Wet Shrublands)	47	293	90	14	46	3	20
Prairies & Meadows	14	532	353	66	244	18	149
Wet Prairies	66	33	26	4	21	2	15
Upland Prairies	22	422	135	24	59	1	13
Sand Barrens	7	113	26	2	5	-	-
Eurasian Meadows	12	543	166	24	59	2	11
Water (Perennial Ponds)	6	11	15	3	13	1	8
Cultural							
Built-up	3	1284	498	81	219	6	76
Dense Urban	<1	32	8	2	3	-	-
Residential / Mixed	3	1289	490	78	210	6	72
Vacant	1	426	227	26	133	9	99
Turf / Pasture	3	382	103	9	21	-	-
Croplands	1	58	124	17	107	7	83
Total mapped			4608				

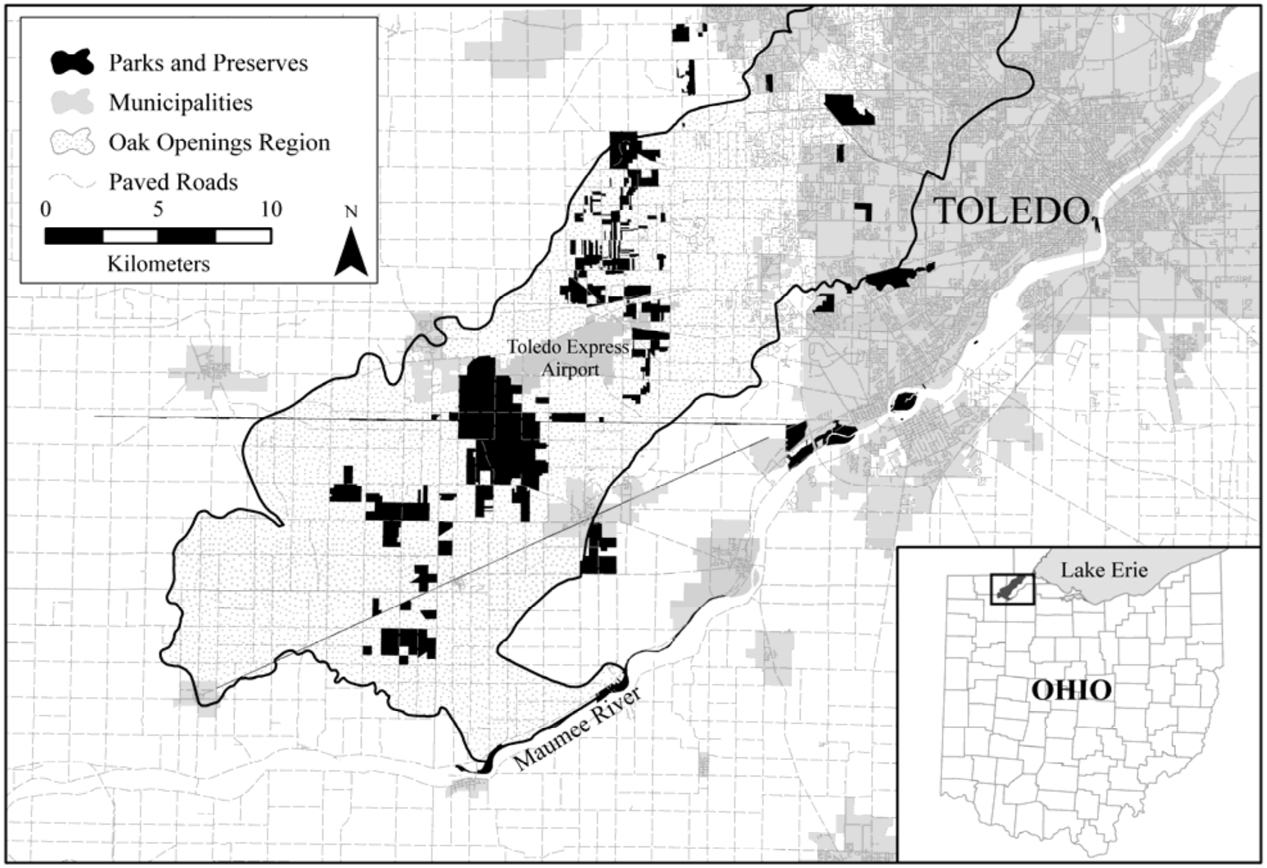

Figure 1. Map of the Oak Openings region of Northwestern Ohio. Parks and Preserves include lands owned & managed by the Metropolitan Park District of the Toledo Area, The Nature Conservancy, Northwestern Ohio Rails-to-Trails Association, Ohio Department of Natural Resources, and The Olander Park System.

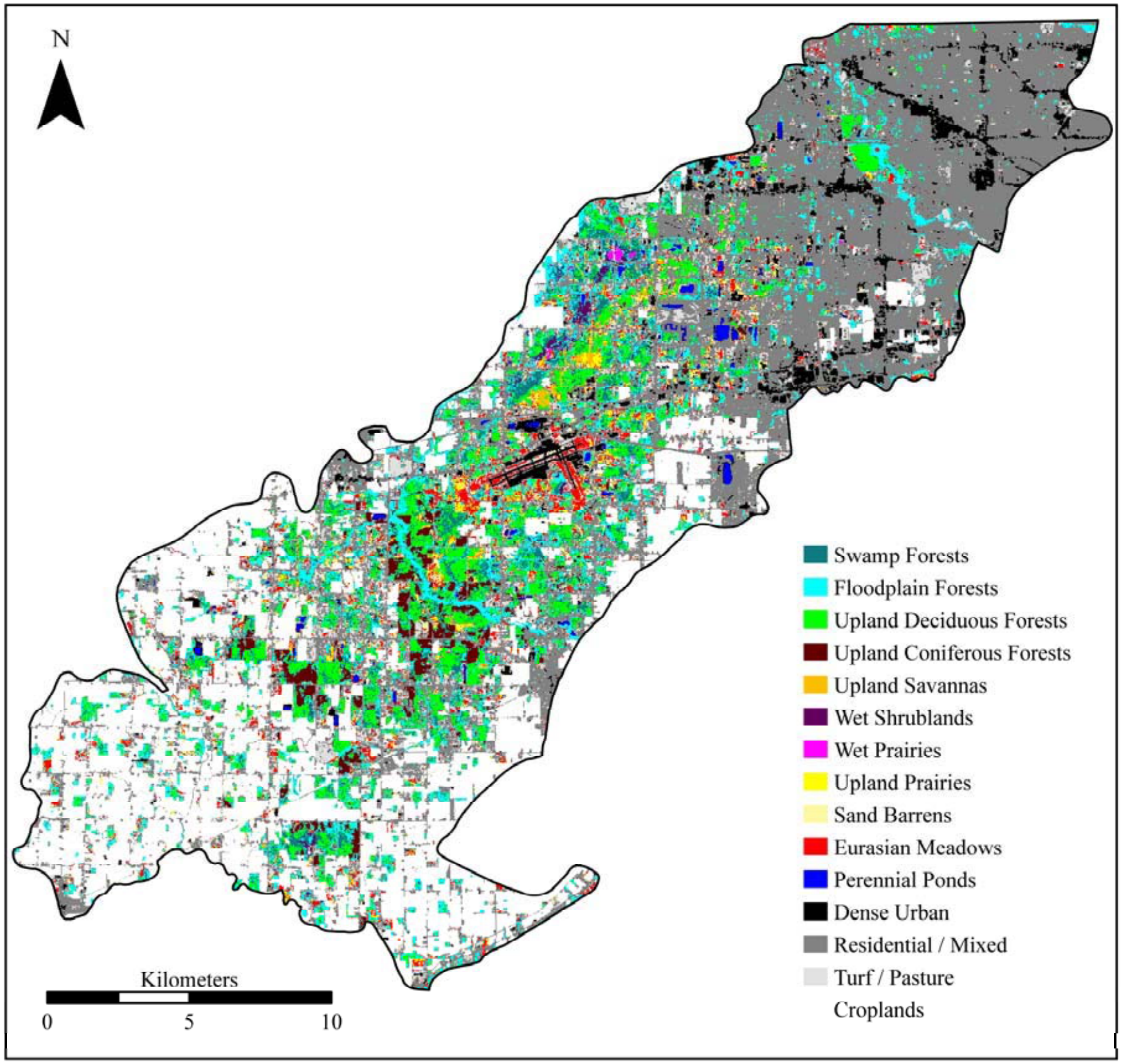

Figure 2. Land cover map of the Oak Openings Region of northwestern Ohio.

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CHAPTER II

A MULTI-SCALE SPATIAL ANALYSIS OF NATIVE AND EXOTIC PLANT SPECIES RICHNESS WITHIN A MIXED-DISTURBANCE OAK SAVANNA LANDSCAPE

ABSTRACT

Impacts of human land use pose an increasing threat to global biodiversity. Resource managers must respond rapidly to this threat by assessing existing natural areas and prioritizing conservation actions across multiple spatial scales. Plant species richness is a useful measure of biodiversity but typically can only be evaluated on small portions of a given landscape. Modeling relationships between spatial heterogeneity and species richness may allow conservation planners to make predictions of species richness patterns within unsampled areas. We utilized a combination of field data, remotely sensed data, and landscape pattern metrics to develop models of native and exotic plant species richness at two spatial extents (60-m and 120-m windows) and at four ecological levels for northwestern Ohio's Oak Openings region. Multivariate models explained 37% to 77% of the variation in plant species richness. These models consistently explained more variation in exotic richness than in native richness. Exotic richness was better explained at the 120-m extent while native richness was better explained at the 60-m extent. Land cover composition of the surrounding landscape was an important component of all models. We found that percentage of human-modified land cover (negatively correlated with native richness and positively correlated with exotic richness) was a particularly

useful predictor of plant species richness and that human-caused disturbances exert a strong influence on species richness patterns within a mixed-disturbance oak savanna landscape. Our results emphasize the importance of using a multi-scale approach to examine the complex relationships between spatial heterogeneity and plant species richness.

INTRODUCTION

Biodiversity is increasingly threatened by growing human impacts throughout the biosphere (Chapin and others 2000, Barnosky and others 2011). Mounting evidence suggests that loss of biodiversity may adversely affect ecosystem functioning (Hooper and others 2005, Cardinale and others 2006, Maestre et al. 2012) along with key ecosystem services that provide for the well-being of humans on Earth such as climate regulation, water and air purification, soil fertility, erosion control, agricultural pest and disease control, and protection from natural hazards (Balvanera and others 2006, Diaz and others 2006, Mooney 2010). Faced with limited financial resources and a narrowing window of time to mitigate further loss of biodiversity, there is urgent need for resource managers to rapidly assess natural areas and prioritize various conservation actions across multiple scales, from individual sites to entire ecoregions (Novacek and Cleland 2001, Rey Benayas and others 2009).

Plant species richness (i.e., number of species) is frequently used to measure biodiversity (Cardinale and others 2011), ecosystem recovery (Ruiz-Jaen and Aide 2005) and ecological restoration (Wang 2010). Plant species richness is a logical choice as a monitoring and evaluation target for conservation because of the important functional role of plants as primary producers and as habitat for animal species (Cardinale and others 2011). Data on plant richness is relatively easy to collect and interpret compared to other formula-based diversity indices.

Additionally, it is useful to differentiate between species that are native to a given region and those that were introduced as a result of human actions (i.e., exotic species). Patterns in native and exotic richness may respond differently to various ecological processes (Denslow and others 2010). For example, in southern California shrublands, severe anthropogenic disturbances associated with urban and agricultural activities led to long-term reductions in native plant species richness and establishment of exotic annual grassland communities (Stylinski and Allen 1999). Thus, evaluation of native and exotic richness patterns in other native communities may provide useful information regarding specific ecological conditions.

Since it is usually possible to sample only a small fraction of a given landscape due to time and financial constraints, it is necessary to develop predictive models to provide information on native and exotic richness for the remaining unsampled landscape (Stohlgren and others 1997). Modeling relationships between richness and spatial heterogeneity (i.e., pattern) of biotic and abiotic resources across a given landscape offers a potentially useful approach. Spatial heterogeneity is hypothesized as one of the primary determinants of biodiversity (Huston 1994, Rosenzweig 1995), though the specific relationship between heterogeneity and diversity is often scale-dependent (Reed and others 1993, Tamme and others 2010). Recent studies evaluating a range of terrestrial ecosystems across multiple spatial scales have confirmed that relationships exist between plant species richness and various aspects of spatial heterogeneity, such as topography (Dogan and Dogan 2006, Dufour and others 2006, Thuiller and others 2006), landscape patch composition / configuration (Kumar and others 2006), soil depth (Lundholm and Larson 2003, Cingolani and others 2010), soil nutrients (Gilliam and Dick 2010), soil pH (Costanza and others 2011), water availability (Pausas and others 2003), grazing pressure

(Olofsson and others 2008), and gradients in natural and human-caused disturbances (Deutschewitz and others 2003, Lilley and Vellend 2009).

To make better management and policy decisions to mitigate future loss of biodiversity, we require a better understanding of the connection between biodiversity and spatial heterogeneity at all scales so that we can make reliable predictions for scenarios of landscape change (Schroder and Seppelt 2006). Recent advances in the application of GIS and remote sensing technologies make these tools appealing for the rapid assessment of spatial heterogeneity and biodiversity (Luoto and others 2002). It is especially important to assess ecosystems or regions that contribute disproportionately to biodiversity (i.e., biodiversity hotspots) and those identified as critically endangered (Hoekstra and others 2005), such as the oak savanna region of the Midwestern United States.

Midwest oak savannas are among the most imperiled North American plant communities, having declined more than 99.9% since European settlement due to land use change and fire exclusion (Nuzzo 1986, Noss and others 1995). Today, remnant oak savannas often represent local hotspots of biodiversity (Leach and Givnish 1999) and serve as refugia for rare species not found elsewhere on the landscape. Remnant oak savanna ecosystems are heavily influenced by mixed natural (fire, hydrologic cycles) and anthropogenic (land use conversion, habitat fragmentation) disturbances within the surrounding landscape (Grossmann and Mladenoff 2007). Studies of remnant oak savannas within a mixed-disturbance landscape have found relationships between plant richness and light availability (Leach and Givnish 1999), fire frequency (Weiher 2003, Peterson and Reich 2008), proximity to possible propagules (Brewer and Vankat 2006), intensity of restoration treatments (Abella and others 2001), and soil characteristics (Leach and Givnish 1999). Lilley and Vellend (2009) evaluated relationships between spatial heterogeneity and plant species richness among remnant oak savannas in British Columbia, finding that gradients in human disturbance were important predictors of both native and exotic richness. However, relationships between spatial heterogeneity and plant richness remain largely unexplored for Midwest oak savannas.

The purpose of this study was to evaluate potential relationships between native / exotic plant species richness and spatial heterogeneity within the context of a mixed-disturbance oak savanna landscape. We followed the general approach offered by Kumar and others (2006), utilizing field data, remotely sensed data, and landscape pattern metrics to develop multi-scale predictive models of native and exotic plant species richness for remnant savanna, prairie and barrens communities. We chose to focus on these specific communities because they remain a target for ongoing conservation and restoration efforts throughout the Midwestern United States (Leach and Ross 1995, Abella and others 2007). We examined the following specific research questions within the context of a mixed-disturbance oak savanna landscape: 1) Can a reduced set of explanatory variables be used to reliably predict native and exotic richness patterns? 2) Do relationships between native / exotic richness and heterogeneity vary at different spatial scales? 3) Do these relationships vary within/among different plant community types?

STUDY AREA

The 478 km^2 Oak Openings region of northwestern Ohio (41^o 25’ to 41^o 44’ N; 83^o 34’ to 84^o 2’ W) occurs near the eastern extent of the historic Midwest Oak Savanna region (Nuzzo 1986). The region’s climate is humid continental; mean monthly temperatures range from -10 ^{o}C to 23 ^{o}C; mean annual precipitation is 81 cm (USDA-NRCS 2010). Historically, the region featured a mosaic of oak savanna uplands and wet prairie lowlands occurring on postglacial sandy soils (Brewer and Vankat 2004). Following European settlement, the region was systematically altered through drainage, fire exclusion, urban development and row-crop agriculture. Today, roughly 73% of the region has been converted to human-modified land cover types while less than 3% of the region remains covered by native savannas, prairies and barrens (Schetter and Root 2011). Despite these changes, the region continues to harbor one-third of Ohio' state-listed rare plant and animal species within an area that collectively represents less than 0.5% of Ohio's total land area.

Currently, 10% of the region's total land area has been permanently protected as public parks and nature preserves by various conservation organizations including the Metropolitan Park District of the Toledo Area, Ohio Department of Natural Resources, and The Nature Conservancy. Although human-caused disturbances persist throughout much of the region, the Oak Openings' remaining natural areas continue to be influenced by natural disturbances such as seasonal flooding and prescribed fires set by preserve managers. A hierarchical land cover classification system has been developed for the region within an ecological framework, dividing the region's savannas, prairies and barrens into five distinct community types: wet prairies, mesic prairies, dry prairies, sand barrens, and oak savannas (Schetter and Root 2011). Today these communities are heavily fragmented, typically occur in discrete patches within a landscape matrix of human-modified and forested land cover types (Figure 1).

METHODS

Site selection and field sampling

Using an existing raster land cover map of our study area (Schetter and Root 2011) imported into ArcGIS 9.1 (ESRI, Redlands, CA, USA), we randomly sampled 30-m map pixels across five community types, resulting in 39 total study sites (Figure 2). At each study site, we established a 20 x 50 m (1000-m^2) modified-Whittaker, multi-scale plot (Kalkhan and Stohlgren 2000) with the long axis randomly assigned to either a north-south or east-west bearing. Plots were centered within two adjacent 30-m map pixels and located on the ground using a high-precision GPS unit (Trimble GPS Pathfinder Pro XRS) set to NAD83 Ohio State Plane North coordinate system. Minimum distance between plots was 100 m. We excluded potential plot locations consisting of mixed community types or those intersected by human features such as roads or ditches.

Each modified-Whittaker plot included 10 1-m^2 non-overlapping subplots, two 10-m^2 non-overlapping subplots, and one 100-m^2 subplot, each nested within the 1000-m^2 plot. Within each 1-m^2 subplot, we estimated foliar cover for each vascular plant species at ground level (<1.7 m height) to the nearest 1%, along with bare ground, litter (attached), duff (detached), coarse woody debris, cryptobiotics (mosses, algae, lichens), and tree/shrub canopy (>1.7 m). Cover for species occupying <1% of a 1-m^2 subplot was recorded as 0.5%. Due to layering of foliage, litter/duff, and cryptobiotocs, it was possible for cumulative cover to exceed 100%. We recorded cumulative number of plant species within each of the 10-m^2 subplots, the 100-m^2 subplot and the 1000-m^2 plot. Within each 1000-m^2 plot, we recorded by species all woody stems $\geq$2.5 cm dbh (diameter at breast height). All upland communities were sampled from 26 July to 20 September, 2008 and from 2 August to 22 September, 2009, corresponding to peak biomass for these communities. For wet prairies, sampling occurred from 23 May to 2 July, 2009, coinciding with availability of flowers and fruits within the Family *Cyperaceae* (necessary for their successful identification) rather than onset of peak biomass within these sedge-dominated communities. Therefore estimates of cover could not be directly compared between upland and wet prairie communities. For all communities, species were classified as either native or exotic to our study area following Andreas and others (2004). Species were identified following Voss (1972, 1985, 2004). Plant species not identified in the field were collected for comparison with appropriate taxonomic keys and herbarium specimens.

Within each modified-Whittaker plot, we collected five soil samples (one from each corner and one from the plot center) to a depth of 40 cm using a 2.5-cm diameter soil probe after removing any surface litter. For each plot, soil samples were pooled into a single sample following Kumar and others (2006) and air dried for 48 hours. Pooled samples were submitted to a commercial analytical lab (Brookside Laboratories, Inc., New Knoxville, Ohio) where they were ground to pass through a 2-mm sieve. Soil texture (sand, silt, and clay fractions) was determined following the standard hydrometer method (ASTM 2002). Soils were analyzed for total nitrogen, total carbon, and organic carbon following Nelson and Sommers (1996). Extractable calcium, magnesium, potassium, sodium, and sulfur were determined following Suarez (1996).

GIS data collection

To evaluate the relationship between specific environmental gradients and plant species richness, we measured proximity of each 1000-m^2 plot to nearest patch edge, paved roadway, water source (dug pond or drainage ditch), and human dwelling using high resolution color orthophotos of our study area (OGRIP 2006, Lucas County ARIES 2004) imported into ArcGIS 9.1. We selected proximity to patch edge as a variable of interest because patch edges are known to influence plant dispersal patterns (Fagan and others 1999). The other variables were selected to evaluate gradients in anthropogenic disturbance. Proximity to natural streams was initially considered as a variable of interest but was later dismissed because no natural surface water drainage occurred within 0.5 km of any of our research plots. We evaluated topographic heterogeneity within and among research plots using 0.762-m grid digital elevation model (DEM) data of our study area (OGRIP 2006). We extracted DEM data for each 1000-m^2 plot (approx. 1,700 data points per plot) and measured the following variables using ArcGIS 9.1 Spatial Analyst (ESRI, Redlands, CA, USA): mean elevation (m), slope (%), and aspect (radians) transformed into north-south and east-west gradients (*see* Kumar and others 2006). We used within-plot standard deviation of elevation to quantify topographic variability following Dufour and others (2006).

Landscape pattern analysis

We evaluated landscape heterogeneity surrounding each 1000-m^2 plot by measuring selected landscape pattern metrics at two nested spatial extents using program FRAGSTATS, version 3.3 (McGarigal and Marks 1995). A raster land cover map of the region was used as the basis for all analyses (Schetter and Root 2011; ESRI GRID format, NAD 1983 datum, Ohio State Plane North projection, 30-m pixel size). We performed moving window analyses using both 60-m and 120-m circular windows around each research plot (corresponding to an area of 1.89 ha and 6.21 ha respectively, *see* McGarigal and Marks 1995). Spatial extents greater than 120-m were not used due to overlap of landscape windows among research plots. The 8-cell patch neighbor rule was applied to all analyses. We used five commonly used landscape pattern metrics (calculated in FRAGSTATS) to quantify specific aspects of landscape composition / configuration (*see* Li and Reynolds 1994):

Cohesion Index: measures physical connectedness of patches on the landscape

Landscape Shape Index: measures total patch edge adjusted for landscape size (edge density)

Patch Richness Density: measures number of different patch types present per total landscape area

Shannon’s Diversity Index: measures the proportional abundance of each patch type on the landscape

Percentage of Landscape: measures total area of all patches of the corresponding patch type per total landscape area

Statistical analyses

Our general statistical approach was to test for linear relationships between native or exotic plant species richness (response variables) and selected physical / landscape variables (predictor variables) at multiple levels within the Oak Openings region ecological hierarchy (Figure 2) and then develop a “best” predictive model among all significant predictor variables for native and exotic richness at each of these levels following Kumar and others (2006). All statistical analyses were performed using JMP ver. 9.0 (SAS Institute, Inc.) unless otherwise referenced. First, we conducted univariate linear regression to identify predictor variables significantly related to native / exotic richness at each ecological level using a critical value of $P = 0.05$. For all datasets, we tested for normality within the residuals using the Shapiro-Wilks test and examined residual plots for obvious patterns indicative of heteroscedasticity. Data were transformed when appropriate prior to analysis to reduce the influence of non-normality / heteroscedasticity within the datasets (e.g., arcsin square root transformation for percent data, log10 ($n + 1$) transformation for count data). Data exhibiting strong nonlinear relationships following transformation were excluded from linear regression analyses.

To account for spatial autocorrelation within the datasets, we followed the procedure developed by Dutilleul (1993) using a computer program written by Legendre (2000). This procedure provides an estimate of the degrees of freedom lost due to spatial dependence between x and y variables, giving a corrected F value and corresponding P-value for each linear regression model (Dale and Fortin 2002). All predictor variables significant at $P < 0.05$ after correcting for spatial autocorrelation were further evaluated using stepwise forward multiple regression ($P = 0.25$ to enter model, $P = 0.10$ to leave model) to develop a set of candidate models of native / exotic richness at both 60-m and 120-m spatial extents within each of the four levels of the Oak Openings ecological hierarchy. Before conducting multiple regression analyses, we examined all predictor variables for cross-correlations and multicollinearity by evaluating correlation matrices and inverse correlation matrices of each set of predictor variables. Any variables with cross correlations $> \pm 0.75$ or those with variance inflation factors > 2.5 were not included in the same model (Neter and others 1996, Kumar and others 2006). At each of the four ecological levels, we used Akaike's Information Criteria adjusted for small sample size (AICc) to select the "best" model among all possible candidate models for native and exotic richness at both 60-m and 120-m spatial extents. Only candidate models with Δ AICc of ≤ 2 were given consideration (Burnham and Anderson 2002). In cases where multiple candidate models had Δ AICc of ≤ 2, the model with the fewest variables was selected as the most parsimonious model. For all multivariate models, we assumed a multivariate normal distribution with constant variance in the residuals and no spatial autocorrelation.

RESULTS

Plant species richness among Oak Openings communities

Among five Oak Opening community types, we recorded 406 vascular plant species (349 native, 57 exotic), including 48 species listed as endangered, threatened, or potentially threatened in Ohio (ODNR 2010). This accounted for one-third of the region's known vascular plant flora (Moseley 1928, Walters 2007) and 34% of the region's documented state-listed rare plant species within a sampled area of 3.9 hectares (<0.01% of the Oak Openings region's total land area). Less than two percent of specimens observed in the field could not be positively identified to species. Total species richness was not significantly different among community types (Table 1). Native richness tended to be greatest in mesic prairies while it tended to be lowest in sand barrens. Exotic richness was four to six times greater in dry prairies and sand barrens compared to the other community types. Native richness was positively correlated with exotic richness only among wet prairies ($R^2 = 0.74$, $F_{1,7} = 9.72$, $P = 0.044$, corrected for spatial autocorrelation following Dutilleul (1993)). For all other communities, there was no statistically significant relationship between native and exotic richness ($P < 0.05$).

Thirty out of 39 research plots occurred within existing managed preserves including all oak savanna, mesic prairie and wet prairie plots; while four of eight dry prairie plots and two of seven sand barrens plots occurred within managed preserves. For dry prairies, there was no significant difference between plots occurring in managed preserves vs. unmanaged areas for native richness ($t = 1.06$, $P = 0.33$), exotic richness ($t = 0.61$, $P = 0.57$), native plant cover ($t = 0.53$, $P = 0.61$), or exotic plant cover ($t = 1.36$, $P = 0.22$). For sand barrens, native richness was significantly greater in managed preserves (44.0 $\pm$ 2.0) compared to unmanaged areas (27.0 $\pm$

7.0; $t = 3.42$, $P = 0.02$), but there was no significant difference for exotic richness ($t = 0.98$, $P = 0.50$), native plant cover ($t = 1.78$, $P = 0.13$), or exotic plant cover ($t = 1.07$, $P = 0.47$).

Physical and landscape attributes among Oak Openings communities

For the various vegetative characteristics measured in the field, it was not possible to directly compare wet prairies with other community types because wet prairies were sampled during the early growing season while all other plots were sampled during the late growing season. Among upland communities, sand barrens had less foliar cover, greater amounts of bare soil and greater cover of cryptobiotics, while oak savannas had the greatest accumulation of ground litter compared to the other community types (Table 2). Oak savannas were typically farther from water sources and patch edges than the other communities while wet prairies and sand barrens were typically closest to water sources. Wet prairies had higher levels of measured soil macronutrients (nitrogen, carbon) and clay / silt fraction than the four upland communities. For the measured topographic variables there was no significant difference in mean elevation or aspect among communities, reflecting the subtle topography of the Oak Openings region. Greatest within-plot topographic heterogeneity occurred among sand barrens, while wet prairies had the most uniform topography.

Measures of landscape heterogeneity varied among the five community types at both the 60-meter and 120-meter spatial extent (Table 3). Sand barrens tended to occur within more heavily fragmented landscapes consisting of smaller patches (higher values for patch richness density and Shannon diversity index) compared to the other community types. Sand barrens also tended to occur in more developed landscapes compared to the other plots (greater percent human-modified land cover), while oak savannas and mesic prairies tended to occur in landscapes with lesser amounts of human-modified land cover.

Relationships between spatial heterogeneity and species richness

At the region level (among all research plots), we observed generally weak relationships between native / exotic richness and the measured physical and landscape variables (Tables 4 and 5). There were no significant relationships for native richness at the region level ($P < 0.05$) while individual physical / landscape variables explained 8 – 46% of the observed variation in exotic richness. Among all upland communities (intermediate level 1), individual physical / landscape variables explained 10 – 52% of observed variation in native richness (Table 4) and 11 – 58% of exotic richness (Table 5). Among upland prairies and barrens (second intermediate level), explanatory power of measured variables generally improved for both native and exotic richness (20 – 50% and 15 – 61% respectively). At these three ecological levels, landscape variables at the 60-meter extent consistently explained more variation in native richness compared to the 120-m extent, while landscape variables at the 120-m extent consistently explained more variation in exotic richness than at the 60-m extent.

