



Herbaceous layer response to 17 years of controlled deer hunting in forested natural areas



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ABSTRACT

Deleterious effects of overabundant deer populations within natural areas have been well documented and hunting programs have been initiated to control populations and facilitate the recovery of vegetation communities. However, few studies have examined whether recovery has occurred following sustained hunting. Hunting was initiated during the 1990s to reduce overabundant deer populations in Indiana state parks. In 2010, we resampled 108 plots established in 1996/97 across 15 state parks and five historically-hunted reference areas to quantify changes in herbaceous-layer vegetation. Species cover was measured along three, 10 m line transects nested within each plot. Data were pooled for all parks and reference areas. We calculated species richness (S), evenness (E), and Shannon-Weiner diversity (H') in 1996/97 and 2010. Compositional changes between sample intervals and contemporary composition across environmental gradients were examined using nonmetric multidimensional scaling (NMS). We observed greater increases in herbaceous-layer cover in parks than in reference areas. S and H' increased significantly in parks, but not reference areas. NMS ordinations revealed unidirectional changes in species composition between parks and their respective reference areas with the composition of parks becoming more similar to that of reference areas through time. Park size, cumulative deer harvest, initial deer abundance, and recent average of harvest/hunter effort were significantly correlated ($p < 0.05$) with ordination scores in four out of five natural regions ($|r| > 0.5$ for at least one axis). Browse-sensitive functional groups increased in cover while that of exotic species decreased. Changes were most pronounced for tree seedlings, which displayed a sixfold increase in cover within parks between sample intervals. These results suggest that hunting has allowed recovery of degraded vegetation communities.

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1. Introduction

Chronic herbivory by overabundant white-tailed deer (*Odocoileus virginianus*) populations represents a serious threat to the diversity and resilience of forest vegetation communities (Waller and Alverson, 1997; Rooney, 2001; Webster et al., 2005; Heckel et al., 2010). The end result of chronic browsing is often local extinctions of browse-sensitive species (Rooney et al., 2004; Thiemann et al., 2009) and a shift in overstory composition towards non-preferred species (Waller and Alverson, 1997; Tanentzap et al., 2011). Common, regionally abundant, or exotic species tend to increase while many native and specialist species

are lost, ultimately leading to biotic homogenization of herbaceous-layer communities (Rooney et al., 2004; Thiemann et al., 2009; Holmes and Webster, 2011). As local extinctions of native plants mount, species diversity is threatened at the landscape level (Rooney et al., 2004). Increased cover of unpalatable species prevents other species from establishing even under reduced browse pressure, thus changing the trajectory of forest composition (Waller and Alverson, 1997; Horsley et al., 2003).

While the effects of chronic herbivory on vegetation communities have been well documented, less is known about how communities recover from long-term herbivory once deer population abundance is reduced. Many studies have employed enclosures to examine vegetation response to the absence of deer (e.g., Rossell et al., 2005; Webster et al., 2005; Knight et al., 2009; Royo et al., 2010a). These studies have demonstrated increased regeneration of browse-sensitive woody species (Anderson and Katz, 1993; Griggs et al., 2006), balanced by the

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slow re-establishment of dispersal-limited herbaceous species (Anderson, 1994; Rooney et al., 2004; Webster et al., 2005). However, relatively few studies have directly compared vegetation community metrics before and after deer reductions or at different levels of browse intensity (Kuiters and Slim, 2002; Tremblay et al., 2006; Hothorn and Müller, 2010; Royo et al., 2010b; Tanentzap et al., 2011).

Overabundant deer populations occur in many parts of the world (Rossell et al., 2005; Perrin et al., 2006; Tremblay et al., 2006; Tanentzap et al., 2009), requiring active management to mitigate ecological damage caused by excessive browsing (Augustine and Frelich, 1998; Webster et al., 2005; Hothorn and Müller, 2010). Natural regulation as a default management technique on public and private lands has proven ineffective in controlling deer populations or reducing the negative effects of chronic herbivory (McShea and Rappole, 1997; Rooney, 2001; Rooney et al., 2004). Under such a system, deer populations typically become very large in the absence of hunting or predation, particularly where there is abundant edge habitat and/or mild winters (Leopold et al., 1947; Alverson et al., 1988).

In many natural areas managed to exclude consumptive use, hunting has long been prohibited in favor of natural regulation. While the negative effects of excessive deer herbivory in natural areas have been well documented (Shelton and Inouye, 1995; Rossell et al., 2005; Webster et al., 2005; Jenkins et al., 2007), the use of hunting to control deer abundance in natural areas has generated considerable controversy (McShea and Rappole, 1997; Mitchell et al., 1997; Dougherty et al., 2003). However, hunting may offer the only economically viable means of control. As more natural areas consider controlled hunts to reduce overabundant deer populations, the need for studies that examine vegetation responses to reduced abundance is highlighted.

Like many natural areas, Indiana state parks have a long history of deer overabundance. For example, in the 1970s deer density in the state's largest park (Brown County) was estimated to be four to eight times higher than on a neighboring national forest where hunting occurred (Mitchell et al., 1997). In 1996, post-mortem measurements of nutritional and physiological stress revealed that deer from two parks, Brown County and Pokagon, were less healthy than deer from hunted areas (Swihart et al., 1998). After much controversy and debate, hunting was implemented in Brown County in 1993 and a state law was passed in 1995 requiring reduction of deer herd sizes in parks sustaining ecological damage from browsing (McCreedy, 1996). Controlled hunts began in other parks in the 1990s and continue today. Repeated hunts have removed approximately 27,000 deer across Indiana state parks since 1993, ranging from 282 to 3458 deer in individual parks (Table 1). This program is unique in both scale and scope in that it was implemented state-wide and has continued according to the original design for nearly two decades.

From 1996 to 1997, permanent plots were established in state parks and reference areas that allow hunting to document herbivory impacts and provide a baseline for quantifying vegetation change. In this study, we resampled these plots to determine if vegetation communities in parks have recovered following 17 years of controlled hunting undertaken to reduce deer abundance and impacts. To our knowledge, ours is the first study to examine plant community response (both herbaceous and woody species) to population reductions of native deer conducted at a state-wide scale as part of permanent non-experimental management program. While much has been learned from previous studies of deer population reductions, these studies were conducted at much smaller spatial scales (Kuiters and Slim, 2002; Royo et al., 2010b; Tanentzap et al., 2011), considered only woody browse (Hothorn and Müller, 2010), or examined deer as a non-native species (Tanentzap et al., 2009; Wright et al., 2012).

