

# Woody Encroachment Removal from Midwestern Oak Savannas Alters Understory Diversity across Space and Time

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## Abstract

Recovering biodiversity is a common goal during restoration; however, for many ecosystems, it is not well understood how restoration influences species diversity across space and time. I examined understory species diversity and composition after woody encroachment removal in a large-scale savanna restoration experiment in central Iowa, United States. Over a 4-year time series, restoration had profound effects across space and time, increasing richness at local and site-level scales. Restoration sites had increased  $\alpha$  (within sample) Simpson's diversity and  $\alpha$  and  $\gamma$  (site level) species richness relative to control sites, although  $\gamma$  and  $\beta$  (among sample) Simpson's diversity,  $\beta$  richness, and  $\alpha$  species evenness were not affected. Changes in richness were driven by graminoids at the  $\alpha$  and  $\gamma$  scales and woody species (and some evidence for forbs) at the  $\alpha$  scale. Interestingly, indicator species analysis revealed that at least some species from all functional

groups were promoted by restoration, although no species were significant indicators of pre-treatment or control sites. Both savanna and nonsavanna species were indicators of restored sites. Restoration promoted exotic species at both scales, although species with spring phenologies were unaffected. Woody encroachment removal may be a means to promote species establishment in savannas; however, in this study, it resulted in establishment and proliferation of native and exotic and savanna and nonsavanna species. Future work might consider reintroduction of key savanna species to supplement those that have established. Work like this demonstrates the utility of restoration experiments for conducting research on large- and multiscale processes, such as species diversity.

**Key words:** additive diversity partitioning, indicator species analysis, restoration ecology, species evenness, species richness, woody encroachment removal.

## Introduction

A common goal during ecosystem restoration is the recovery of lost biodiversity (Bakker et al. 2000; SER Science & Policy Working Group 2004; Clewell & Aronson 2006). Such a motivation is necessarily wide sweeping and encompasses spatial and temporal elements, ranging from local to regional scales and from individual organisms to entire ecosystems (Bestelmeyer et al. 2003). Because biodiversity is controlled by different factors at different spatial and temporal scales (Menge & Olson 1990; Huston 1999), restoration success should be assessed across time and space. Repeated sampling coupled with evaluation of diversity using  $\alpha$  (within sample),  $\beta$  (among sample), and  $\gamma$  (composite) spatial components provides a framework for such assessments (Veech et al. 2002). Unfortunately, when evaluated, restorations frequently fail to replicate the levels of biodiversity observed in reference sites. For

example, recent work in North American prairies demonstrated that grasslands restored from agricultural fields are less species diverse than remnant (reference) prairies across all spatial scales (Martin et al. 2005; Polley et al. 2005). To improve restoration methodologies, replicated restoration experiments allow for statistical testing of management protocol (Holl et al. 2003). Furthermore, restoration experiments provide unique opportunities to perform large-scale manipulations, in which ecological theories may be tested that improve our understanding of large- and multiscale processes (Holl et al. 2003). This is especially important for testing species diversity theory because our understanding of how local and regional processes contribute to species diversity is based almost entirely on observational studies (Huston 1999).

Species diversity can be additively partitioned into  $\alpha$ ,  $\beta$ , and  $\gamma$  spatial components (Lande 1996; Veech et al. 2002). Although originally proposed to understand diversity at regional scales (Lande 1996), this is a flexible framework allowing for work at any scale, provided that  $\gamma$  is larger than  $\alpha$  (Veech et al. 2002). In this article, I define  $\alpha$  as diversity in 1-m<sup>2</sup> plots,  $\beta$  as diversity among plots, and  $\gamma$  as restoration site-level diversity (multiple hectares). By these definitions, species interactions take place at the  $\alpha$  scale, and promoting  $\alpha$  diversity may be important for

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restoring ecosystem functions such as primary productivity and invasion resistance (e.g., Tilman et al. 2001; Kennedy et al. 2002).  $\beta$  diversity is influenced by within-site habitat structure (Hewitt et al. 2005), making this a potential indicator of success because structure is an important consideration during restoration (Bakker et al. 2000; SER Science & Policy Working Group 2004). As defined in this article,  $\gamma$  is the scale of the local species pool (Zobel et al. 1998) and, frequently, the scale at which management takes place (Bestelmeyer et al. 2003). Species restored to the site level overcome significant dispersal limitations, which is critical during restoration of dispersal-limited ecosystems (Tilman 1997; Foster & Tilman 2003; Kirkman et al. 2004). Restoration might influence  $\gamma$  diversity by altering  $\alpha$  (via establishment opportunities provided by increased resources and/or disturbance; Huston 1999) and/or  $\beta$  components (via altered habitat heterogeneity) and it is important to understand their relative influences.

Diversity has two components—species richness, or the number of species, and species evenness, or their equitability (Magurran 2004). Species richness is determined by local immigrations and extinctions, whereas evenness is also influenced by species interactions that drive dominance and rarity, such as competition (Wilsey & Stirling 2007). As described above, if restoration results in increased species establishment, diversity might increase via the richness component. Alternately, if restoration primarily influences species interactions, diversity might be altered due to changes in the evenness component (Huston 1999).