At these higher ecological levels, native and exotic richness showed contrasting relationships with various measures of spatial heterogeneity (Tables 4 and 5). For example, for native species richness we found positive correlations with measures of vegetative cover and percent Oak Openings land cover while we observed negative relationships between native richness and measures of topographic heterogeneity, landscape heterogeneity, and percent human-modified land cover. In contrast, we found negative relationships between exotic richness and measures of vegetative cover and percent Oak Openings land cover while we observed positive relationships between exotic richness and measures of landscape heterogeneity and percent human-modified land cover. Within individual community types, there were fewer physical / landscape predictor variables that were statistically significant compared to the higher ecological levels, which can be attributed at least in part to decreasing sample size. Individual variables at the community level explained 60 – 89% and 44 – 66% of variability in native and exotic richness, respectively (Figure 3).

Best explanatory models of native and exotic richness

At the three highest ecological levels a single "best" multivariate model was developed separately for native and exotic richness, explaining 50 – 69% and of the variation observed within our data (Tables 6 and 7). At these three ecological levels, models of exotic richness consistently explained more variation in our data than models of native richness. A model for native richness could not be developed at the region level due to lack of statistical significance. At both intermediate levels, the best models of native richness included landscape variables at the 60-m scale. Best models of exotic richness at the region and intermediate levels included landscape variables at the 120-m scale. At the individual community level, multivariate models of native and exotic richness could not be developed because of the small number of variables that were statistically significant after adjusting for spatial autocorrelation and/or high levels of cross-correlation when more than one variable was significant.

DISCUSSION

Our results show that within the context of a mixed-disturbance oak savanna landscape, measures of spatial heterogeneity derived from a combination of field data, remotely sensed data, and landscape pattern metrics can be used to explain trends in plant species richness and that these trends are different when comparing native and exotic species. Within our dataset, we evaluated numerous aspects of spatial heterogeneity including vegetative cover, soil nutrients, environmental gradients, topography, landscape configuration, and landscape composition. We found that in most cases, landscape composition derived from raster land cover data explained more variation in our data than other possible explanatory variables. Specifically, we found that percentage of human-modified land cover within the surrounding landscape was negatively correlated with native species richness but positively correlated with exotic species richness. We found that multivariate models of plant species richness explained more variation for exotic species than for native species, consistent with the findings of Kumar and others (2006). Further, we found that exotic richness was better explained at a larger spatial extent (roughly six hectares) while native richness was better explained at a smaller spatial extent (roughly two hectares). We attribute these findings, at least in part, to differences in life history traits between native and exotic species; i.e., exotic species are typically associated with early successional stages resulting from human disturbances in the surrounding landscape (McIntyre and Lavorel 1994, Sutherland 2004).

In contrast to studies of plant species richness in mountainous regions linking species richness and gradients in elevation (Dogan and Dogan 2006, Kumar and others 2006), we found no such relationship within the relatively flat Oak Openings region. However, for upland communities (especially sand barrens) we found a negative relationship between native species richness and measures of within-plot topographic heterogeneity. Other studies have shown the importance of topographic heterogeneity in explaining plant species richness (Dufour and others 2006, Thuiller and others 2006). However these studies found a positive relationship between species richness and heterogeneity. Similarly, Costanza and others (2011) found a positive correlation between land cover heterogeneity and plant species richness. Although we found a positive correlation between land cover heterogeneity and exotic species richness at the three higher ecological levels, we found the opposite trend for native species richness among upland sites, suggesting that habitat fragmentation associated with human disturbance may be limiting dispersal of native plant species (Honnay and others 1999).

In the case of the Oak Openings region, our data suggest that human-caused disturbances exert a strong influence over the observed relationships between spatial heterogeneity and species richness. As gradients in human disturbance increase, we would expect a corresponding increase in exotic richness and a decrease in native richness. Much of our data is consistent with this hypothesis. Although broad-scale topography within the Oak Openings can be attributed to glacial and post-glacial natural processes (Forsyth 1970), site-level topographic heterogeneity within our study can be attributed to more recent human disturbances. For example, among our study sites, we found the greatest topographic heterogeneity among sand barrens communities. A quick review of available USGS topographic maps and aerial photos of our study sites revealed that all seven of the sand barrens we evaluated originated from human disturbances since the mid-twentieth century (sand pits, former homesteads, off-road vehicle use). Although native richness was significantly greater for the two sand barrens sites occurring within established preserves, these sites have also been protected from human disturbance for 40-70 years compared to sand barrens occurring on unprotected sites which have all seen ongoing disturbances within the past ten years.

Further evidence of the influence of human disturbance in the Oak Openings can be seen in the positive relationship between exotic richness and proximity to roads (among uplands) and ditches/ponds (among uplands, but especially pronounced among sand barrens), both of which are known to serve as ongoing vectors for the introduction of exotic species (Jodoin and others 2008, Lilley and Velland 2009). Observed soil nutrient levels in relation to species richness patterns further support the influence of human-caused disturbance in the Oak Openings. For example, the positive correlation between native richness and soil organic carbon that we observed among upland sites could be related to the well-established effects of soil disturbance on reducing soil organic carbon (e.g., Post and Kwon 2000). Additionally, levels of soil sodium among upland prairies and barrens were positively correlated with exotic richness but also positively correlated with proximity to roads ($R = 0.56$, $P < 0.01$), a likely source of soil sodium through runoff of road salt.

At the three highest ecological levels, the various landscape metrics we evaluated showed that exotic species richness was positively correlated with patch edge, patches richness, and patch diversity but negatively correlated with patch connectedness, while native species richness among uplands was negatively correlated with patch edge. These results point to the influence of habitat fragmentation, widely known to negatively influence native species richness (Fahrig 2003) but promote the occurrence of exotic plant species (Minor and others 2009). Perhaps the most convincing evidence of the influence of human-caused disturbance in the Oak Openings is the strong relationship between percentage of landscape occupied by human-modified land cover and native richness (negatively correlated) and exotic richness (positively correlated) across all levels of the ecological hierarchy. For the Oak Openings region, the influence of human disturbance in the surrounding landscape is especially pronounced for exotic species richness, which exhibited stronger relationships with human-induced heterogeneity at a broader spatial extent compared with native species richness. While our results are generally consistent with the findings of Kumar and others (2006) that exotic species richness exhibits a stronger relationship with spatial heterogeneity compared to native species richness, we found that in the case of a mixed-disturbance oak savanna landscape, this relationship was largely driven by human disturbance in contrast to other more “natural” landscapes, where exotic species richness exhibits a stronger link with gradients in elevation and hydrology (e.g. Kumar and others 2006).

We acknowledge that our findings are based on a single observation of each of our research plots and that the correlations we observed do not necessarily point to causal relationships between heterogeneity and richness. We also note that although our study area is referred to as the Oak Openings “region”, the land area under investigation in our study was on the order of several hundred square kilometers in contrast to other larger “regions”, for example the Midwestern United States. With these caveats in mind, our results are consistent with a growing body of scientific literature showing that relationships exist between spatial heterogeneity and plant species richness and that these relationships are both ecologically and spatially scale-dependant. We do not discount the importance of other factors known to influence the relationship between heterogeneity and plant species richness, such as climate, geology, and natural disturbances (e.g., fire regime, hydrologic cycles) which were not evaluated in our study. We also emphasize that our findings do not necessarily apply to other ecosystems or at other spatial scales. Within the context of a mixed-disturbance oak savanna landscape, our results clearly point to the important influence of human disturbance on natural areas occurring within a matrix of human-modified land cover types. Further, our results emphasis the importance of using a multi-scale approach to examine the complex relationships between spatial heterogeneity and plant species richness.

Management Implications for Midwest Oak Savannas

Due to human activities across the landscape, remnant savanna and prairie communities in the Oak Openings are typically found in discrete patches scattered within a matrix of human-modified land cover types. To be considered as a potential study site, we required a minimum patch size of 30 x 60 m (1.8 ha) consisting of a single community type. Three of the five Oak Openings communities we examined (oak savannas, mesic prairies and wet prairies) were found only within existing managed preserves. We were not able to directly evaluate relationships between ecological restoration treatments and species richness. Because preserves are often initially placed within areas of high biological diversity, it would be difficult to evaluate the true effects of restoration activities on species richness without establishing separate control and manipulated experimental plots. However, it appears obvious that management treatments, such as prescribed fire, are critical for maintaining these imperiled plant communities, given that we could not find suitable study sites for three of the five communities outside of existing managed preserves.

Within remnant Midwest oak savannas, overhead tree canopy cover has been found to influence plant species richness in the understory (Weiher and Howe 2003, Peterson and Reich 2008). However, we found no relationships between plant species richness and overhead canopy, tree frequency, or total woody stem basal area. In the nine oak savanna sites we evaluated, mean total canopy cover ranged from 22–65% compared to these previous studies where measures of tree canopy approached 100% in some research plots. Given that all of our savanna plots occurred within managed preserves where numerous restoration treatments have been applied over many years, it is possible that overhead tree canopy in these areas has been reduced below some threshold level so that relationships between tree canopy and plant species richness are no longer detectable. We did however find a strong negative relationship between horizontal forest cover (i.e., percent cover in the surrounding landscape) and native species richness among our savanna plots. While it is possible that increased amounts of forest cover surrounding our study sites may result in lower native species richness by limiting dispersal of native savanna and prairie species, it is also possible that greater percent forest cover in the surrounding landscape is a reflection of less intensive management activities such as prescribed burning which might also decrease native richness.

Among oak savannas, exotic species richness also appears to be influenced by the composition of the surrounding landscape. While exotic richness at the higher ecological levels was positively correlated with proportion of human-modified land cover, for savannas we instead found a significant positive correlation between exotic richness and proportion of upland prairies and barrens in the surrounding landscape (Figure 3). This suggests that closed-canopy forests surrounding restored savannas may serve as dispersal barriers for exotic species compared to prairies and barrens, which may allow easier dispersal of exotic species into adjacent savannas. It is clear from these results that resource managers should carefully consider the landscape surrounding existing preserves or potential restoration sites when making resource planning and management decisions for Midwest oak savannas.

Landscape Composition as a Rapid Assessment Tool

A clear justification has previously been established for using plant species richness as a basis for measuring ecosystem restoration success, both theoretically (Wang 2010) and in practice (Ruiz-Jaen and Aide 2005). However, it is usually not practical to measure species richness across an entire area of interest, especially at larger spatial scales. Therefore it is critical for effective regional conservation planning that appropriate surrogates are developed to quantify patterns of plant species richness (Ferrier 2002). Much of the physical data we collected in the field (such as vegetative cover and soil characteristics) have been shown to reliably predict plant species richness across multiple spatial scales and ecosystems. However, these data can be time-consuming and costly to collect. Therefore it is especially appealing to find appropriate surrogates of plant species richness through remote sensing and GIS applications for rapidly assessing a given area for conservation planning. For the Oak Openings region, we found percentage of human-modified land cover in the landscape to be especially promising in this regard. Percentage of landscape has been used to reliably predict wetland condition (Mack 2006) and is currently used by regulatory agencies as part of a rapid assessment method for wetlands (Mack 2001). Based on our results, percentage of landscape should be given strong consideration as a rapid assessment tool for predicting plant species richness across mixed-disturbance landscapes.

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Table 1. Plant species richness (per 1,000 m^2 plot) among five Oak Openings community types (mean with 1 SE in parentheses).

Community	*n*	Total richness	Native richness	Exotic richness	% Exotic richness
Wet prairies	9	46.3 (8.2) ^{a}	43.8 (7.4) ^{ab}	2.4 (1.0) ^{c}	4.0 (1.2) ^{b}
Mesic prairies	6	70.5 (5.2) ^{a}	66.7 (5.5) ^{a}	3.3 (1.5) ^{bc}	4.8 (2.4) ^{b}
Dry prairies	8	61.9 (5.9) ^{a}	49.3 (6.0) ^{ab}	12.6 (1.8) ^{a}	21.4 (3.3) ^{a}
Sand barrens	7	48.3 (3.7) ^{a}	39.1 (3.7) ^{b}	9.1 (2.4) ^{ab}	19.2 (4.3) ^{a}
Oak savannas	9	52.0 (5.5) ^{a}	49.9 (5.1) ^{ab}	2.0 (0.5) ^{c}	3.8 (0.9) ^{b}
$F_{4,34}$		2.36	2.56	10.77	12.41
P		0.073	0.056	<0.0001	<0.0001
R^2		0.22	0.23	0.56	0.59

Means with different lowercase letters within columns are significantly different at $P < 0.05$, Tukey's test.

Table 2. Physical characteristics of five Oak Openings community types (mean with 1 SE in parentheses).

	Community								
Physical variables	Wet prairie	Mesic prairie	Dry prairie	Sand barren	Oak Savanna	*F*	*P*	R^2	
Vegetation									
Total foliar cover <1.7m (%)	30.2 (3.9)	102.3 (7.5) ^{a}	74.5 (10.2) ^{ab}	44.7 (5.5) ^{b}	89.4 (11.3) ^{a}	6.07	0.003	0.41	
Native	29.0 (3.7)	97.4 (8.8) ^{a}	70.3 (10.4) ^{ab}	41.0 (6.9) ^{b}	89.2 (11.4) ^{a}	5.76	0.004	0.40	
Exotic	2.0 (1.2)	5.7 (3.1) ^{ab}	5.4 (1.6) ^{a}	4.7 (2.0) ^{ab}	0.8 (0.4) ^{b}	4.18	0.015	0.33	*
% Exotic	5.2 (0.03)	5.9 (0.03) ^{ab}	8.0 (0.03) ^{ab}	14.4 (0.09) ^{a}	1.4 (0.01) ^{b}	3.76	0.023	0.30	*
Bare ground (%)	12.5 (6.0)	6.0 (1.8) ^{b}	7.8 (2.2) ^{b}	30.9 (11.2) ^{a}	2.7 (1.4) ^{b}	7.37	0.001	0.46	*
Total ground litter (%)	72.9 (8.7)	69.4 (8.0) ^{ab}	66.3 (8.9) ^{b}	33.9 (7.9) ^{c}	96.0 (2.0) ^{a}	14.29	<.0001	0.62	
Cryptobiotics (%)	2.6 (1.2)	1.4 (0.6) ^{bc}	7.1 (2.5) ^{ab}	12.2 (4.5) ^{a}	0.1 (0.03) ^{c}	8.38	0.001	0.49	*
Tree canopy (%)	0	0.3 (0.3) ^{a}	0 ^{a}	1.3 (1.3) ^{a}	36.8 (5.2) ^{b}	69.67	<.0001	0.89	*
Woody stem basal area (m^2/ha)	0.27 (0.17) ^{a}	0.14 (0.13) ^{a}	0.05 (0.04) ^{a}	0.78 (0.43) ^{a}	13.4 (2.3) ^{b}	43.98	<.0001	0.84	**
Environmental gradients									
Nearest paved road (m)	161 (56) ^{a}	187 (43) ^{a}	127 (34) ^{a}	192 (35) ^{a}	275 (52.1) ^{a}	1.47	0.233	0.15	**
Nearest water source (m)	112 (22) ^{b}	200 (67) ^{ab}	202 (39) ^{ab}	129 (22) ^{b}	353 (48.9) ^{a}	6.02	0.001	0.41	**
Nearest human dwelling (m)	262 (36) ^{a}	259 (37) ^{a}	263 (72) ^{a}	311 (107) ^{a}	341 (69.8) ^{a}	1.25	0.308	0.13	**
Nearest patch edge (m)	22.2 (3.7) ^{b}	27.0 (4.9) ^{b}	38.5 (6.3) ^{ab}	18.6 (3.3) ^{b}	62.8 (10.4) ^{a}	7.53	0.000	0.47	

Means with different lowercase letters within rows are significantly different at $P < 0.05$, Tukey's test. A single asterisk indicates data were arcsin-square root transformed prior to analysis. Double asterisk indicates data were log transformed prior to analysis.

Table 2. (cont.)

	Community							
Physical variables	Wet prairie	Mesic prairie	Dry prairie	Sand barren	Oak Savanna	*F*	*P*	R^2
Soil variables								
N (%)	0.27 (0.03) ^{a}	0.11 (0.02) ^{b}	0.10 (0.01) ^{b}	0.06 (0.01) ^{b}	0.06 (0.0) ^{b}	16.79	<.0001	0.67
C_{total} (%)	3.6 (0.4) ^{a}	1.5 (0.2) ^{b}	1.4 (0.1) ^{b}	0.9 (0.1) ^{b}	1.0 (0.3) ^{b}	18.21	<.0001	0.69
$C_{organic}$ (%)	2.2 (0.3) ^{a}	1.4 (0.2) ^{ab}	1.2 (0.1) ^{ab}	0.7 (0.1) ^{b}	0.9 (0.2) ^{b}	6.80	0.000	0.45 *
Ca (ppm)	2480 (195) ^{a}	417 (304) ^{b}	243 (53) ^{b}	148 (28) ^{b}	191 (55.4) ^{b}	24.96	<.0001	0.75 **
Mg (ppm)	146.5 (11.4) ^{a}	44.5 (26.1) ^{b}	30.8 (4.8) ^{b}	22 (3.9) ^{b}	24 (2.5) ^{b}	20.15	<.0001	0.71 **
K (ppm)	18.9 (1.1) ^{a}	29.2 (3.8) ^{a}	26.8 (3.7) ^{a}	28 (2.5) ^{a}	24 (3.0) ^{a}	2.27	0.083	0.22 **
Na (ppm)	35.1 (2.8) ^{a}	23.8 (1.0) ^{a}	30.5 (4.6) ^{a}	29 (5.3) ^{a}	37 (3.5) ^{a}	2.43	0.067	0.23 **
S (ppm)	17.6 (2.4) ^{a}	24.8 (3.9) ^{a}	20.5 (2.8) ^{a}	19 (2.8) ^{a}	22 (3.8) ^{a}	0.68	0.611	0.08
Clay (%)	8.3 (0.8) ^{a}	7.6 (0.7) ^{ab}	6.2 (0.7) ^{ab}	5.7 (0.6) ^{ab}	5.0 (0.7) ^{b}	3.90	0.011	0.32
Silt (%)	6.8 (0.8) ^{a}	2.8 (0.7) ^{b}	2.5 (0.6) ^{b}	1.7 (0.5) ^{b}	2.4 (0.7) ^{b}	7.26	0.000	0.47 **
Sand (%)	84.9 (0.9) ^{a}	89.6 (0.9) ^{b}	91.2 (0.9) ^{b}	92.5 (1.0) ^{b}	92.6 (1.2) ^{b}	9.98	<.0001	0.55
Topographic variables								
Elevation (m)	668.3 (0.5) ^{a}	671.7 (2.0) ^{a}	673.0 (4.9) ^{a}	667.1 (5.4) ^{a}	678.1 (1.4) ^{a}	1.87	0.139	0.18 **
North aspect (radians)	-0.03 (0.12) ^{a}	0.21 (0.12) ^{a}	-0.03 (0.14) ^{a}	-0.08 (0.14) ^{a}	0.02 (0.01) ^{a}	0.75	0.565	0.08
East aspect (radians)	-0.09 (0.13) ^{a}	-0.07 (0.12) ^{a}	-0.03 (0.09) ^{a}	-0.20 (0.07) ^{a}	0.01 (0.01) ^{a}	0.69	0.606	0.07
Topographic variability (m)	0.11 (0.0) ^{c}	0.25 (0.0) ^{bc}	0.52 (0.2) ^{abc}	1.13 (0.2) ^{a}	0.82 (0.2) ^{ab}	7.12	0.000	0.46
Slope (%)	0.5 (0.1) ^{d}	1.3 (0.2) ^{cd}	2.1 (0.7) ^{bc}	5.4 (1.1) ^{a}	3.8 (0.5) ^{ab}	15.91	<.0001	0.65 *

Table 3. Landscape characteristics of five Oak Openings community types (mean with 1 SE in parentheses).

			60-m spatial extent					
Landscape pattern metric	Wet prairie	Mesic prairie	Dry prairie	Sand barren	Oak savanna	*F*	*P*	R^2
Cohesion index (0-100)	71.3 (6.0) ^{a}	79.6 (4.5) ^{a}	82.6 (4.0) ^{a}	63.7 (3.1) ^{a}	78.0 (4.5) ^{a}	2.42	0.067	0.22
Landscape shape index (≥1)	1.61 (0.08) ^{a}	1.53 (0.07) ^{a}	1.53 (0.07) ^{a}	1.75 (0.04) ^{a}	1.56 (0.07) ^{a}	1.52	0.218	0.15
Patch richness density (no. patches / 1 ha)	3.04 (0.33) ^{ab}	1.99 (0.26) ^{b}	2.30 (0.28) ^{b}	3.60 (0.28) ^{a}	2.56 (0.29) ^{ab}	4.00	0.009	0.32
Shannon diversity index (≥0)	0.89 (0.14) ^{ab}	0.62 (0.13) ^{b}	0.61 (0.13) ^{b}	1.21 (0.08) ^{a}	0.71 (0.12) ^{ab}	3.60	0.015	0.30
Percentage of Landscape								
<u>Individual land cover classes</u>								
Wet prairie	66.3 (8.7) ^{a}	0 ^{b}	0 ^{b}	0.5 (0.5) ^{b}	0 ^{b}	30.3	<.0001	0.78 *
Upland prairie [1]	5.8 (4.0) ^{b}	71.5 (8.3) ^{a}	77.4 (5.7) ^{a}	26.4 (8.3) ^{b}	10.3 (4.4) ^{b}	32.2	<.0001	0.80
Sand barren	0 ^{b}	0 ^{b}	0.5 (0.5) ^{b}	36.3 (7.1) ^{a}	0.9 (0.9) ^{b}	28.8	<.0001	0.75 *
Savanna	0.9 (0.9) ^{b}	16.0 (7.8) ^{b}	5.8 (3.8) ^{b}	1.6 (1.1) ^{b}	70.1 (7.2) ^{a}	31.5	<.0001	0.79 *
Upland deciduous forest	0 ^{b}	0.6 (0.6) ^{ab}	0 ^{b}	0 ^{b}	9.8 (4.6) ^{a}	6.83	0.000	0.45 *
Eurasian meadow	7.2 (3.8) ^{ab}	6.2 (5.2) ^{ab}	7.7 (2.2) ^{ab}	18.7 (3.7) ^{a}	3.8 (1.7) ^{b}	3.18	0.026	0.28 *
<u>Composite land cover classes</u>								
Oak Openings [2]	73.1 (5.0) ^{a}	90.8 (6.5) ^{a}	83.7 (4.5) ^{a}	64.8 (6.4) ^{a}	81.2 (5.5) ^{a}	1.13	0.361	0.12 *
Human-modified [3]	22.6 (4.8) ^{ab}	6.2 (5.2) ^{c}	13.5 (4.0) ^{abc}	30.8 (5.4) ^{a}	7.7 (3.0) ^{bc}	6.07	0.001	0.42 *

Means with different lowercase letters within rows are significantly different at $P < 0.05$, Tukey's test. A single asterisk indicates data were arcsin-square root transformed prior to annalysis. Double asterisk indicates data were log transformed prior to analysis.

[1] Mesic prairie and dry prairie land cover types were included as a single land cover class by Schetter and Root (2011)

[2] Composite of all five Oak Openings land cover classes (wet prairie, mesic prairie, dry prairie, sand barren, oak savanna)

[3] Composite of Eurasian meadow, perennial ponds, dense urban, residential/mixed, turf/pasture, cropland, and conifer plantings (Schetter and Root 2011)

Table 3. (cont.)

			120-m spatial extent					
Landscape pattern metric	Wet prairie	Mesic prairie	Dry prairie	Sand barren	Savanna	*F*	*P*	R^2
Cohesion index (0-100)	71.7 (3.9) ^{a}	80.2 (4.5) ^{a}	76.7 (3.4) ^{a}	66.3 (3.4) ^{a}	77.6 (3.7) ^{a}	1.92	0.129	0.18
Landscape shape index (≥1)	2.53 (0.17) ^{a}	2.25 (0.20) ^{a}	2.42 (0.14) ^{a}	2.84 (0.11) ^{a}	2.42 (0.16) ^{a}	1.55	0.210	0.15 **
Patch richness density (no. patches / 1 ha)	1.36 (0.15) ^{a}	1.17 (0.24) ^{a}	1.19 (0.11) ^{a}	1.75 (0.15) ^{a}	1.28 (0.14) ^{a}	2.08	0.105	0.20
Shannon diversity index (≥0)	1.40 (0.15) ^{a}	1.15 (0.21) ^{a}	1.19 (0.16) ^{a}	1.72 (0.11) ^{a}	1.17 (0.15) ^{a}	2.26	0.083	0.21
Percentage of Landscape								
<u>Individual land cover classes</u>								
Wet prairie	46.9 (7.6) ^{a}	1.5 (1.5) ^{b}	0 ^{b}	0.3 (0.3) ^{b}	0.1 (0.1) ^{b}	60.5	<.0001	0.88 *
Upland prairie [1]	5.0 (3.2) ^{d}	49.8 (10.1) ^{ab}	55.6 (7.1) ^{a}	23.3 (5.5) ^{bc}	12.6 (4.8) ^{cd}	14.7	<.0001	0.65 *
Sand barren	0 ^{b}	0 ^{b}	0.8 (0.5) ^{b}	19.5 (6.2) ^{a}	1.4 (0.8) ^{b}	15.4	<.0001	0.64 *
Savanna	2.0 (1.9) ^{c}	24.8 (9.8) ^{b}	6.0 (2.6) ^{bc}	4.1 (0.9) ^{bc}	52.9 (7.9) ^{a}	18.1	<.0001	0.68 *
Upland deciduous forest	0.2 (0.2) ^{b}	7.0 (3.2) ^{ab}	4.3 (2.2) ^{ab}	4.2 (1.3) ^{ab}	14.3 (4.5) ^{a}	4.70	0.004	0.36 *
Eurasian meadow	5.6 (2.7) ^{b}	6.1 (3.5) ^{ab}	14.7 (2.5) ^{a}	15.6 (2.9) ^{a}	5.3 (1.7) ^{ab}	4.42	0.006	0.15 *
<u>Composite land cover classes</u>								
Oak Openings [2]	54.2 (4.5) ^{a}	79.0 (9.8) ^{a}	62.4 (7.1) ^{a}	47.2 (8.7) ^{a}	67.0 (7.6) ^{a}	2.20	0.091	0.22
Human-modified [3]	29.8 (5.0) ^{ab}	7.3 (4.7) ^{b}	25.5 (6.3) ^{ab}	36.6 (7.1) ^{a}	13.3 (3.7) ^{b}	4.21	0.008	0.34

Table 4. Relationship between native species richness and individual predictor variables at three levels of ecological hierarchy.

Variable type	Predictor variable	adj. R^2	Coeff.	modified df	F	P
ENTIRE REGION (n=39)	*no variables significant at p<0.05*					
UPLANDS (n=30)						
Physical	Slope (%)	0.23	-0.033	27.1	9.60	0.004
	C_{total} (%)	0.11	0.103	29.0	4.62	0.040
	$C_{organic}$ (%)	0.13	0.111	29.0	5.52	0.026
	Clay (%)	0.10	0.028	29.0	4.25	0.049
Landscape (60-m extent)	Oak Openings land cover (%)	0.52	0.007	13.2	15.3	0.002
	Human-modified land cover (%)	0.32	-0.006	15.3	8.02	0.012
Landscape (120-m extent)	Oak Openings land cover (%)	0.21	0.003	20.0	6.20	0.022
	Human-modified land cover (%)	0.18	-0.004	20.0	5.41	0.031
UPLAND PRAIRIES & BARRENS (n=21)						
Physical	Total foliar cover (%)	0.40	0.003	16.5	12.5	0.003
	Total ground litter (%)	0.24	0.003	20.0	7.46	0.013
	Bare ground (%)	0.42	-0.005	17.2	13.7	0.002
	Topographic variability (m)	0.34	-0.676	20.0	11.1	0.003
	Slope (%)	0.38	-1.379	17.7	12.6	0.002
Landscape (60-m extent)	Oak Openings land cover (%)	0.48	0.006	7.5	11.0	0.012
	Human-modified land cover (%)	0.50	-0.007	10.0	11.3	0.007
Landscape (120-m extent)	Savanna land cover (%)	0.20	0.005	15.2	4.88	0.043
	Human-modified land cover (%)	0.27	0.012	12.5	5.37	0.038

Values for df, F, and P were adjusted for spatial autocorrelation following Dutilleul (1993).

$\log_{10}$ (native species richness +1) transformation used prior to analysis

Table 5. Relationship between exotic species richness and individual predictor variables at three levels of ecological hierarchy.