Specific questions addressed in this study were: (1) Have herbaceous-layer composition and diversity recovered in parks relative to reference areas? We hypothesize that reduced deer densities will result in a compositional convergence between parks and reference areas. (2) Are observed changes in herbaceous-layer composition related to changes in deer abundance following the initiation of hunting? We hypothesize that variables related to deer density will display significant correlations with compositional changes between sample periods. (3) Has recovery varied among species functional groups with differing sensitivities to chronic herbivory? We hypothesize that woody species have displayed greater recovery due to a readily available seed source and rapid dispersal. However, we also hypothesize that cover of perennial herbs increased as a result of re-expansion of existing populations and exotic species cover decreased as a result of reduced browsing of native competitors.

2. Methods

2.1. White-tailed Deer in Indiana State Parks

White-tailed deer were extirpated from Indiana in the 1880s following unregulated harvest and habitat destruction. Following reintroductions in the 1930–40s, the prevalence of edge habitat, absence of predators, and cessation of unregulated hunting allowed deer populations to recover and greatly expand (Webster, 1997). By the mid-1900s, high populations occurred throughout the state with extremely high densities in state parks where hunting was prohibited (Mitchell et al., 1997). This increased deer abundance is reflected in hunting statistics prepared by the Indiana Department of Natural Resources (IDNR): harvested deer statewide increased from 51,778 in 1987 to a record 136,248 in 2012. The first state hunting season was held in 1951 at various sites, including Brown County State Park (McCreedy, 1996). However, parks were not hunted in subsequent years and served as refuges to deer until controlled hunts were initiated in the 1990s. The first hunt occurred in 1993, with hunting beginning at most parks after 1996 (Table 1).

Since hunting in state parks began, individual park managers have decided on a yearly basis whether to conduct a hunt. Hunts are held during two weekends in November and hunters are allocated to achieve a target density of one hunter per eight ha of parkland (Mycroft, 2012). Hunting began as early as 1993 at Brown County and as late as 1999 in Shakamak, Turkey Run, and Spring Mill (M. Mycroft, IDNR, personal communication).

2.2. Study areas

In 1996/97 monitoring plots were established in 15 parks across Indiana to examine the effect of deer herbivory on vegetation communities. Parks varied in size, shape, and landscape matrix, but all plots were established on north-facing slopes in closed-canopy hardwood forest. Using the same criteria, Webster (1997) established plots in one or more reference areas per natural region as delineated by Homoya et al. (1985). Deer were historically hunted at all reference areas. We evaluated Palmer Drought Severity Index state-wide to compare soil moisture between sample periods (1996/97 and 2010). Values across regions and sample periods were within normal ranges, suggesting that observed differences in cover were not the result of precipitation (NOAA, 2011).

Parks and associated reference areas were grouped by natural region (Homoya et al., 1985) to reduce variability in composition due to differences in topography and land use. Six natural regions were included in this study: (1) Northern Lakes (2) Northwestern Morainal, (3) Central Till, (4) Southwestern Lowlands, (5)

Table 1

Deer hunting and landscape attributes of Indiana state parks across six natural regions (HR = Highland Rim, NL = Northern Lakes/Northwestern Morainial, SW = Southwestern Lowlands, CT = Central Till, BG = Bluegrass). HE recent average = harvest/hunter effort for the last three hunts at a park.

Park	Natural region	Size (ha)	First hunt	Initial abundance ^a	Cumulative harvest	Harvest km ⁻²	Total hunts	H/E recent average	Landscape context
Brown County	HR	6384	1993	3994	3458	54	10	0.25 ± 0.035	Forest
McCormick's Creek	HR	779	1996	867	637	82	10	0.21 ± 0.015	Forest
Spring Mill	HR	550	1999	538	282	51	8	0.23 ± 0.046	Mixed
Pokagon	NL	510	1995	758	671	132	13	0.27 ± 0.003	Agriculture
Potato Creek	NL	1554	1995	2789	2526	163	12	0.33 ± 0.049	Agriculture
Chain O'Lakes	NL	1100	1998	4186	2096	191	12	0.46 ± 0.078	Agriculture
Indiana Dunes	NL	883	1998	1332	895	101	10	0.25 ± 0.033	Mixed
Harmonie	SW	1402	1995	3827	3305	236	14	0.30 ± 0.036	Agriculture
Lincoln	SW	707	1996	6308	852	121	13	0.34 ± 0.018	Forest
Shakamak	SW	715	1999	556	328	46	8	0.25 ± 0.028	Agriculture
Turkey Run	CT	964	1999	2127	874	91	11	0.25 ± 0.034	Forest
Shades	CT	1247	1997	2962	1597	128	13	0.22 ± 0.056	Mixed
Versailles	BG	2423	1997	4760	2637	109	11	0.27 ± 0.042	Forest
Whitewater	BG	692	1997	2374	1308	189	13	0.43 ± 0.030	Agriculture
Clifty Falls ^b	BG	573	1998	785	618	108	12	0.14 ± 0.015	Urban

^a Initial abundance represents the total number of deer utilizing the park as part of their home range and was calculated using the linear regression method of catch/effort estimation where catch was equivalent to deer removal (Bishir and Lancia, 1996).

^b Clifty Falls SP was hunted with archery, all other parks were hunted with firearms.

Bluegrass, and (6) Highland Rim Natural Regions (NR). The reference area for the Southwestern Lowlands was not resampled due to a change in ownership. Agriculture dominates the landscape in the northern, glaciated portion of the state while the southern, unglaciated portion is more forested (Table 1).

2.3. Field sampling

In 2010, we resampled 108 plots originally sampled in 1996/97 in 15 state parks and five reference areas (85 plots in state parks and 23 plots in reference areas; Webster, 1997). All resampled parks were hunted eight to 13 times between 1997 and 2010. All plots were sampled from May to August 2010 using techniques outlined in Webster (1997). To replicate the sampling chronology of Webster (1997), we began sampling in southern Indiana and worked northward.