In addition to species diversity metrics, it is important to consider species identities during land management and restoration (Bestelmeyer et al. 2003). Restoration of functional groups may have impacts on numerous ecosystem processes, which are controlled by both functional group richness and identity (Tilman et al. 1997). However, very few studies have explored the impact of restoration on functional group diversity at multiple spatial scales. Furthermore, restoration should promote native species (SER Science & Policy Working Group 2004), and in areas like the Midwestern United States with concerns about early-season nutrient run-off (Mitsch et al. 2001), retention of species with spring phenologies is a pertinent restoration goal because these species can act as nutrient sinks during this period (Muller & Bormann 1976). Finally, it is important to evaluate the species-level impacts of restoration, in part because reestablishing target species is a frequent goal (Bakker et al. 2000) and also because important patterns may be missed when only species diversity or functional groups are evaluated (e.g., Brudvig et al. 2007).

Midwestern North American oak savannas represent an ideal system to investigate changes in biodiversity during experimental restoration. Midwestern oak savannas are defined by a sparse, fire-maintained oak overstory and a continuous herbaceous understory (Anderson 1998), which is exceptionally species diverse relative to Midwestern prairies and woodlands (Curtis 1959; Leach & Givnish 1999). High diversity is thought to result from species

turnover along resource gradients, including light, produced by scattered overstory trees (Leach & Givnish 1999; Meisel et al. 2002), and environmental factors may have varying effects on species richness at different spatial scales (Weiher & Howe 2003). Thus, there is an important spatial component to Midwestern oak savanna understory diversity. Although once widespread (approximately 10- to 13-m ha prior to Euro-American settlement), Midwestern oak savannas are now rare (<1% of original range) due to agricultural conversion (Nuzzo 1986). Remaining remnants are commonly degraded by fire suppression and subsequent woody encroachment (Nuzzo 1986), which may alter understory flora (Cottam 1949; Curtis 1959). Efforts to restore encroached remnants generally operate at the stand scale (multiple hectares) and first involve mechanical removal of encroachment, followed later by prescribed understory fires (Packard 1993). During this process, reestablishing overstory structure may be critical to restoring the spatial structure of understory resources and biodiversity (Nielsen et al. 2003). In other words, restoring overstory structure may increase  $\beta$  diversity, and this may help to produce the high  $\gamma$  diversity of pristine Midwestern oak savannas. However, this has not been verified, making it important to assess savanna restoration success across spatial scales.

In this article, I use a replicated large-scale restoration experiment with Midwestern oak savannas to assess changes in understory biodiversity. To do this, I pursue three main research questions: (1a) How does restoration impact species diversity over time and across space? As a corollary to question 1a (1b), if restoration affects diversity at the local scale, are changes a result of altered richness and/or evenness components? (2) How does restoration impact richness within functional groups? (3) What are the effects of restoration on individual species?

## Methods

### Study Sites and Restoration Methodology

This study was conducted within a replicated large-scale oak savanna restoration experiment near Des Moines, Iowa. In 2002, eight degraded oak savanna study sites were identified along Saylorville Lake, a U.S. Army Corps of Engineers Reservoir (lat 41°76'N, long 93°82'W). Sites ranged in size from 1.5 to 3.3 ha and were located on parallel, linear upland ridges separated by stream valleys. Soils at these sites have never been plowed and are a mosaic of Hayden (fine-loamy, mixed, superactive, mesic Glossic Hapludalf, developed under oak/hickory forest) and Lester series (fine-loamy, mixed superactive, mesic Mollic Hapludalf, developed under oak savanna; U.S. Department of Agriculture 2007). Mean annual temperature, precipitation, and frost-free days for the city of Des Moines are 10°C, 882 mm, and 133 (National Oceanic and Atmospheric Administration 2007). All sites were grazed by livestock until purchased by the U.S. Army Corps of

Engineers between 1965 and 1975 (Karnitz & Asbjornsen 2006). Following purchase, sites were unmanaged and sparse overstories dominated by *Quercus alba* were heavily encroached by mesophytic tree species (e.g., *Ostrya virginiana*, *Fraxinus americana*, and *Ulmus* sp.; Karnitz & Asbjornsen 2006).

To restore overstory structure and species composition to the preencroachment condition, all encroaching woody vegetation greater than 1.5 m height was cut by chain saws and burned in off-site slash piles (restoration treatment; Asbjornsen et al. 2005). No herbicides were applied. We chose to retain only *Quercus* species, in accordance with early surveyor notes that described uplands in and around our research sites dominated by this genus (Asbjornsen et al. 2005). Due to the necessity to conduct the restoration treatment during winter months (when soil disturbances are reduced) and the time required for its implementation (1–2 months/site), treatments were conducted at two sites during winter 2002–2003 and at the remaining two treatment sites during winter 2003–2004. The remaining four sites were retained as controls.

Pre-treatment canopy cover values ranged from 84 to 89% at control sites and 86 to 87% at treatment sites, while following the restoration treatment, canopy cover values ranged from 8 to 52% at treatment sites and 85 to 92% at control sites (assessed by hemispherical photographs; Brudvig & Asbjornsen 2007). Values at treatment sites now fall roughly within those published for Midwestern oak savannas (10–50%: Curtis 1959; 10–30%: Packard 1993). Canopy cover standard deviations increased from 4.0 to 18.4 at treatment sites (control sites declined from 5.6 to 4.3), suggesting that restoration increased not only the amount of light reaching the understory but also the variability of understory light microhabitats.

#### Data Collection

I used permanently marked 1 × 1-m plots to sample understory vegetation at the eight savanna sites. Plots were located every 10 m along a 100- to 200-m linear transect that ran through the center of each site ( $n = 11$ – $21$  plots/site; transects varied in length due to differences in site sizes). I sampled plots twice annually (early May and late June/early July) beginning the year before and for three subsequent years after the restoration treatment. For four sites, the sampling duration was 2002–2005 and for the remaining four sites the duration 2003–2006 (see above; Study Sites and Restoration Methodology). During each sampling period, I recorded percent covers for all species present in each plot (visually estimated to the nearest percent). Two sampling periods per year were necessary to record species with both early- and mid-season phenologies.

