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Community-Level Impacts of Management and Disturbance in Western Michigan Oak Savannas

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ABSTRACT.—Midwestern oak savanna systems are typically defined by their open canopy and the co-existence of scattered mature oak trees and a ground layer dominated by herbaceous vegetation. The structure of these systems is thought to be primarily maintained by disturbance such as fire. In this study we examined the plant community of 21 different oak savanna sites in western Lower Michigan, U.S.A., across a coarse disturbance gradient created by different management practices. Herbaceous community composition differed significantly across a variety of management approaches, while overall diversity remained similar. Indicator species analysis (ISA) identified several species commonly associated with mixed oak forest understories (*e.g., Maianthemum canadense*) as indicators for recently abandoned oak savanna sites, whereas the indicators identified for managed or heavily disturbed sites included common savanna-associates (*e.g., Lupinus perennis*). Variation in soil characteristics (C:N ratio and pH) and canopy cover may be driving these differences in plant community composition between management approaches. These results reinforce the importance of disturbance to Midwestern oak savanna ecosystems. Furthermore, if long-term management goals include encouraging the establishment and maintenance of herbaceous oak savanna-associated plant species, disturbance created through management activities, such as hand cutting, will likely yield better results over inaction, especially where using fire is not an option.

INTRODUCTION

North American Midwestern oak savannas are characterized by sparsely distributed mature oak trees and a ground layer dominated by forbs and graminoids. This distinctive ecosystem structure is thought to have been maintained primarily by fire and to a lesser extent animal grazing (Olson, 1996; Sankaran *et al.,* 2004; Anderson, 2007). These ecosystems were fairly common historically throughout the Midwestern United States and Canada (Anderson, 2007). Today less than one percent of the estimated presettlement oak savanna remains (Nuzzo, 1986). This loss of savanna has largely been attributed to land use change, fragmentation, and fire suppression (Abrams, 1992; Scholes and Archer, 1997).

In recent decades there has been a growing effort to maintain savanna remnants and restore oak savanna habitat across the Midwestern United States (*e.g.,* Apfelbaum and Haney, 1991; Peterson and Reich, 2001; Nielsen *et al.*, 2003; Asbjornsen *et al.,* 2005; Brudvig

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and Asbjornsen, 2008; Brudvig, 2010; Lettow *et al.*, 2014). Given their heavy herbaceous component and historical dependence on fire, these systems can have significant spatial variation in both composition and structure (Asbjornsen *et al.,* 2005; Anderson, 2007). This variability makes setting restoration goals and defining desired future conditions difficult. What makes 'good' oak savanna? What metrics should we use to define success? Historical conditions have often been used to inform restoration and management goals (Landres *et al.,* 1999; Swetnam *et al.*, 1999) because they help us to understand the ecological processes that structure the community of interest. Unfortunately, little to no historical reference data exists for Midwestern oak savanna systems, and our understanding of their vegetation dynamics is relatively limited (Brudvig and Asbjornsen, 2008). We can set restoration goals based on our understanding of savanna remnants (*e.g.*, White, 1994; Delong and Hooper, 1996), but even those remnants may differ from historical savannas (Anderson, 1998; Asbjornsen *et al.,* 2005; Anderson, 2007). Even historical conditions may not be useful as ecological references when considering modern anthropogenic influences, such as climate change, on landscapes where restored oak savannas will be managed into the future (*see* Harris *et al.*, 2006; Millar *et al.*, 2007).

One possible restoration approach is to set management goals based on a detailed picture of the extant regional oak savanna community. Desired future conditions can be defined by targeting certain community compositions, creating habitat for focal species, and minimizing risk of invasion by exotics. Using plant community composition as a management target in and of itself could make monitoring efforts difficult because it requires the simultaneous consideration of a large number of different plant species. One increasingly popular solution to this problem is to conduct an indicator species analysis (ISA) and use individual indicator species as management targets. ISA identifies individual or groups of species that act as ecological indicators for a given community (Dufrêne and Legendre, 1997). Because indicator species are, by definition, indicative of a larger community and/or site conditions, managers can use these species as foci to aid in setting management goals based around particular communities and to more easily monitor the success of their efforts (sensu Lambeck, 1997).

Here we examine differences in western Michigan oak savanna plant community structure and composition across a range of management practices and their associated disturbance regimes. We quantified differences in community composition, species richness, and the abundances of individual species of special concern. We also examine some of the potential disturbance-mediated factors that may be acting as drivers of community assembly across management practices, including canopy structure and soil physical and chemical characteristics. Contingent on the identification of distinct plant communities, we also conducted an indicator species analysis to obtain a list of indicator species for each distinct community. This work has the potential to shed light on the relatively poorly studied, biologically important, and exceedingly rare (Nuzzo, 1986) oak savanna plant communities of western Michigan by examining different disturbances and management practices and their influence on community assembly, while informing potential management efforts aimed at restoring these ecosystems.