Within each plot, three parallel 10 m line transects (30 m total transect distance) were placed random distances apart and perpendicular to the slope (Fig. 1). In order to sample herbaceous-layer vegetation, we tallied the total transect distance (cm)

covered by all herbaceous and woody species less than 50 cm tall over all three transects. Diameter at breast height (dbh) of trees taller than 2.0 m and greater than 2.5 cm dbh was recorded by species within a 300 m² circular plot.

2.4. Data analysis

Deer abundance on state parks prior to hunting initiation was estimated by regressing cumulative deer harvest against annual estimates of harvest per unit effort and calculating the intercept term where harvest per unit effort was zero as an index of initial abundance. Data on annual harvest and hunter effort at each state park were available from 1993 through 2010 (Indiana Department of Natural Resources, unpublished data). This approach of linearly regressing catch/effort against cumulative harvest to estimate initial abundance is frequently employed in fisheries studies (Bishir and Lancia, 1996). In our application, catch was measured as number of deer harvested and effort was records of number of hunter days. We treated the results of this analysis as an index of initial abundance rather than a precise estimate. This index

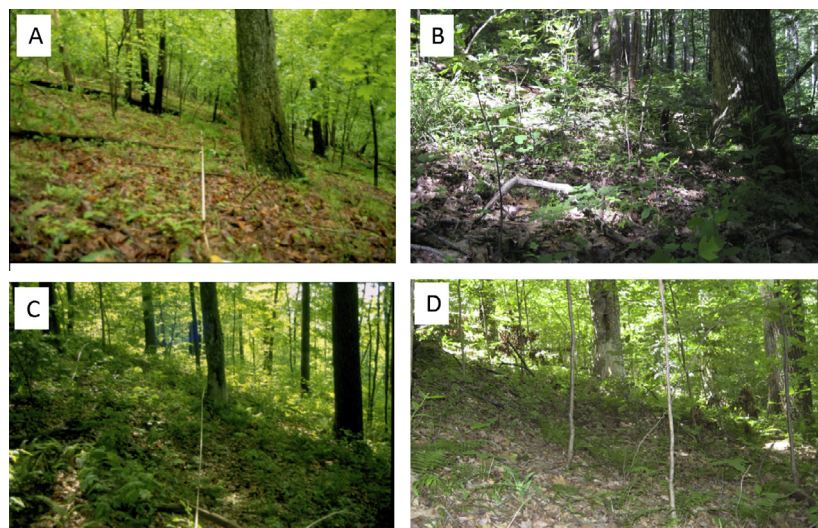


Fig. 1. Transect photos from Brown County State Park (BCSP) and Morgan-Monroe State Forest (MMSF; reference area for the Highland Rim Natural Region). (A) BCSP in 1996, (B) BCSP in 2010, (C) MMSF in 1996, and (D) MMSF in 2010. For reference, note the locations of large trees in each photo.

interpretation was taken in part because deer home ranges typically expand well outside a smaller park's boundaries (Hurley et al., 2012) making it infeasible to develop a true density estimate of number of deer per hectare of park. Additional deer harvest metrics calculated from IDNR data included cumulative deer reduction over all hunts in each park and recent abundance reductions. The latter were quantified as the average harvest per hunter effort (H/E) for the three most recent hunts, occurring anywhere between every year for three years and an annually alternating hunt (three hunts over six years, Mycroft, 2012).

Plant species cover values were combined into seven functional groups or growth forms: tree, shrub, herb, fern, exotic, lily, and graminoid. Vines, including *Toxicodendron radicans* and *Parthenocissus quinquefolius*, were included in the herb functional group. Species nomenclature follows USDA Plants Database (USDA, NRCS, 2011). Percent cover for each species in each plot was calculated by dividing transect overlap distance by total plot transect distance (3000 cm). An arcsine square root transformation was used to improve normality of the cover data. We examined the relative percent cover [(mean cover of a functional group/mean cover of all groups) \times 100] of each functional group in parks and reference areas and in both study periods. Species richness (S), evenness (E), and Shannon-Weiner diversity (H') were calculated from percent cover data (McCune and Mefford, 2011). Temporal changes in percent cover, S, E, and H' for parks and reference areas, respectively, were compared by natural region with two-way repeated measures analysis of variance (ANOVA). This technique was also used to examine temporal changes in percent cover within functional groups in both parks and reference areas. When ANOVA revealed significant main effects or a significant interaction, we used Holm-Sidak multiple comparison tests for post hoc comparisons. Parks in two neighboring natural regions, Northern Lakes and Northwestern Morainial, were combined for all analyses since we only sampled one park (Indiana Dunes) in the Northern Lakes NR.

We used non-metric multidimensional scaling (NMS) ordinations to examine composition changes in parks and reference areas by natural region between sample periods. Autopilot mode in PC-ORD Version 5.1 (McCune and Mefford, 2011) was used with the Sørensen distance measure, 0.0000001 stability criterion, 250 runs with real data, 250 runs with randomized data, and 500 maximum iterations for each. Separate NMS analyses were performed for each natural region. Plot scores were averaged across each park or reference area. In each natural region, changes in ordination space over time were visually compared between parks and reference areas with successional vectors. We examined associations between ordination axis scores and the following environmental variables: percent slope, transformed aspect (Beers et al., 1966), percent change in basal area, park size, cumulative deer harvest, H/E, and initial deer abundance using Pearson's correlation analysis. Environmental gradients were overlaid onto the 2010 NMS plot based upon Pearson correlation coefficients to examine their relationship to contemporary vegetation composition in parks and reference areas.

3. Results

3.1. Deer abundance

Initial abundance of deer varied widely across parks (Table 1). However, estimates of abundance were correlated with both cumulative harvest ($r = 0.63$, $p = 0.01$) and H/E ($r = 0.50$, $p = 0.06$). Total deer reduction over all hunts ranged from 46 deer/km² in Shakamak to 236 deer/km² in Harmonie. Average H/E (total number of deer killed in a given year/number of hunters present at all four hunting days) for the three most recent hunts ranged from

0.14 \pm 0.01 deer/hunter effort in Clifty Falls to 0.46 \pm 0.08 deer/hunter effort in Chain O'Lakes (Table 1).