#### Species Diversity Indices

For each site and year of study, I assessed species evenness at the  $\alpha$  level and species richness and Simpson's

diversity at the  $\alpha$ ,  $\beta$ , and  $\gamma$  levels (Magurran 2004). I used species occurrence and cover data from summer samples to calculate evenness and Simpson's diversity and species occurrence data from spring and summer samples to calculate richness. In the instance that a species was present during both spring and summer sampling periods for a given plot, I counted it only once. I defined  $\alpha$  richness and Simpson's diversity as mean values per 1 × 1 m-plot and  $\gamma$  richness and diversity as restoration site-level values by pooling plots together. I partitioned  $\gamma$  richness and diversity into  $\alpha$  and  $\beta$  components by the additive method, whereby  $\gamma = \alpha + \beta$  (Lande 1996; Veech et al. 2002). This framework allows for direct comparison of  $\alpha$  and  $\beta$  diversity and is useful for understanding patterns of species diversity at multiple spatial scales (Veech et al. 2002).

#### Functional Group Classification

For each site and year of study, I calculated richness of species within functional groups at the plot and site levels for the following groups: graminoids (grasses, sedges, and rushes), forbs, woody species (tree seedlings, shrubs, and woody vines), and species with spring phenologies. I also calculated the percentage of total species that were native at the plot and site levels. Finally, I assessed the number of common species in each year (present in >10% of plots/treatment) and species identified by indicator species analysis (ISA) (see below) that were present on DeLong and Hooper's (1996) Iowa oak savanna species list.

#### Statistical Analyses

To understand changes in species and functional group diversity due to restoration and over time, I used repeated measures analyses of variance (PROC GLM; SAS 2002), with treatment ( $n = 2$ ) and year ( $n = 4$ ) as independent variables. I tested the following dependent variables: species richness ( $\alpha$ ,  $\beta$ ,  $\beta$  proportion of  $\gamma$ , and  $\gamma$  scales), Simpson's diversity ( $\alpha$ ,  $\beta$ ,  $\beta$  proportion of  $\gamma$ , and  $\gamma$  scales), species evenness ( $\alpha$  scale), the percentage of species that were native ( $\alpha$  and  $\gamma$  scales), and richness of graminoids, forbs, woody species, and species with early-season phenology (each at  $\alpha$  and  $\gamma$  scales). All  $\alpha$  (plot)-level dependent variables were assessed as means/site ( $n = 4$ /treatment). Treatment and control sites did not differ in any dependent variable before treatments were conducted (maximum  $t = 2.03$ ,  $p = 0.0884$ ; plot-level woody species richness). I considered treatment effects significant over the course of the study at  $\alpha < 0.05$  for the treatment × year interaction. However, because replication of sites was limited by funding and logistics (as is the case in most large-scale experiments; Carpenter 1990), I considered the biological importance of results with trends for significance (e.g.,  $p < 0.15$ ).

To investigate impacts of restoration on species identity, I ran ISA (McCune & Grace 2002) in PC-ORD

(McCune & Mefford 1999). ISA is a multivariate test that describes species associations with predefined units of study. I defined units as the study sites, coded by treatment and the 4 years of study (32 units total), and ran ISA using the frequency of occurrence for the 75 species that were present in greater than or equal to 10% of plots in any year  $\times$  treatment (Appendix S1). I considered species to be significant indicators of a year  $\times$  treatment at  $p < 0.05$  for 1,000 Monte Carlo permutations.

## Results

### Species Richness and Diversity Across Spatial Scales

Over the course of this study,  $\gamma$  richness increased by 215% in treatment sites, which was significantly more than the 149% increase in control sites (treatment  $\times$  year  $F_{[3,18]} = 3.53$ ,  $p = 0.0361$ ; Fig. 1a). Across all sites and years, the  $\beta$  component consistently explained three to four times more of the  $\gamma$  richness than did  $\alpha$  (Fig. 1a). Over the course of the study, the overall levels of  $\alpha$  and  $\beta$  richness increased more in treatment sites ( $\alpha$  225% and  $\beta$  210%) than control sites ( $\alpha$  145% and  $\beta$  150%). However, due to the increase in  $\gamma$  richness with restoration, changes in the relative proportion of the  $\beta$  component were not different between treatments (treatment  $\times$  year  $F_{[3,18]} = 0.80$ ,  $p = 0.5101$ ; Fig. 1a).

Over the course of the study,  $\gamma$  Simpson's diversity increased by 250% in treatment sites, which was not different from the 224% increase in control sites (treatment  $\times$  year  $F_{[3,18]} = 0.96$ ,  $p = 0.4322$ ; Fig. 1b). In general, the amount of  $\gamma$  diversity explained by the  $\beta$  component was similar to the amount explained by the  $\alpha$  component (Fig. 1b).  $\beta$  represented a low of 42.2% in pre-treatment control sites and a high of 53.7% in treatment sites 2 years following restoration (Fig. 1b). Over the course of the study, overall levels of  $\alpha$  and  $\beta$  diversity increased by similar magnitudes in control ( $\alpha$  187% and  $\beta$  274%) and treatment sites ( $\alpha$  228% and  $\beta$  275%), and changes in the relative proportion of the  $\beta$  component were not different between treatments (treatment  $\times$  year  $F_{[3,18]} = 0.08$ ,  $p = 0.9711$ ; Fig. 1a).