Variable type	Predictor variable	adj. R^2	Coeff.	modified df	F	P
ENTIRE REGION (n=39)						
Physical	Total ground litter (%)	0.24	-0.007	36.3	12.91	0.001
	Bare ground (%)	0.10	0.008	37.0	5.17	0.029
Landscape (60-m extent)	Shannon diversity index	0.08	0.320	38.0	4.34	0.046
	Eurasian meadow land cover (%)	0.23	0.021	28.7	9.73	0.004
	Human-modified land cover (%)	0.22	0.014	32.5	10.37	0.003
Landscape (120-m extent)	Landscape shape index	0.12	0.333	38.0	6.25	0.017
	Patch richness density	0.08	0.003	37.5	4.30	0.045
	Shannon diversity index	0.11	0.308	38.0	5.46	0.025
	Savanna land cover(%)	0.24	-0.008	25.4	8.76	0.007
	Eurasian meadow land cover (%)	0.46	0.034	22.4	20.02	0.000
	Oak Openings land cover (%)	0.12	-0.007	30.9	5.31	0.028
	Human-modified land cover (%)	0.31	0.014	37.0	16.80	0.000
UPLANDS (n=30)						
Physical	Total foliar cover (%)	0.27	-0.007	29.0	11.78	0.002
	Distance from roads (m)	0.19	-0.001	17.3	4.84	0.042
	Distance from water (m)	0.29	-0.001	29.0	12.64	0.001
Landscape (60-m extent)	Patch richness density	0.13	0.002	24.3	4.77	0.039
	Eurasian meadow land cover (%)	0.11	0.013	26.3	6.40	0.018
	Human-modified land cover (%)	0.31	0.016	15.5	7.77	0.014
Landscape (120-m extent)	Cohesion index	0.20	-0.017	24.3	4.77	0.039
	Eurasian meadow land cover (%)	0.38	0.030	20.9	13.82	0.001
	Savanna land cover(%)	0.58	-0.011	12.0	17.48	0.001
	Human-modified land cover (%)	0.43	0.015	15.6	12.79	0.003
UPLAND PRAIRIES & BARRENS (n=21)						
Physical	Total foliar cover (%)	0.16	-0.005	20.0	4.95	0.039
	Soil Na	0.24	0.016	17.1	6.59	0.020
	Soil S	0.23	-0.022	20.0	6.85	0.017
Landscape (60-m extent)	Oak Openings land cover (%)	0.25	-0.011	14.8	5.77	0.030
	Human-modified land cover (%)	0.24	0.012	14.0	5.47	0.035
Landscape (120-m extent)	Cohesion index	0.25	-0.017	20.0	7.74	0.012
	Landscape shape index	0.26	0.428	20.0	7.96	0.011
	Patch richness density	0.15	0.003	20.0	4.47	0.048
	Savanna land cover(%)	0.61	-0.018	13.8	23.16	0.000
	Eurasian meadow land cover (%)	0.37	0.028	19.0	12.31	0.003
	Oak Openings land cover (%)	0.38	-0.010	14.9	10.78	0.005
	Human-modified land cover (%)	0.43	0.012	15.0	12.42	0.003

Values for df, F, and P were adjusted for spatial autocorrelation following Dutilleul (1993).

$\log_{10}$ (exotic species richness +1) transformation used prior to analysis

Table 6. Best models of native plant species richness at three levels of ecological hierarchy.

Spatial extent	Native Species Richness Predictor variable	Parameter estimate	P	Adjusted R^2	AICc	Δ AICc
ENTIRE REGION (n=37)*						
60-m	*no variables significant at p<0.05*					
120-m	*no variables significant at p<0.05*					
UPLANDS (n=29)**						
60-m	**Clay soil (%)**	**0.018**	**<0.0001**	**0.56**	**-44.21**	**0**
	Oak Openings land cover (%)	**0.006**				
120-m	Slope (%)	-0.021	0.002	0.37	-32.29	11.93
	Clay soil (%)	0.023				
	Oak Openings land cover (%)	0.002				
UPLAND PRAIRIES & BARRENS (n=20)**						
60-m	**Human-modified land cover (%)**	**-0.007**	**0.007**	**0.50**	**-26.12**	**0**
120-m	Bare ground (%)	-0.004	0.0029	0.49	-21.59	3.6518
	Human-modified land cover (%)	-0.0001				
	Savanna land cover (%)	0.004				

Native species richness was $\log_{10}(n + 1)$ transformed prior to analysis. The best model at each ecological level is shown in bold type.

* sample size reduced by 2 due to missing data

** sample size reduced by 1 due to missing data

Table 7. Best models of exotic plant species richness at three levels of ecological hierarchy.

Spatial extent	Exotic Species Richness Predictor variable	Parameter estimate	P	Adjusted R^2	AICc	Δ AICc
ENTIRE REGION (n=37)*						
60-m	Total ground litter (%)	0.003	<0.0001	0.56	15.34	9.43
	Upland prairies / barrens land cover (%)	0.008				
	Human-modified land cover (%)	0.017				
120-m	**Total ground litter (%)**	**0.002**	**<0.0001**	**0.62**	**6.59**	**0.68**
	Upland prairies / barrens land cover (%)	**0.010**				
	Human-modified land cover (%)	**0.017**				
UPLANDS (n=29)**						
60-m	Total foliar cover (%)	-0.003	<0.0001	0.60	14.80	12.17
	Distance from roads	-0.001				
	Distance from water	-0.001				
	Human-modified land cover (%)	0.007				
	Upland prairies / barrens land cover (%)	0.003				
120-m	**Total foliar cover (%)**	**-0.323**	**<0.0001**	**0.69**	**3.32**	**0.70**
	Distance from roads	**-0.001**				
	Savanna land cover (%)	**-0.009**				
UPLAND PRAIRIES & BARRENS (n=20)**						
60-m	Soil Na (ppm)	0.016	<0.0001	0.65	4.24	8.59
	Soil S (ppm)	-0.028				
	Oak Openings land cover (%)	-0.003				
120-m	**Soil Na (ppm)**	**0.132**	**<0.0001**	**0.77**	**-4.35**	**0.00**
	Soil S (ppm)	**-0.016**				
	Savanna land cover (%)	**-0.011**				

Exotic species richness was $\log_{10}(n + 1)$ transformed prior to analysis. The best model at each ecological level is shown in bold type.

* sample size reduced by 2 due to missing data

** sample size reduced by 1 due to missing data

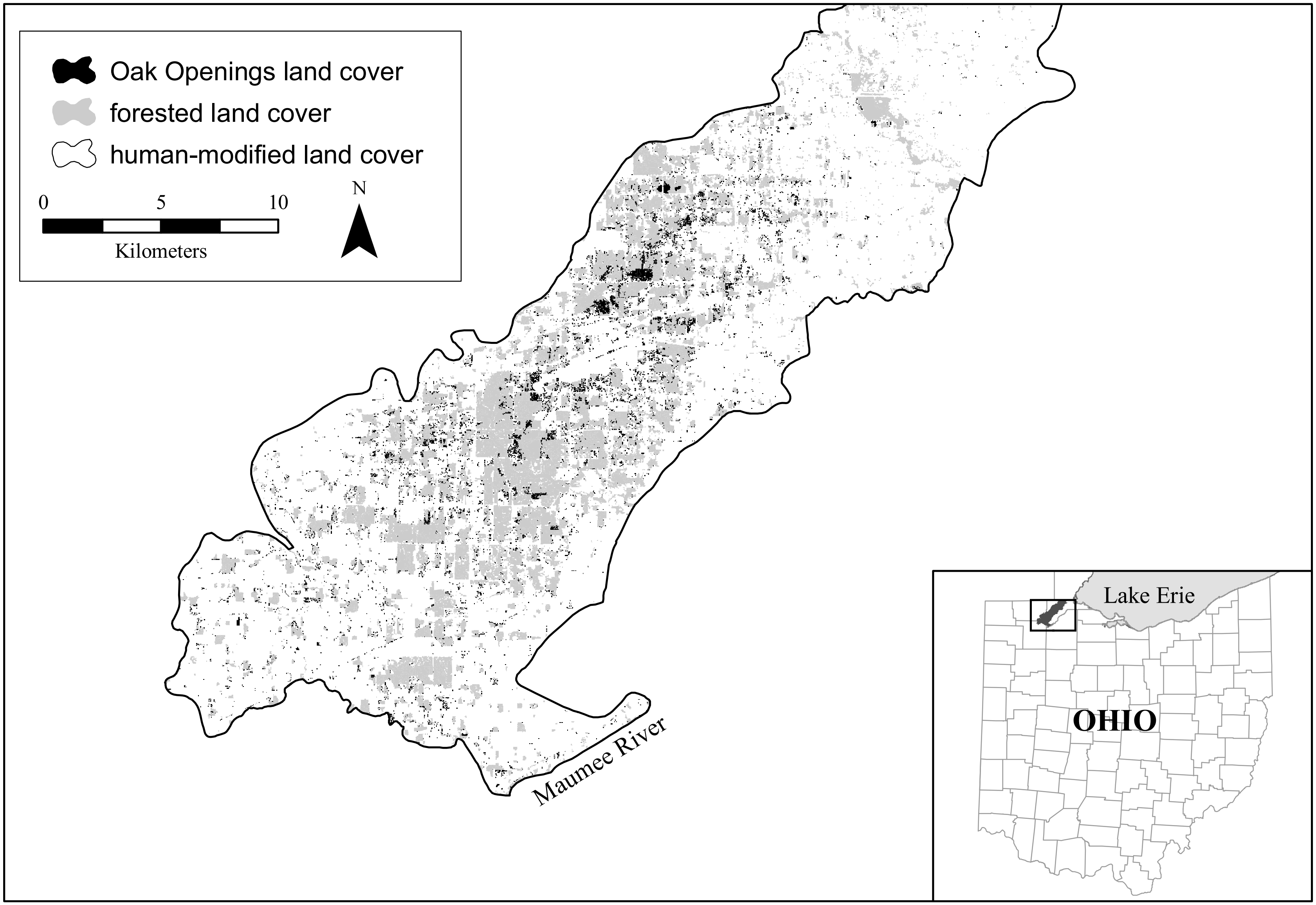

Figure 1. Current extent of Oak Openings land cover (adapted from Schetter and Root 2011). Oak Openings land cover includes wet prairies, dry prairies, mesic prairies, sand barrens, and oak savannas.

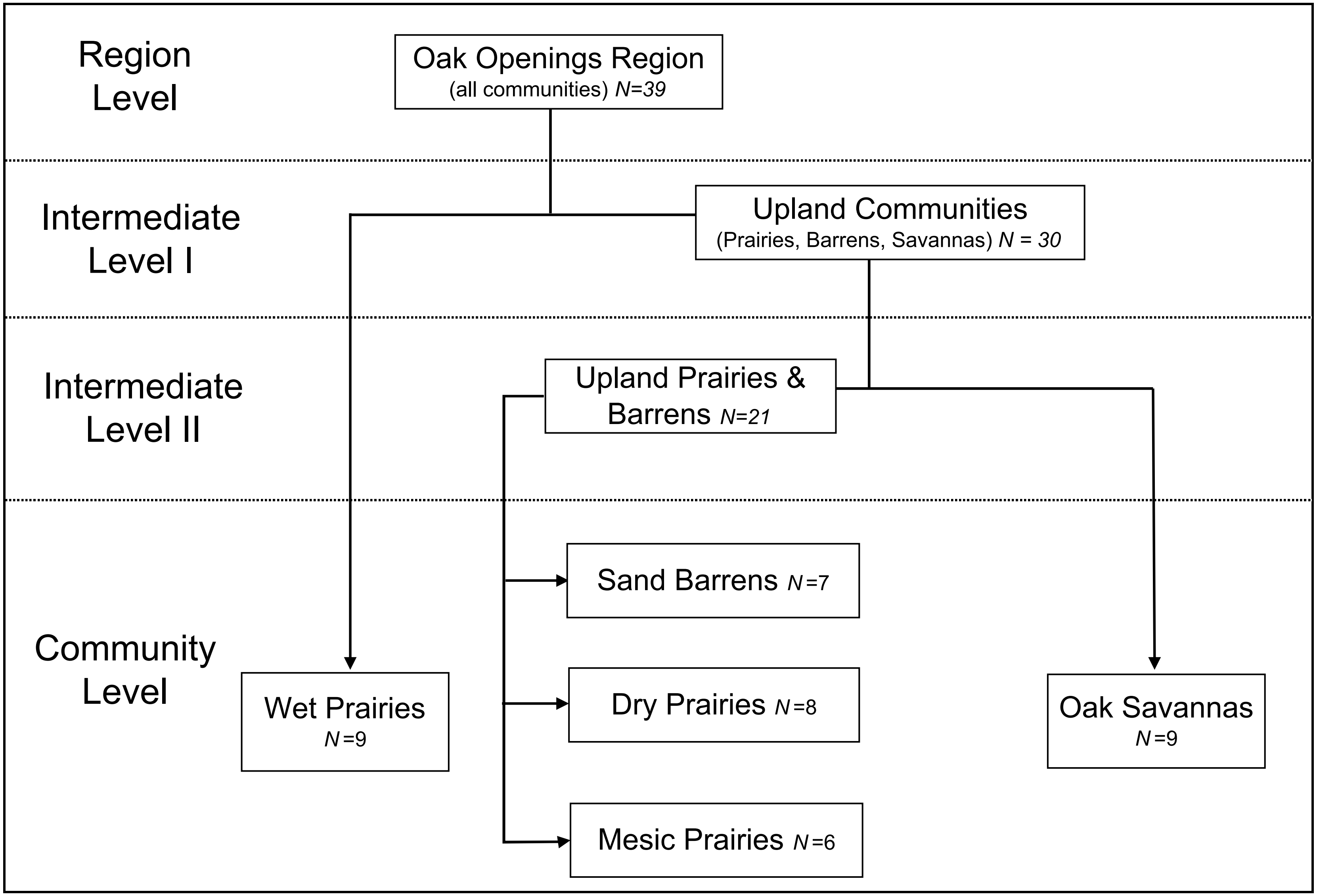

Figure 2. Five Oak Openings plant communities within the context of an ecological classification hierarchy

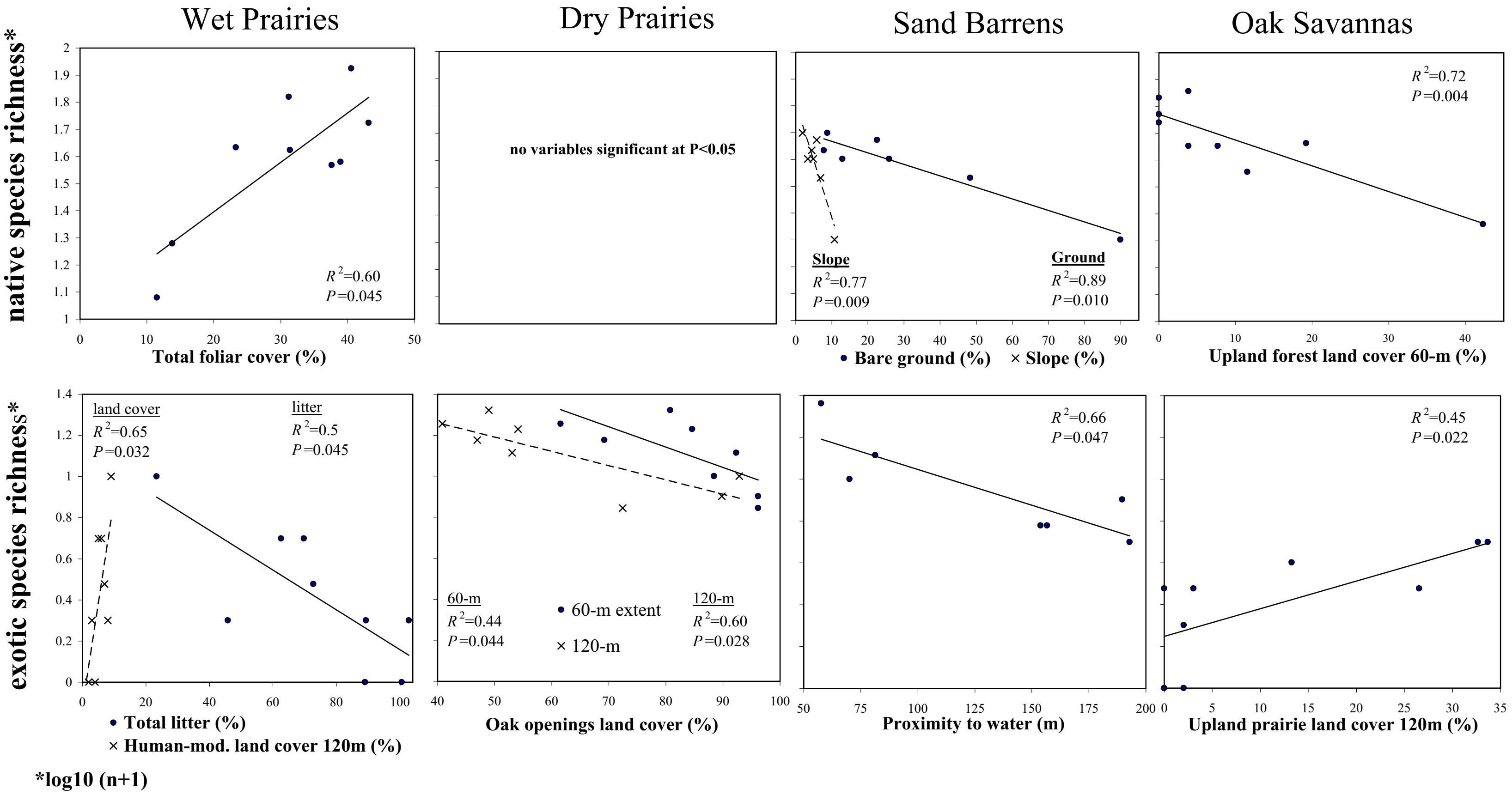

Figure 3. Relationship between native / exotic species richness and individual predictor variables for four Oak Openings community types. For mesix prairies, no variables were significant at P = 0.05.

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CHAPTER III

A MULTISPECIES HABITAT SUITABILITY MODEL OF RARE OAK OPENINGS PLANTS WITH IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

INTRODUCTION

The Oak Openings region of northwestern Ohio supports populations of over 140 plant species listed as endangered, threatened, or potentially threatened in Ohio (ODNR 2010). However, there is limited information on the current distribution of many of these species, especially outside of existing parks and preserves. In the face of limited time and financial resources, conservation planners and land managers require accurate information on the potential distribution and habitat suitability of these rare plant species in order to make informed decisions on reserve design and implementation of management and restoration treatments.

Niche-based species distribution models (SDMs), which quantify species-environment relationships, are widely used in ecology to 1) make predictions on the potential geographic distribution of species under a given set of environmental variables and 2) to evaluate the relative habitat suitability for species under varying levels of those parameters (Guisan and Zimmerman 2000, Guisan and Thuiller 2005). SDMs are especially appealing when dealing with rare or endangered species because there is often limited information on the distribution of these species and insufficient time and/or resources available to conduct ground-based surveys needed to find them (Wilson et al. 2005). Recent advances in GIS technology and modeling techniques, combined with the availability of spatially explicit, high resolution environmental data (e.g., Landsat) provide conservation planners with new opportunities to make empirically based decisions on the conservation of rare species using SDMs (Lahoz-Monfort et al. 2010).

One common SDM approach is to evaluate environmental data at locations where a given species is known to occur in comparison with locations where that species is found to be absent (i.e., presence/absence models). However, when presence/absence models are used to identify potentially suitable habitat for a given species, observed absence of that species at a specific location does not necessarily provide useful information on whether or not that location is actually capable of providing suitable habitat (Pearson et al. 2007). This may be especially true for managed landscapes such as the Oak Openings region where rare plant species may persist for years in the seed bank and emerge in response to restoration treatments in areas that were considered to be unsuitable habitat under pre-restoration conditions.

An alternative SDM approach is to evaluate environmental conditions where species are known to occur in relation to background environmental conditions across the entire study area. One such modeling technique known as maximum entropy modeling or Maxent (Phillips et al. 2006) has gained recent popularity among ecologists as a robust modeling algorithm shown to perform favorably when compared to other SDMs (Elith et al. 2006, Phillips et al. 2006, Pearson et al. 2007). Maxent is a deterministic, general-purpose algorithm based in machine learning methods and Bayesian statistics, which makes predictions based on incomplete information. Over a finite set of pixels (with each pixel representing a combination of environmental variables within a study area), Maxent estimates the target probability distribution by calculating the probability distribution of maximum entropy (i.e., closest to uniform) subject to a set of constraints based only on the information that is available (Philips et al. 2006). Maxent has been shown to perform well when sample sizes are small (i.e., less than 25; Hernandez et al. 2006, Pearson et al. 2007, Kumar and Stohlgren 2009) and at fine spatial resolutions (i.e., 30-m pixel; Gogol-Prokurat 2011), making it especially useful for evaluating potential habitat suitability for rare and endangered species for which limited site-specific information is available. Additionally, evaluation of Maxent models for multiple species within the same geographic area offers a potentially useful prioritization tool for conservation planners along with information on regional species richness patterns (Aranda and Lobo 2011, Larrea-Alcazar et al. 2011).

The objectives of this study were (1) to develop Maxent species distribution models for rare and endangered plant species of the Oak Openings region to evaluate potential habitat suitability, (2) to develop a multispecies habitat suitability model to help identify and prioritize areas for conservation and management of selected species within the Oak Openings region, and (3) to determine which environmental factors are most important for predicting habitat suitability among those species selected for model development.

METHODS

My initial objective for model development was to consider a broad range of rare plant species from various taxonomic groups, growth forms, and Oak Openings habitats. Because sampling bias in occurrence records is known to affect model performance (Wolmarans et al. 2010), I obtained site-specific location records of Oak Openings plant species from three separate sources with the expectation that this would reduce the influence of sampling bias from any one data source. These sources included: (1) thirty-nine 0.1-ha research plots established at randomly selected locations during 2008 and 2009 (further described in Chapter II), (2) records from Metroparks of the Toledo Area's ongoing rare plant monitoring program, conducted by park district employees and volunteers within established parks using an intensive non-random sampling protocol, and (3) records from the Ohio Department of Natural Resources (ODNR) Biodiversity Database collected haphazardly from a variety of sources and locations but typically verified by ODNR botanists from voucher specimens.

To be considered for model development, each species was required to meet the following criteria: (1) species must be on Ohio’s 2010-2011 rare plant list (ODNR 2010), (2) species records must have site-specific GPS coordinates collected between 2001 and 2011, (3) records for individual species must be $\geq$150m apart (equivalent to 5 map pixels) to reduce the potential influence of spatial autocorrelation in the dataset, and (4) a minimum of 10 site records must be available for each species. Species not meeting all four of these criteria were eliminated from further consideration. All records were converted to X-Y coordinates (UTM Datum WGS84) prior to analysis.

Environmental data representing a variety of potential habitat variables were obtained from four primary sources: (1) a 0.762-m grid digital elevation model (OGRIP 2006) used to derive the following topographic indices: aspect, elevation, roughness (measured as standard deviation of elevation within a 3-pixel window around each map pixel), slope, and solar insolation (calculated using the area solar radiation tool in ArcGis 9.2; ESRI, Redlands, CA); (2) digital soils data obtained from county soil surveys (Flesher et al. 1974, Stone et al. 1980, Stone et al. 1984), converted into the following three categories: a) Oak Openings indicator soils (hydric), b) Oak Openings indicator soils (nonhydric), c) other soil types; (3) a Landsat-based categorical land cover map of the Oak Openings region (Schetter and Root 2011); and (4) two separate spectral indices derived from Landsat 5 TM reflectance data (obtained from a single frame, 15 July 2008; USGS 2009); Normalized Difference Vegetation Index (NDVI) and soil brightness index (Huang et al. 2002). From these four data sources, a total of 16 environmental data layers were evaluated.

All environmental data were imported into ArcGIS 9.2, clipped to an area representing the Oak Openings region (Brewer and Vankat 2004), and resampled to a 30-m pixel. The various topographic indices were calculated using ArcGIS 9.2 Spatial Analyst. All categorical data (i.e., soils and land cover data) were converted to continuous data using the PLAND metric in program FRAGSTATS (McGarigal and Marks 1995) set to a circular 120-m neighborhood moving window, which provided a measure of percent area occupied by a given categorical variable within the 120-m circular window. The resulting data layers derived from FRAGSTATS thus represented the percentage of each pixel composed of a given soil / land cover type. All final environmental layers were converted to ASCII grid format (composed of 1301 columns and 1123 rows).

Maxent is capable of processing many environmental layers within a single model using an intrinsic regularization procedure to assign weights to each input environmental layer (Philips et al. 2006). Maxent begins with a uniform probability distribution, iteratively changing one weight at a time to achieve maximum likelihood of occurrence for the presence-only dataset (Hernandez et al. 2006). This process will always converge on the optimum probability distribution for the given dataset, making pre-selection of environmental layers prior to model development generally unnecessary (Elith et al 2010). However, Warren and Seifert (2011) found that inappropriately complex models reduced the ability to infer habitat quality from final models. Therefore, in the interest of model parsimony and to ease interpretation of results, I used a pre-screening process following Wollan et al. (2008) to eliminate insignificant environmental variables (out of 16 possible variables) prior to running Maxent models. For each species, I used logistic regression to compare environmental layers at presence locations with 200 randomly generated background points in program JMP 9.0 (SAS Institute, Inc.). For each species, only environmental variables where presence locations were significantly different from the random background values ($P < 0.05$) were considered for Maxent model development. Variables were also evaluated for cross-correlation in JMP 9.0 prior to model development. In cases where two or more variables were significantly cross-correlated ($r \geq 0.6$, $P < 0.05$), a single variable was retained based on my understanding of the data.

I used program MaxEnt 3.3 (Philips et al. 2006) to develop all models using default settings following Phillips and Dudik (2008). For each species, ten model replicates were run with occurrence records randomly partitioned into model building (70%) and model validation (30%) datasets prior to each run (Phillips et al. 2006, Yost et al. 2008). In this way, potential effects of spatial autocorrelation resulting from any single random partition of the validation dataset were reduced (Gogol-Prokurat 2011). For each species, the average results over all ten runs were used to evaluate model performance while all records were used to build the final model. All model outputs were on a logistic scale, where each pixel was assigned a value between zero and one, representing the relative habitat suitability for that species (from low to high, respectively). The following assumptions were implicit in the final models: 1) the species occurrence records (i.e., samples) used for analysis represented an unbiased sampling of all possible occurrence records, 2) the samples represented the full range of environmental conditions under which that species occurs within the study area, 3) the final model represented the realized niche for that species, and 4) each species is at equilibrium with its environment.

I evaluated model performance by considering both omission (false negative) and commission (false positive) errors within the model validation dataset using two separate approaches. First, as a threshold-independent evaluation of model performance, I used the 'receiver operating characteristic' (ROC) curve and the 'area under ROC curve' (AUC) statistic to determine whether each model performed better than would be expected for a random model (Phillips and others 2006). The ROC curve plots sensitivity vs. [1 – specificity], where sensitivity is equal to [1 – omission rate] and specificity is equal to the commission rate (i.e., false positive error rate). Note that with presence-only data, the true commission rate is unknown, and therefore, the fractional predicted area is used to approximate the true commission rate (Philips et al. 2006). An AUC value of 0.5 indicates that a given model performs no better than random, AUC values > 0.75 are considered potentially useful (Elith et al. 2006), and AUC values > 0.9 are considered 'good' (Wolmarans et al. 2010). The second, threshold-dependent approach to evaluate model performance was to calculate a one-tailed binomial test (approximated using X^2) at specific omission error thresholds to determine whether a given model was able to predict the validation locations significantly better than random at that given threshold (Philips et al. 2006). Fixed thresholds of one, five, and ten percent omission error rates were evaluated along with the 'maximum sensitivity plus specificity' (MSS) threshold which balances omission and commission errors among the validation dataset resulting in varying omission rates for each species (Liu and others 2005).

Following final development of all single-species Maxent models, I evaluated multispecies habitat suitability in two ways. First, the logistic output from each single-species model was normalized to a continuous scale from zero to one and averaged to create an equally weighted multispecies model. Second, I used the various omission thresholds to create a binomial output for each species where zero represented unsuitable habitat and one represented suitable habitat. Habitat suitability maps for each species were then combined into a single map where each pixel in the map contained a value from zero to *N*, where *N* is the total number of species for which that pixel is considered to be suitable habitat.

RESULTS

Based on initial species selection criteria, there were sufficient occurrence records for nine rare plant species to be considered for model development, including representatives of eight different families and a variety of growth forms (Table 1). Eight out of the nine selected species (including five upland and three facultative species) occur primarily on open sandy soils such as prairies, barrens and savannas. The remaining species (*Salix petiolaris*) is considered an obligate wetland species found mainly in wet prairies within the Oak Openings portion of its range. ODNR (2010) lists encroachment of woody vegetation as a conservation threat for all nine selected species.

Logistic regression was used to prescreen a total of 16 possible environmental variables for each plant species, resulting in three to six variables per species being selected for model development (Table 2). Based on individual models developed for all nine species, areas predicted as highly suitable habitat tended to occur in the central portion of the Oak Openings region while areas predicted as unsuitable habitat tended to occur in the northeastern and southwestern portions of region (Figure 1). Using mean AUC as an evaluation criterion, model performance for all nine species was considered ‘good’ based on generally accepted standards (Wolmarans et al. 2010; Table 3). The minimum AUC value reported for any single model replicate was 0.799 (for *A. purpurascens*) while the highest mean AUC value achieved was 0.992 (for *S. triglomerata*).