3.2. Herbaceous-layer cover, species richness, evenness, and diversity

In state parks, we observed a significant increase in percent cover from 1996/97 to 2010 ($F_{(1, 80)} = 159.7$, $p < 0.001$) and a significant interaction effect between sample period and natural region ($F_{(4, 80)} = 3.6$, $p = 0.009$). Percent cover across all reference areas also increased from 1996/97 to 2010 ($F_{(1, 19)} = 7.9$, $p = 0.011$), but there was not a significant interaction effect ($F_{(3, 19)} = 0.3$, $p = 0.796$). Total herbaceous-layer cover exhibited a three times greater increase in parks compared to reference areas (102% vs. 30%; Figs. 1 and 2). Mean species richness (S) in parks increased from 20.1 \pm 0.7 to 26.9 \pm 0.9 between 1996/97 and 2010 ($F_{(1, 80)} = 111.6$, $p < 0.001$), but did not change significantly in reference areas (26.0 \pm 1.2 to 27.3 \pm 1.3; $F_{(1, 19)} = 1.3$, $p = 0.276$). Mean species evenness (E) also increased significantly from 0.91 \pm 0.005 to 0.92 \pm 0.003 ($F_{(1, 80)} = 14.9$, $p < 0.001$) in parks, but did not change in reference areas (0.92 \pm 0.006 to 0.92 \pm 0.005; $F_{(1, 19)} = 0.0008$, $p = 0.977$). Similarly, Shannon-Weiner diversity (H') increased significantly in parks (2.7 \pm 0.04 to 3.0 \pm 0.04; $F_{(1, 80)} = 94.8$, $p < 0.001$), but not in reference areas (3.0 \pm 0.06 to 3.0 \pm 0.06; $F_{(1, 19)} = 0.9$, $p = 0.353$; Fig. 2).

3.3. Cover of species functional groups

Mean percent cover of tree seedlings increased from 2.2 \pm 0.3% to 13.4 \pm 1.1% in parks ($F_{(1, 80)} = 241.7$, $p < 0.001$; Fig. 3) and there was a significant interaction effect between natural region and time period ($F_{(4, 80)} = 4.8$, $p = 0.002$). Reference area cover of tree seedlings increased from 4.2 \pm 0.7% to 11.4 \pm 1.8% ($F_{(1, 19)} = 68.7$, $p < 0.001$). Relative cover of seedlings increased from 8% to 23% in parks and from 10% to 20% in reference areas. Mean cover of shrubs increased from 0.5 \pm 0.1% to 2.7 \pm 0.5% in parks and from 1.0 \pm 0.3% to 3.1 \pm 0.6% in reference areas ($F_{(1, 80)} = 45.5$, $p < 0.001$ in parks and $F_{(1, 19)} = 15.0$, $p = 0.001$ in reference areas) and relative cover of shrubs increased from 2% to 5% in parks and from 2% to 6% in reference areas. Mean cover of herbs increased in the parks from 20.4 \pm 1.7% to 32.0 \pm 2.8% ($F_{(1, 80)} = 37.6$, $p < 0.001$) and remained the same in reference areas (31.0 \pm 3.3% and 31.4 \pm 4.1%; $F_{(1, 19)} = 0.6$, $p = 0.45$), though relative percent cover decreased in parks from 72% to 55% and in reference areas from 72% to 56%. While the total cover of exotics species was low in both parks and reference areas, mean cover of this group decreased in parks from 2% to 1% ($F_{(1, 80)} = 7.9$, $p = 0.006$), and remained at 1% in reference areas. Relative cover of exotics decreased from 5% to 2% in state parks and increased slightly from 1% to 2% in reference areas (Fig. 2). In 1996/97, graminoids constituted 1% of the mean percent cover in both state parks and reference areas and increased to 3% in both categories (state parks: $F_{(1, 80)} = 56.5$, $p < 0.001$; reference areas: $F_{(1, 19)} = 16.1$, $p < 0.001$) by 2010. In state parks, there was a significant interaction for the graminoids group ($F_{(4, 80)} = 3.3$, $p = 0.015$). Relative cover of graminoids increased from 2% to 5% in both parks and reference areas. The relative percent cover of the liliaceous group remained at 3% in state parks and decreased from 4% to 1% in reference areas. Increases in fern mean percent cover were similar in parks and reference areas (2–4%, $F_{(1, 80)} = 18.3$, $p < 0.001$ and 4–5%, $F_{(1, 19)} = 3.3$, $p = 0.084$, respectively) and neither site type changed substantially in relative percent cover (8–7% in parks and 9–10% in reference areas).

3.4. Cover of individual species

In the 1990s, four species unpalatable to deer, *Polystichum acrostichoides*, *Arisaema triphyllum*, *Podophyllum peltatum*, and

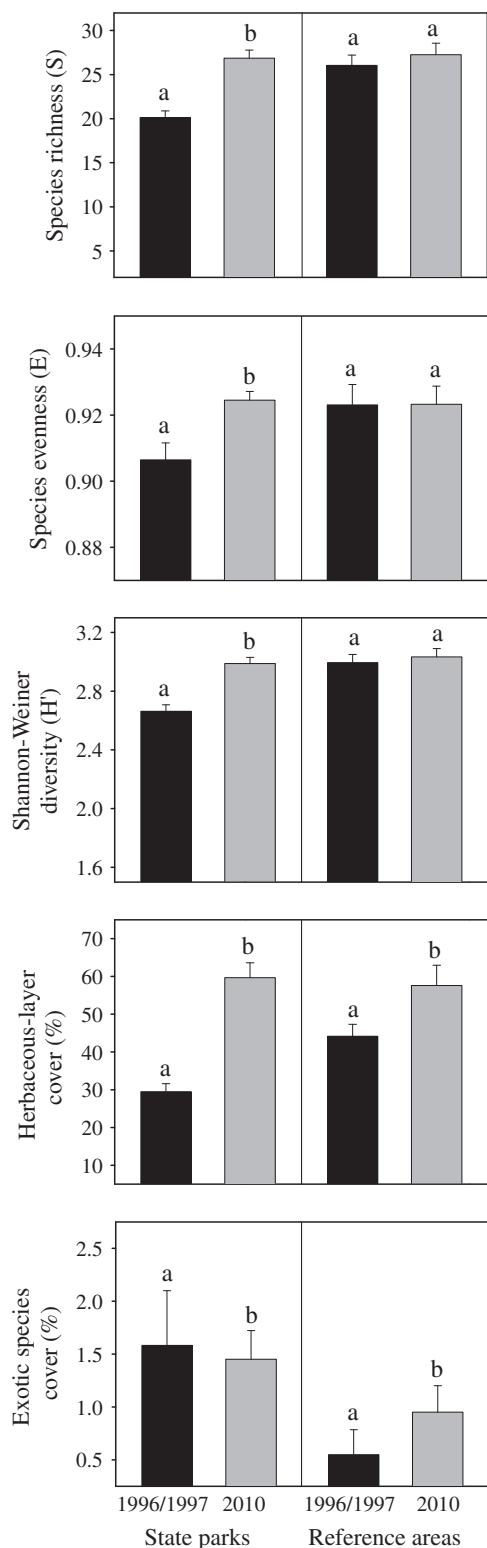


Fig. 2. Mean species richness (S), evenness (E), Shannon-Weiner diversity (H'), herbaceous percent cover, and exotic plant percent cover (mean \pm SE) across state parks and reference areas in 1996/97 and 2010.