### Local Diversity and Components

At the local scale, there was some evidence that Simpson's diversity increased more in treatment (228%) than control sites (187%; treatment  $\times$  year  $F_{[3,18]} = 2.30$ ,  $p = 0.1116$ ; Fig. 2a). Species richness was strongly influenced by the restoration treatment (treatment  $\times$  year  $F_{[3,18]} = 5.78$ ,  $p = 0.0060$ ; Fig. 2b), as richness increased 225% in treatment sites, relative to 145% in control sites. Species evenness was unaffected by restoration (treatment  $\times$  year  $F_{[3,18]} = 0.80$ ,  $p = 0.5101$ ; Fig. 2c).

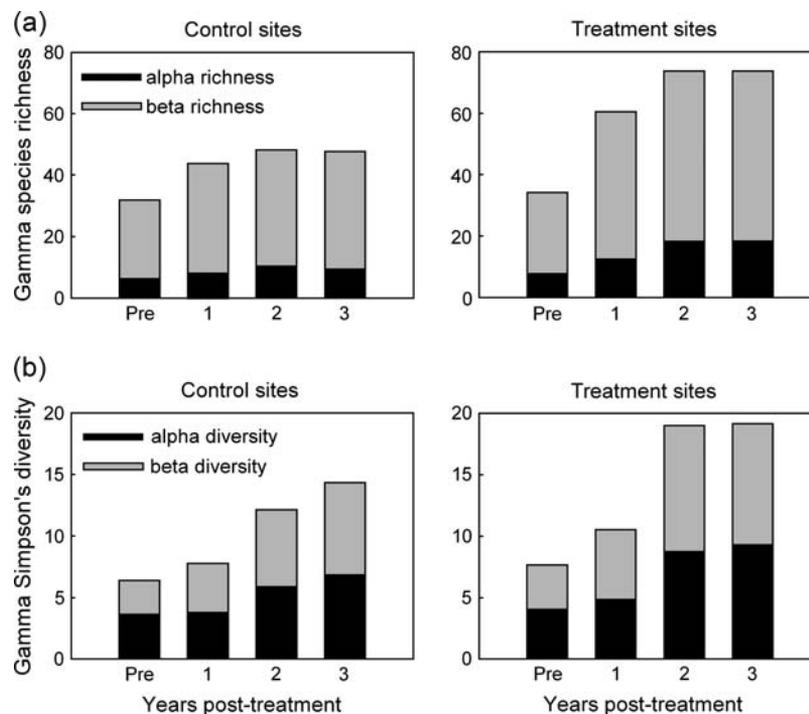


Figure 1. Site-level ( $\gamma$ ) (a) understory species richness and (b) Simpson's diversity and the relative proportions comprised by local ( $\alpha$ ) and among-patch ( $\beta$ ) components 1 year before and for 3 years after restoration treatment of Midwestern oak savanna remnants ( $n = 4$ ) and unmanipulated control remnants ( $n = 4$ ). The restoration treatment increased  $\gamma$  richness ( $p < 0.05$ ); however, the proportions of  $\alpha$  and  $\beta$  richness were unaffected by treatment. There was no effect of treatment on  $\gamma$  Simpson's diversity ( $p > 0.4$ ) or on the proportions of  $\alpha$  and  $\beta$  diversity.

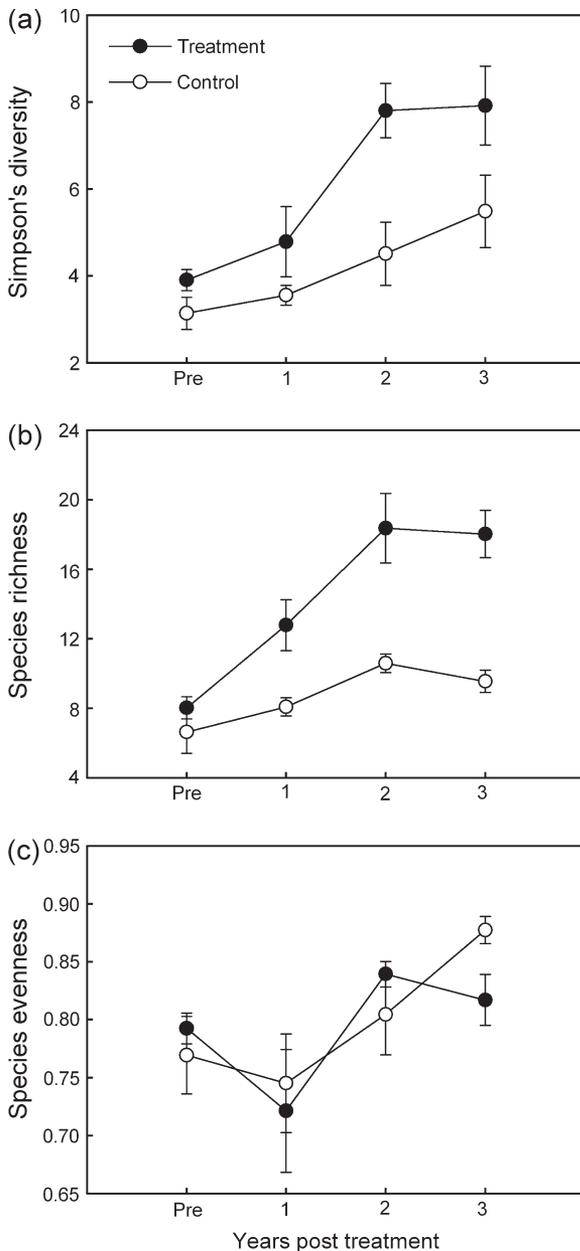


Figure 2. Plot-level (a) understory Simpson's diversity, (b) species richness, and (c) species evenness 1 year before and for 3 years after restoration treatment of Midwestern oak savanna remnants ( $n = 4$ ) and unmanipulated control remnants ( $n = 4$ ). The restoration treatment increased species richness ( $p < 0.01$ ), produced a trend for increase in Simpson's diversity ( $p < 0.15$ ), and did affect species evenness ( $p > 0.5$ ). Values are mean  $\pm$  1 SE.