METHODS

STUDY SITE

This study was conducted on the Huron-Manistee National Forests (HMNF) in Lower Michigan, U.S.A. Our study sites were located on the southern portion of the Manistee

National Forest, in western Lower Michigan between 43.55°N, 86.09°W and 43.48°N, 86.32°W. The area has a humid continental climate with a mean annual (1901–2000) temperature of 7.16 C (NOAA, 2016). Annual precipitation is variable, with an average (1901–2000) of 810 ± 150 mm per y (NOAA, 2016). Upland soils in the region are sandy and largely glacial in origin and consist largely of entisols and spodosols (NRCS, 2015).

Historically oak savanna systems were fairly common in this region (Nuzzo, 1986), existing within a matrix of mixed oak-pine forest (Albert and Comer, 2008). Today the landscape is dominated by mixed oak forest, red pine (*Pinus resinosa*) plantations, and agricultural fields. Early successional native plant communities like oak savanna, jack pine (*Pinus banksiana*) barrens, and dry sand prairies exist only in small patches. The oak savanna systems in this study region are typically dominated by white oak (*Quercus alba*) and black oak (*Q. velutina*), with smaller components of red oak (*Q. rubra*), pine (*Pinus* spp.; especially *P. banksiana*), and cherry (*Prunus* spp.). These systems typically fall under the 'Black Oak / Lupine Barrens' classification within the U.S. National Vegetation Classification System (CEGL002492; Faber-Langendoen, 1998). The ground layer is often dominated by forbs and grasses, though sedges (*Carex* spp.) can become very abundant following heavy disturbance (Abrams and Dickmann, 1983, 1984). Woody shrubs and tree seedlings are also common. Canopy cover is often heterogeneous, with either single or small groups of trees scattered throughout the site, creating a mix of open and shaded habitat. Managed oak savanna systems on the HMNF have an average canopy cover of 35%.

DATA COLLECTION

Plant community data were collected from a total of 21 sites in 2013 and 2014. Sites ranged in size from 2 to 8 ha and were <10 km apart. Sites were selected based on their physiographic and environmental similarity. There were no significant differences ($P > 0.05$) in elevation (203 ± 9 m ASL), average slope (1.4 ± 1.1%), or aspect (183 ± 34°) between sites. All sites were located on similar soils (Typic Udipsamments, Entic Haplorthods, or a mixture of both). Within each site a multiscale random sampling approach was used to collect vegetation data: 1-m^2 quadrats for herbaceous vegetation, 4-m^2 plots for small (*i.e.*, <2.54 cm diameter) woody vegetation, and 0.04 ha plots for larger woody vegetation. Within each plot the identity, number of stems, and estimated cover (%) class was recorded for each plant species. Only identity and cover class were recorded for grasses and sedges. Because sites varied in size, the number of randomly placed plots within each site was based on total site area such that 5×10^{-4}% of the area was sampled for herbaceous vegetation, 1×10^{-3}% for small woody, and 0.02% was sampled for larger woody vegetation. Using this sampling intensity, an 8 ha site would have 40 1-m^2 quadrats, 20 4-m^2 quadrats, and four 0.04 ha plots.

Forest structure and environmental variables were also recorded for each site. In 2013 and 2014 canopy cover (%) class was estimated using a convex densiometer at all vegetative sampling locations. In 2012 several soil characteristics were recorded at each site using a transect-based systematic sampling design and the same sampling scheme as our herbaceous vegetation measurements (*see above*). At each sampling location the depth of the soil A horizon was measured using a ruler and samples were collected for the analysis of soil pH and elemental carbon and nitrogen in the laboratory. Soil samples were collected using a 3 cm diameter × 25 cm long hand probe (AMS, Inc.). Soil pH was recorded using an Oakton 2700 benchtop pH meter in a 1:1 soil:water mixture. To determine elemental C and N content, soils were ground to powder using a Retsch RM 100 mortar grinder and analyzed using a Fisons NA1500 elemental analyzer which uses microcombustion to estimate elemental composition.

The sites used in this study represent a range of disturbance intensities as a result of current management practices. Of the 21 sites, seven are actively managed as oak savanna (Managed), six are heavily disturbed and actively surveyed by the HMNF as savanna sites (Disturbed), and eight are recently abandoned sites formerly managed as oak savanna (Abandoned). Actively managed sites are maintained using hand tools (chainsaws, brushsaws) to control woody vegetation. Hand cutting treatments are typically conducted in late summer on a 4 y rotation. All woody shrubs and trees with a diameter at breast height (dbh) of <20 cm are targeted for removal from the site; this diameter threshold forestalls woody plant recruitment while maintaining a constant level of canopy cover (typically ~35%) from mature trees. Due to the presence of the federally endangered Karner Blue butterfly (Lepidoptera: *Lycaeides melissa samuelis*), fire is not currently used as a regular management tool on the Managed sites.