Asarum canadense, were common in the parks (Webster, 1997). However, we observed decreased relative cover of these species in our study (*P. acrostichoides* 4–3%, *A. triphyllum* 4–2%, *P. peltatum* 22–4%, and *A. canadense* 9–4%). In many parks, the decrease in the cover of exotic species was driven by decreases in the cover of *Alliaria petiolata*. For example, in the 1990s Pokagon was

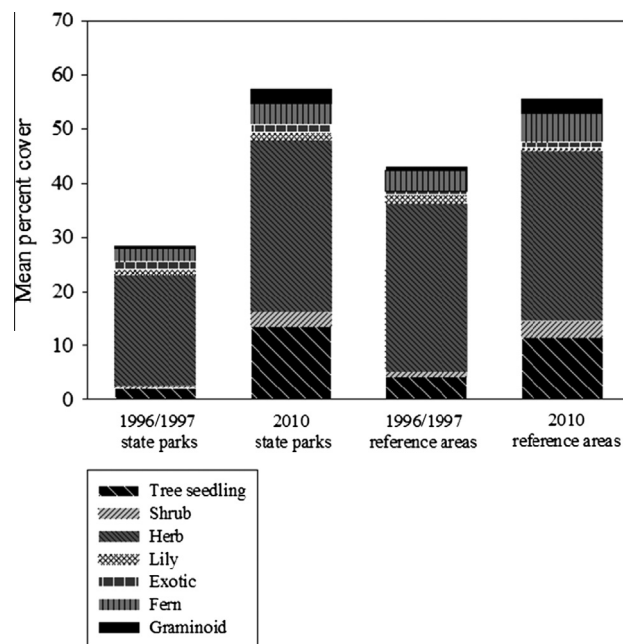


Fig. 3. Mean percent cover of species functional groups in state parks and reference areas at the initiation of controlled deer hunts in state parks (1996/97) and following more than a decade of hunting (2010).

dominated by *A. petiolata* (Webster, 1997). Cover of this species decreased at Pokagon from 9% in 1996/97 to 0.4% in 2010. Percent cover of *A. petiolata* across parks in 2010 (0.2%) was less than half of that found in 1996/97 (1.4%). Declines in invasive species cover in the parks were not universal, each of the nine plots that contained *Rosa multiflora* in 1996/97 displayed increased cover in 2010 (0.1–0.5%), and this species expanded to 16 additional plots between 1996/97 and 2010. *R. multiflora* cover increased from 0.02% to 0.3% in reference areas, but *A. petiolata* cover remained largely unchanged.

3.5. NMS ordinations

NMS ordination revealed a three dimensional solution as the best fit for each natural region. In the Highland Rim, axes 1, 2, and 3 accounted for 75.3% of total variance in the data, with axes 2 and 3 explaining 40.8% and 19.7%, respectively, and a final stress equal to 15.06. The Northern Lakes/Northwestern Morainial ordination had a final stress of 19.18. Axes 1, 2, and 3 accounted for 64.6% of total variance, with axes 2 and 3 explaining 23.0% and 26.6%, respectively. The final stress equaled 15.9 in the Southwestern Lowlands. Axes 1, 2, and 3 accounted for 70.8% of total variance, with axes 1 and 3 explaining 28.0% and 27.2%, respectively. The Central Till ordination had a final stress equal to 14.70. Axes 1, 2, and 3 accounted for 76.8% of the total variance, with axes 1 and 2 explaining 44.9% and 17.5%, respectively. The final stress was equal to 15.64 in the Bluegrass NR. Axes 1, 2, and 3 accounted for 75.0% of total variance, with axes 1 and 3 explaining 30.5% and 29.7%, respectively.

Park size, cumulative harvest, initial deer abundance, and H/E were the environmental variables with the greatest correlations with at least one axis in most natural regions ($r > 0.50$, $p \leq 0.05$; Table 2). The Central Till NR was the notable exception where percent slope, percent change in basal area, and aspect were more strongly related to axis values than park size or variables related to deer abundance (Table 2). Percent slope was also an important variable in the Northern Lakes/Northwestern Morainial, Southwestern Lowlands, and Bluegrass NRs and percent change in basal

Table 2
Pearson correlation of state park NMS (non-metric multidimensional scaling) plot scores in each natural region with hunting-related and environmental variables (H/E = harvest per hunter effort for the three most recent hunts). Significant correlations ($p < 0.1$) are bolded for ease of interpretation.