Models were also evaluated using threshold-dependent measures of performance, with higher omission error thresholds corresponding to smaller predicted area of suitable habitat (a proxy measure of commission error). At the 1% omission threshold (meaning that 1% of the validation dataset was incorrectly predicted as unsuitable habitat), seven of nine models performed significantly better than random ($P < 0.05$) while all nine models performed significantly better than random at the higher omission thresholds (Table 4). The 'maximum sensitivity plus specificity' threshold, which balances omission and commission errors individually for each model, consistently provided the most conservative estimate of habitat suitability for all species, with 2 – 16% of total land area predicted as suitable habitat.

The relative contribution of various environmental variables for the final Maxent models differed by species. However, land cover consistently accounted for a large proportion of the predictive power of all models, ranging from a combined low of 53% relative contribution for *S. petiolaris* to a combined high 93% for *J. greenei*. Soils were included in every model, but contribution varied widely among species, from 0% for *S. triglomerata* to 46% for *S. petiolaris*. At least one topographic variable was included in eight out of nine models (Table 3). However, topographic variables generally provided little contribution to overall model performance, ranging from a low of 0.1% for *L. perennis* to a combined high of 9% for *A. purpurascens*. Spectral indices were included in six out of nine models. For five of these, NDVI contributed from 0.5 to 8% of overall predictive power. Soil brightness index was included in only a single model, *A. purpurascens*, contributing 27% to model performance. Individual response curves for environmental variables used to develop each model are provided in Appendix III.

A multispecies model was developed to include eight of the nine species for which single-species models were constructed. *S. petiolaris* was excluded from the multispecies model as the only obligate wetland species of all those evaluated. Therefore the resulting eight-species model is not appropriate for evaluating wetlands. As with the individual species models, highest relative habitat suitability for the multispecies model was predicted in the central portion of the Oak Openings region, especially within existing parks and preserves (Figure 2).

Based on the various omission thresholds, between 21% and 69% of the Oak Openings region is considered suitable habitat for at least one of the eight species, while between 1% and 16% of the region is considered suitable for all eight species (Figure 3, Table 5). As expected for the multispecies model, as omission thresholds increased the amount of predicted suitable habitat across the region decreased. However, as omission thresholds increased, the proportion of available suitable habitat occurring within parks and preserves increased, suggesting that parks and preserves disproportionately include greater amounts of suitable habitat compared with the Oak Openings region in general. For example, nearly half of areas predicted suitable for all eight species at the most stringent MSS (maximum sensitivity plus specificity) threshold occur within parks and preserves. Under this MSS threshold, the range of environmental conditions for areas predicted as suitable habitat were narrower than for the region in general, especially for land cover and soils variables (Table 6).

DISCUSSION

Of the more than 140 species of rare plants known to occur in the Oak Openings region, only a small fraction of these species (less than seven percent) were available for modeling after applying a rigorous species-selection criteria to eliminate occurrence records that might negatively impact model performance. Of the nine species selected for model development, none are currently listed as endangered in Ohio (out of 60+ known endangered species in the region), and only one out of nine species (11%) is an obligate wetland plant. This is generally consistent with the proportion of obligate wetland species among the entire subset of Oak Openings rare plants (19%). The final results of this selection process, in which only nine species were available for modeling, highlight two issues regarding the status of rare plants in the Oak Openings: first, that there is limited information available on the regional distribution of most of these species; and second, these results reflect the imperiled status of many of these rare species, especially those that persist in wet prairies.

Despite the small number of available occurrence records (between 10 and 34) for the nine modeled species, all Maxent models performed well based on currently accepted evaluation criteria, consistent with the findings of other Maxent models developed with small sample sizes (Hernandez et al. 2006, Pearson et al. 2007, Kumar and Stohlgren 2009). Of the four classes of environmental variables that I evaluated, measures of proportional land cover derived from Landsat imagery were largely responsible for driving model performance for all nine species. Given the unique geological history of the Oak Openings and the important role of the resulting topography in shaping the region's plant communities (Forsyth 1970), it is perhaps surprising that topographic variables did not have a larger influence on model performance. However, the model results from this study do not necessarily suggest that topography has no predictive value in the Oak Openings, but rather that land cover has an especially strong influence on model performance. The results of single-variable jackknife tests on model performance (Appendix III) show that topographic variables are potentially useful for predicting habitat suitability for rare Oak Openings plants.

The single-species habitat suitability models developed in this study are generally consistent with the observed range of environmental conditions under which the modeled species are known to occur. For example, anecdotally *A. purpurascens* is one of the most widely distributed "rare" plants in the Oak Openings, being more tolerant of anthropogenic disturbances than other rare Oak Openings plants (T. Walters, *pers. comm*.), occurring frequently in recently-disturbed sandy soils. Concurrently, *A. purpurascens* had the largest predicted area of all modeled species, while soil brightness index (an indicator of bare sand) contributed 27% to model performance for this species. In contrast, the extent of suitable habitat for *S. petiolaris* (an obligate wetland plant) was much narrower, roughly following the extent of existing wet prairie and shrub/scrub wetlands in the region. Concurrently, hydric Oak Openings soils contributed to nearly half of model performance for this species.

While these Maxent models appear to have performed well, it is important to also evaluate potential caveats along with the utility of these models. I used a combination of logistic regression and heuristic selection to choose model variables for each species out of 16 possible environmental variables. While the rationale behind this decision is sound, it is possible (even likely) that other combinations of variables may be as good (or better) than the selected variables at driving model performance. Although it might be worthwhile to investigate other alternatives, the practical constraints of limited time and resources that one must face while making conservation planning decisions preclude focusing intensive effort in this regard. Although Wolmarans et al. (2010) found that intentionally-introduced sampling bias did not significantly affect model performance, it is possible that sampling bias among occurrence records in this study, which occurred disproportionately within managed preserves, may have impacted model performance, especially given the small sample sizes used. Further, spatial autocorrelation among occurrence records used for Maxent modeling is known to artificially inflate measures of model performance such as AUC (Veloz 2009, Merckx et al. 2011). Thus, the high AUC values reported in this study may be (at least partially) indicative of spatial autocorrelation rather than model performance. Finally, Philips et al. (2006) caution that Maxent model performance is unpredictable when environmental variables are strongly correlated. While I have taken reasonable precautions to address sampling bias, spatial autocorrelation, and cross-correlation among environmental variables, it is possible that any of these issues may have affected model performance to some extent.

Despite the possible limitations of the modeling approach used in this study, the resulting multispecies habitat suitability model has immediate applicability for evaluating various conservation planning alternatives for the Oak Openings region, especially given the time and expense required to build a similar model based on extensive field sampling. Depending on the intended use of this model, it is important to consider an appropriate omission error threshold. Lie et al. (2005) found that the MSS threshold, balancing both omission and commission errors), predicted true model performance better than other arbitrary thresholds. However, given the high omission error rate for most species in this study under the MSS threshold, it is likely that some areas of truly suitable habitat were excluded from the final model. Therefore a reasonable application of the MSS threshold for the Oak Openings would be to identify areas that have the highest habitat suitability for the eight modeled plant species under current conditions. The five and ten percent omission thresholds would perhaps be better suited for evaluating whether a given location might be capable of supporting suitable habitat following application of restoration treatments. For the species modeled in this study, the one percent omission threshold is likely too broad (i.e., commission errors are too high) to be of practical use given the large land area predicted as suitable under this threshold.

It is not surprising that according to the final multispecies model, up to half of all predicted suitable habitat in the Oak Openings region occurs within existing parks and preserves. However, the final model clearly shows that there are many unprotected / unmanaged areas throughout the region that may provide suitable habitat for eight species of Oak Openings plants that I evaluated. The results of the final model clearly point to the importance of land cover within the surrounding landscape as a predictor of habitat suitability for rare plants in the Oak Openings. These results are consistent with the findings in Chapter II of this dissertation that land cover in the surrounding landscape is an important predictor of both native and exotic plant species richness.

Table 1. Nine rare Oak Openings plant species for which Maxent habitat suitability models were developed.

Scientific Name	Common Name	Family	Wet Status	Form	Status	CofC	# Records
Aristida purpurascens	Purple Triple-awned Grass	Poaceae	upland	grass	P	7	28
Desmodium sessilifolium	Sessile Tick-trefoil	Fabaceae	upland	legume	T	8	20
Euthamia remota	Great Lakes Goldenrod	Asteracea	facultative	forb	T	9	28
Helianthemum canadense	Canada Frostweed	Cistaceae	upland	forb	T	9	29
Juncus greenei	Greene's Rush	Juncaceae	facultative	rush	T	7	24
Lupinus perennis	Wild Lupine	Fabaceae	upland	legume	P	7	29
Polygala polygama	Racemed Milkwort	Polygalaceae	upland	forb	T	10	34
Salix petiolaris	Slender Willow	Salicaceae	obligate	shrub	T	8	10
Scleria triglomerata	Tall Nut-rush	Cyperaceae	facultative	sedge	P	7	17

For status, "P" indicates potentially threatened and "T" indicates threatened. 'CofC' (coefficient of conservatism) and 'Wet Status' (wetland status) were obtained from Andreas et al. 2004.

Table 2. Prescreening of 16 environmental variables using logistic regression to determine Maxent model parameters for nine rare Oak Openings plant species.

Species Explanatory variable	*Aristida purpurascens*	*Desmodium sessilifolium*	*Euthamia remota*	*Helianthemum canadense*	*Juncus greenei*	*Lupinus perennis*	*Polygala polygama*	*Salix petiolaris*	*Scleria triglomerata*
Topographic									
Aspect (North)	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.01
Aspect (East)	**0.02** *	0.00	0.00	0.01	0.00	0.01	0.00	0.02	**0.04** *
Elevation	**0.09** ***	0.02	~~0.04~~ *	**0.04** **	**0.07** **	**0.11** ***	0.01	0.02	0.01
Roughness	0.01	0.00	**0.08** ***	0.01	0.02	0.02	0.02	~~0.15~~ ***	**0.12** ***
Slope	0.00	0.01	~~0.05~~ **	0.01	0.01	0.00	0.01	**0.11** **	~~0.06~~ **
Solar insolation	0.02	0.00	**0.03** *	**0.03** *	0.01	0.00	0.00	0.01	**0.03** *
Soil type (% area)									
Oak Openings (non-hydric)	**0.04** *	**0.18** ***	0.00	**0.22** ***	**0.12** ***	**0.25** ***	**0.24** ***	~~0.15~~ ***	~~0.03~~ *
Oak Openings (hydric)	0.01	0.02	~~0.11~~ ***	~~0.04~~ **	0.00	~~0.03~~ *	0.04 **	**0.49** ***	0.03
Oak Openings (combined)	~~0.05~~ **	~~0.06~~ **	**0.12** ***	~~0.04~~ **	~~0.12~~ ***	~~0.06~~ **	~~0.05~~ **	~~0.16~~ ***	**0.09** ***
Land Cover type (% area)									
Developed	**0.20** ***	**0.26** ***	**0.30** ***	**0.30** ***	**0.37** ***	**0.37** ***	**0.33** ***	**0.23** ***	**0.41** ***
Forested	0.01	0.00	0.00	~~0.04~~ *	0.00	0.02	~~0.06~~ ***	0.01	0.00
Oak Openings (all)	~~0.52~~ ***	~~0.48~~ ***	**0.53** ***	~~0.44~~ ***	**0.70** ***	~~0.60~~ ***	~~0.37~~ ***	**0.55** ***	**0.69** ***
Oak Openings (upland)	~~0.47~~ ***	**0.48** ***	~~0.38~~ ***	**0.44** ***	~~0.70~~ ***	**0.60** ***	**0.37** ***	~~0.06~~ *	~~0.68~~ ***
Wetland	0.00	0.00	~~0.04~~ **	0.00	0.00	0.14	0.00	~~0.34~~ ***	0.00
Spectral									
NDVI	0.00	0.01	~~0.02~~ *	**0.03** *	**0.04** *	**0.04** *	**0.05** **	0.02	~~0.09~~ **
Brightness	**0.04** *	0.01	0.02	0.00	0.01	0.00	0.00	~~0.22~~ ***	0.01
No. of variables selected	5	3	5	6	5	5	4	4	6

R^2 values are reported for each species. Bold type indicates variables selected for Maxent model development. Strike-through type indicates variables removed from consideration due to cross correlation. "*" denotes $P < 0.05$, "**" denotes $P < 0.01$, "***" denotes $P < 0.001$. For soils, "Oak Openings (combined)" includes both hydric and non-hydric soils. For land cover type, "developed" includes dense urban, residential/mixed, turf/pasture, and croplands land cover types; "forested" includes swamp forests, floodplain forests, and upland deciduous forests; "Oak Openings (all)" includes wet praires, upland prairies, sand barrens, and oak savannas; Oak Openings (upland) includes upland prairies, sand barrens, and oak savannas.

Table 3. Percent contribution of environmental variables to Maxent species distribution models develoepd for nine plant rare Oak Openings plant species.

Species Explanatory variable	*Aristida purpurascens*	*Desmodium sessilifolium*	*Euthamia remota*	*Helianthemum canadense*	*Juncus greenei*	*Lupinus perennis*	*Polygala polygama*	*Salix petiolaris*	*Scleria triglomerata*
Topographic									
Aspect (East)	3.8 +								1.3 irr
Elevation	5.2 +			0.2 -	0.4 irr	0.1 irr			
Roughness			4.6 -						6.5 -
Slope								1.9 -	
Solar insolation			0.7 +	1.1 +					1.0 +
Soil type (% area)									
Oak Openings (non-hydric)	6.4 irr	15.8 +		16.1 +	6.6 +	16.9 +	19.9 +		
Oak Openings (hydric)								45.6 +	
Oak Openings (combined)			1.4 +						0 -
Developed	57.4 -	45.8 -	23.8 -	33.1 -	11.3 -	28.6 -	41.4 -	9.2 -	33.7 -
Oak Openings (all)			67.0 +		81.2 +			43.4 +	57.3 +
Oak Openings (upland)		38.4 +		41.8 +		52.0 +	37.9 +		
Spectral									
NDVI			2.5 -	7.8 irr	0.5 -	2.3 -	0.9 irr		
Brightness	27.3 +								
Minimum AUC	0.799	0.944	0.940	0.931	0.976	0.972	0.910	0.966	0.983
Mean AUC	0.890	0.972	0.961	0.961	0.985	0.981	0.953	0.981	0.992
SD AUC	0.045	0.017	0.012	0.021	0.007	0.006	0.019	0.011	0.004

The symbol following each number describes the response curve for the corresponding environmental variable in each Maxent model ("+" for increasing, "-" for decreasing, "irr" for irregular). Minimum AUC indicates the lowest AUC value out of ten replicate models for each species. For soils, "Oak Openings (combined)" includes both hydric and non-hydric soils. For land cover type, "developed" includes dense urban, residential/mixed, turf/pasture, and croplands land cover types; "forested" includes swamp forests, floodplain forests, and upland deciduous forests; "Oak Openings (all)" includes wet praires, upland prairies, sand barrens, and oak savannas; Oak Openings (upland) includes upland prairies, sand barrens, and oak savannas.

Table 4. Proportional predicted area of suitable habitat within the Oak Openings region for nine rare plant species. Predictions are based on Maxent species distribution models evaluted using four separate ommission thresholds.

Species Ommission threshold	*Aristida purpurascens*	*Desmodium sessilifolium*	*Euthamia remota*	*Helianthemum canadense*	*Juncus greenei*	*Lupinus perennis*	*Polygala polygama*	*Salix petiolaris*	*Scleria triglomerata*
1%	0.39	0.54 *	0.40 **	0.38 **	0.27 ***	0.22 ***	0.30 ***	0.51	0.22 ***
5%	0.34 *	0.30 **	0.22 ***	0.20 ***	0.11 ***	0.11 ***	0.19 ***	0.27 *	0.14 ***
10%	0.24 *	0.21 ***	0.14 ***	0.12 ***	0.05 ***	0.07 ***	0.12 ***	0.16 **	0.09 ***
MSS threshold	**18%**	**29%**	**15%**	**19%**	**13%**	**10%**	**15%**	**32%**	**31%**
	0.16 ***	0.06 ***	0.09 ***	0.06 ***	0.02 ***	0.07 ***	0.09 ***	0.03 ***	0.02 ***

MSS threshold refers to ‘maximum sensitivity plus specificity’ which balances both ommission and commission errors within the test dataset. "*" denotes $P < 0.05$, "**" denotes $P < 0.01$, "***" denotes $P < 0.001$. MSS refers to ‘maximum sensitivity plus specificity’ which varies for each species. Percentages shown in the row for MSS threshold indicate the corresponding omission error rate for each species. Each number in the table can be multiplied by 45,882 ha (total land area modeled) to determine number of hectares predicted as suitable for each species under each omission threshold.

Table 5. Cumulative predicted area of suitable habitat within the Oak Openings region for eight rare plant species evaluated using four different omission thresholds. Numbers reported under 'Parks and Preserves' indicate the proportion of available suitable habitat under each ommission threshold that occurs within existing parks and preserves.

	Cumulative predicted area: Oak Openings Region				Percent area within Parks and Preserves			
	omission threshold				omission threshold			
No. Species	1%	5%	10%	MSS	1%	5%	10%	MSS
1 of 8	0.69	0.39	0.30	0.21	0.14	0.24	0.30	0.34
2 of 8	0.50	0.29	0.22	0.11	0.19	0.31	0.36	0.42
3 of 8	0.41	0.25	0.17	0.08	0.23	0.34	0.39	0.46
4 of 8	0.35	0.21	0.13	0.06	0.27	0.37	0.40	0.46
5 of 8	0.30	0.17	0.09	0.05	0.30	0.39	0.42	0.45
6 of 8	0.28	0.14	0.07	0.03	0.32	0.39	0.42	0.43
7 of 8	0.24	0.10	0.05	0.02	0.34	0.39	0.42	0.47
all 8	0.16	0.05	0.02	0.01	0.37	0.39	0.43	0.48

MSS threshold refers to ‘maximum sensitivity plus specificity’ which balances both ommission and commission errors within the test dataset. Each number in the table can be multiplied by 45,882 ha

Table 6. Values for 16 environmental variables evaluated for Maxent model development for rare Oak Openings plant species.

		Oak Openings Region			8-Species Suitabilitiy Model		
Explanatory variable	Unit	Range	Mean	SD	Range	Mean	SD
Topographic							
Aspect (North)	degrees	-1 - 1	0.06	0.70	-1 - 1	0.15	0.727
Aspect (East)	degrees	-1 - 1	-0.04	0.71	-1 - 1	0.12	0.675
Elevation	m	579.5 - 718.0	660.5	20.0	624.4 - 692.2	672.6	9.88
Roughness	m	0 - 16.35	0.70	0.72	0 - 1.64	0.38	0.216
Slope	m	0 - 98.8	2.8	3.6	0 - 9.3	1.5	1.2
Solar insolation	KWH/m2	186.9 - 596.8	522.5	133.3	493.3 - 526.4	526.4	593.1
Soil type (% area)							
Oak Openings (non-hydric)	%	0 - 100	33.8	24.7	8 - 100	55.1	22.93
Oak Openings (hydric)	%	0 - 100	34.3	29.8	0 - 92	39.7	23.6
Oak Openings (combined)	%	0 - 100	68.0	38.8	27 - 100	94.8	12.79
Land Cover type (% area)							
Developed	%	0 - 100	72.9	33.2	0 - 49	10.5	10.14
Forested	%	0 - 100	21.2	30.4	0 - 94	26.7	20.29
Oak Openings (all)	%	0 - 100	3.0	7.5	6 - 100	47.9	18.87
Oak Openings (upland)	%	0 - 100	2.9	7.3	6 - 100	47.7	18.88
Wetland	%	0 -100	12.7	19.5	0 - 67	13.1	12.67
Spectral							
NDVI	index	0 - 255	207.4	41.5	89 - 253	230.1	20.43
Brightness	index	45 - 255	164.6	24.3	116 - 255	167.5	14.6

Values reported under 'Oak Openings Region' are based on all map pixels within the study area. Values reported under '8-Species Suitabilitiy Model' represent only map pixels predicted as suitable habitat for all eight species in the final multispecies model using the ‘maximum sensitivity plus specificity’ omission threshold.

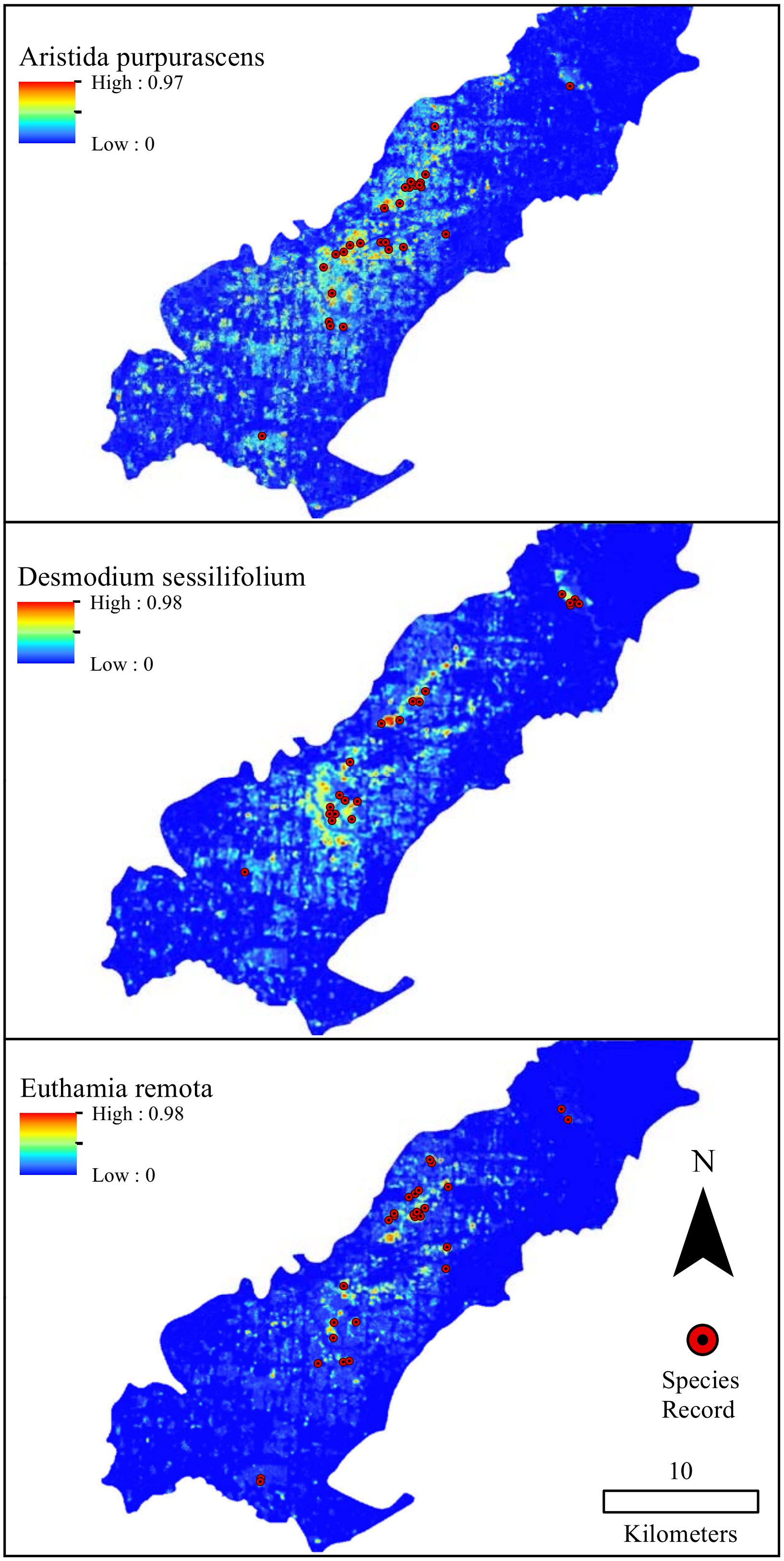

Figure 1. Maxent habitat suitability models for nine Oak Openings plant species. Logistic output shows relative suitability from low (blue) to high (red). Red circles show locations of species occurance records.

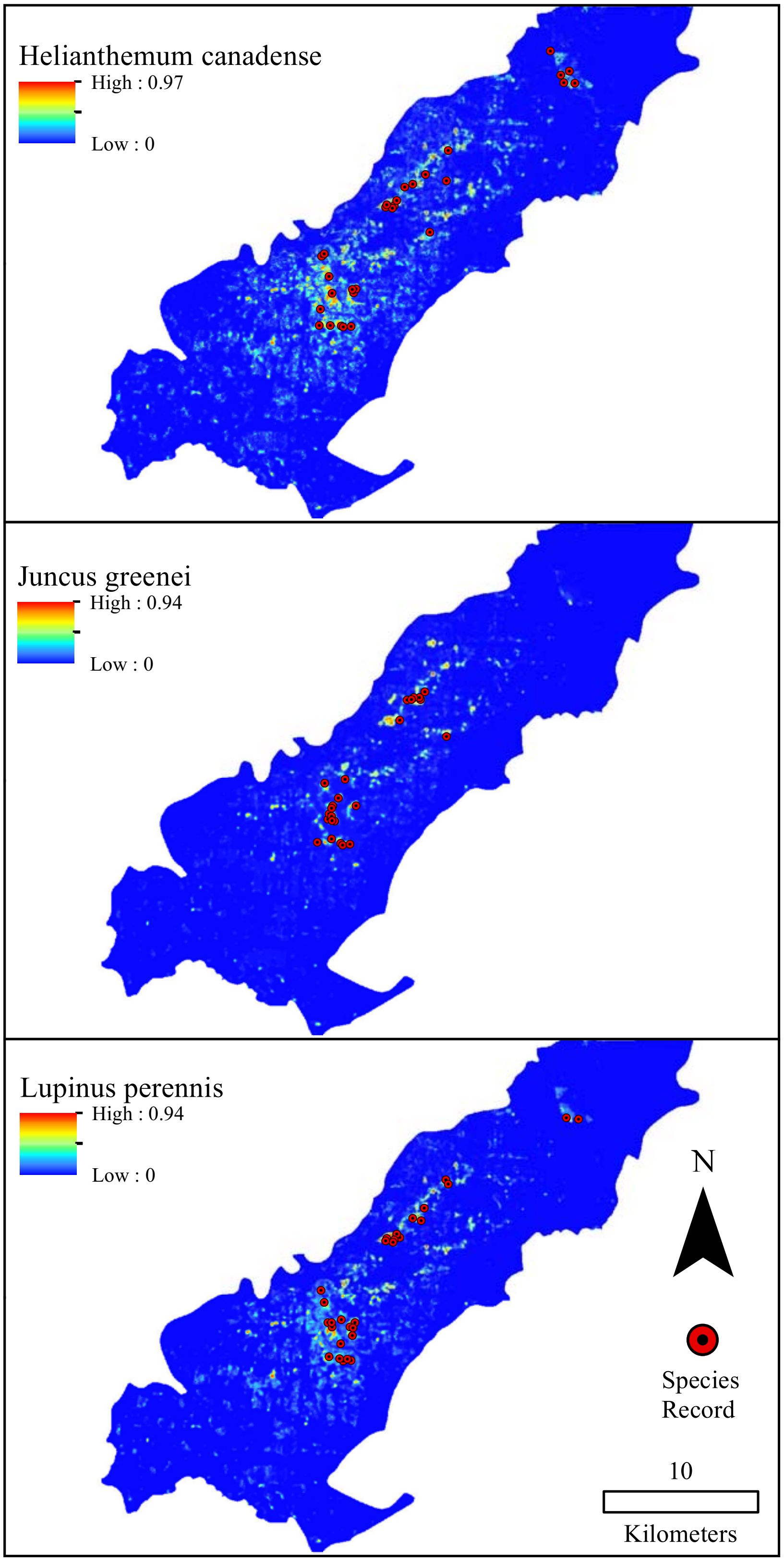

Figure 1. (continued)