The Disturbed sites represent locations demonstrating heavy anthropogenic (*e.g.*, offroad vehicle) or other disturbance (*e.g.*, high frequency fire) that maintains or creates a savanna-like structure. The Abandoned sites in this study were once managed similarly to sites in the Managed group but have recently (within the last 10 y) been abandoned and have only a light disturbance regime (*e.g.*, windthrow, minimal animal browse).

DATA ANALYSIS

We used nonmetric multidimensional scaling (NMDS) and permutational multivariate analysis of variance (perMANOVA) to explore community level differences between sites in species space. Plotting the sites in species space using NMDS provides a visual interpretation of the differences in plant community composition between sites or groups of sites. We used a Bray-Curtis dissimilarity index (Bray and Curtis, 1957) to run the NMDS. PerMANOVA was used to determine whether our *a priori* site groupings were significantly different from each other in terms of community composition. Because we suspected herbaceous and woody species would have variable responses to differences in management approach, we split the dataset into two separate units: herbaceous-only and woody-only, and ran separate NMDS and perMANOVA analyses for each. Dissimilarity matrices used in these analyses were constructed using percent cover data.

Contingent on any differences between site groups in terms of plant community composition, we were also interested in identifying indicator species. Indicator species analysis (ISA) examines the relationship between species occurrence and abundance data and groups of sites (Dufrêne and Legendre, 1997). We performed ISA for our site groups (*i.e.*, Managed, Disturbed, Abandoned) as well as pairs of site groups (*i.e.*, Managed+Disturbed, *etc.*). We also computed potential indicator species-pair combinations—pairs of species that, together, may be a good indicator of a distinct community. We considered plants to be indicator species only when species IndVal scores were above 0.85 ($P < 0.05$). Separate ISAs were performed on both the herbaceous and woody plant communities.

To address some of the underlying causes of any potential differences in plant communities between site groups, we examined percent canopy cover, soil pH, soil C:N ratio, and depth of soil A horizon thickness (cm) across sites. The relationships between these environmental factors and the continuous NMDS ordination axes for each community dataset were explored using separate linear models, with environmental variables as the response and NMDS axes as the predictor variables. Separately, we also constructed linear

TABLE 1.—perMANOVA table for both the herbaceous and woody plant communities; effects of *a priori* site groups on plant community composition

Community	Source	df	SS	MSS	*F*	r^2	P
Herbaceous							
	Community type	2	1.1619	0.5809	2.7984	0.2372	0.001
	Residuals	18	3.737	0.2076		0.7628	
	Total	20	4.8989			1	
Woody							
	Community type	2	0.7116	0.3558	1.7127	0.1599	0.052
	Residuals	18	3.7391	0.2078		0.8401	
	Total	20	4.4513			1	

models to look at the relationship between these environmental factors and our categorical *a priori* site groupings (Managed, Disturbed, Abandoned).

Given potential differences in community composition between our site groups, we were also interested in exploring trends in species richness and the abundances of individual species of conservation concern. Species accumulation curves were used to quantify species richness, and two-way analysis of variance was used to assess differences in accumulation curves between site groups. We used linear models to explore between-group differences in the abundances of four species of conservation interest: wild lupine (*Lupinus perennis*), butterfly weed (*Asclepias tuberosa*), spotted knapweed (*Centaurea maculosa*), and St. John's wort (*Hypericum perforatum*). Wild lupine and butterfly weed are uncommon but nonthreatened species that serve as important food sources for several endangered or threatened butterflies (Grundel *et al.,* 2000; USFWS, 2003; Yarrish, 2011). Spotted knapweed and St. John's wort are nonnative invasive species (Higman and Campbell, 2009) that are becoming more common in early successional habitats across Michigan. Spotted knapweed is a plant of particular concern because it may exhibit allelopathic properties (Bais *et al.,* 2002; Duke *et al.,* 2009). Area-normalized stem counts, rather than the percent cover values used in the community analyses, were used as the response variable in these analyses.

RESULTS

Across the 21 sites surveyed, we found a total of 98 plant species, 76 of which were herbaceous and 22 were woody. The most common species overall in terms of both frequencies of occurrence and average percent cover was Pennsylvania sedge (*Carex pensylvanica*), a native sedge that can become abundant following disturbance (including frequently burned areas). Big bluestem (*Andropogon gerardi*) and little bluestem (*Schizachyrium scoparium*) were the most abundant grass species. The most abundant forb species were sheep sorrel (*Rumex acetosella*) and hawkweed (*Hieracium aurantiacum*). Cherries (*Prunus* spp.) were the most abundant woody understory species.