Natural region	Environmental variable	Axis 1		Axis 2		Axis 3	
		<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>
Highland Rim	Park size	0.542	−0.154	<0.001	0.749	<0.001	0.881
	Cumulative harvest	0.407	−0.208	0.001	0.726	<0.001	0.871
	Initial deer abundance	0.437	−0.196	0.001	0.731	<0.001	0.874
	H/E	0.167	0.340	<0.001	0.801	<0.001	0.791
	Percent slope	0.552	−0.15	0.929	0.0227	0.173	0.336
	Percent Δ in basal area	0.687	0.102	0.240	0.292	0.376	0.222
	Aspect	0.346	0.236	0.714	−0.0928	0.978	0.007
Northern Lakes/Northwestern Morainial	Park size	0.005	0.607	0.001	0.694	0.208	−0.294
	Cumulative harvest	0.002	0.648	<0.001	0.812	0.786	−0.065
	Initial deer abundance	0.074	0.409	<0.001	0.815	0.206	0.295
	H/E	0.225	0.284	<0.001	0.720	0.017	0.529
	Percent slope	0.094	0.385	0.132	0.349	<0.001	0.775
	Percent Δ in basal area	0.773	−0.0687	0.983	−0.005	0.292	−0.248
	Aspect	0.701	−0.0915	0.795	0.0621	0.087	−0.393
Southwestern Lowlands	Park size	0.044	−0.494	0.181	−0.341	<0.001	−0.813
	Cumulative harvest	0.096	−0.417	0.404	−0.217	<0.001	−0.823
	Initial deer abundance	0.186	0.337	0.009	0.615	0.485	−0.182
	H/E	0.205	0.324	0.010	0.605	0.436	−0.202
	Percent slope	0.142	−0.372	0.022	−0.551	0.335	−0.249
	Percent Δ in basal area	0.827	0.0575	0.692	0.104	0.005	0.649
	Aspect	0.401	−0.218	0.580	0.145	0.426	−0.207
Central Till	Park size	0.454	0.239	0.845	0.063	0.406	−0.265
	Cumulative harvest	0.454	0.239	0.845	0.063	0.406	−0.265
	Initial deer abundance	0.454	0.239	0.845	0.063	0.406	−0.265
	H/E	0.454	−0.239	0.845	−0.063	0.406	0.265
	Percent slope	0.147	−0.445	0.206	0.393	0.071	0.538
	Percent Δ in basal area	0.021	0.655	0.477	−0.227	0.313	0.318
	Aspect	0.301	0.326	0.838	−0.0661	0.076	−0.53
Bluegrass	Park size	0.006	0.625	0.083	−0.420	0.304	0.256
	Cumulative harvest	0.019	0.547	0.019	−0.548	0.086	0.416
	Initial deer abundance	0.026	0.522	0.013	−0.571	0.062	0.448
	H/E	0.453	−0.189	0.029	−0.513	0.008	0.603
	Percent slope	0.010	0.588	0.023	−0.534	0.256	−0.283
	Percent Δ in basal area	0.584	0.138	0.998	0.001	0.519	−0.163
	Aspect	0.128	0.372	0.294	−0.262	0.876	−0.040

area was important in the Southwestern Lowlands. Park size, cumulative harvest, H/E, and initial deer abundance were highly correlated ($r > 0.70$, $p \leq 0.001$) with plot scores along the two dominant axes (1 and 2) in the Highland Rim NR (Table 2). The environmental overlay onto 2010 plot scores in this natural region showed that plots within Brown County were associated with larger park size, cumulative harvest, and initial abundance while plots in Spring Mill and McCormick's Creek were associated with lower values of these variables (Fig. 4a). In the Northern Lakes/Northwestern Morainial NR, park size, cumulative harvest, H/E, and initial deer abundance were also highly correlated to plot axis scores ($r > 0.60$, $p \leq 0.005$) with plots in Chain O'Lakes and Potato Creek associated with larger values of these variables (Fig. 4b).

Successional vectors revealed that the compositional trajectories of herbaceous-layer vegetation in parks and reference areas were generally unidirectional, suggesting that similar changes occurred within reference areas and parks following deer reductions (Fig. 5). Vectors at three parks (Brown County, Pokagon, and Whitewater) converged with those of their reference areas, reflecting increased similarity in species composition. Each of these three parks was the spatially-closest park to their respective reference areas and very similar in topography and disturbance history, suggesting that differences in pre-hunting composition between these parks and their reference areas resulted from disparate deer abundances and not environmental variability.

4. Discussion

Our results suggest that the nearly two decade-long hunting program in Indiana state parks has resulted in the recovery of degraded vegetation communities. Between our sample intervals, we observed greater increases in herbaceous-layer cover, S, E, and H' in parks than in reference areas (Fig. 2) and the composition of the herbaceous layer in parks exhibited changes similar to those of reference areas (Fig. 5). Because herbaceous species richness and diversity increased in parks and remained constant in reference areas, this compositional convergence is not due to concurrent species loss but rather to increased similarity in species pools and relative cover. The association of cumulative harvest, H/E, and initial deer abundance with 2010 composition in the NMS ordination further suggests that deer population reductions are driving compositional changes in parks (Table 2; Fig. 4). Moderate levels of deer herbivory promote herbaceous layer diversity when combined with other concurrent natural disturbances (such as fire or canopy gaps; Royo et al., 2010a). Therefore, reduced deer abundances following the initiation of hunting and the occurrence of canopy gaps with stand development likely explain observed increases in herbaceous species cover and diversity in state parks. Because our data only represent two points in time, we were unable to assess the rate of recovery following the initiation of hunting. Exclosure studies suggest that this rate is non-linear and varies for different elements of vegetation composition and structure (Ross et al., 1970; Perrin et al., 2006; Webster et al., 2008).