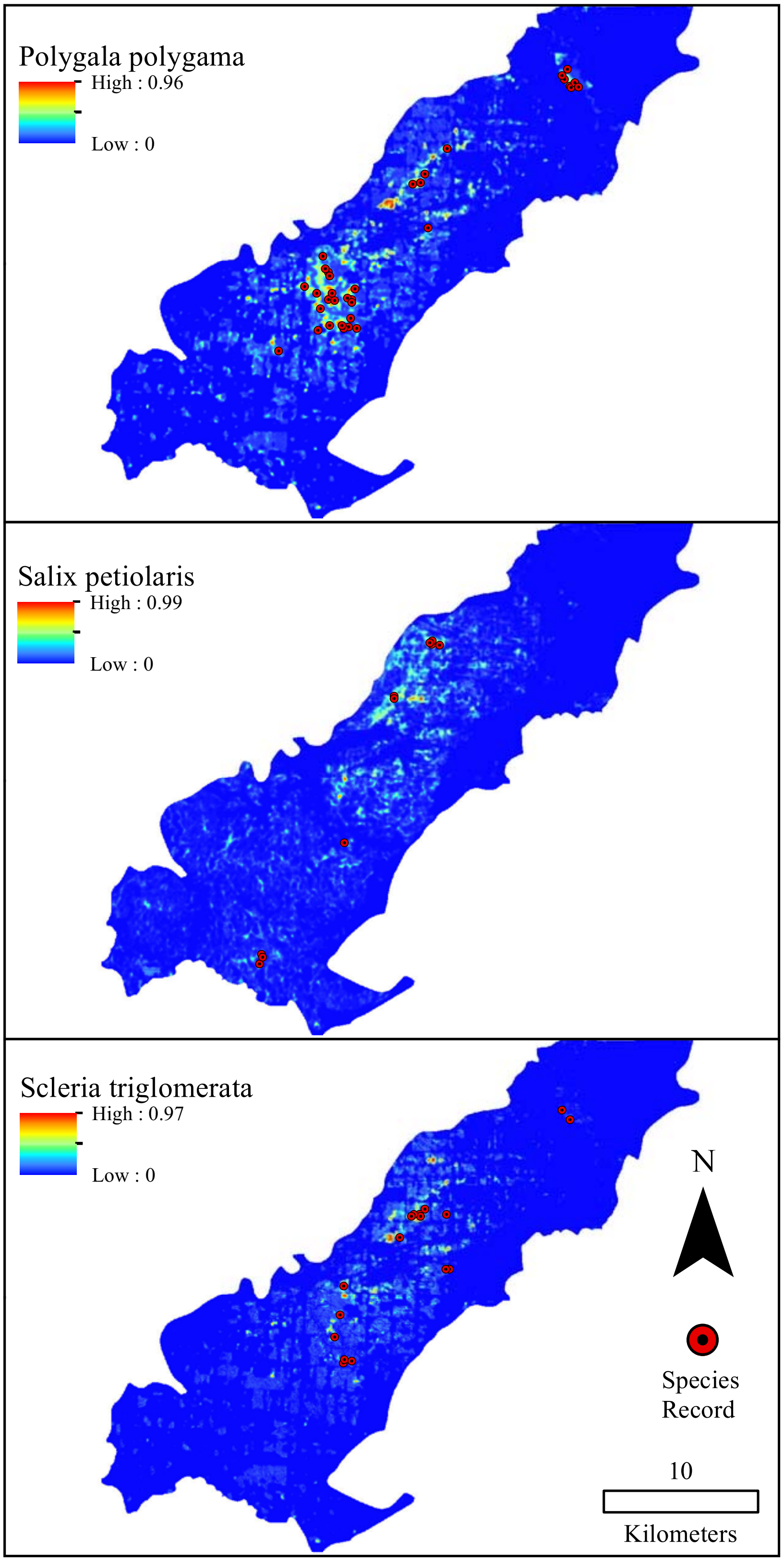

Figure 1. (continued)

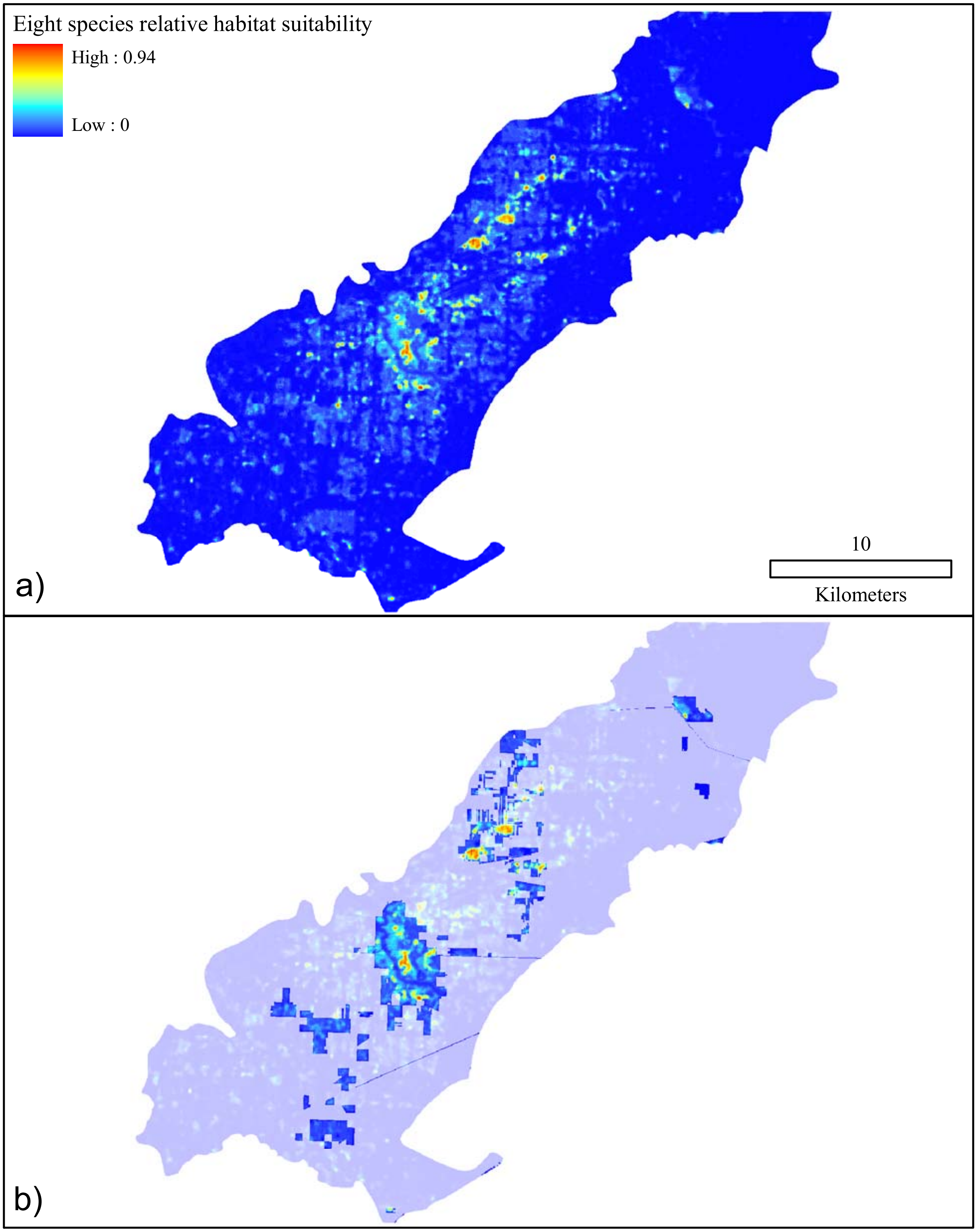

Figure 2. a) Multispecies Maxent habitat suitability model averaged across 8 Oak Openings species. Logistic output shows relative suitability from low (blue) to high (red). b) Same model featuring existing parks and preserves.

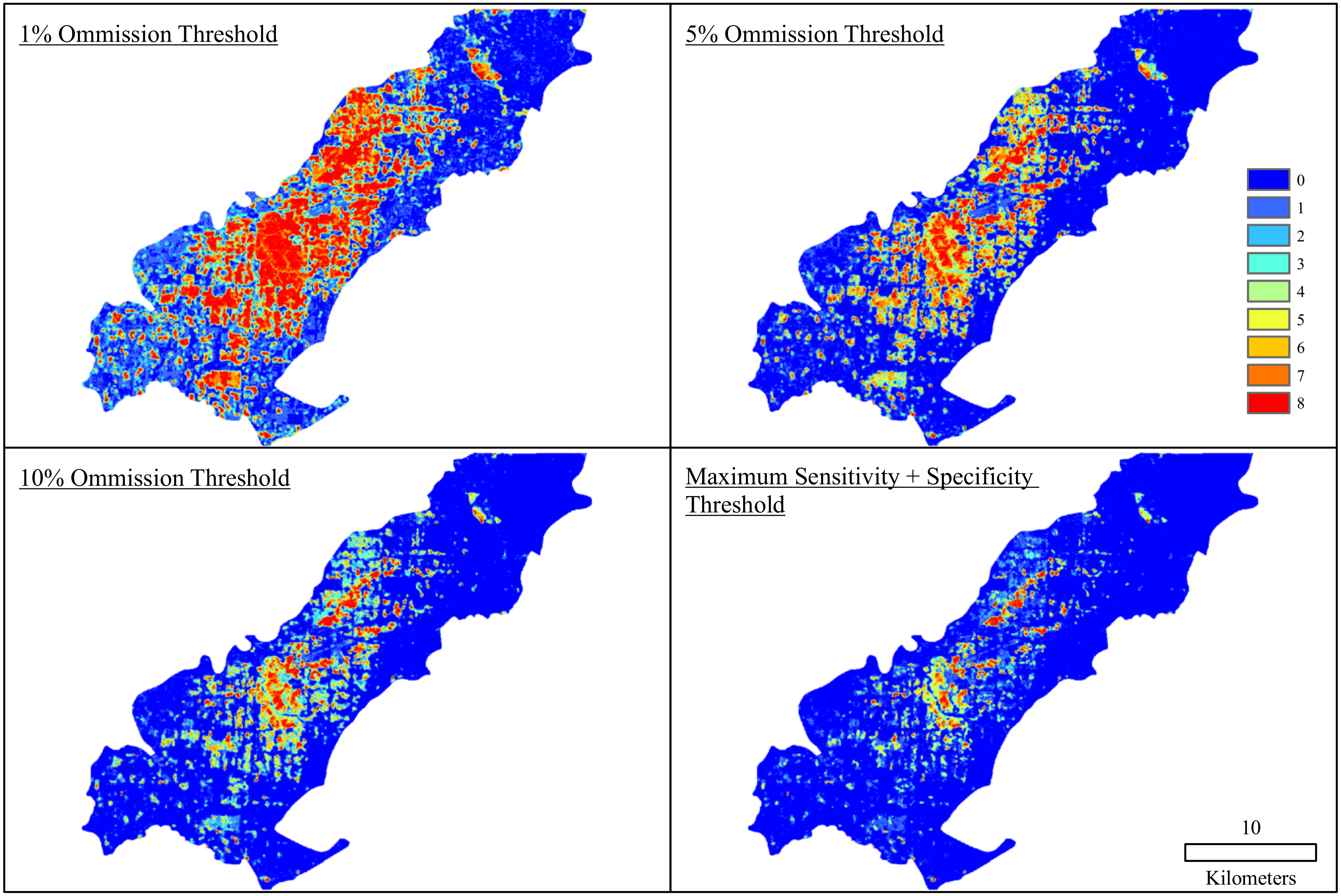

Figure 3. Absolute habitat suitability for eight Oak Openings plant species using four separate ommission thresholds. Each color shows the respective number of species for which habitat is considered suitable.

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CHAPTER IV

Conclusions

In this dissertation, I explored patterns of plant diversity in the Oak Openings region across multiple spatial and ecological scales. In the first chapter, I used multi-seasonal Landsat images to map the current extent and distribution of native plant communities within the context of the surrounding human-dominated landscape. I determined that less than 3% of the Oak Openings region remains covered by native savanna, prairie, and barrens communities, compared to human-dominated land cover types (e.g., urban, residential, agricultural), which now occupy nearly three-fourths of the region. Among native communities, which are now heavily fragmented, wet prairies have faced the sharpest declines, now covering less than 0.1% of the region's total land area. Further, I found that nearly all large (>1 hectare) remnant savannas and wet prairies occur within existing parks and preserves, although opportunities for restoration of these communities in additional areas within their historic extent certainly exist.

Methodologically, I found that classification accuracy of individual land cover types was driven at least in part, by patch size on the landscape. Thus, land cover types consisting of small (< 0.2 ha), isolated patches on the landscape, such as sand barrens, were difficult to classify within an acceptable range of accuracy, given the constraint of the 30-m Landsat pixel. Further, I found that use of fuzzy-set theory (i.e., the concept that individual pixels may represent multiple land cover classes) improved overall map accuracy by as much as nine percent. This is an important consideration for land areas such as the Oak Openings, where narrow, but ecologically-significant ecotones may exist across community types. These findings highlight the utility of using Landsat images to evaluate mixed-use landscapes at regional scales but demonstrate the limitations of using these images at local scales.

In the second chapter, I evaluated patterns of native and exotic plant species richness within and among thirty-nine, randomly selected study sites stratified across five Oak Openings communities. I found that measures of spatial heterogeneity derived from a combination of field data, remotely sensed data, and landscape pattern metrics were able to explain trends in species richness at multiple ecological levels (from whole-region to individual community). Further, I found that these trends differed for native and exotic species in three main ways. First, multivariate models of species richness consistently explained more variation for exotic species (up to 77%) than for native species (up to 56%). Second, exotic species richness was better explained at a larger spatial extent (roughly six hectares) while native richness was better explained at a smaller spatial extent (roughly two hectares). Finally, native species richness tended to be negatively correlated with environmental variables indicative of human disturbance, while exotic species richness tended to be positively correlated with those same variables. In particular, I found that percentage of human-modified land cover (negatively correlated with native richness and positively correlated with exotic richness) was a particularly useful predictor of species richness.

While I cannot rule out the contribution of other variables known to influence patterns of plant species richness patterns such as climate, geology, and natural disturbances (e.g., fire regime, hydrologic cycles), based on the results of this chapter I conclude that human-caused disturbances exert a strong influence on species richness patterns within a mixed-disturbance oak savanna landscape. It is therefore important for resource managers to carefully consider the context of the landscape surrounding remnant Oak Openings communities when evaluating potential management and restoration treatments.

In the third chapter, I developed species distribution models for nine rare plant species within the Oak Openings region using the Maxent modeling algorithm with two primary goals in mind. My first goal was to determine which environmental variables were most important for predicting habitat suitability for these species. My second goal was to construct a multispecies habitat suitability model to help identify and prioritize areas for conservation and management within the Oak Openings region.

Despite the low number of occurrence records for each species, all models performed well based on accepted evaluation statistics, although it is possible that spatial bias in occurrence records and correlations among predictor variables may have artificially inflated estimates of model performance. While the relative contribution of individual environmental variables differed by species, proportional land cover (derived from Chapter I) consistently accounted for a large proportion of the predictive power of all models. Specifically, as percentage of human development increased in the surrounding landscape, the relative habitat suitability for modeled plant species typically decreased. Based on the final multispecies model, up to half of all predicted suitable habitat in the Oak Openings region occurs within existing parks and preserves. However, potentially suitable habitat was identified within unprotected areas throughout the region.

The combined results of these three chapters demonstrate the strong influence of anthropogenic land cover on native communities and species. Further, these results emphasize the importance of using a multi-scale approach to examine the complex relationships between spatial heterogeneity and plant diversity. Multispectral data derived from Landsat images proved to be an especially important tool for implementing this study in its entirety. These data were used to develop the categorical land cover map in Chapter I, and to predict both species richness and habitat suitability in the subsequent chapters. The Landsat program provides an inexpensive, long-term dataset for continued diversity research. In particular, proportional land cover provides a potentially useful rapid assessment tool for evaluating heterogeneity-diversity relationships at multiple spatial scales. While the field-based multi-scale research plots used in Chapter II were shown to yield a large amount of data that is useful for many potential research objectives, these data were time-consuming and therefore costly to collect. It is therefore promising that predictions from the habitat suitability models derived from a small number of occurrence records in Chapter III yielded similar results to the species richness models from Chapter II; especially given that conservation planning decisions on reserve design and implementation of management and restoration treatments are often made in the face of limited time and financial resources.

APPENDIX I: SPECIES LIST

Table 1. Complete list of 406 plant species (349 native, 57 exotic) sampled among five community types within the Oak Openings region. Number of 1000-m^2 plots occupied by each species is shown with number of occupied 1-m^2 subplots in parentheses. Scientific names shown in all capital letters are considered exotic to Ohio (Andreas et al. 2004). For status, E = Ohio endangered, T = Ohio threatened, P = Ohio potentially threatened (ODNR 2010). CofC is '*Coefficient of Conservatism*' from Andreas et al. (2004). Total number of 1000-m^2 plots sampled within each community type is as follows: wet prairie (9), mesic prairie (6), dry prairie (8), sand barrens (7), wet prairie (9). Ten 1-m^2 subplots were sampled per 1000-m^2 plot. For taxonomic authority and additional species information, refer to Andreas et al. (2004). For methodology and complete list of references, refer to Chapter II.

Status	CofC	Scientific Name	Common Name	Family	Total	Wet prairie	Mesic prairie	Dry prairie	Sand barrens	Oak savanna
	2	*Acer rubrum*	red maple	Aceraceae	16 (22)	2 (1)	3 (3)	2 (3)	3 (7)	6 (8)
	3	*Acer saccharinum*	silver maple	Aceraceae	13 (12)	2 (4)	2	2 (2)	2 (1)	5 (5)
	1	*Achillea millefolium*	yarrow	Asteraceae	15 (35)	2 (4)	4 (13)	4 (16)	5 (2)	
T	7	*Actaea rubra*	red baneberry	Ranunculaceae	1					1
T	8	*Agalinis gattingeri*	Gattinger's foxglove	Scophulariaceae	1 (4)		1 (4)			
	6	*Agalinis purpurea* var. *purpurea*	large purple foxglove	Scophulariaceae	3 (4)		1 (4)	1		1
	4	*Agalinis tenuifolia*	slender foxglove	Scophulariaceae	8 (13)	2 (2)	5 (9)			1 (2)
	2	*Agrimonia parviflora*	small-flowered agrimony	Rosaceae	5 (2)	2 (1)	2 (1)	1		
	*	*AGROSTIS GIGANTEA*	redtop	Poaceae	10 (17)	3 (5)	3 (9)	3 (3)		1
	3	*Agrostis hyemalis*	ticklegrass	Poaceae	11 (25)		5 (14)	3 (3)	2 (8)	1
	4	*Agrostis perennans*	autumn bent grass	Poaceae	1 (2)			1 (2)		
	*	*AILANTHUS ALTISSIMA*	tree-of-heaven	Simaroubaceae	1				1	
	8	*Aletris farinosa*	colic-root	Liliaceae	5 (5)		4 (5)	1		
	2	*Alisma subcordatum*	southern water-plantain	Alismataceae	3 (6)	3 (6)				
	0	*Ambrosia artemisiifolia*	common ragweed	Asteraceae	19 (42)	1 (2)	3 (4)	6 (20)	6 (13)	3 (3)
	5	*Amelanchier arborea*	downy serviceberry	Rosaceae	4 (2)			1		3 (2)
	7	*Amelanchier spicata*	dwarf serviceberry	Rosaceae	1					1
	4	*Amphicarpaea bracteata*	hog-peanut	Fabaceae	1		1			
	5	*Andropogon gerardii*	big bluestem	Poaceae	14 (31)	2 (4)	6 (24)	3 (1)	1 (1)	2 (1)
	3	*Andropogon virginicus*	common broom-sedge	Poaceae	7 (22)		1 (3)	2 (7)	3 (12)	1
T	8	*Anemone cylindrica*	prairie thimbleweed	Ranunculaceae	2				1	1
	3	*Anemone virginiana*	woodland thimbleweed	Ranunculaceae	4 (1)	1	1 (1)	2		

Table 1. Continued

Status	CofC	Scientific Name	Common Name	Family	Total	Wet prairie	Mesic prairie	Dry prairie	Sand barrens	Oak savanna
	1	*Antennaria neglecta*	field pussy-toes	Asteraceae	2 (6)	1 (5)	1 (1)			
	1	*Antennaria parlinii*	Parlin's pussytoes	Asteraceae	3 (2)	1	1 (2)			1
	3	*Apios americana*	common groundnut	Fabaceae	4 (10)		3 (10)		1	
	6	*Apocynum androsaemifolium*	spreading dogbane	Apocynaceae	3 (4)					3 (4)
	1	*Apocynum cannabinum*	indian hemp	Apocynaceae	12 (7)	4 (2)	3 (4)	2	2 (1)	1
	*	*ARABIDOPSIS THALIANA*	mouse-ear cress	Brassicaceae	2 (3)			1 (2)	1 (1)	
	5	*Aralia nudicaulis*	wild sarsaparilla	Araliaceae	1 (1)					1 (1)
	*	*ARENARIA SERPYLLIFOLIA*	thyme-leaved sandwort	Caryophyllaceae	2 (2)			2 (2)		
	4	*Aristida longespica* var. *longespica*	three-awned grass	Poaceae	2			2		
P	7	*Aristida purpurascens*	purple three-awned grass	Poaceae	10 (25)		1 (1)	5 (6)	3 (14)	1 (4)
	5	*Aronia melanocarpa*	black chokeberry	Rosaceae	6 (12)	1	1			4 (12)
	8	*Asclepias hirtella*	sand milkweed	Asclepiadaceae	2 (1)		1 (1)		1	
	4	*Asclepias incarnata*	swamp milkweed	Asclepiadaceae	4 (1)	4 (1)				
	1	*Asclepias syriaca*	common milkweed	Asclepiadaceae	6 (1)			4	2 (1)	
	4	*Asclepias tuberosa*	butterfly-weed	Asclepiadaceae	4 (2)				2 (2)	2
	6	*Aster laevis*	smooth aster	Asteraceae	2 (1)		1 (1)	1		
	3	*Aster lanceolatus*	eastern lined aster	Asteraceae	3 (5)		2 (2)			1 (3)
	5	*Aster macrophyllus*	big-leaved aster	Asteraceae	3 (8)					3 (8)
	2	*Aster novae-angliae*	New England aster	Asteraceae	3 (7)	2 (6)	1 (1)			
	1	*Aster pilosus*	awl aster	Asteraceae	12 (8)		2 (3)	6 (4)	2 (1)	2
	6	*Aster praealtus*	veiny lined aster	Asteraceae	15 (33)	3 (6)	6 (22)	3 (4)	1	2 (1)
	3	*Aster sagittifolius*	arrow-leaved aster	Asteraceae	3 (3)		2 (3)	1		
	3	*Aster umbellatus*	flat-topped white aster	Asteraceae	5 (4)		2			3 (4)
E	10	*Aureolaria pedicularia* var. *ambigens*	prairie fern-lvd. false foxglove	Scrophulariaceae	1					1
	6	*Baptisia tinctoria*	yellow false indigo	Fabaceae	8 (8)		3 (1)	1		4 (7)
	6	*Bartonia virginica*	screw-stem	Gentianaceae	4 (12)		2 (9)			2 (3)
	*	*BERTEROA INCANA*	hoary-alyssum	Brassicaceae	2 (3)			1 (1)	1 (2)	
	*	*BETULA PENDULA*	European white birch	Betulaceae	1	1				
	5	*Betula populifolia*	gray birch	Betulaceae	2 (2)		1 (2)	1		
	2	*Bidens frondosa*	devil's beggar's-tick	Asteraceae	1 (1)	1 (1)				
	3	*Botrychium dissectum*	lace-frond grape fern	Ophioglossaceae	1 (2)			1 (2)		
	*	*BROMUS INERMIS*	hungarian brome	Poaceae	3 (6)			1 (4)	2 (2)	

Table 1. Continued. Note: *Calamagrostis* spp. includes both *C. canadensis and C. stricta* (could not be differentiated due to time of sampling).

Status	CofC	Scientific Name	Common Name	Family	Total	Wet prairie	Mesic prairie	Dry prairie	Sand barrens	Oak savanna
	*	*BROMUS TECTORUM*	downy brome	Poaceae	5 (15)			3 (6)	2 (9)	
	3	*Bulbostylis capillaris*	thread-leaved sedge	Cyperaceae	5 (8)		2 (5)	2 (1)	1 (2)	
	4	*Calamagrostis canadensis*	canada bluejoint	Poaceae	6 (9)	2 (2)	2 (4)			2 (3)
	7	*Calamagrostis stricta*	northern reed grass	Poaceae	2 (11)	2 (11)				
	n/a	*Calamagrostis* spp. *(see note above)*	reed grass	Poaceae	5 (20)	5 (20)				
	1	*Calystegia sepium*	hedge bindweed	Convolvulaceae	3 (4)		2 (3)	1 (1)		
	4	*Calystegia spithamaea*	upright bindweed	Convolvulaceae	1 (1)			1 (1)		
P	7	*Carex alata*	broad-winged sedge	Cyperaceae	1 (1)	1 (1)				
	8	*Carex albicans* var. *emmonsii*	emmons' sedge	Cyperaceae	4 (1)				1	3 (1)
P	7	*Carex atherodes*	wheat sedge	Cyperaceae	2 (2)	2 (2)				
P	7	*Carex aurea*	golden-fruited sedge	Cyperaceae	2 (1)	2 (1)				
P	7	*Carex bebbii*	Bebb's sedge	Cyperaceae	2 (2)	2 (2)				
T	9	*Carex bicknellii*	Bicknell's sedge	Cyperaceae	2 (2)		1 (1)	1 (1)		
	1	*Carex blanda*	common wood sedge	Cyperaceae	2 (1)		1 (1)			1
	8	*Carex buxbaumii*	Buxbaum's sedge	Cyperaceae	7 (22)	6 (16)	1 (6)			
T	8	*Carex conoidea*	field sedge	Cyperaceae	2 (9)	2 (9)				
	3	*Carex cristatella*	crested sedge	Cyperaceae	1	1				
	9	*Carex cryptolepis*	little yellow sedge	Cyperaceae	6 (26)	6 (26)				
	4	*Carex gracillima*	graceful sedge	Cyperaceae	3 (2)	1	1			1 (2)
	3	*Carex granularis*	meadow sedge	Cyperaceae	6 (17)	6 (17)				
	8	*Carex interior*	interior sedge	Cyperaceae	1 (1)	1 (1)				
	5	*Carex lacustris*	lake sedge	Cyperaceae	1 (2)	1 (2)				
P	8	*Carex lasiocarpa*	quill-leaved sedge	Cyperaceae	8 (62)	8 (62)				
	7	*Carex muhlenbergii*	muhlenberg's sedge	Cyperaceae	14 (35)		1	6 (20)	5 (10)	2 (5)
	6	*Carex pellita*	woolly sedge	Cyperaceae	4 (8)	2 (1)	2 (7)			
	3	*Carex pensylvanica*	Pennsylvania sedge	Cyperaceae	14 (96)		1 (2)	3 (8)	1 (2)	9 (84)
	8	*Carex sartwellii*	Sartwell's sedge	Cyperaceae	3 (3)	3 (3)				
	3	*Carex scoparia*	pointed broom sedge	Cyperaceae	5 (6)		4 (5)	1 (1)		
	2	*Carex stipata*	crowded sedge	Cyperaceae	1	1				
	5	*Carex stricta*	tussock sedge	Cyperaceae	5 (6)	1	2 (5)			2 (1)
	4	*Carex swanii*	Swan's sedge	Cyperaceae	13 (28)	1 (1)	5 (18)	2 (6)	2	3 (3)
	8	*Carex tenera* var. *tenera*	slender sedge	Cyperaceae	13 (19)	4 (4)	4 (9)	2 (1)	1 (1)	2 (4)

Table 1. Continued

Status	CofC	Scientific Name	Common Name	Family	Total	Wet prairie	Mesic prairie	Dry prairie	Sand barrens	Oak savanna
	7	*Carex tetanica*	rigid sedge	Cyperaceae	1 (1)	1 (1)				
	8	*Carex tonsa*	low sand sedge	Cyperaceae	7 (6)			3 (1)	3 (5)	1
	4	*Carex tribuloides*	blunt broom sedge	Cyperaceae	1	1				
	1	*Carex vulpinoidea*	fox sedge	Cyperaceae	5 (6)	1 (2)	2 (2)	2 (2)		
	5	*Ceanothus americanus*	New Jersey tea	Rhamnaceae	5 (4)		2	1 (2)		2 (2)
	*	*CELASTRUS ORBICULATUS*	oriental bittersweet	Celastraceae	1 (1)			1 (1)		
	2	*Celastrus scandens*	bittersweet	Celastraceae	1		1			
	4	*Celtis occidentalis*	hackberry	Ulmaceae	1	1				
	3	*Cenchrus longispinus*	common sandbur	Poaceae	2 (9)			1 (8)	1 (1)	
	6	*Cephalanthus occidentalis*	buttonbush	Rubiaceae	3 (9)	2 (9)				1
	*	*CERASTIUM VULGATUM*	common chickweed	Caryophyllaceae	1 (1)	1 (1)				
	3	*Chamaecrista fasciculata*	partridge-pea	Fabaceae	1 (1)			1 (1)		
	*	*CHRYSANTHEMUM LEUCANTHEMUM*	ox-eye daisy	Asteraceae	2 (5)			1 (5)	1	
	3	*Cicuta bulbifera*	bulblet-bearing water-hemlock	Apiaceae	2 (2)	2 (2)				
	3	*Cicuta maculata*	water-hemlock	Apiaceae	2	1	1			
	3	*Circaea lutetiana*	enchanter's-nightshade	Onagraceae	1					1
	4	*Cirsium discolor*	field thistle	Asteraceae	5 (7)		1 (5)	4 (2)		
	8	*Cirsium muticum*	swamp thistle	Asteraceae	2 (2)	2 (2)				
	9	*Cladium mariscoides*	twig-rush	Cyperaceae	9 (56)	9 (56)				
	5	*Comandra umbellata*	bastard toad-flax	Santalaceae	5 (16)	1	1 (2)	1 (5)		2 (9)
E	8	*Comptonia peregrina*	sweet-fern	Myricaceae	2 (6)			1 (6)	1	
	7	*Conopholis americana*	squawroot	Orobanchaceae	1					1
	0	*Conyza canadensis*	horseweed	Asteraceae	15 (65)			7 (40)	6 (25)	2
	*	*COREOPSIS TINCTORIA*	plains tickseed	Asteraceae	1 (2)					1 (2)
	5	*Coreopsis tripteris*	tall tickseed	Asteraceae	18 (33)	4 (16)	6 (10)	4 (2)		4 (5)
	2	*Cornus amomum*	silky dogwood	Cornaceae	4 (3)	3 (3)			1	
	3	*Cornus drummondii*	rough-leaved dogwood	Cornaceae	5 (4)		1 (1)	3 (3)	1	
	1	*Cornus racemosa*	gray dogwood	Cornaceae	22 (44)	7 (16)	5 (16)	2 (5)	2	6 (7)
	4	*Corylus americana*	american hazel	Betulaceae	4 (3)			1 (1)	1	2 (2)
	3	*Crataegus mollis*	downy hawthorn	Rosaceae	1			1		
	3	*Crataegus punctata*	dotted hawthorn	Rosaceae	1 (1)			1 (1)		
	3	*Cuscuta gronovii*	common dodder	Cuscutaceae	1 (1)		1 (1)			