### Species Composition

The restoration treatment had varying effects on richness within functional groups at local and site-level scales (Fig. 3). Relative to controls, richness of graminoids increased with restoration at both the site (treatment  $\times$  year  $F_{[3,18]} = 16.51$ ,  $p < 0.0001$ ) and the plot levels (treatment  $\times$  year  $F_{[3,18]} = 5.77$ ,  $p = 0.0060$ ; Fig. 3a). Treatment

sites had an average addition of 9.0 graminoid species/site and 1.93 species/plot compared to 1.5 species/site and a reduction by 0.01 graminoid species/plot at control sites. Forb species richness increased at both scales over the course of study in treatment (21.75 species/site and 4.87 species/plot) and control sites (9.5 species/site and 1.90 species/plot), although changes were not significantly different between treatment and control sites at either scale (site level: treatment  $\times$  year  $F_{[3,18]} = 1.79$ ,  $p = 0.1851$ ; plot level: treatment  $\times$  year  $F_{[3,18]} = 2.58$ ,  $p = 0.0852$ ; Fig. 3b). However, by the final year of study, plot-level forb richness was greater in treatment than control sites ( $t = 2.79$ ,  $p = 0.0317$ ). Relative to control sites, woody species richness increased with restoration at the plot level (treatment  $\times$  year  $F_{[3,18]} = 8.06$ ,  $p = 0.0013$ ) but not at the site level (treatment  $\times$  year  $F_{[3,18]} = 1.98$ ,  $p = 0.1538$ ; Fig. 3c). In treatment sites, this corresponded with increases of 7.25 species/site and 3.14 species/plot, whereas in control sites, increases were 3.75 species/site and 1.08 species/plot. The restoration treatment did not alter the richness of species with spring phenologies, relative to control sites, at either scale (site level: treatment  $\times$  year  $F_{[3,18]} = 0.67$ ,  $p = 0.5786$ ; plot level: treatment  $\times$  year  $F_{[3,18]} = 0.20$ ,  $p = 0.8965$ ). Over the course of this study, treatment sites averaged 4.00–6.25 spring species/site and 0.95–1.97 spring species/plot, whereas control sites averaged 4.00–7.00 spring species/site and 0.65–1.36 spring species/plot.

Prior to restoration at treatment sites and at control sites in all years, richness was dominated by native species (site level: 94–97%; plot level: 97–99%); however, following restoration, the percentage of native species declined at both the site (treatment  $\times$  year  $F_{[3,18]} = 4.90$ ,  $p = 0.0116$ ) and the plot levels (treatment  $\times$  year  $F_{[3,18]} = 3.30$ ,  $p = 0.0440$ ; Fig. 4). Changes were abrupt, with native species reduced to 89% for 2 years following treatment at the site level (corresponding to an average addition of 5.75 and 7.25 exotic species/site in posttreatment years 1 and 2, respectively) and 92 and 90% in years 1 and 2 following treatment at the plot level (corresponding with the average addition of 1.04 and 2.34 exotic species/plot in posttreatment years 1 and 2, respectively). There was a trend toward a return to pre-treatment/control levels 3 years after the restoration treatment, with respective values of 91 and 95% at the site and plot levels.

### Individual Species

Twenty-five species were significant indicators of sites undergoing restoration, whereas no species were indicators of control sites (Table 1). One species was an indicator of sites 1 year following the restoration treatment, 10 species were indicators of sites 2 years after treatment, and 14 species were indicators of sites 3 years after treatment. In total, 5 graminoids, 12 forbs, and 8 woody species were significant indicators of sites undergoing restoration. Of these, four were exotic species. Both savanna and non-savanna species were represented (Delong & Hooper