Both NMDS ordinations (herbaceous and woody) were constructed using two dimensions (herbaceous 2D stress: 0.139, woody 2D stress: 0.165, stress values < 0.2 are considered acceptable (Clarke, 1993; Oksanen *et al.,* 2015)). Both the herbaceous and woody plant datasets also met the multivariate homogeneity of group variances assumption of perMANOVA (β-dispersion test: herbaceous $P = 0.108$, woody $P = 0.449$). We found differences in herbaceous plant community composition between our *a priori* site groupings using perMANOVA (Table 1, Fig. 1). All three site groupings seemed to represent distinct

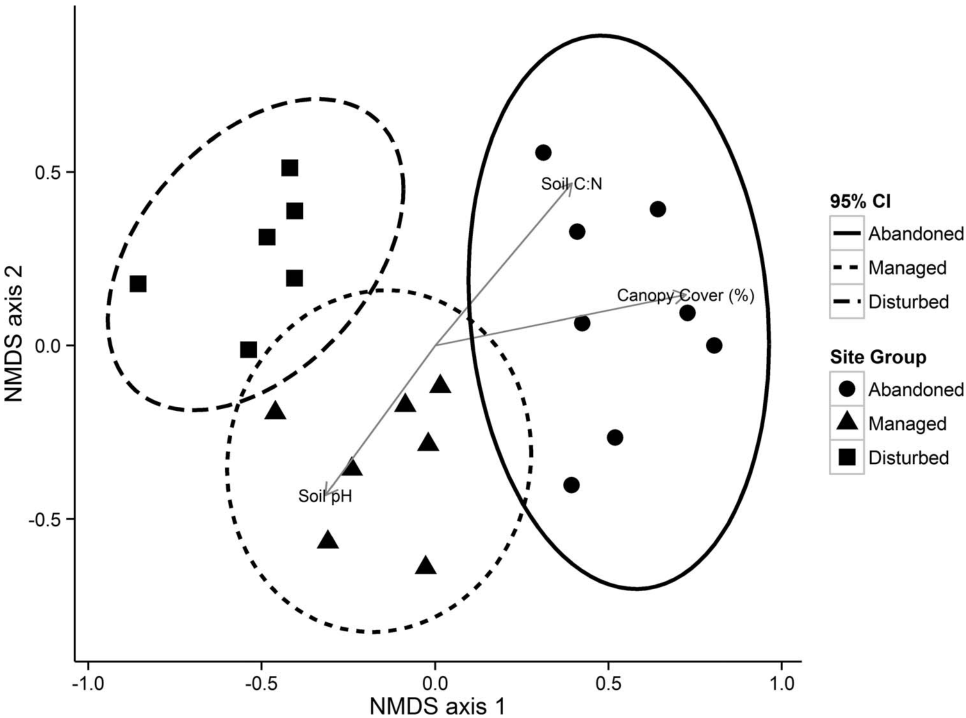

FIG. 1.—NMDS plot, plant community composition, for herbaceous plants. Ellipses represent 95% confidence intervals. Statistically significant relationships with environmental variables are displayed as vectors in species-space. Stress (2D): 0.139

communities, with the largest apparent differences between the Disturbed and Abandoned groups. Woody plant community composition between site groups was not different (Table 1), though the P-value (0.052) was not far from an α-threshold of 0.05. In addition the woody plant NMDS showed an apparent separation of the Abandoned group compared to the Managed and Disturbed groups (Fig. 2), suggesting distinct plant communities in the Abandoned sites.

For the herbaceous community, canopy cover and soil C:N ratio were positively correlated with NMDS axes 1 and 2 (Table 2, Fig. 1). Soil pH had a marginally significant negative correlation with both axes (Table 2, Fig. 1). The NMDS axes for the woody plant dataset were oriented differently (Fig. 2). Canopy cover and soil pH had a strong negative correlation with axis 2 and little correlation with axis 1 (Table 2, Fig. 2). Soil C:N ratio had a marginally significant negative correlation with both axes (Table 2).