Table 1. Continued

Status	CofC	Scientific Name	Common Name	Family	Total	Wet prairie	Mesic prairie	Dry prairie	Sand barrens	Oak savanna
	*	*CYCLOLOMA ATRIPLICIFOLIUM*	winged pigweed	Chenopodiaceae	1				1	
	4	*Cyperus lupulinus*	slender umbrella-sedge	Cyperaceae	18 (79)		1 (6)	7 (28)	7 (41)	3 (4)
	1	*Cyperus strigosus*	straw-colored umbrella-sedge	Cyperaceae	6 (5)		3 (3)	1	1 (1)	1 (1)
	4	*Danthonia spicata*	poverty oat grass	Poaceae	2 (6)			1 (6)		1
	*	*DAUCUS CAROTA*	queen-anne's-lace	Apiaceae	10 (14)	1 (1)	2 (2)	5 (6)	2 (5)	
	4	*Desmodium canadense*	Canada tick-trefoil	Fabaceae	10 (7)	1 (1)	3 (2)	3 (4)	1	2
	5	*Desmodium marilandicum*	Maryland tick-trefoil	Fabaceae	16 (25)	1	4 (12)	4 (10)	3 (1)	4 (2)
	5	*Desmodium nudiflorum*	naked tick-trefoil	Fabaceae	2					2
T	8	*Desmodium sessilifolium*	sessile tick-trefoil	Fabaceae	4 (3)			3 (3)		1
	*	*DIANTHUS ARMERIA*	Deptford-pink	Caryophyllaceae	11 (24)			6 (16)	4 (8)	1
	*	*DIGITARIA ISCHAEMUM*	smooth crab grass	Poaceae	3 (1)			1	2 (1)	
	*	*DIGITARIA SANGUINALIS*	northern crab grass	Poaceae	1			1		
	4	*Dioscorea villosa*	wild yam	Dioscoreaceae	1 (1)		1 (1)			
	6	*Dulichium arundinaceum*	three-way sedge	Cyperaceae	1 (2)	1 (2)				
	*	*ELAEAGNUS UMBELLATA*	autumn-olive	Elaeagnaceae	6 (3)		1	4 (2)	1 (1)	
	7	*Eleocharis elliptica*	yellow-seeded spike-rush	Cyperaceae	13 (53)	9 (44)	4 (9)			
	*	*ELYTRIGIA REPENS*	quackgrass	Poaceae	8 (12)			5 (9)	2 (3)	1
	0	*Equisetum arvense*	field horsetail	Equisetaceae	4 (3)	1	2 (3)	1		
	6	*Equisetum laevigatum*	smooth scouring-rush	Equisetaceae	4 (3)	1 (1)	2 (1)	1 (1)		
	2	*Eragrostis spectabilis*	purple love grass	Poaceae	7 (10)		1 (1)	3 (7)	3 (2)	
	2	*Erechtites hieracifolia*	pilewort	Asteraceae	1					1
	0	*Erigeron annuus*	daisy fleabane	Asteraceae	1					1
	1	*Erigeron strigosus*	rough fleabane	Asteraceae	11 (8)	1 (1)	2 (2)	4 (3)	4 (2)	
	0	*Eupatorium altissimum*	tall boneset	Asteraceae	2			2		
	6	*Eupatorium maculatum*	spotted joe-pye weed	Asteraceae	1		1			
	3	*Eupatorium perfoliatum*	common boneset	Asteraceae	6 (2)	1	3 (1)	1		1 (1)
	4	*Euphorbia corollata*	flowering spurge	Euphorbiaceae	13 (33)		3 (15)	4 (10)	4 (7)	2 (1)
	*	*EUPHORBIA CYPARISSIAS*	cypress spurge	Euphorbiaceae	1			1		
	*	*EUPHORBIA DENTATA*	toothed spurge	Euphorbiaceae	1				1	
	0	*Euphorbia maculata*	spotted spurge	Euphorbiaceae	2 (4)				2 (4)	
	2	*Euthamia graminifolia*	flat-topped goldenrod	Asteraceae	20 (41)	2 (2)	6 (24)	5 (10)	3 (1)	4 (4)
T	9	*Euthamia remota*	Great Lakes goldenrod	Asteraceae	12 (42)	6 (30)	4 (11)	1 (1)	1	

Table 1. Continued

Status	CofC	Scientific Name	Common Name	Family	Total	Wet prairie	Mesic prairie	Dry prairie	Sand barrens	Oak savanna
	*	*FESTUCA PRATENSIS*	meadow fescue	Poaceae	1			1		
	1	*Fragaria virginiana*	wild strawberry	Rosaceae	18 (49)	2 (8)	5 (19)	6 (8)	3 (8)	2 (6)
	3	*Fraxinus pennsylvanica*	green ash	Oleaceae	5 (2)	5 (2)				
	0	*Galium aparine*	cleavers	Rubiaceae	1 (1)			1 (1)		
	4	*Galium circaezans*	wild licorice	Rubiaceae	2 (1)					2 (1)
	4	*Galium pilosum*	hairy bedstraw	Rubiaceae	8 (7)	1 (1)	1 (2)	2 (1)	1 (1)	3 (2)
	4	*Galium tinctorium*	small three-lobed bedstraw	Rubiaceae	3 (1)	3 (1)				
	4	*Galium triflorum*	sweet-scented bedstraw	Rubiaceae	1					1
	5	*Gaultheria procumbens*	teaberry	Ericaceae	5 (7)			1 (3)		4 (4)
	6	*Gaylussacia baccata*	huckleberry	Ericaceae	9 (24)			1 (4)		8 (20)
	5	*Gentiana andrewsii*	bottle gentian	Gentianaceae	1	1				
P	7	*Gentianopsis crinita*	fringed gentian	Gentianaceae	1	1				
	4	*Geranium maculatum*	wild geranium	Geraniaceae	1					1
	4	*Gleditsia triacanthos*	honey locust	Caesalpinaceae	1					1
T	9	*Glyceria acutiflora*	sharp-glumed manna grass	Poaceae	1 (2)		1 (2)			
	2	*Glyceria striata*	fowl manna grass	Poaceae	5 (13)	5 (13)				
	2	*Gnaphalium obtusifolium*	fragrant cudweed	Asteraceae	13 (18)		1 (2)	5 (7)	4 (9)	3
	2	*Hackelia virginiana*	virginia stickseed	Boraginaceae	1					1
	5	*Hamamelis virginiana*	witch-hazel	Hamamelidaceae	6 (29)			1		5 (29)
P	7	*Hedeoma hispida*	rough pennyroyal	Lamiaceae	2 (3)			2 (3)		
	*	*HELENIUM FLEXUOSUM*	naked sneezeweed	Asteraceae	1 (1)	1 (1)				
P	9	*Helianthemum bicknellii*	plains frostweed	Cistaceae	2 (1)				1	1 (1)
T	9	*Helianthemum canadense*	canada frostweed	Cistaceae	5 (5)				2	3 (5)
	4	*Helianthus divaricatus*	woodland sunflower	Asteraceae	11 (14)		2	1 (1)		8 (13)
	6	*Helianthus giganteus*	swamp sunflower	Asteraceae	4 (2)	1	1			2 (2)
	7	*Helianthus occidentalis*	western sunflower	Asteraceae	5 (7)			3 (6)	1 (1)	1
	*	*HIERACIUM CAESPITOSUM*	yellow king-devil	Asteraceae	1 (3)				1 (3)	
	5	*Hieracium gronovii*	beaked hawkweed	Asteraceae	5 (1)		1	1	2 (1)	1
	5	*Hieracium scabrum*	rough hawkweed	Asteraceae	1 (1)		1 (1)			
	3	*Hypericum gentianoides*	orange-grass	Clusiaceae	3 (1)			2	1 (1)	
T	8	*Hypericum kalmianum*	Kalm's st. john's-wort	Clusiaceae	2	2				
	6	*Hypericum majus*	tall St. John's-wort	Clusiaceae	3 (4)	2 (3)	1 (1)			

Table 1. Continued

Status	CofC	Scientific Name	Common Name	Family	Total	Wet prairie	Mesic prairie	Dry prairie	Sand barrens	Oak savanna
	3	*Hypericum mutilum*	slender St. John's-wort	Clusiaceae	1 (1)			1 (1)		
	*	*HYPERICUM PERFORATUM*	common St. John's-wort	Clusiaceae	3 (1)		1 (1)	1		1
	3	*Hypericum prolificum*	shrubby St. John's-wort	Clusiaceae	1			1		
	6	*Ilex verticillata*	winterberry	Aquifoliaceae	7 (6)	5 (5)	1 (1)			1
	6	*Iris virginica*	southern blue flag	Iridaceae	7 (9)	6 (9)	1			
	4	*Juncus anthelatus*	branched rush	Juncaceae	6 (12)		1 (8)	4 (4)	1	
	3	*Juncus articulatus*	jointed rush	Juncaceae	3 (6)	3 (6)				
	5	*Juncus brachycarpus*	short-fruited rush	Juncaceae	4		3			1
	4	*Juncus canadensis*	Canada rush	Juncaceae	1 (3)	1 (3)				
	3	*Juncus dudleyi*	Dudley's rush	Juncaceae	17 (37)	8 (23)	4 (9)	1 (3)	2 (1)	2 (1)
	1	*Juncus effusus*	soft rush	Juncaceae	4 (4)	1 (1)	2 (3)		1	
T	7	*Juncus greenei*	Greene's rush	Juncaceae	9 (20)		4 (11)	2 (5)	1	2 (4)
	4	*Juncus marginatus*	grass-leaved rush	Juncaceae	10 (5)	4 (1)	4 (4)			2
	5	*Juncus nodosus*	knotted rush	Juncaceae	2 (4)	2 (4)				
	1	*Juncus tenuis*	path rush	Juncaceae	13 (19)		5 (9)	4 (4)	3 (5)	1 (1)
	3	*Juncus torreyi*	Torrey's rush	Juncaceae	5 (8)	4 (8)	1			
	3	*Juniperus virginiana*	eastern red cedar	Cupressaceae	1			1		
E	1	*Koeleria pyramidata*	june grass	Poaceae	2 (4)			1		1 (4)
	5	*Krigia biflora*	orange dwarf-dandelion	Asteraceae	2 (2)	1 (1)	1 (1)			
T	8	*Krigia virginica*	dwarf-dandelion	Asteraceae	1				1	
	1	*Lactuca canadensis*	wild lettuce	Asteraceae	7 (1)			4 (1)	2	1
P	7	*Lechea intermedia*	round-fruited pinweed	Cistaceae	2 (1)		1	1 (1)		
	7	*Lechea mucronata*	hairy pinweed	Cistaceae	2			1		1
T	7	*Lechea pulchella*	Leggett's pinweed	Cistaceae	3 (4)		2 (4)	1		
	1	*Leersia oryzoides*	rice cut grass	Poaceae	3 (5)	3 (5)				
	1	*Lepidium virginicum*	common pepper-grass	Brassicaceae	11 (20)			6 (12)	5 (8)	
	4	*Leptoloma cognatum*	fall witch grass	Poaceae	12 (27)		1 (1)	6 (16)	4 (10)	1
	5	*Lespedeza capitata*	round-headed bush-clover	Fabaceae	20 (40)		4 (14)	7 (12)	4 (7)	5 (7)
	5	*Lespedeza hirta*	hairy bush-clover	Fabaceae	1 (2)			1 (2)		
	5	*Leucospora multifida*	leucospora	Scrophulariaceae	1 (2)	1 (2)				
	6	*Liatris aspera*	rough blazing-star	Asteraceae	9 (34)		1 (2)	4 (12)	2 (14)	2 (6)
	7	*Liatris spicata*	spiked blazing-star	Asteraceae	11 (25)	3 (16)	6 (8)	1		1 (1)

Table 1. Continued

Status	CofC	Scientific Name	Common Name	Family	Total	Wet prairie	Mesic prairie	Dry prairie	Sand barrens	Oak savanna
P	8	*Liatris squarrosa*	scaly blazing-star	Asteraceae	2 (1)				2 (1)	
	*	*LIGUSTRUM VULGARE*	common privet	Oleaceae	1 (1)			1 (1)		
E	7	*Lilium philadelphicum*	wood lily	Liliaceae	1		1			
E	4	*Linaria canadensis*	old-field toadflax	Scrophulariaceae	3 (13)		1 (4)		2 (9)	
	5	*Linum medium*	stiff yellow flax	Linaceae	2 (9)	1 (6)	1 (3)			
	7	*Liparis loeselii*	bog twayblade	Orchidaceae	2 (1)	2 (1)				
T	8	*Lipocarpha micrantha*	dwarf bulrush	Cyperaceae	1 (1)				1 (1)	
	6	*Liriodendron tulipifera*	tulip tree	Magnoliaceae	1					1
T	9	*Lithospermum caroliniense*	plains puccoon	Boraginaceae	1				1	
	5	*Lobelia spicata*	pale-spike lobelia	Campanulaceae	2 (1)	2 (1)				
	*	*LONICERA JAPONICA*	Japanese honeysuckle	Caprifoliaceae	1 (1)			1 (1)		
	*	*LONICERA MORROWII*	Morrow's honeysuckle	Caprifoliaceae	3 (1)		1	1 (1)	1	
	3	*Ludwigia alternifolia*	seedbox	Onagraceae	6 (2)	2	2 (2)	1		1
	3	*Ludwigia palustris*	water-purslane	Onagraceae	4 (2)	4 (2)				
P	7	*Lupinus perennis*	wild lupine	Fabaceae	7 (13)			2 (5)	2 (1)	3 (7)
	4	*Luzula echinata*	round-leaved woodrush	Juncaceae	2 (3)	1 (2)	1 (1)			
	3	*Lycopus americanus*	american water-horehound	Lamiaceae	8 (9)	4 (3)	4 (6)			
	3	*Lycopus uniflorus*	northern water-horehound	Lamiaceae	3 (11)	3 (11)				
	3	*Lycopus virginicus*	virginia bugle-weed	Lamiaceae	2 (2)	2 (2)				
	4	*Lysimachia ciliata*	fringed loosestrife	Primulaceae	1 (1)			1 (1)		
	6	*Lysimachia lanceolata*	lance-leaved loosestrife	Primulaceae	2 (2)		1	1 (2)		
	5	*Lysimachia quadrifolia*	whorled loosestrife	Primulaceae	10 (42)		2 (10)			8 (32)
	6	*Lysimachia terrestris*	swamp-candles	Primulaceae	1 (4)	1 (4)				
	6	*Lysimachia thyrsiflora*	tufted loosestrife	Primulaceae	3 (8)	3 (8)				
	6	*Lythrum alatum*	winged loosestrife	Lythraceae	6 (11)	5 (10)	1 (1)			
	*	*LYTHRUM SALICARIA*	purple loosestrife	Lythraceae	1	1				
	6	*Maianthemum canadense*	Canada mayflower	Liliaceae	2 (1)					2 (1)
	4	*Maianthemum racemosum*	false solomon's-seal	Liliaceae	8 (14)		1			7 (14)
	7	*Maianthemum stellatum*	starry false solomon's-seal	Liliaceae	1				1	
	6	*Medeola virginiana*	indian cucumber-root	Liliaceae	1					1
	*	*MEDICAGO LUPULINA*	black medick	Fabaceae	1 (1)				1 (1)	
	*	*MELILOTUS ALBA*	white sweet-clover	Fabaceae	2	1			1	

Table 1. Continued

Status	CofC	Scientific Name	Common Name	Family	Total	Wet prairie	Mesic prairie	Dry prairie	Sand barrens	Oak savanna
	3	*Monarda fistulosa*	wild bergamot	Lamiaceae	7 (7)	1 (2)	2 (3)	3 (1)		1 (1)
E	7	*Monarda punctata*	dotted horsemint	Lamiaceae	3 (4)			2 (4)	1	
	4	*Muhlenbergia mexicana*	leafy satin grass	Poaceae	3 (1)			1 (1)	1	1
	0	*Muhlenbergia schreberi*	nimblewill	Poaceae	1			1		
	7	*Nyssa sylvatica*	black-gum	Cornaceae	3 (1)		2 (1)	1		
	1	*Oenothera biennis*	common evening-primrose	Onagraceae	8 (1)		2 (1)	2	3	1
E	8	*Oenothera clelandii*	Cleland's evening-primrose	Onagraceae	1 (1)			1 (1)		
	4	*Oenothera laciniata*	cut-leaved evening primrose	Onagraceae	1 (1)			1 (1)		
	2	*Onoclea sensibilis*	sensitive fern	Dryopteridaceae	6 (13)	1	4 (13)		1	
P	8	*Opuntia humifusa*	common prickly-pear	Cactaceae	2 (10)			2 (10)		
	6	*Osmunda cinnamomea*	cinnamon fern	Osmundaceae	2 (2)		1			1 (2)
	7	*Osmunda regalis*	royal fern	Osmundaceae	6 (4)		4 (4)			2
	0	*Oxalis dillenii*	southern yellow wood-sor.	Oxalidaceae	9 (24)		1 (1)	5 (21)	2 (2)	1
	2	*Panicum acuminatum*	tapered rosette grass	Poaceae	10 (15)	2 (5)	1 (2)	1 (1)	3 (3)	3 (4)
P	6	*Panicum boreale*	northern panic grass	Poaceae	2	1	1			
	2	*Panicum clandestinum*	deer's-tongue panic grass	Poaceae	8 (15)		2 (7)	4 (8)	2	
	6	*Panicum columbianum*	American panic grass	Poaceae	16 (25)			6 (7)	7 (16)	3 (2)
	8	*Panicum depauperatum*	starved panic grass	Poaceae	4 (9)			1 (2)	2 (6)	1 (1)
	0	*Panicum dichotomiflorum*	fall panic grass	Poaceae	1					1
	9	*Panicum implicatum*	southern hairy panic grass	Poaceae	10 (25)	4 (7)	3 (12)	2 (5)		1 (1)
	4	*Panicum latifolium*	broad-leaved panic grass	Poaceae	2 (3)					2 (3)
T	9	*Panicum meridionale*	southern hairy panic grass	Poaceae	3 (8)		1 (2)		1 (4)	1 (2)
	6	*Panicum oligosanthes*	few-flowered panic grass	Poaceae	12 (28)		1	4 (17)	6 (11)	1
	5	*Panicum rigidulum*	rigid panic grass	Poaceae	2 (1)	1 (1)		1		
E	9	*Panicum spretum*	narrow-headed panic grass	Poaceae	4 (9)		1 (4)	1 (4)	2 (1)	
	2	*Parthenocissus quinquefolia*	Virginia creeper	Vitaceae	7 (16)	1 (1)		1 (1)		5 (14)
	2	*Paspalum setaceum*	thin paspalum	Poaceae	6 (7)			4 (6)	2 (1)	
	6	*Pedicularis canadensis*	common lousewort	Scrophulariaceae	2 (4)	1 (3)	1 (1)			
	2	*Penstemon digitalis*	foxglove beard-tongue	Scrophulariaceae	1 (4)		1 (4)			
	*	*PHLEUM PRATENSE*	timothy	Poaceae	3 (3)		1 (3)	2		
	*	*Phragmites australis*	giant reed	Poaceae	3	3				
	1	*Physalis heterophylla*	clammy ground-cherry	Solanaceae	2 (2)			1 (1)	1 (1)	

Table 1. Continued

Status	CofC	Scientific Name	Common Name	Family	Total	Wet prairie	Mesic prairie	Dry prairie	Sand barrens	Oak savanna
	4	*Physocarpus opulifolius*	ninebark	Rosaceae	3 (4)	2 (3)		1 (1)		
	*	*PINUS STROBUS*	white pine	Pinaceae	2				1	1
	*	*PINUS SYLVESTRIS*	Scotch pine	Pinaceae	4 (1)			1	3 (1)	
	*	*PLANTAGO LANCEOLATA*	English plantain	Plantaginaceae	9 (8)	1 (1)	1 (1)	4 (3)	3 (3)	
	*	*PLANTAGO MAJOR*	common plantain	Plantaginaceae	2 (1)		1		1 (1)	
	3	*Platanthera lacera*	ragged fringed orchid	Orchidaceae	2 (1)	2 (1)				
	7	*Platanus occidentalis*	sycamore	Platanaceae	2 (1)	1			1 (1)	
	*	*POA COMPRESSA*	canada bluegrass	Poaceae	15 (24)	1 (1)	3 (8)	6 (10)	2 (1)	3 (4)
	*	*POA PRATENSIS*	kentucky bluegrass	Poaceae	6 (16)			5 (14)	1 (2)	
T	10	*Polygala polygama*	racemed milkwort	Polygalaceae	6 (13)		1	1 (1)	2 (10)	2 (2)
	2	*Polygala sanguinea*	field milkwort	Polygalaceae	4 (1)		3 (1)		1	
	2	*Polygala verticillata*	whorled milkwort	Polygalaceae	1 (1)	1 (1)				
	4	*Polygonatum biflorum*	smooth solomon's-seal	Liliaceae	4 (3)					4 (3)
	4	*Polygonum amphibium*	water smartweed	Polygonaceae	2 (1)	1 (1)			1	
	0	*Polygonum pensylvanicum*	pinkweed	Polygonaceae	1 (1)			1 (1)		
	*	*POLYGONUM PERSICARIA*	lady's thumb	Polygonaceae	1				1	
	2	*Polygonum scandens*	climbing false buckwheat	Polygonaceae	1			1		
	4	*Polygonum tenue*	slender knotweed	Polygonaceae	4 (3)			2	1	1 (3)
	3	*Populus deltoides*	eastern cottonwood	Salicaceae	10 (16)	2 (1)	4 (11)	1 (1)	3 (3)	
	2	*Populus grandidentata*	big-tooth aspen	Salicaceae	2 (2)				1 (1)	1 (1)
	2	*Populus tremuloides*	quaking aspen	Salicaceae	16 (27)	4 (1)	4 (15)	2	3 (5)	3 (6)
	1	*Potentilla simplex*	old field cinquefoil	Rosaceae	27 (86)	4 (7)	6 (32)	4 (12)	4 (8)	9 (27)
	5	*Prenanthes alba*	white rattlesnake-root	Asteraceae	2 (1)					2 (1)
P	8	*Prenanthes racemosa*	prairie rattlesnake-root	Asteraceae	4 (1)	1	1			2 (1)
	7	*Proserpinaca palustris*	mermaid-weed	Haloragaceae	6 (18)	6 (18)				
	0	*Prunella vulgaris*	self-heal	Lamiaceae	5 (8)	2 (6)	2 (1)	1 (1)		
	4	*Prunus pensylvanica*	fire cherry	Rosaceae	1 (1)		1 (1)			
E	10	*Prunus pumila*	sand cherry	Rosaceae	2 (1)		1		1 (1)	
	3	*Prunus serotina*	black cherry	Rosaceae	25 (52)	1 (1)	4 (2)	5 (7)	6 (5)	9 (37)
	2	*Prunus virginiana*	choke cherry	Rosaceae	5 (3)		1	1		3 (3)
	1	*Pteridium aquilinum*	bracken fern	Dennstaedtiaceae	12 (64)		2 (7)	1 (8)		9 (49)
	4	*Pycnanthemum virginianum*	virginia mountain-mint	Lamiaceae	8 (19)	4 (11)	3 (5)	1 (3)		

Table 1. Continued

Status	CofC	Scientific Name	Common Name	Family	Total	Wet prairie	Mesic prairie	Dry prairie	Sand barrens	Oak savanna
	7	*Pyrola elliptica*	shinleaf	Pyrolaceae	1 (2)					1 (2)
	6	*Quercus alba*	white oak	Fagaceae	12 (41)		2 (1)	1 (2)	1	8 (38)
	6	*Quercus coccinea*	scarlet oak	Fagaceae	17 (20)			4 (8)	7 (6)	6 (6)
	5	*Quercus palustris*	pin oak	Fagaceae	11 (7)	6 (2)	4 (1)			1 (4)
	6	*Quercus rubra*	red oak	Fagaceae	2 (3)		1			1 (3)
	7	*Quercus velutina*	black oak	Fagaceae	20 (54)		2 (1)	5 (6)	4 (5)	9 (42)
	8	*Rhamnus alnifolia*	alder-leaved buckthorn	Rhamnaceae	2	2				
	*	*RHAMNUS CATHARTICA*	European buckthorn	Rhamnaceae	2 (2)		1 (1)	1 (1)		
	*	*RHAMNUS FRANGULA*	glossy buckthorn	Rhamnaceae	14 (25)	6 (12)	1 (9)	1 (2)	2 (1)	4 (1)
	4	*Rhus copallinum*	winged sumac	Anacardiaceae	21 (45)	1 (1)	5 (10)	5 (9)	6 (19)	4 (6)
	2	*Rhus typhina*	staghorn sumac	Anacardiaceae	2			1	1	
	7	*Rhynchospora capitellata*	brownish beak-rush	Cyperaceae	2		1			1
	1	*Rhynchospora recognita*	grass-like beak-rush	Cyperaceae	1		1			
	*	*ROBINIA HISPIDA*	bristly locust	Fabaceae	1			1		
	0	*Robinia pseudoacacia*	black locust	Fabaceae	1				1	
	4	*Rosa carolina*	pasture rose	Rosaceae	9 (24)		1 (3)	1 (1)		7 (20)
	*	*ROSA MULTIFLORA*	multiflora rose	Rosaceae	5 (1)	1		3 (1)	1	
	5	*Rosa palustris*	swamp rose	Rosaceae	11 (18)	8 (17)	2			1 (1)
	4	*Rosa setigera*	climbing prairie rose	Rosaceae	1 (1)	1 (1)				
	1	*Rubus allegheniensis*	common blackberry	Rosaceae	20 (75)	1 (3)	1 (8)	5 (20)	5 (13)	8 (31)
	1	*Rubus flagellaris*	northern dewberry	Rosaceae	22 (99)	3 (8)	4 (19)	6 (37)	5 (28)	4 (7)
	5	*Rubus hispidus*	swamp dewberry	Rosaceae	5 (8)	1 (1)				4 (7)
	6	*Rubus idaeus* L. var. *strigosus*	wild red raspberry	Rosaceae	1 (1)					1 (1)
	1	*Rubus occidentalis*	black raspberry	Rosaceae	2 (1)				1	1 (1)
	7	*Rubus pubescens*	dwarf raspberry	Rosaceae	15 (53)		3 (17)	3 (5)	2 (2)	7 (29)
	1	*Rudbeckia hirta*	black-eyed susan	Asteraceae	10 (13)	2 (6)	3 (5)	3 (1)	1	1 (1)
	*	*RUMEX ACETOSELLA*	sheep sorrel	Polygonaceae	18 (47)		2 (7)	8 (20)	6 (19)	2 (1)
	*	*RUMEX CRISPUS*	curly dock	Polygonaceae	2 (1)		1 (1)	1		
	5	*Salix bebbiana*	Bebb's willow	Salicaceae	2 (8)	1	1 (8)			
	3	*Salix discolor*	pussy willow	Salicaceae	6 (4)	4 (3)	2 (1)			
	2	*Salix eriocephala*	heart-leaved willow	Salicaceae	7 (2)	5 (2)	1	1		
	1	*Salix exigua*	sandbar willow	Salicaceae	1 (2)	1 (2)				