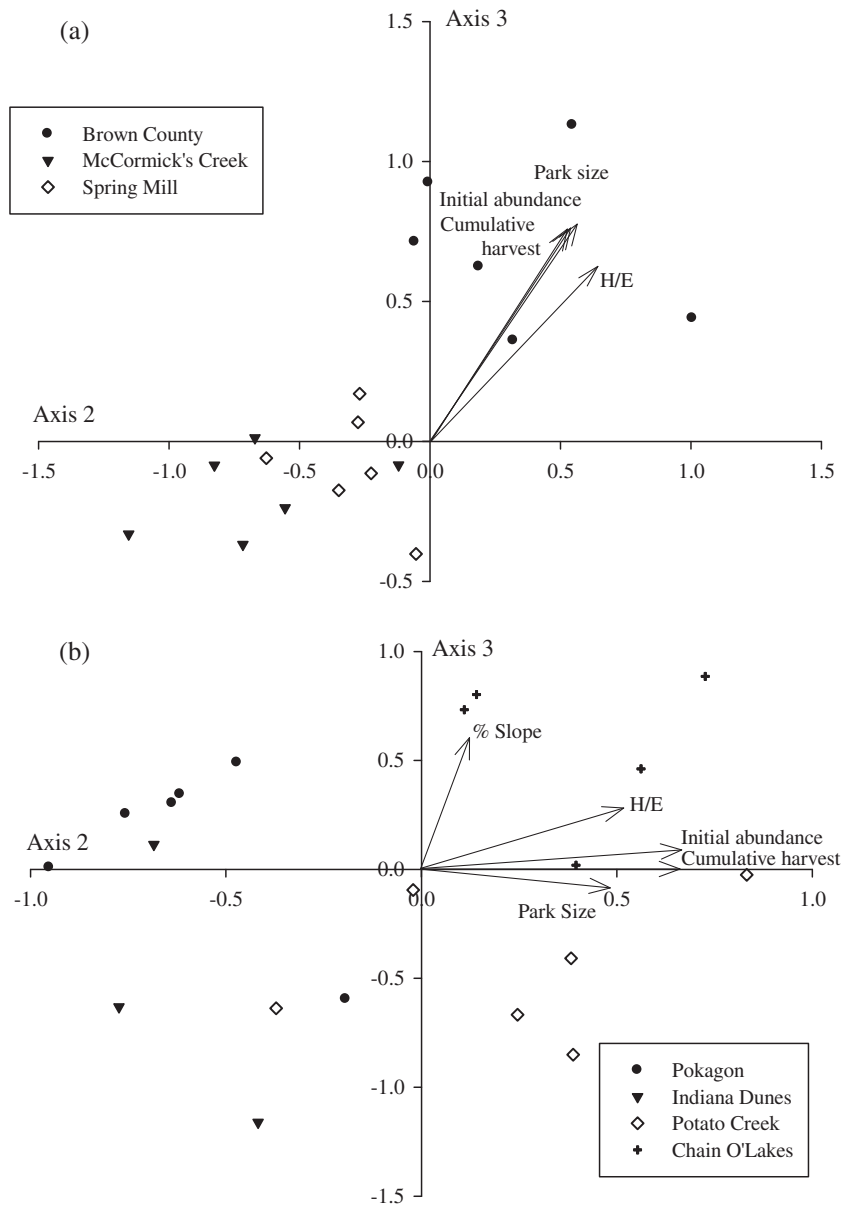


Fig. 4. NMS ordination results from state park plots derived from 2010 data for (a) Highland Rim and (b) Northern Lakes/Northwestern Morainal Natural Regions. Highland Rim axis 2: $r^2 = 0.41$ and axis 3: $r^2 = 0.20$; dominant environmental variables including initial deer abundance, park size, cumulative harvest, and harvest/hunter effort recent average (H/E) are shown as vectors. Northern Lakes/Northwestern Morainal axis 2: $r^2 = 0.23$ and axis 3: $r^2 = 0.27$; dominant environmental variables including initial deer abundance, cumulative harvest, H/E, park size, and percent slope are shown as vectors.

While the detailed hunting data collected in the state parks allowed us to examine the relationships between measures of deer abundance and changes in plant community composition, we lacked similar data resolution in our reference areas. In addition, hunting outside the parks consisted of widely dispersed hunters and multiple seasons (archery, firearm, and black powder) extended over more than three months. This differs greatly from the short-term high hunter density hunts that occurred within the parks. In the counties that contain the parks we studied, the total number of deer harvested increased 24% between 1997 and 2009 (25,817–31,988 deer; Indiana Department of Natural Resources, unpublished data). However, we were unable to deduce whether this change reflects constant hunting pressure on a growing population or a reduction in population density driven by increased hunting pressure.

We observed distinct shifts in the cover of functional groups in state parks. Heavy and sustained herbivory by deer has been

shown to favor dominance by non-preferred, browse-resilient species such as ferns, graminoids, and exotic species (Horsley et al., 2003; Webster et al., 2005; Royo et al., 2010b; Nuttle et al., 2014). This was evident in Indiana state parks during the late 1990s when the herbaceous layer was dominated by less palatable species such as *A. triphyllum*, *P. peltatum*, and *A. canadense* (Webster and Parker, 2000; Webster et al., 2001). In 2010, we observed increased cover of species in functional groups that are more palatable to deer and hence more sensitive to browse, such as tree seedlings and shrubs (Anderson, 1994; Rooney and Waller, 2003; Royo et al., 2010b).

Liliaceous species such as those in the genera *Trillium*, *Maianthemum*, and *Polygonatum* were present in parks in the 1990s but were scattered in distribution and had very low cover (Fig. 3). The increased cover of this functional group in 2010 suggests that these preferred-browse species were able to persist during years of chronic herbivory and recolonized or expanded from existing