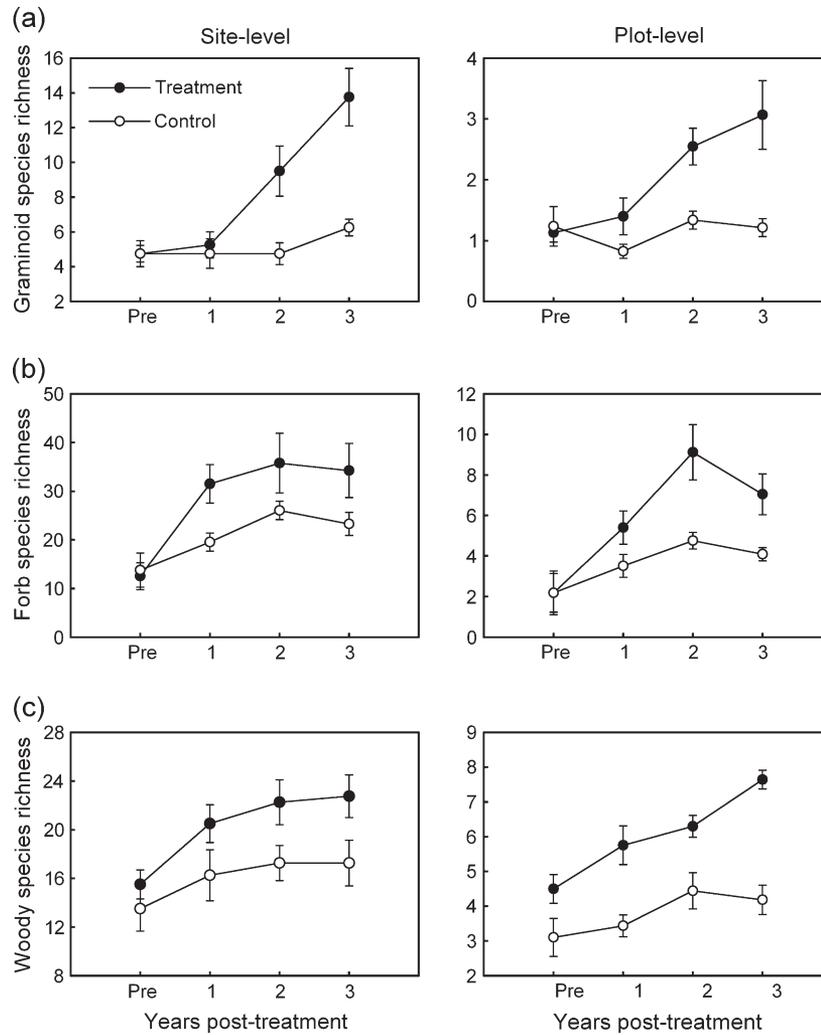


Figure 3. Richness of (a) graminoids, (b) forbs, and (c) woody species at the site ( $\gamma$ ) and plot levels ( $\alpha$ ) 1 year before and for 3 years after restoration treatment of Midwestern oak savanna remnants ( $n = 4$ ) and unmanipulated control remnants ( $n = 4$ ). The restoration treatment increased richness of graminoids at the site ( $p < 0.0001$ ) and plot levels ( $p < 0.01$ ) and woody species at the plot level ( $p < 0.01$ ). Values are mean  $\pm$  1 SE. Note variable vertical axes.

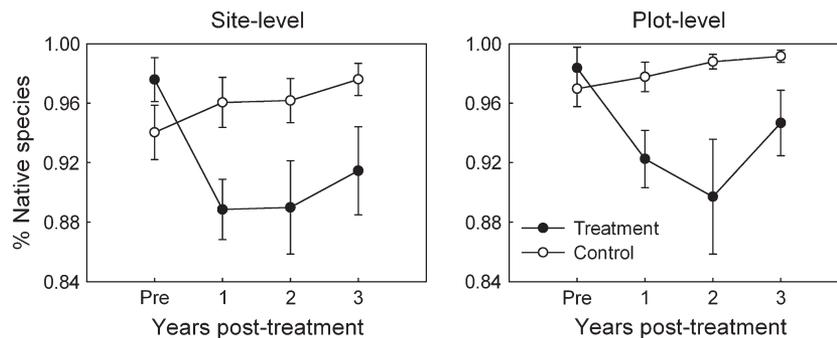


Figure 4. Percent native species at the site ( $\gamma$ ) and plot levels ( $\alpha$ ) 1 year before and for 3 years after restoration treatment of Midwestern oak savanna remnants ( $n = 4$ ) and unmanipulated control remnants ( $n = 4$ ). The restoration treatment decreased the percentage of native species at the site ( $p < 0.05$ ) and plot levels ( $p < 0.05$ ). Values are mean  $\pm$  1 SE.

**Table 1.** Species identified as indicators of sites undergoing restoration from ISA.

Years Posttreatment	Species	Life-Form <sup>a</sup>	Native/Exotic	Frequency of Occurrence (%)
1	<i>Laportea canadensis</i>	P-forb	Native	14.3
2	<i>Carex amphibola turgida</i>	Sedge	Native	57.1
	<i>Ca. jamesii</i>	Sedge	Native	41.4
	<i>Conyza canadensis</i>	A-forb	Native	47.1
	<i>Erigeron strigosus</i> <sup>b</sup>	P-forb	Native	55.7
	<i>Hackelia virginiana</i>	P-forb	Native	51.4
	<i>Oxalis stricta</i> <sup>b</sup>	P-forb	Native	35.7
	<i>Potentilla simplex</i> <sup>b</sup>	P-forb	Native	24.3
	<i>Sonchus oleraceus</i>	A-forb	Exotic	10.0
	<i>Trifolium repens</i>	P-forb	Exotic	57.1
	<i>Verbascum thapsus</i>	B-forb	Exotic	31.4
3	<i>Ca. grvida</i>	Sedge	Native	54.3
	<i>Celtis occidentalis</i>	Tree	Native	27.1
	<i>Cornus racemosa</i> <sup>b</sup>	Shrub	Native	58.6
	<i>Dactylis glomerata</i>	P-grass	Exotic	15.7
	<i>Galium triflorum</i>	P-forb	Native	38.6
	<i>Gleditsia triacanthos</i>	Tree	Native	15.7
	<i>Juncus tenuis</i> <sup>b</sup>	Rush	Native	25.7
	<i>Morus rubra</i>	Tree	Native	12.9
	<i>Rubus occidentalis</i> <sup>b</sup>	Shrub	Native	32.9
	<i>Solidago canadensis</i> <sup>b</sup>	P-forb	Native	34.3
	<i>Symphoricarpos orbiculatus</i> <sup>b</sup>	Shrub	Native	62.9
	<i>Viola sororia</i>	P-forb	Native	62.9
	<i>Vitis riparia</i> <sup>b</sup>	W-vine	Native	25.7
	<i>Zanthoxylum americanum</i> <sup>b</sup>	Shrub	Native	12.9

No species were significant indicators of pre-treatment sites or control sites in any year.