Table 1. Continued

Status	CofC	Scientific Name	Common Name	Family	Total	Wet prairie	Mesic prairie	Dry prairie	Sand barrens	Oak savanna
	4	*Salix humilis*	prairie willow	Salicaceae	9 (15)		3 (11)	2	1 (1)	3 (3)
T	8	*Salix petiolaris*	slender willow	Salicaceae	7 (4)	7 (4)				
	*	*SAPONARIA OFFICINALIS*	soapwort	Caryophyllaceae	2 (1)			1 (1)	1	
	3	*Sassafras albidum*	sassafras	Lauraceae	20 (56)		4 (2)	3 (4)	4 (2)	9 (48)
	5	*Schizachyrium scoparium*	little bluestem	Poaceae	19 (81)	2 (9)	5 (18)	6 (39)	3 (10)	3 (5)
	7	*Schoenoplectus acutus*	hard-stemmed bulrush	Cyperaceae	1 (2)	1 (2)				
	2	*Schoenoplectus tabernaemontani*	soft-stemmed bulrush	Cyperaceae	1 (1)	1 (1)				
	1	*Scirpus atrovirens*	green bulrush	Cyperaceae	1			1		
	1	*Scirpus cyperinus*	wool-grass	Cyperaceae	4 (7)	2 (7)			1	1
	1	*Scirpus hattorianus*	smooth-lvd. dark green bulrush	Cyperaceae	1	1				
	2	*Scirpus pendulus*	drooping bulrush	Cyperaceae	4 (20)	4 (20)				
P	7	*Scleria triglomerata*	tall nut-rush	Cyperaceae	7 (11)		3 (6)	3 (2)		1 (3)
	3	*Scutellaria lateriflora*	mad-dog skullcap	Lamiaceae	1 (1)	1 (1)				
	4	*Senecio aureus*	golden ragwort	Asteraceae	1	1				
	*	*SETARIA FABERI*	giant foxtail grass	Poaceae	2			2		
	*	*SILENE LATIFOLIA*	white campion	Caryophyllaceae	2			2		
	6	*Sisyrinchium albidum*	pale blue-eyed-grass	Iridaceae	1 (1)		1 (1)			
	2	*Sisyrinchium angustifolium*	stout blue-eyed-grass	Iridaceae	3 (4)	3 (4)				
	6	*Sium suave*	water-parsnip	Apiaceae	2 (1)	2 (1)				
	5	*Smilax glauca*	cat greenbrier	Smilacaceae	14 (37)		3 (5)	3 (10)	2 (1)	6 (21)
	3	*Smilax hispida*	bristly greenbrier	Smilacaceae	5 (4)	1 (1)	1			3 (3)
	*	*SOLANUM CAROLINENSE*	horse nettle	Solanaceae	13 (25)		1	5 (16)	6 (9)	1
	1	*Solidago canadensis*	canada goldenrod	Asteraceae	21 (45)	2 (6)	6 (18)	7 (18)	3 (2)	3 (1)
	3	*Solidago gigantea*	smooth goldenrod	Asteraceae	3 (5)	2 (4)	1 (1)			
	2	*Solidago juncea*	plume goldenrod	Asteraceae	14 (29)	1 (1)	5 (10)	3 (9)	3 (4)	2 (5)
	2	*Solidago nemoralis*	gray goldenrod	Asteraceae	18 (26)	1 (1)	4 (4)	5 (12)	5 (7)	3 (2)
	6	*Solidago patula*	rough-leaved goldenrod	Asteraceae	1	1				
	8	*Solidago riddellii*	Riddell's goldenrod	Asteraceae	1 (2)	1 (2)				
	2	*Solidago rugosa*	rough goldenrod	Asteraceae	27 (81)	3 (6)	6 (24)	7 (22)	3 (10)	8 (19)
T	5	*Solidago speciosa*	showy goldenrod	Asteraceae	1					1
	5	*Sorghastrum nutans*	indian grass	Poaceae	12 (21)		4 (15)	4 (3)	2 (2)	2 (1)
T	8	*Sphenopholis obtusata* var. *obtusata*	prairie wedge grass	Poaceae	1			1		

Table 1. Continued

Status	CofC	Scientific Name	Common Name	Family	Total	Wet prairie	Mesic prairie	Dry prairie	Sand barrens	Oak savanna
	3	*Spiraea alba*	meadow-sweet	Rosaceae	15 (66)	8 (45)	5 (19)			2 (2)
	4	*Spiraea tomentosa*	steeplebush	Rosaceae	7 (23)		4 (19)	2 (3)	1 (1)	
	6	*Sporobolus cryptandrus*	sand dropseed	Poaceae	2 (1)				2 (1)	
	4	*Stachys tenuifolia*	smooth hedge-nettle	Lamiaceae	1	1				
	4	*Stellaria longifolia*	long-leaved stitchwort	Caryophyllaceae	2 (2)	2 (2)				
	*	*TARAXACUM OFFICINALE*	common dandelion	Asteraceae	5 (5)			2 (2)	1 (3)	2
	6	*Tephrosia virginiana*	goat's-rue	Fabaceae	1					1
	4	*Thalictrum dasycarpum*	purple meadow-rue	Ranunculaceae	1 (2)		1 (2)			
	6	*Thelypteris palustris*	marsh fern	Thelypteridaceae	7 (2)	4	1 (1)			2 (1)
	1	*Toxicodendron radicans*	poison-ivy	Anacardiaceae	11 (10)	2 (1)		1 (1)	2 (1)	6 (7)
	*	*TRAGOPOGON DUBIUS*	field goat's-beard	Asteraceae	6 (3)			4 (2)	2 (1)	
	4	*Trichostema dichotomum*	bluecurls	Lamiaceae	1 (1)				1 (1)	
	1	*Tridens flavus*	grease grass	Poaceae	2 (2)		1 (1)	1 (1)		
	*	*TRIFOLIUM PRATENSE*	red clover	Fabaceae	2 (2)			2 (2)		
P	9	*Triplasis purpurea*	purple sand grass	Poaceae	2 (7)			1 (1)	1 (6)	
	*	*TYPHA ANGUSTIFOLIA*	narrow-leaved cat-tail	Typhaceae	1 (2)	1 (2)				
	*	*ULMUS PUMILA*	Siberian elm	Ulmaceae	2 (7)			1	1 (7)	
	5	*Uvularia sessilifolia*	merry-bells	Liliaceae	8 (37)		1 (2)			7 (35)
	7	*Vaccinium angustifolium*	low sugarberry	Ericaceae	10 (29)		2 (5)			8 (24)
	6	*Vaccinium pallidum*	low blueberry	Ericaceae	8 (37)			2 (4)		6 (33)
	*	*VERBASCUM THAPSUS*	common mullein	Scrophulariaceae	12 (2)			5 (1)	7 (1)	
	4	*Verbena hastata*	blue vervain	Verbenaceae	2 (1)	1 (1)	1			
	3	*Verbena urticifolia*	white vervain	Verbenaceae	1		1			
	2	*Vernonia gigantea*	tall ironweed	Asteraceae	4 (1)	3 (1)	1			
P	8	*Viola lanceolata*	lance-leaved violet	Violaceae	1 (1)		1 (1)			
	4	*Viola sagittata*	arrow-leaved violet	Violaceae	9 (22)	2 (5)	3 (13)		1 (2)	3 (2)
	4	*Vitis aestivalis*	summer grape	Vitaceae	6 (6)					6 (6)
	3	*Vitis riparia*	riverbank grape	Vitaceae	19 (12)	4 (5)	3 (1)	6 (4)	2 (1)	4 (1)
	4	*Vulpia octoflora*	six-weeks fescue	Poaceae	1 (1)				1 (1)	
	*	*XANTHIUM STRUMARIUM*	common cocklebur	Asteraceae	1				1	
T	10	*Xyris torta*	twisted yellow-eyed-grass	Xyridaceae	1 (1)		1 (1)			
	3	*Zanthoxylum americanum*	prickly-ash	Rutaceae	1	1				

APPENDIX II: SPECIES RICHNESS PATTERNS

The following supplemental information is provided to further characterize species richness patterns within and among the five Oak Openings plant communities evaluated in Chapter II. For proper interpretation of the following data, it is important to consider that the minimum contiguous patch size of all 39 sampled study sites was 30 m by 60 m (1800 m^2; refer to Chapter II, Methods). Therefore, smaller or irregular-shaped patches on the landscape would not be expected to follow these patterns.

Site-level species richness – Summary information for all 39 individual 1000-m^2 sampling plots is provided in Table 1. Floristic Quality Assessment Index (FQAI) scores were determined following Adreas et al. (2004) and are given to provide a range of example scores for these five Oak Openings communities.

Species area curves – To generate species-area curves for the five sampled Oak Openings communities, at each sampling location I calculated mean number of species per 1-m^2 and 10-m^2 subplots and totaled the number of species for the 100-m^2 subplot and the 1000-m^2 sampling plot. This resulted in a total of 39 data points at each of the four nested scales from which species-area curves were generated by community type. While all curves were statistically significant at $P = 0.05$, among all community types more variation in the data was explained for total species richness and native species richness than for exotic species richness (Figure 1).

Species composition overlap – To evaluated species composition overlap within and among the five plant communities, I used Jaccard's Coefficient, which indicates the similarity between two datasets as follows: C / (U1 + U2 + C); where U1 = the number of species unique to the first set, U2 = the number of species unique to the second set, and C = the number of species common to both sets. A coefficient score of ‘0’ indicates total dissimilarity among sets, while a score of ‘1’ indicates total similarity among sets. While the mean total species richness among community types was not significantly different at $P = 0.05$ (Chapter II, Table 1), the number of sampled species unique to each community type was highest for wet prairies (Table 2). Overall species composition overlap among the five community types is shown in Table 3, while mean species composition overlap within each individual community type is shown in Table 4.

I evaluated relationships between species composition overlap and proximity of individual sampling plots using linear regression. This provided a measure of the influence of spatial autocorrelation in determining species composition overlap. For mesic prairies, a majority (68%) of variation in species composition overlap was explained by geographic distance between plots (Figure 2). For oak savannas and wet prairies, a lesser amount of the variation in species composition overlap (26% and 13%, respectively) was explained by geographic distance between plots. For dry prairies and sand barrens this relationship was not statistically significant at $P = 0.05$.

Table 1. Summary of results for 39 1000-m^2 vegetation sampling plots, by community type. FQAI indicates '*floristic quality assessment index*' score (from Andreas et al. 2004).

Location of sampling plot within Oak Openings region	Date sampled	Coordinates		Native richness	Exotic richness	FQAI score
		W Longitude	N Latitude			
Wet prairies						
Irwin Prairie State Nature Preserve	05/23/09	-83.77887042	41.65334780	19	0	24.5
Irwin Prairie State Nature Preserve	05/29/09	-83.77840607	41.65511520	38	1	28.3
Irwin Prairie State Nature Preserve	05/31/09	-83.77253922	41.65282516	12	0	22.9
Irwin Prairie State Nature Preserve	06/05/09	-83.77882399	41.65226821	37	4	25.0
Kitty Todd Nature Preserve	06/06/09	-83.80669469	41.62214104	66	4	32.7
Kitty Todd Nature Preserve	06/10/09	-83.80698409	41.62051289	53	2	32.7
Maumee State Forest	06/24/09	-83.90453599	41.46340989	42	1	28.7
Irwin Prairie State Nature Preserve	06/27/09	-83.78051887	41.65398335	43	1	32.0
Kitty Todd Nature Preserve	07/02/09	-83.81119463	41.61797831	84	9	33.9
Mesic prairies						
Kitty Todd Nature Preserve	08/09/08	-83.78611093	41.62075088	70	2	31.7
Kitty Todd Nature Preserve	08/12/08	-83.79058951	41.62023690	70	1	34.4
Kitty Todd Nature Preserve	08/24/08	-83.79137876	41.62183880	52	0	34.5
Oak Openings Preserve Metropark	09/20/08	-83.85210987	41.53740181	52	10	20.1
Irwin Prairie State Nature Preserve	08/02/09	-83.78040282	41.65547214	68	5	26.4
Kitty Todd Nature Preserve	08/16/09	-83.78706248	41.62194360	88	2	43.5
Dry prairies						
Kitty Todd Nature Preserve	08/09/08	-83.78694618	41.61924463	38	7	25.8
Kitty Todd Nature Preserve	08/20/08	-83.80194450	41.60807258	74	12	32.4
Toledo Express Airport	08/30/08	-83.84403705	41.57880442	68	6	34.8
Wildwood Preserve Metropark	09/03/08	-83.67225674	41.67992386	64	16	28.9
Toledo Express Airport	09/06/08	-83.84304573	41.57261482	35	9	14.7
Toledo Express Airport	09/06/08	-83.84498095	41.57162129	39	14	16.8
Kitty Todd Nature Preserve	08/30/09	-83.78546098	41.61819993	46	20	24.5
Toledo Express Airport	09/12/09	-83.81798125	41.57539378	30	17	16.1
Sand barrens						
Oak Openings Preserve Metropark	07/26/08	-83.84265229	41.53493436	43	5	29.9
Oak Openings Preserve Metropark	07/29/08	-83.85249850	41.55441354	47	5	30.9
Metroparks corridor	08/01/08	-83.76540501	41.59963676	40	9	19.6
Toledo Express Airport	08/08/08	-83.85026180	41.57716417	40	12	20.2
Metroparks corridor	08/27/08	-83.76483574	41.60316282	50	4	20.5
Toledo Express Airport	08/25/09	-83.78235114	41.58774489	20	7	20.3
Toledo Express Airport	09/11/09	-83.81621933	41.57624753	34	22	16.6
Oak Savannas						
Kitty Todd Nature Preserve	08/07/09	-83.80967020	41.60774878	36	0	22.8
Oak Openings Preserve Metropark	08/09/09	-83.84691919	41.53793580	23	2	23.1
Kitty Todd Nature Preserve	08/14/09	-83.81316272	41.60941948	45	0	25.5
Oak Openings Preserve Metropark	08/23/09	-83.84997917	41.55028826	45	2	23.9
Kitty Todd Nature Preserve	08/30/09	-83.80418403	41.60990919	46	1	29.5
Kitty Todd Nature Preserve	09/13/09	-83.79670408	41.62008870	59	2	34.1
Kitty Todd Nature Preserve	09/17/09	-83.81199005	41.60728675	55	4	26.6
Kitty Todd Nature Preserve	09/20/09	-83.79330439	41.62057474	68	3	35.4
Kitty Todd Nature Preserve	09/22/09	-83.79253861	41.61951407	72	4	39.4

Table 2. Total number of species, by community type, among 39 1000-m^2 vegetation sampling plots within the Oak Openings region.

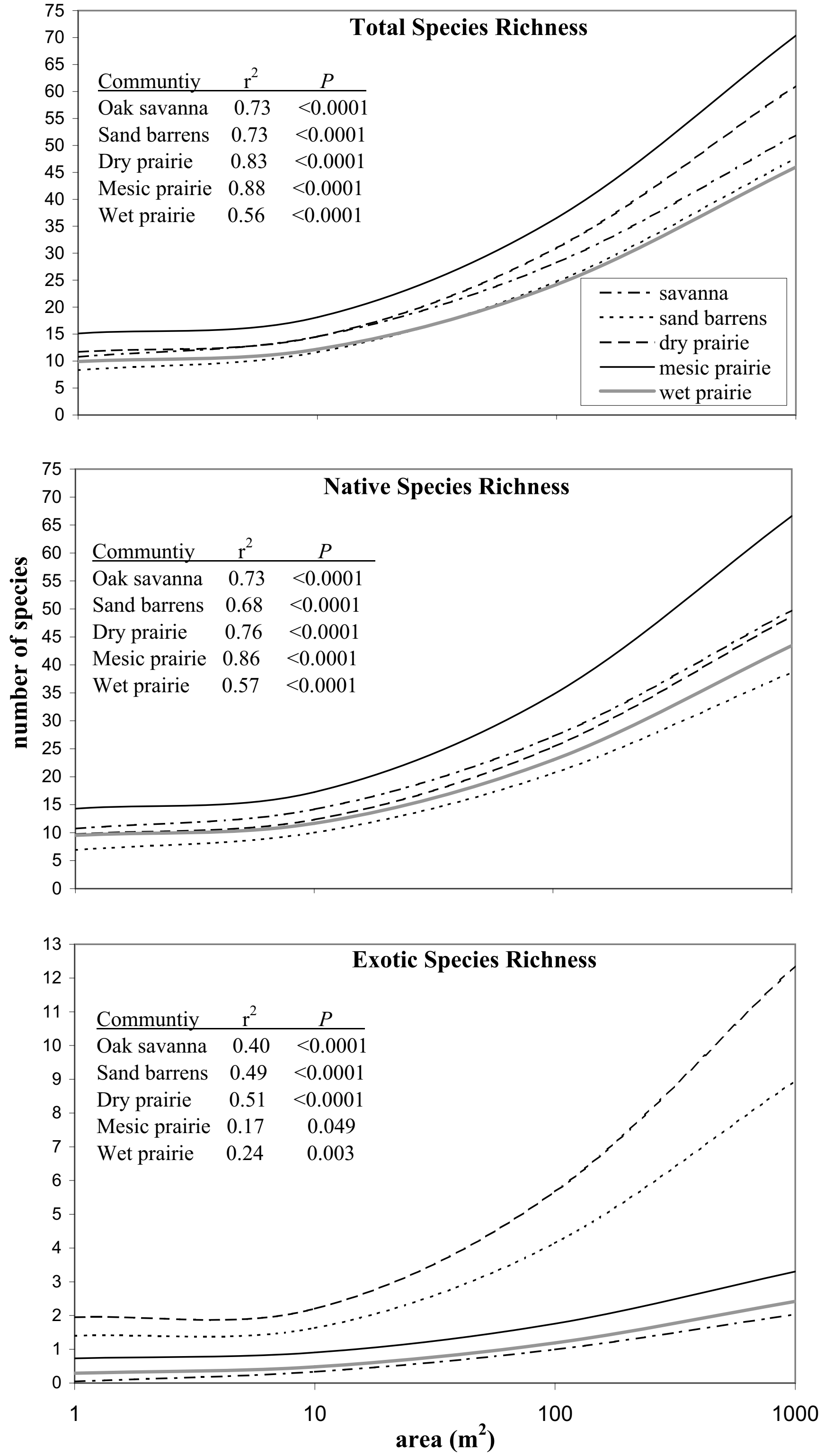
Community type	Plots	No. species	No. unique species	Percent unique
Wet prairie	9	175	70	40.0
Mesic prairie	6	199	18	9.0
Dry prairie	8	201	19	9.5
Sand barren	7	153	36	23.5
Oak savanna	9	173	30	17.3

Table 3. Species composition overlap (Jaccard's Coefficient) among five Oak Openings plant communities.

Community type	Wet prairie	Mesic prairie	Dry prairie	Sand barrens	Oak savanna
Wet prairie	-	0.322	0.182	0.167	0.213
Mesic prairie	0.322	-	0.423	0.375	0.431
Dry prairie	0.182	0.423	-	0.469	0.375
Sand barren	0.167	0.375	0.469	-	0.353
Oak savanna	0.213	0.431	0.375	0.353	-
Mean	0.221	0.388	0.362	0.341	0.343

Table 4. Species composition overlap (Jaccard's Coefficient) within each of five Oak Openings plant communities (mean with standard error).

Community type	Mean (SE)
Wet Prairie	0.218 (0.030)
Mesic Prairie	0.274 (0.037)
Dry Prairie	0.253 (0.030)
Sand Barren	0.247 (0.033)
Savanna	0.292 (0.029)



Total Species Richness

Communtiy	r^2	*P*
Oak savanna	0.73	<0.0001
Sand barrens	0.73	<0.0001
Dry prairie	0.83	<0.0001
Mesic prairie	0.88	<0.0001
Wet prairie	0.56	<0.0001

Native Species Richness

Communtiy	r^2	*P*
Oak savanna	0.73	<0.0001
Sand barrens	0.68	<0.0001
Dry prairie	0.76	<0.0001
Mesic prairie	0.86	<0.0001
Wet prairie	0.57	<0.0001

Exotic Species Richness

Communtiy	r^2	*P*
Oak savanna	0.40	<0.0001
Sand barrens	0.49	<0.0001
Dry prairie	0.51	<0.0001
Mesic prairie	0.17	0.049
Wet prairie	0.24	0.003

Figure 1. Species area curves for five Oak Openings plant communities based on 39 1000-m2 modified-Whittaker, multi-scale plots. Statistical relationships are based on log10 transformed data for both area and number of species.

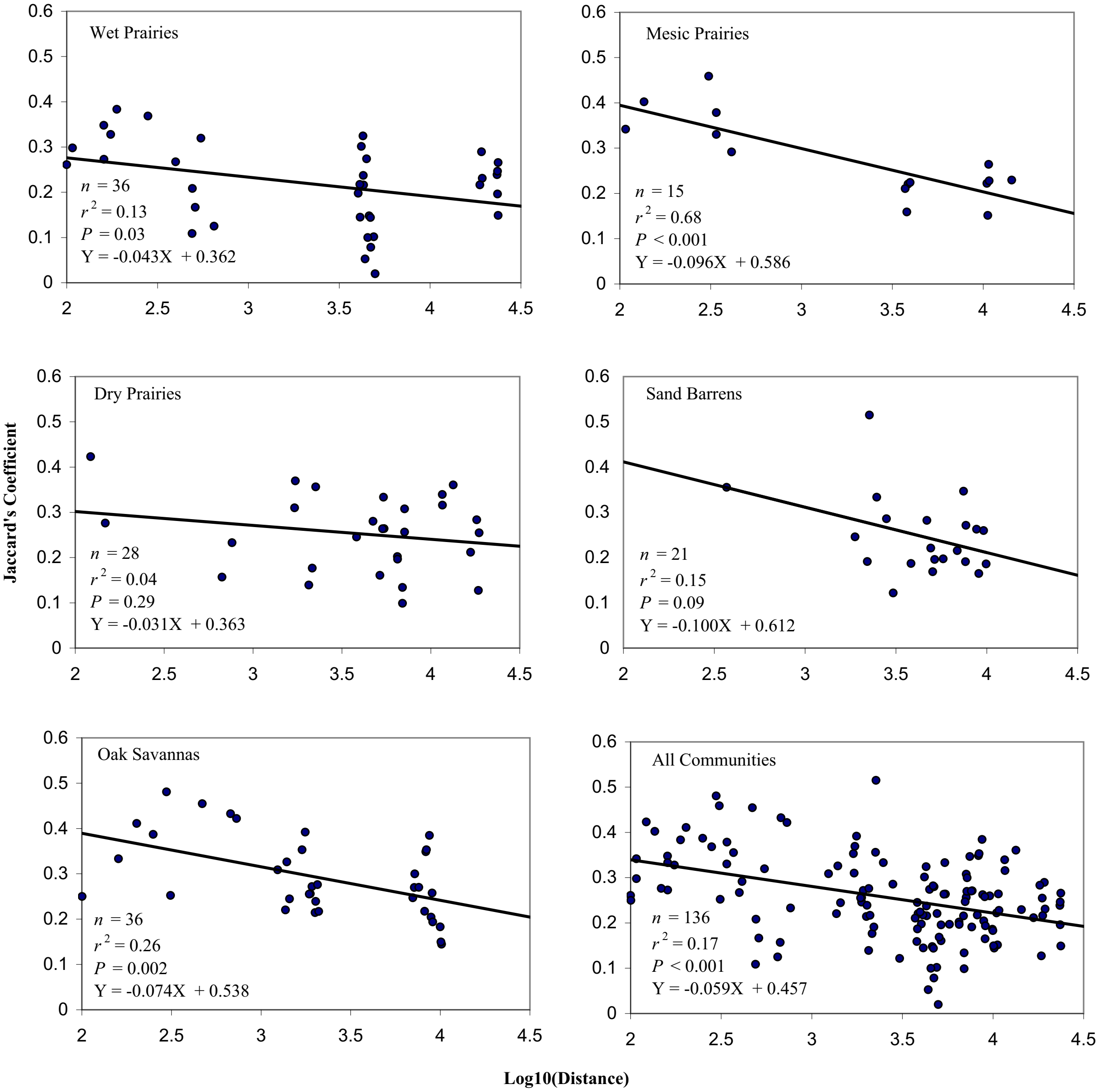


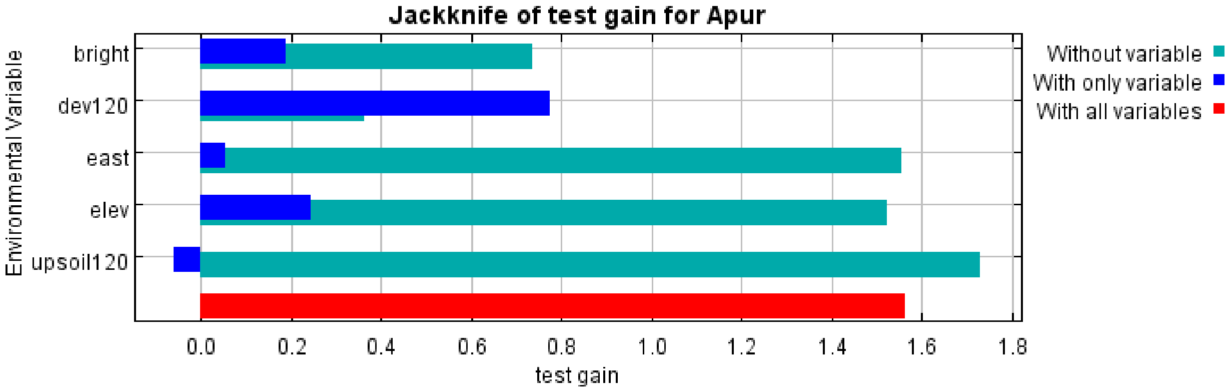
Figure 2. Relationship between species composition overlap (Jaccard's Coefficient) and proximity of sampling plots for five Oak Openings plant communities. Distance units are in meters.

APPENDIX III: MAXENT MODEL PARAMETERS

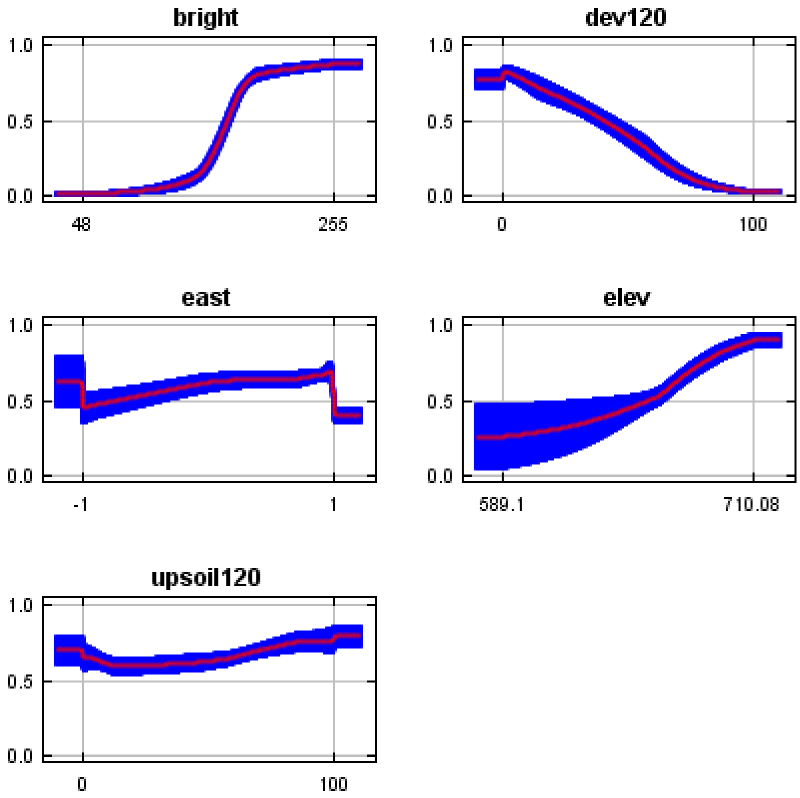
In Chapter III, I evaluated the percent contribution of selected environmental variables to Maxent species distribution models for nine rare Oak Openings plant species. The following appendix provides additional information on the importance of each environmental variable for these nine models. Figure 1 contains the model outputs for the selected species generated from program MaxEnt 3.3 (Phillips et al. 2006), and is displayed following the format of Wollan et al. (2008). For complete citations of these references, refer to Chapter III.

In Figure 1, the ‘jackknife of test gain’ for each model provides an estimate of the relative gain or loss in mode performance for each variable when that variable is used in isolation for model development, and when omitted from the model. For example, for *Aristida purpurascens*, the environmental variable with highest gain in model performance when used in isolation is ‘percent of developed land cover’, which thus appears to have more predictive power by itself than the other model variables. ‘Percent of developed land cover’ is also the variable that has the greatest negative effect on model performance when omitted from the model, and thus appears to have the most information that is not present in the other model variables. The response curves for each variable show how the logistic prediction changes across the entire range of that variable when keeping all other environmental variables at their average sample value. The curves show the mean response over ten replicate Maxent runs (mean values shown in red with one standard deviation shown in blue.