Linear models between site groups showed that canopy cover was significantly higher ($P < 0.001$, $F_{2,18} = 17.64$) in Abandoned sites compared with the Managed and Disturbed sites, as shrubs and trees have apparently experienced an increase in recruitment in the absence of disturbance. In terms of soil characteristics, we found differences in the C:N ratio ($P = 0.024$, $F_{2,18} = 4.652$) as well as soil pH between site groups ($P < 0.001$, $F_{2,18} = 11.67$). Soils in Abandoned sites generally had a higher C:N ratio and higher acidity (mean: 20:1 C:N and 5.30 pH) than those in Managed sites (mean: 18:1 C:N and 4.75 pH). We did not, however,

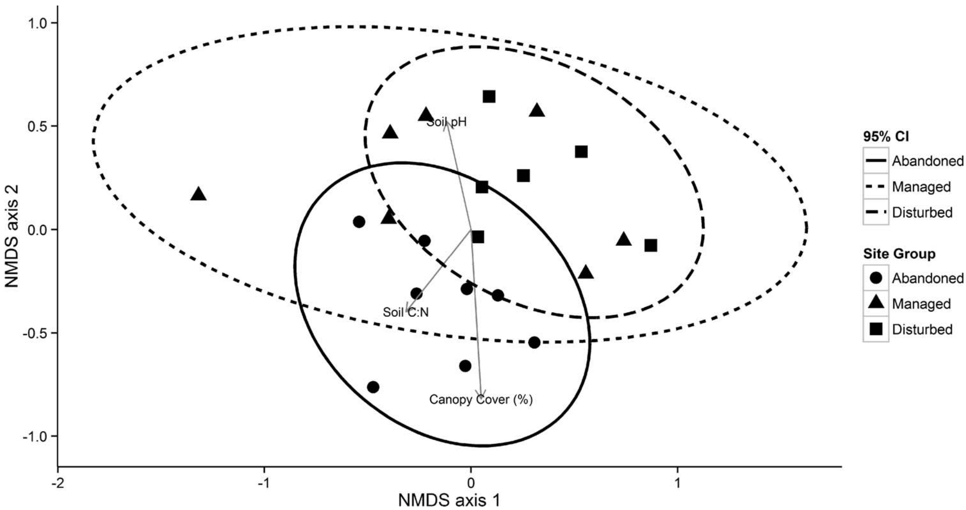

FIG. 2.—NMDS plot, plant community composition, for woody plants only. Ellipses represent 95% confidence intervals. Statistically significant relationships with environmental variables are displayed as vectors in species-space. Stress (2D): 0.165

find any differences between site groups with respect to the depth of the soil A horizon ($P = 0.249$, $F_{2,18} = 1.501$), suggesting little to no difference between site groups in terms of heavy mineral soil disturbance.

A number of plant species demonstrated significant correlations with NMDS axes, illustrating different habitat preferences. Most notably, wild lupine ($r^2 = 0.25$; Axis 1: –0.34, Axis 2: –0.94), butterfly weed ($r^2 = 0.40$; Axis 1: –0.12, Axis 2: –0.99), and spotted knapweed ($r^2 = 0.24$; Axis 1: –0.30, Axis 2: –0.95) were correlated with sites in the Managed group (Fig. 1). St. John's wort, on the other hand, was weakly correlated ($r^2 = 0.15$; Axis 1: 0.63, Axis 2: –0.77) with NMDS axes associated with sites in the Abandoned group.

These ordination correlations are partially reflected in our linear analyses of *a priori* site groupings: we found differences in wild lupine ($P = 0.007$, $F_{2,18} = 6.551$) and butterfly weed ($P = 0.043$, $F_{2,18} = 3.758$) abundance between site groups, with the Managed sites having significantly more lupine stems per m^2 than either the Disturbed or Abandoned sites. We

TABLE 2.—Summary of the relationships between measured environmental variables and community NMDS axes (Fig. 1) for herbaceous and woody plants

Community	Variable	Axis 1	Axis 2	r^2	P
Herbaceous	Canopy cover (%)	0.979	0.203	0.545	0.001
	A horizon thickness	−0.520	−0.854	0.196	0.158
	Soil pH	−0.610	−0.792	0.286	0.050
	Soil C:N ratio	0.646	0.763	0.371	0.019
Woody	Canopy cover (%)	0.060	−0.998	0.674	0.001
	A horizon thickness	0.519	0.855	0.123	0.299
	Soil pH	−0.221	0.975	0.288	0.045
	Soil C:N ratio	−0.621	−0.784	0.258	0.076