<sup>a</sup> Life-forms are as follows: A-forb, annual forbs; B-forb, biennial forbs; P-forb, perennial forbs, P-grass, perennial grasses; rush, perennial rushes; sedge, perennial sedges; shrub, shrubs; tree, trees; W-vine, woody vine.

<sup>b</sup> Components of the Iowa oak savanna understory community in Delong and Hooper (1996).

1996), with the number and proportion of savanna species increasing over time: 0/1 indicator species were savanna species 1 year following restoration, 3/10 2 years following restoration, and 7/14 were savanna species 3 years following restoration (Table 1). Similar patterns were evident for common species (present in >10% of plots/year; Appendix S1). Prior to treatment, there were eight common savanna species at control sites, and this number remained relatively constant throughout the duration of the study (1 year following treatment: eight common savanna species, 2 years: six common savanna species, and 3 years following treatment: eight common savanna species; Appendix S1). Prior to treatment, there were seven common savanna species at treatment sites. Following treatment, the number of savanna species increased each year (1 year following treatment: 12 common savanna species, 2 years following treatment: 16 common savanna species, and 3 years following treatment: 19 common savanna species; Appendix S1).

## Discussion

### Species Diversity

In spite of being heralded as laboratories for testing large-scale processes, restoration efforts are rarely used for this purpose (Holl et al. 2003). This study represents an experi-

mental setting in which I tested multiscale changes in species diversity and composition during restoration of savannas. Restoration increased species richness at  $\alpha$  and  $\gamma$  scales, suggesting that both species interactions ( $\alpha$  scale) and immigrations ( $\gamma$  scale) were important (Huston 1999). At the  $\alpha$  scale, restoration may have produced microsites suitable for disturbance-adapted species to colonize (Hobbs & Huenneke 1992). Furthermore, restoration likely reduced competition by overstory trees on understory plants, an important asymmetric interaction in forested ecosystems (Weiner 1990). Potentially, release from competition led to increased species richness after overstory removal (Huston 1999). At the  $\gamma$  scale, restoration increased the size of the species pool, potentially through dispersal from off-site and/or stimulation of the soil seed bank (Bakker et al. 1996; Zobel et al. 1998). Theoretical work has shown the potential importance of dispersal from the regional species pool on local species coexistence and richness (Loreau & Mouquet 1999).

Simpson's diversity increased at the  $\alpha$  scale during restoration, which was due to the species richness component. Despite evidence for local interactions promoting graminoids, forbs, and woody species, local-scale species evenness did not change during restoration, which is contrary to expectation because evenness is thought to be influenced by species interactions (Huston 1999). Potentially, these interactions occurred at scales larger than the  $1 \times 1$  m at

which I calculated species evenness, though still within the site-level scale. Such mesoscale interactions might be a result of short-distance dispersals (i.e., within site), vegetative growth, or stimulation of the soil seed bank (Bakker et al. 1996; Zobel et al. 1998), followed by within-site proliferation of species present prior to restoration. This might help to explain the dramatically increased  $\alpha$  species richness observed in this study. This occurred, however, without altering local species evenness, a result found also for Midwestern prairies (Polley et al. 2005).

Similar to findings in Midwestern prairies (e.g., Martin et al. 2005; Polley et al. 2005), I found that a majority of  $\gamma$  richness was explained by the  $\beta$  component, suggesting high levels of spatial variability within both treatment and control sites. Many processes may operate at the among-plot scale, and restoration efforts sometimes seek to re-create these. For example, Fuhlendorf and Engle (2004) describe restoration of a shifting mosaic of habitat in prairies by use of prescribed fire and ungulate grazers. During oak savanna restoration, the intention of re-creating a patchy overstory is to increase the variability of understory microhabitats (Packard 1993). This was successfully accomplished at my research sites because removing encroaching woody vegetation from degraded savannas increased the variability of light reaching the understory (assessed by hemispherical photographs). However, this did not translate into an increase in the proportions of  $\beta$  diversity or richness. There are several possible explanations for this finding. It is possible that important resource gradients have not yet established in these savannas. Past work has shown that savanna vegetation is organized across multiple environmental gradients, including light, soil texture and nutrients, and fire-return interval (Leach & Givnish 1999; Meisel et al. 2002); however, Weiher and Howe (2003) found that a majority of variation in species richness was left unexplained by these physical factors in Wisconsin oak savannas, suggesting that critical drivers remain uninvestigated. During restoration, some gradients that serve to organize vegetation may take more time and/or reimplementation of prescribed understory fire before they fully develop. Alternately, the time frame of my study may have been insufficient for vegetation to fully reorganize along environmental gradients. In either of these cases, further long-term investigation in these savannas may help to elucidate vegetation development and contribute to  $\beta$  diversity theory. Finally, this study is one of the first to investigate  $\beta$  diversity in savannas (see also Leach & Givnish 1999), and it is possible that savanna restoration simply does not increase the proportions of  $\beta$  diversity and richness relative to encroached sites. To test this possibility, comparison with nonencroached reference sites will be necessary.

### Species Composition

Analysis of functional groups revealed that richness of forbs and woody species increased at the local scale, but

not at the site level, suggesting that these changes occurred due to proliferation of species that existed prior to restoration rather than immigration of new species. Conversely, graminoid richness increased at both scales, revealing both proliferation of preexisting species and establishment of new species. Furthermore, both ISA and examination of common species demonstrated that restoration promoted numerous species from all functional groups. Many of these species were not present prior to restoration, suggesting novel establishments across functional groups (Brudvig, unpublished data).