Aristida purpurascens



Response curves:

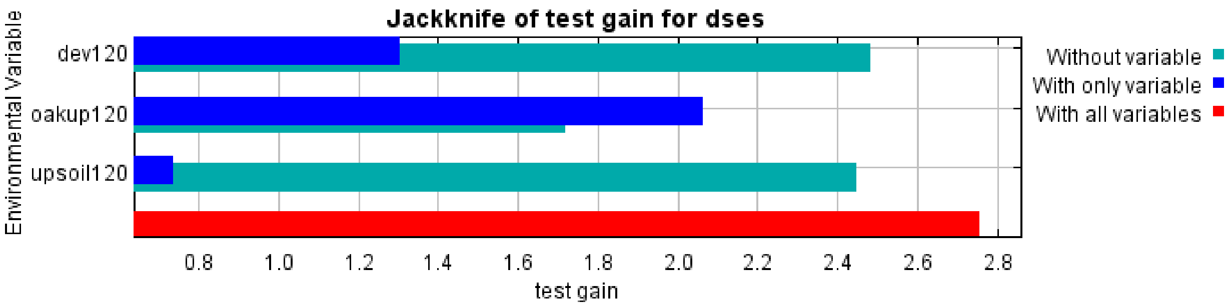


Key to variables:

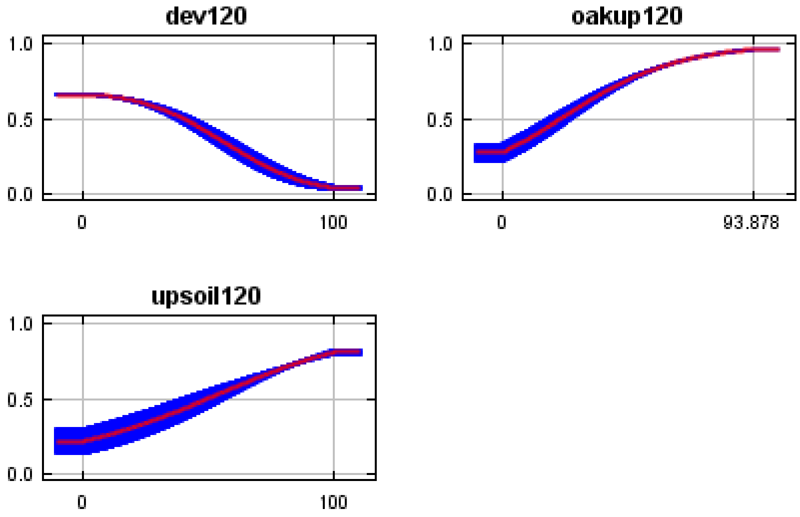
bright:	brightness index
dev120:	percent of developed land cover
east:	east aspect
elev:	elevation
upsoil120:	percent Oak Openings soils (non-hydric)

Figure 1. Jackknife tests of variable importance with response curves for each environmental variable used to develop Maxent models for nine rare Oak Openings plant species. For each species, results were averaged over ten replicate model runs. For response curves, mean values are shown in red, +/- one standard deviation in blue.

Desmodium sessilifolium



Response curves:

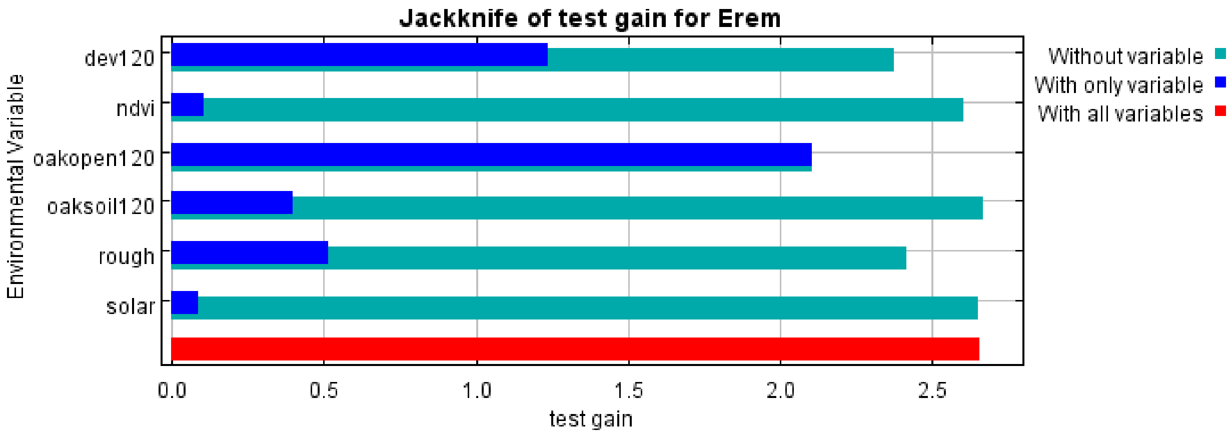


Key to variables:

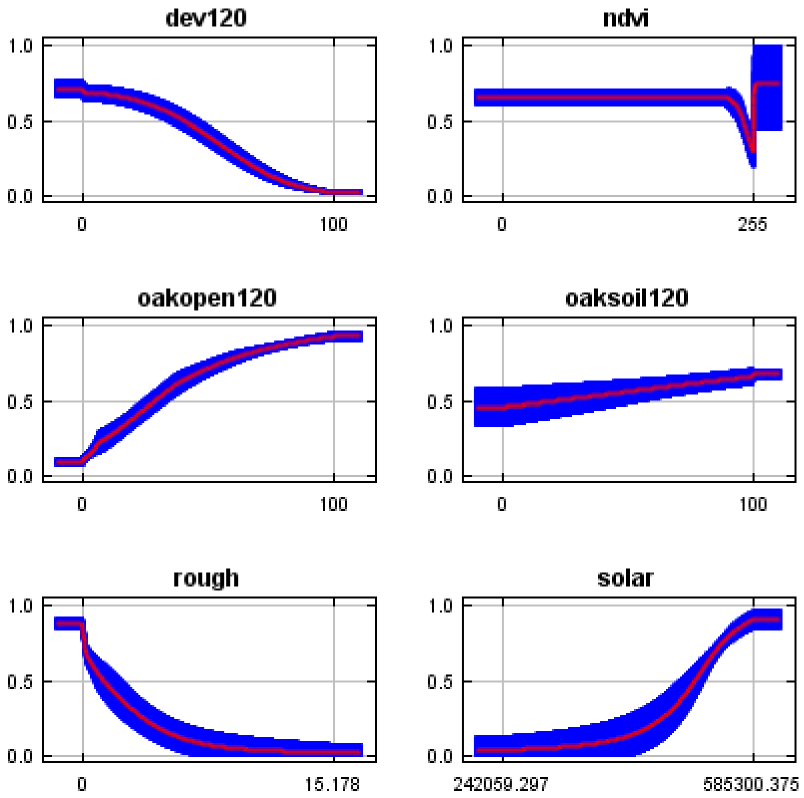
dev120:	percent of developed land cover
oakup120:	percent Oak Openings land cover (upland)
upsoil120:	percent Oak Openings soils (non-hydric)

Figure 1. Continued

Euthamia remota



Response curves:

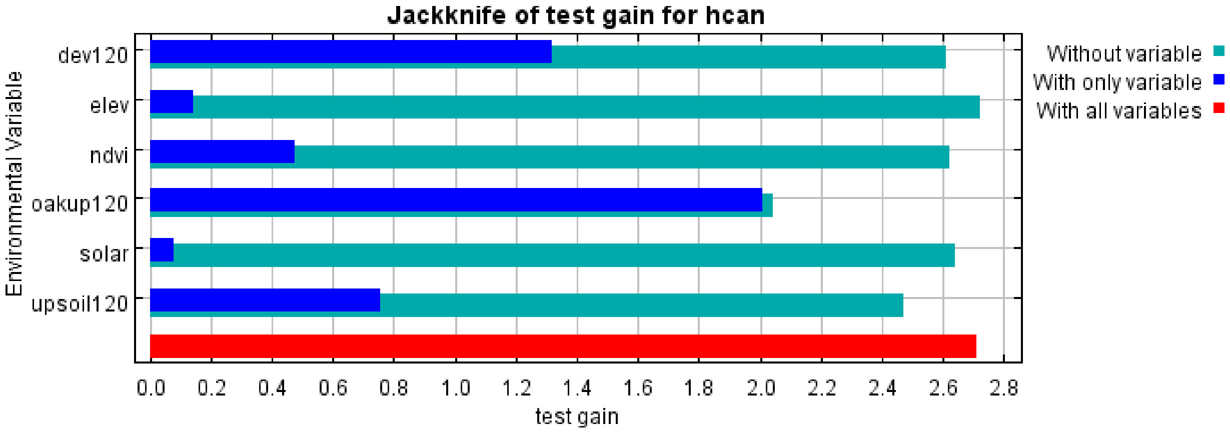


Key to variables:

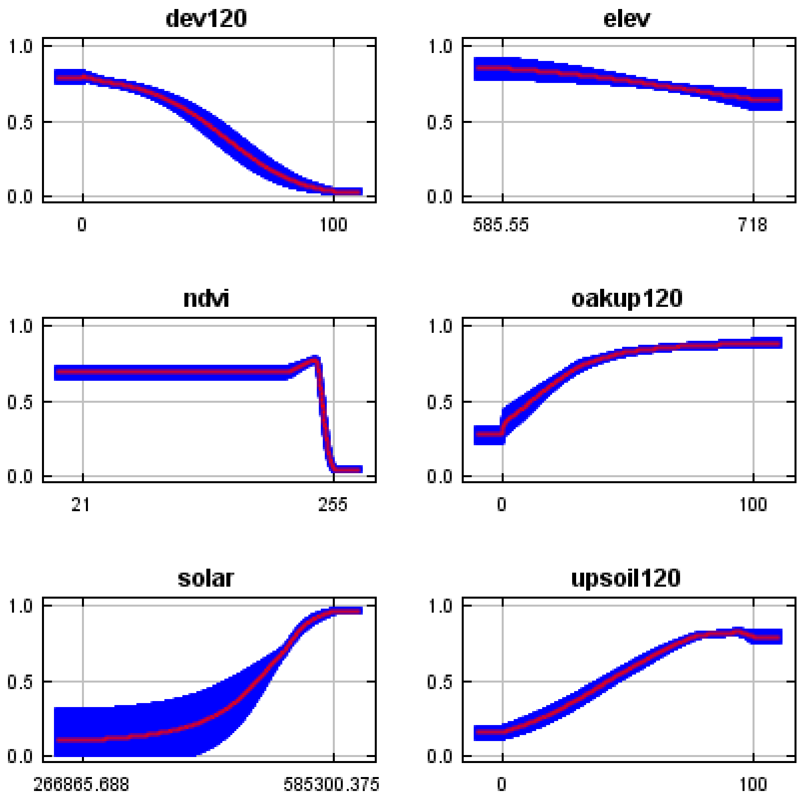
dev120:	percent of developed land cover
ndvi:	NDVI index
oakopen: 120	percent Oak Openings land cover
rough:	roughness index
solar:	solar insolation
upsoil120:	percent Oak Openings soils (non-hydric)

Figure 1. Continued

Helianthemum canadense



Response curves:

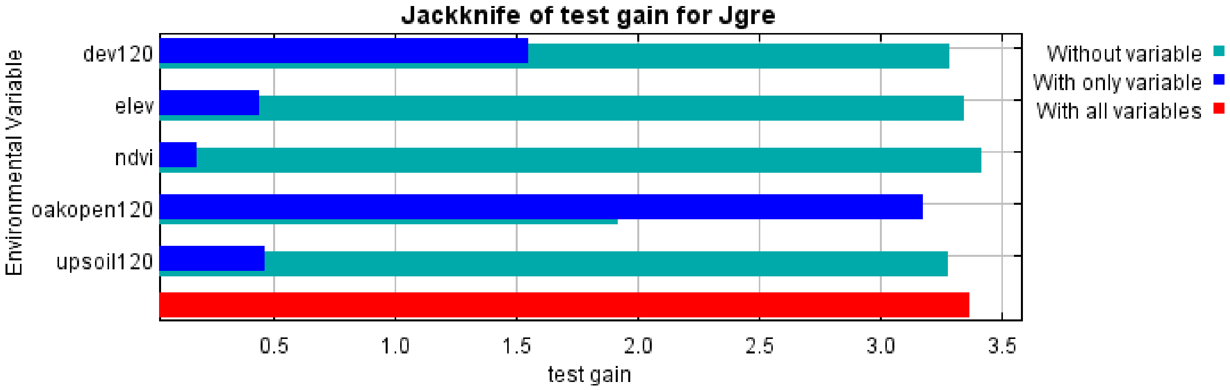


Key to variables:

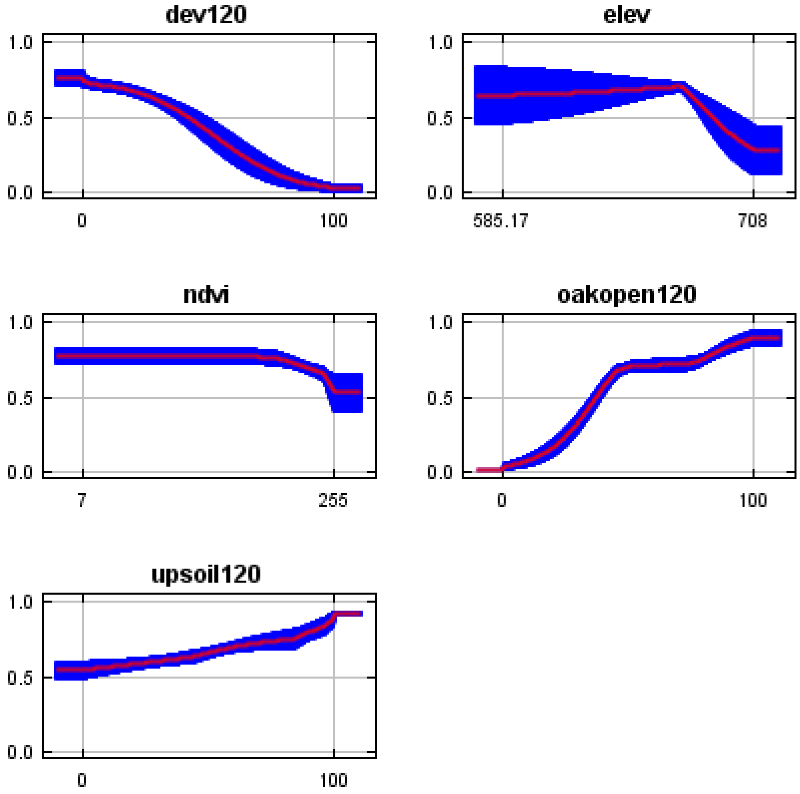
dev120:	percent of developed land cover
elev:	elevation
ndvi:	NDVI index
oakup120:	percent Oak Openings land cover (upland)
solar:	solar insolation
upsoil120:	percent Oak Openings soils (non-hydric)

Figure 1. Continued

Juncus greenei



<u>Response curves</u>:

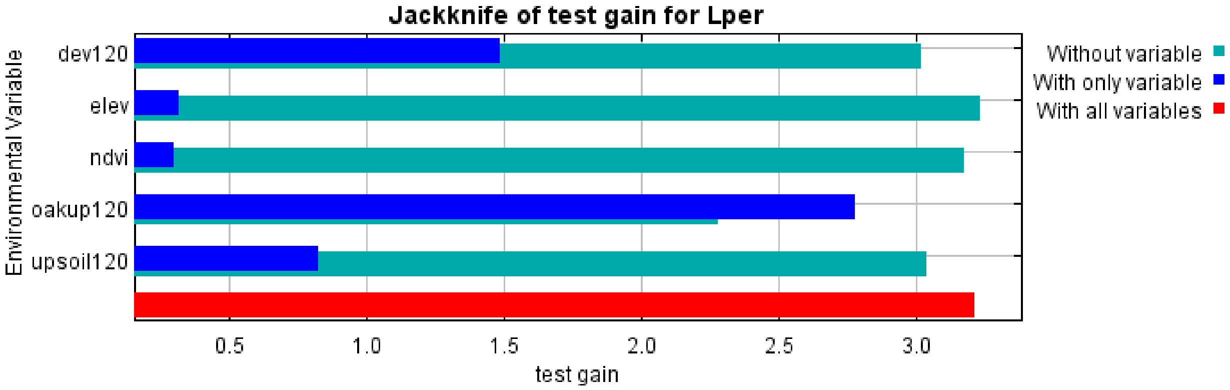


<u>Key to variables</u>:

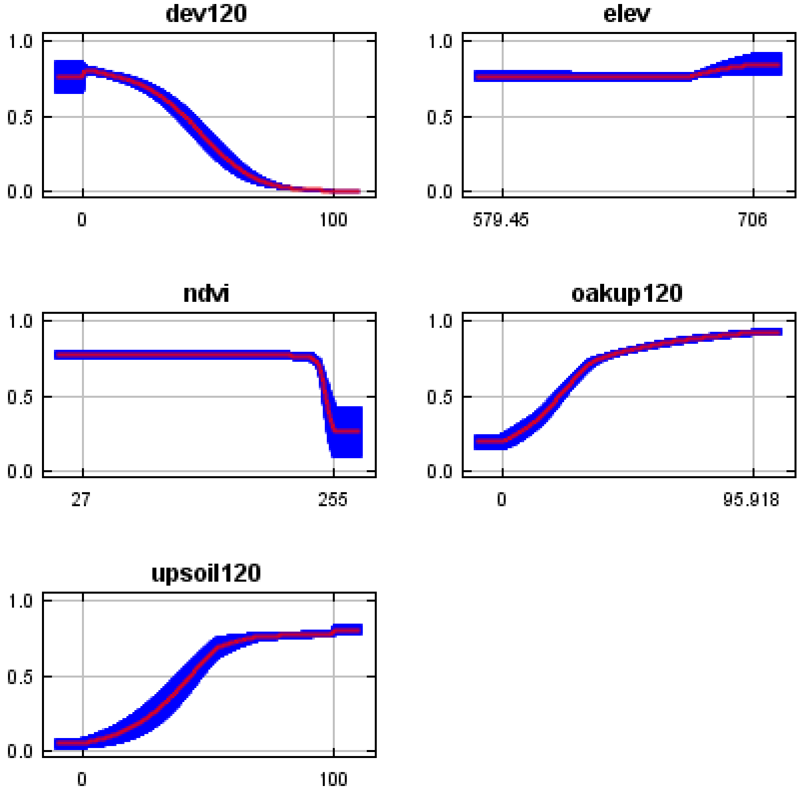
dev120:	percent of developed land cover
elev:	elevation
ndvi:	NDVI index
oakopen: 120	percent Oak Openings land cover
upsoil120:	percent Oak Openings soils (non-hydric)

Figure 1. Continued

Lupinus perennis



Response curves:



Key to variables:

dev120: percent of developed land cover

elev: elevation

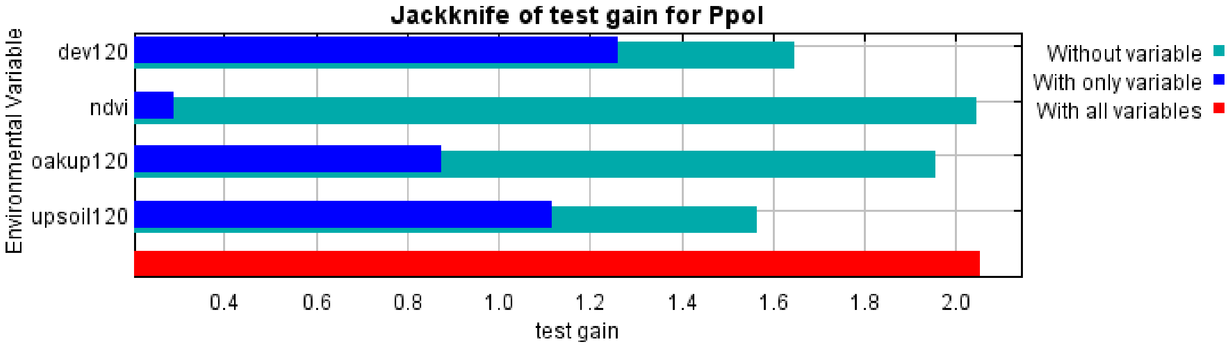
ndvi: NDVI index

oakup120: percent Oak Openings land cover (upland)

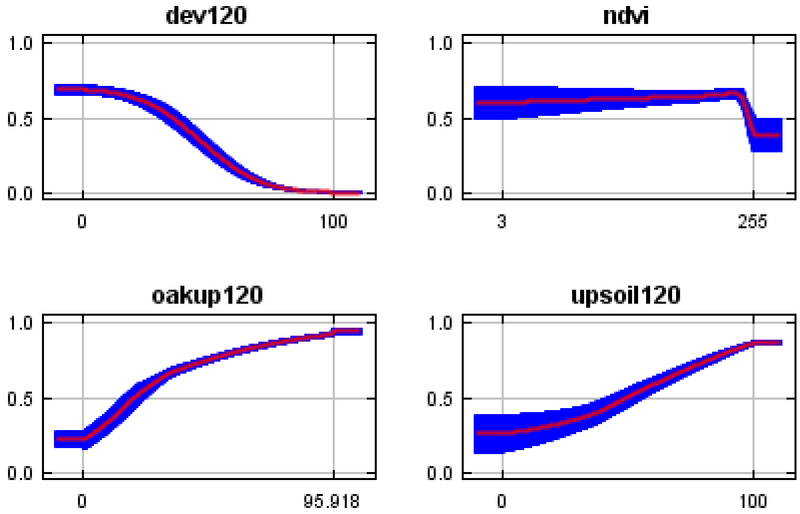
upsoil120: percent Oak Openings soils (non-hydric)

Figure 1. Continued

Polygala polygama



Response curves:

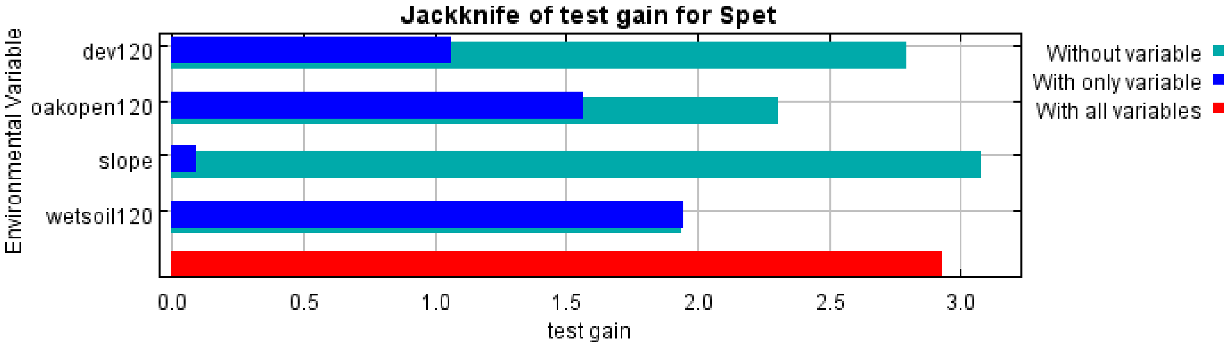


Key to variables:

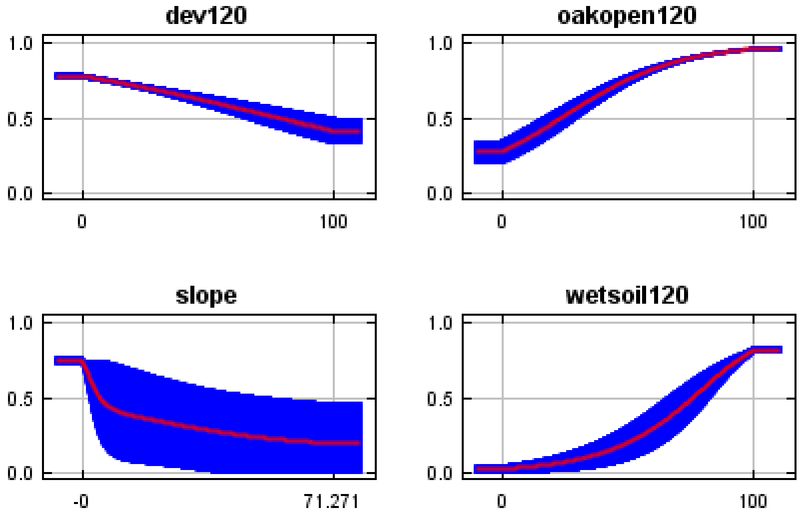
dev120:	percent of developed land cover
ndvi:	NDVI index
oakup120:	percent Oak Openings land cover (upland)
upsoil120:	percent Oak Openings soils (non-hydric)

Figure 1. Continued

Salix petiolaris



<u>Response curves</u>:

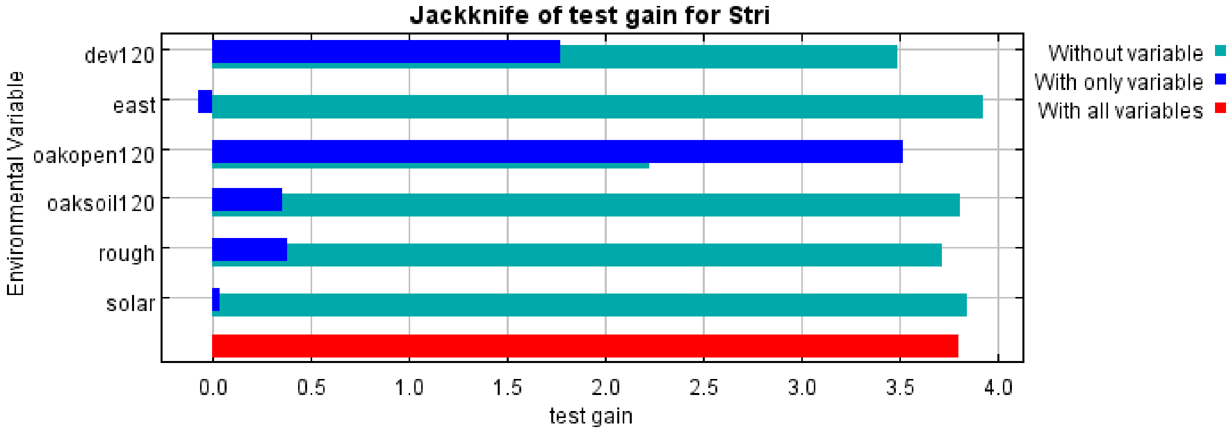


<u>Key to variables</u>:

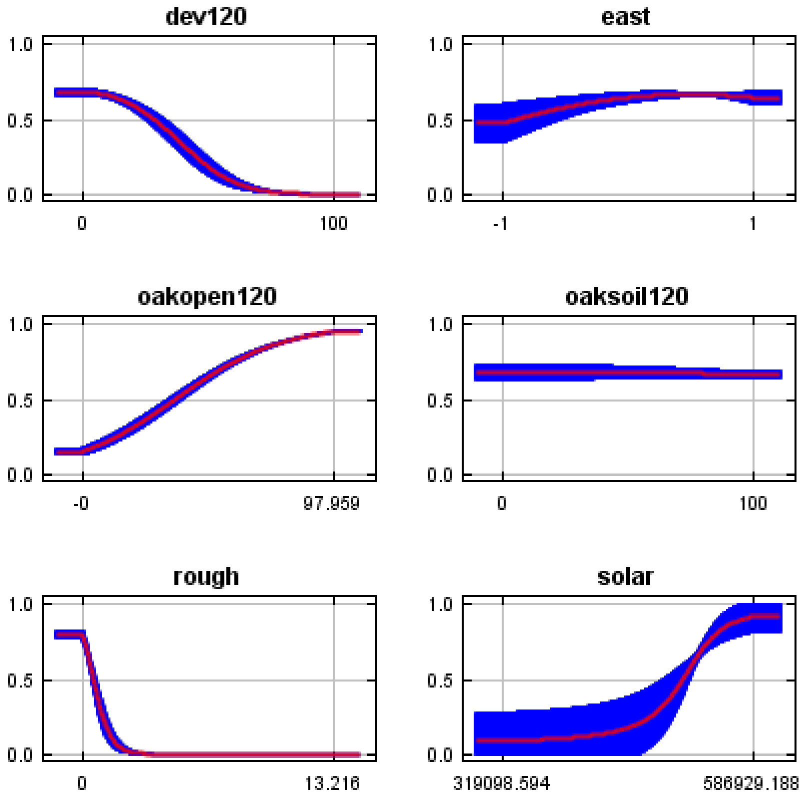
dev120:	percent of developed land cover
oakopen: 120	percent Oak Openings land cover
slope:	percent slope
wetsoil: 120	percent Oak Openings soils (hydric)

Figure 1. Continued

Scleria triglomerata



Response curves:



Key to variables:

dev120:	percent of developed land cover
east:	east aspect
oakopen: 120	percent Oak Openings land cover
upsoil120:	percent Oak Openings soils (non-hydric)
rough:	roughness index
solar:	solar insolation

Figure 1. Continued