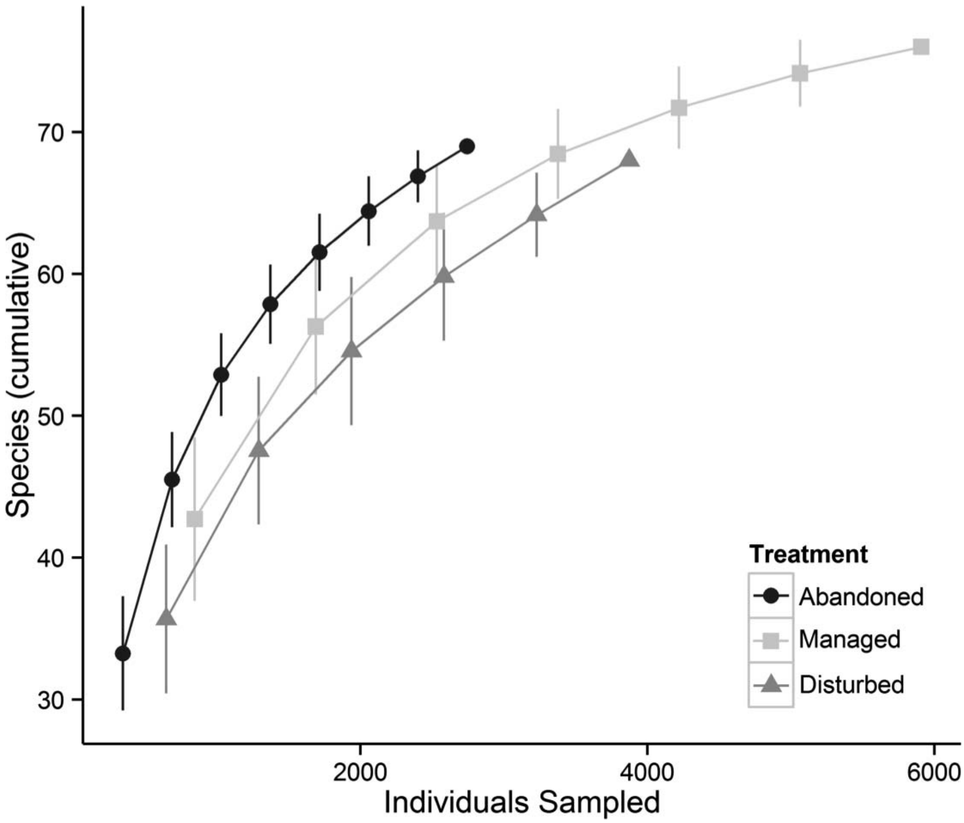

FIG. 3.—Species accumulation curves (number of species per individual sampled) for each site group. Mean ±1 SE species from randomized site additions

did not find any differences between site groups in spotted knapweed abundance (P = 0.852, $X^2 = 0.322$) and found only a marginal difference in St. John's wort abundance (P = 0.071, $X^2 = 5.303$) between site groups, likely due to the high amount of variability in stem counts across sites.

We found a significant difference between site groups (P = 0.001, $F_{2,15} = 12.316$) in species richness, primarily driven by the contrast between Disturbed and Abandoned sites (Fig. 3). Species accumulation curves (Fig. 3) indicated differences in spatial grain between site groups: sites in the Managed group had higher plant densities than either Disturbed or Abandoned sites, and Abandoned sites tended to have more species per individual than either Managed or Disturbed sites. These differences in accumulation curve shapes suggests there may be between-group variation in the spatial structure of sites.

Our analysis identified several indicator species for the Managed and Abandoned site groups, and one indicator, bastard toadflax (*Comandra umbellata*), for the Disturbed site group (Table 3). Several species were also identified as indicators for pairs of site groups—Abandoned Managed and Disturbed+Managed (Table 3). No indicator species were identified for the Abandoned+Disturbed pair (Table 3), perhaps due to the relatively larger differences between plant communities (Fig. 1). When considering pairs of species, we

TABLE 3.—Indicator species by site group. Statistically significant indicators are listed for each site group, as well as two group pairs (Abandoned + Managed, Disturbed + Managed). Two species pairs, identified by *, which when found together function as a significant indicator, are also shown

Site group	Species	Common name	Specificity (*A*)	Fidelity (*B*)	IndVal	P
Abandoned	*Maianthemum canadense*	False Solomon's Seal	1	1	1	0.001
	Oenothera biennis	Primrose	1	1	1	0.001
	Vaccinium augustifolium	Lowbush Blueberry	1	1	1	0.001
	Taenidia integerrima	Yellow Pimpernel	1	1	1	0.001
	Lactuca canadensis	Canada Lettuce	0.9852	0.75	0.86	0.003
Managed	*Galium pilosum*	Hairy Bedstraw	0.8661	1	0.931	0.006
	Tradescantia ohiensis	Common Spiderwort	1	0.8571	0.926	0.001
	Symphyotrichum laeve	Smooth Aster	0.9576	0.8462	0.9	0.001
	Coreopsis lanceolata	Lanceleaf Coreopsis	0.837	1	0.915	0.005
	Asclepias tuberosa	Butterfly Weed	0.7597	1	0.872	0.002
	Monarda punctata	Horsemint	0.8469	0.8571	0.852	0.031
	Andropogon gerardii + *Danthonia spicata**	Big Bluestem + Poverty Grass*	0.8399	1	0.9164	0.005
Disturbed	*Comandra umbellata*	Bastard Toadflax	1	1	1	0.002
	Asclepias syriaca + *Tephrosia virginiana**	Common Milkweed + Goat's Rue*	0.8682	1	0.9318	0.007
Group Pair	**Species**		**Specificity (*A*)**	**Fidelity (*B*)**	**IndVal**	**P**
Abandoned + Managed	*Pteridium aquilinum*	Bracken Fern	0.9759	1	0.988	0.002
	Pedicularis canadensis	Wood Betony	1	0.7333	0.856	0.015
	Potentilla simplex	Cinquefoil	0.9884	0.7333	0.851	0.015
Disturbed + Managed	*Lupinus perennis*	Wild Lupine	0.8595	1	0.927	0.019
	Andropogon gerardii	Big Bluestem	0.8582	1	0.926	0.026
	Schizachyrium scoparium	Little Bluestem	0.9576	0.8462	0.9	0.007
	Asclepias syriaca	Common Milkweed	0.949	0.8462	0.896	0.009
	Krigia virginica	False Dandelion	0.9491	0.7692	0.894	0.025