Restoration promoted the establishment of exotic species at both the plot and the site levels. This is not surprising, given that many invasive exotic species are favored by disturbed conditions (Sakai et al. 2001) and restoration represented a disturbance that promoted the establishment of many new species (native and exotic). However, relative to native species, exotic species proliferation was short lived, with the proportion of exotic species at both scales decreasing by 3 years following restoration. Because local species richness and site-level species richness did not decline over this time period, this suggests that, over time, native species were displacing exotics. This result is promising for management; however, future restoration efforts will involve prescribed understory fire at these sites. Determining whether or not this disturbance will also promote establishment of exotic species requires future study. This question is coupled with the potential that increased species richness may confer invasion resistance to restored savannas (Kennedy et al. 2002).

ISA revealed that 25 species were indicators of restored sites (and more as time passed), whereas none were indicators of control sites. Furthermore, the number of indicator species that were savanna species (DeLong & Hooper 1996) increased over time, and this pattern was paralleled by common species, which also showed the number of savanna species increasing over time. This suggests two things. First, savanna restoration promoted a novel set of species, and although this set included both native and exotic species and savanna and nonsavanna species, the proportion of exotic species decreased over time, whereas the number of savanna species increased throughout the study. Second, because numbers of indicator and savanna species did not plateau, this new set of species may have still been evolving at the end of this study. This further supports the conclusion that  $\gamma$  richness is increasing via species establishment and demonstrates that restoration promotes establishment of some members of the target savanna community. Furthermore, nearly half of indicator species were forbs, which was surprising, given that there was only some evidence that this functional group was promoted by restoration. Thus, forbs did respond positively to restoration, and this underscores the importance of examining species-level data when evaluating management because responses may be obscured if only broad life-form groups are evaluated (Brudvig et al. 2007).

### Restoration Implications

Pristine Midwestern oak savannas are exceptionally species diverse and dominated by native forbs and graminoids (Leach & Givnish 1999; Meisel et al. 2002). Woody encroachment removal promoted species richness and diversity at local and site levels and, thus, appears to be a promising first step in restoration. Furthermore, restoration promoted graminoids at both local and site levels, and there was some evidence that forbs were promoted at local scales. Although these results are encouraging, further monitoring during restoration will help elucidate which dispersal-limited species will require active reintroduction (Brudvig & Mabry 2008). Active reintroduction will help supplement those savanna species that are less dispersal limited and have already established (Bakker et al. 2000; Bestelmeyer et al. 2003). This approach might be especially helpful for targeting key forbs for reintroduction because this group showed a relatively weak response and is an especially important component of pristine Midwestern oak savannas (Leach & Givnish 1999). The increase in woody species at local scales was less promising. Although there was no evidence for establishment of new woody species (i.e., site-level increase), these savannas may be reverting back toward the pre-restoration (encroached) state. Reimplementation of prescribed fire at these sites may be critical for controlling woody encroachment (Brudvig & Asbjornsen 2007); however, this may be a long process requiring as much as several decades of prescribed fires before woody encroachment can be checked (Anderson et al. 2000; Nielsen et al. 2003).

The increases in understory diversity presented in this article were coupled with a reduction in overstory diversity and cover during restoration (Brudvig & Asbjornsen 2007). Such dramatic shifts in ecosystem state are often the goal of restoration and may have dramatic impacts on ecosystem function (Suding et al. 2004). For example, by manipulating tree densities, savanna restoration alters site hydrology (Asbjornsen et al. 2007). In the present study, I found that restoration did not reduce richness of species with spring phenologies at the local or site scales, suggesting that degraded and restored savannas may function similarly with regard to springtime nutrient capture (Muller & Bormann 1976), an important consideration in the Midwestern United States (Mitsch et al. 2001). However, overstory reduction coupled with graminoid proliferation following restoration suggests that nutrient uptake may differ later in the growing season. The full significance of this should be investigated, if savannas are to be restored to their historically prominent landscape position along waterways in the Midwest (Anderson 1998).

A final direction for future work would be to investigate how changes in species diversity and composition during restoration compare with values from pristine remnants because this is a common means for evaluating restoration

success (SER Science & Policy Working Group 2004). Comparison with reference sites is complicated in the Midwest, however, because pristine oak savanna remnants are extremely rare due to agricultural conversion and fire suppression (Nuzzo 1986). This suggests that references for success may have to come from nontraditional sources. In this article, I made a preliminary assessment of savanna species response by comparing my results with a generic list of Iowa savanna species (DeLong & Hooper 1996). These results were quite promising and suggested that at least some oak savanna species will establish following removal of woody encroachment. Furthermore, ecological studies, like this one, during restoration of degraded remnants may provide an important source of reference information and help to guide future restoration efforts (Asbjornsen et al. 2005).

### Implications for Practice

- In fire-suppressed ecosystems, mechanical removal of woody encroachment may be an important first step in restoration.
- Encroachment removal increased understory species richness at local and site-level scales for 3 years in degraded white oak savannas in Iowa (United States).
- Graminoids showed the strongest response to restoration, increasing in richness at local and site-level scales, whereas forbs and woody species increased at local scales.
- Both native and exotic species and savanna and non-savanna species were promoted; however, exotic species decreased over time, whereas savanna species richness increased.

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### Supplementary material

The following supplementary material is available for this article online:

## Appendix S1.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1526-100X.2008.00431.x>

(This link will take you to the article abstract).

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