found a single indicator species pair each for the Abandoned and Disturbed site groups (Table 3). The only woody indicator species identified was lowbush blueberry (*Vaccinium augustifolium*) in the Abandoned site group (Table 3).

DISCUSSION

Plant community composition varied among management practices (Managed, Disturbed, and Abandoned), primarily in the herbaceous layer, with less variation in woody vegetation across sites. This trend is not surprising, given there are more herbaceous than woody plant species across landscapes in general (Stevens, 2001). As a result, there is a wider variety of species available to respond to variations in environmental filtering and competition (sensu Pärtel *et al.,* 1996; Zobel, 1997; Díaz and Cabido, 2001).

We found management practice to have a significant impact on species richness, with Disturbed sites in particular having lower species counts than Abandoned sites (Fig. 3). These differences were most apparent at higher sample grains; at 2000 individuals sampled, the Abandoned species accumulation curve had a mean of 64 cumulative species while Disturbed sites had only 55 (Fig. 3). These differences in the slope and grain size of the accumulation curves between management types suggests the factors or processes driving community composition may differ in terms of spatial scale (*e.g.*, He and Legendre, 2002; Powell *et al.*, 2013). The large grain size in the Managed curve may reflect the spatial homogeneity and site-wide consistency of the hand-pruning treatments. In contrast the initial steep slope and small grain size of the Abandoned curve may indicate a high degree of spatial aggregation among species or individual plants (He and Legendre, 2002; Chase *et al.*, 2013). This may be a result of higher canopy cover (Fig. 1) restricting forb and graminoid establishment to gaps. The relatively low species densities in the Disturbed sites may be due to the nature of the disturbance occurring there: both off-road vehicles (Luckenbach and Bury, 1983; Kutiel *et al.*, 2000) and high frequency fire (Peterson *et al.*, 2007) have been demonstrated to have significant impacts on forb and woody plant diversity and abundance in early successional systems.

These potential differences in the spatial scale of community composition drivers may be reflected in the abundances of some individual species of regional conservation concern. Wild lupine and butterfly weed were significantly more abundant in Managed sites than either Disturbed or Abandoned. Both of these species are of particular interest in western Michigan oak savanna management due to their importance for butterfly conservation. Wild lupine is the obligate larval food source for three rare and threatened butterflies occurring in scattered pockets around the region: The Karner blue, frosted elfin (*Callophrys irus*), and persius duskywing (*Erynnis persius*) (USFWS, 2003). Butterfly weed is a milkweed primarily pollinated by Hymenoptera and Lepidoptera (Fishbein and Venable, 1996) and is known to serve as a preferred nectar source for the adult form of the Karner blue (Grundel *et al.,* 2000; Yarrish, 2011). These two plant species are known to perform well on sites that experience regular mineral soil disturbance (Smith *et al.,* 2002; *see* also USDA, 2015), but our results suggest that the level of soil disturbance in the Disturbed group may be either intense or heterogeneous enough to reduce their abundance.

Of the two invasive species of particular concern in these communities, only St. John's wort demonstrated a marginally significant difference in abundance between community type, occurring in greater abundance in Abandoned sites. This is not unexpected given the species' ability to tolerate higher amounts of shade (USDA, 2015). Spotted knapweed, on the other hand, demonstrated no difference in abundance between community types and exhibited high variation across sites. On sites where spotted knapweed did occur (*i.e.*, Managed sites), it was quite abundant, often exceeding densities of 3 plants per m^2. From a management and conservation perspective, the higher abundance of wild lupine and butterfly weed on sites in the Managed group is encouraging, but the elevated abundance of spotted knapweed is concerning.

Indicator species for Managed sites consisted of species frequently associated with oak savanna habitat in the upper Midwestern United States (Table 3; Betz and Lamp, 1990; Grundel *et al.,* 2000; USFWS, 2003), especially lanceleaf coreopsis (*Coreopsis lanceolata*), butterfly weed, and horsemint (*Monarda punctata*). The sole indicator species for Disturbed sites, bastard toadflax (*Comandra umbellata*), is a semiparasitic plant often found on sandy, gravelly, or heavily grazed sites (Zentz and Jacobi, 1989; Leicht-Young *et al.,* 2009). On Abandoned sites, indicator species consisted of plants one would expect to find in both upland forests and semi-open habitats, including false solomon's seal (*Maianthemum racemosum*), yellow pimpernel (*Lysimachia nemorum*), and Canada lettuce (*Lactuca canadensis*) (USDA, 2015). Indicator species were also identified for two site group pairs: Abandoned+Managed and Managed+Disturbed (Table 3). Noteworthy is the presence of species traditionally associated with oak savannas in the Managed+Disturbed indicator list, including wild lupine. The Managed and Disturbed groups each had indicator species-pairs, that when found together, act as a significant ecological indicator (Table 3).

The types of indicator species identified for each site group reinforces the apparent differences in compositional drivers between management practices. The early successional species identified as indicators for the Disturbed group, particularly bastard toadflax, suggest a site with heavy mineral soil disturbance. This is consistent with the types of disturbance that maintain sites in the Disturbed group (off-road vehicle usage, high frequency surface fire). The savanna associates identified as indicators for Managed sites suggests that hand-cutting may be doing a reasonable job at maintaining oak savanna structure. On Abandoned sites, the identification of several forest understory species as indicators may suggest succession is moving those sites further toward woodland or forest.

The contrasts identified between site groups seem to be due in part to differences in environmental characteristics (Fig. 1), which in turn are a result of the different management practices. For instance the differences in community composition between Managed and Abandoned sites seems to be at least partially driven by differences in canopy cover, soil C:N ratio, and soil pH. Canopy cover affects plants by limiting photosynthetic capacity in the understory (Bazzaz, 1979). Similarly, the soil C:N ratio affects plants as it is a measure of nitrogen availability (Paul, 2007) and along with soil pH, also contributes to variation in macronutrient uptake (Paul, 2007). These factors, especially canopy cover (Bazzaz, 1979), but also soil C:N ratio and pH (Rose *et al.,* 2002; Reynolds *et al.,* 2003; Dovčiak *et al.,* 2003; Ehrenfeld *et al.,* 2005), are known to act as filters for the regional species pool, ultimately leading to distinct plant communities (Díaz *et al.,* 1998).

The apparent differences we found between management practices has the potential to be useful for managers working with oak savanna systems in Michigan and perhaps more broadly. Managing oak savanna systems can be challenging, particularly the task of identifying the appropriate disturbance type and level of intensity (Peterson and Reich, 2001; Brudvig and Asbjornsen, 2007, 2008). Though the sites in this study were located on similar soil types, shared similar physiographies, and were surrounded by similar mixed oak forest, differences in management approach and therefore disturbance type has resulted in three distinct plant communities. The recently Abandoned oak savanna sites have started to undergo vegetation change in the absence of active management or major disturbance, as evidenced by increased levels of canopy cover (Fig. 1) and a quantitative association with plants typically found in mixed-oak forest understories (Table 3). The relatively short ecological timeframe of abandonment (<10 y) highlights the high rate of compositional change in these systems, especially with respect to the herbaceous layer. This rapid compositional change is consistent with similar results and predictions from previous work (*e.g.*, Cottam, 1949; Nuzzo, 1986; Tester, 1989; Cole and Taylor, 1995; Peterson and Reich, 2001) and reinforces the importance of active management to the long-term maintenance of oak savanna systems.

The differences between Managed oak savanna sites and heavily Disturbed savanna sites is noteworthy because disturbance, primarily fire, was a major component of many savanna ecosystems and maintained the co-existence of mature trees and herbaceous vegetation (Sankaran *et al.,* 2004; Anderson, 2007). Results from our study sites suggest, however, that some major disturbances (including recreational off-road vehicles, heavy equipment use, and high frequency surface fires) may result in a plant community with fewer species overall (Fig. 3), and further, lacking in some important savanna associates (*e.g.*, lanceleaf coreopsis, butterfly weed, horsemint) while retaining others (wild lupine, big bluestem, common milkweed; Table 3). This suggests our actively managed sites more closely reflect historical disturbance regimes than the heavily disturbed sites in this study.

The results reported in this study suggest the type and intensity of disturbance can significantly alter plant community composition of oak savanna ecosystems. If long-term management goals include encouraging the establishment and maintenance of herbaceous oak savanna-associated plant species, disturbance created through management activities, such as hand cutting, will likely yield better results over inaction, especially where using fire is not an option. This point should be considered in context, as different regions may contain different species pools (including invasives) and different abiotic environmental factors.

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