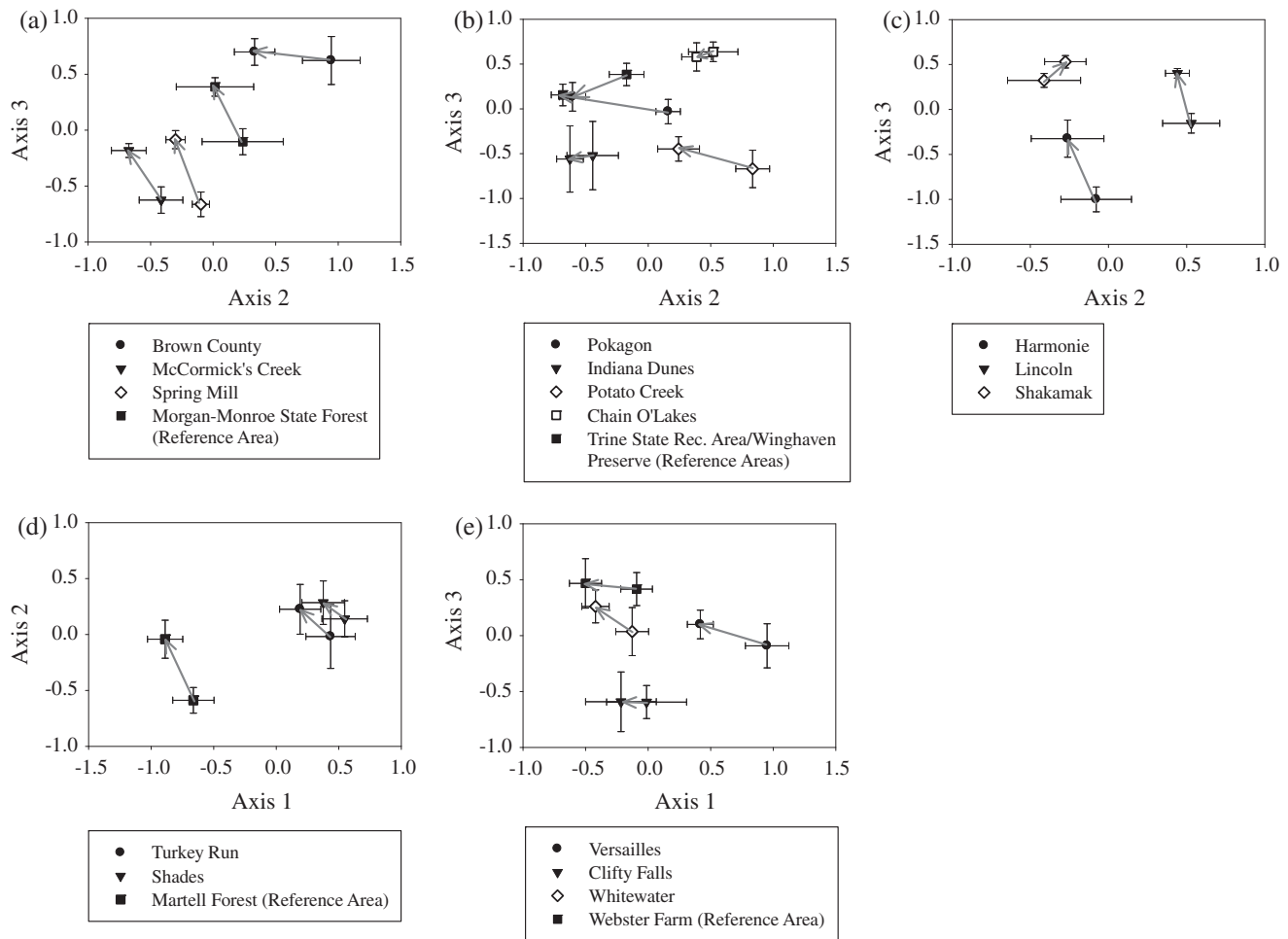


Fig. 5. Mean change in composition based upon NMS centroids between 1996/97 and 2010 in each park or reference area in the (a) Highland Rim, (b) Northern Lakes/Northwestern Morainal, (c) Southwestern Lowlands, (d) Central Till, and (e) Bluegrass Natural Regions.

rhizomes and seeds as deer populations were reduced. Exclosure studies have shown that recolonization by dispersal-limited herbaceous perennials is a slow process once a species is extirpated and reestablishment requires dispersal from distant populations (Webster et al., 2005; Royo et al., 2010b). Though not completely extirpated, *Trillium* spp. (an ant-dispersed genus), were lost from thirteen park plots between 1996/97 and 2010. Percent cover of this genus increased on plots where it remained, suggesting an expansion of existing populations. However, these species were not found on any additional plots in 2010, suggesting limited recolonization.

Despite their slightly increased cover in state parks, neither ferns nor graminoids dominated understories in parks in 2010 because other functional groups increased substantially in cover. Dense fern carpets that block tree regeneration and out-compete other herbaceous species often form following heavy deer herbivory (Rooney, 2001; Horsley et al., 2003; Royo et al., 2010b; Nuttle et al., 2014), but were not found in Indiana state parks in either 1996/97 or 2010. Between sampling intervals, we observed a greater increase in the cover of tree seedlings in parks than in reference areas (Fig. 3). This finding is consistent with other research that observed increased recruitment of tree seedlings after 10–20 years of deer reduction (Anderson and Katz, 1993; Tanentzap et al., 2011).

While the cover of exotic species was small in both parks and reference areas, our results show reduced importance of these species in the parks, compared to generally stable importance in reference areas. We also observed reduced cover of *A. petiolata* in

parks, while cover of this species remained unchanged in reference areas. This species was not controlled by park managers and is unpalatable to deer (Knight et al., 2009; Waller and Maas, 2013). Numerous exclosure studies have found that deer facilitate dominance of invasive species through selective browsing of native competitors (Webster et al., 2008; Knight et al., 2009; Abrams and Johnson, 2012). This finding further supports our hypothesis that the hunts have been effective in reducing deer abundance and allowing the recovery of herbaceous communities and supports the passenger model of invasibility (Didham et al., 2005; MacDougall and Turkington, 2005). Under this model, deer herbivory serves as the environmental condition driving the susceptibility of forest communities to invasion. Once deer populations were reduced, dominance of invasives was no longer enforced, allowing preferred browse species to increase in cover (Webster et al., 2008; Knight et al., 2009).

The potential for recovery following deer reduction is a function of initial deer density as well as initial plant abundance (Rooney and Waller, 2003). The effects of herbivory measured in 1996/97 varied by park; therefore, resulting recovery may have varied due to differences in initial deer densities and plant abundances as well as different levels of reduction. Because deer exhibit habitat selectivity, landscape configuration strongly influences the per capita impact of deer herbivory on forest understories (Hurley et al., 2012). According to Hurley et al. (2012) increased availability of annual forage within a landscape is related to increased forest herb cover at a given abundance of deer. While we observed that metrics related to initial deer abundance and the number of deer

removed from parks formed significant gradients in all natural regions (Table 2; Fig. 4), these gradients were stronger in the Highland Rim NR. Forest cover dominates this natural region and annual forage is uncommon, suggesting that metrics related to deer abundance would predominate. Conversely, metrics related to deer abundance formed weaker gradients in the Central Till NR where the landscape matrix includes a greater proportion of patches comprised of annual forage. We offer the caveat that our initial deer abundance values represent indices rather than precise estimates. Nonetheless, these index values were among the environmental variables with the greatest correlations in the NMS ordination supporting the utility of this index.

5. Conclusions

Our results suggest that regular hunting in Indiana state parks since the 1990s has successfully allowed vegetation communities to recover from several decades of chronic herbivory by overabundant deer populations. We observed increased cover by an assemblage of herbaceous and woody species since 1996/97, resulting in increased species richness and diversity. These increases in cover occurred among functional groups that are sensitive to chronic herbivory, in conjunction with reduced relative cover of exotic species. However, many dispersal-limited perennials exhibited limited recovery due to a lack of reestablishment in areas from which they were extirpated. Additional work is needed to determine if landscape context has contributed to variable rates of recovery in vegetation communities of parks within different natural regions. While our study supports the effectiveness of hunting, deer populations have the capacity to grow rapidly once released from control and continued management of deer herds under current guidelines is recommended to sustain community recovery. Controlled hunts may offer a viable option to reduce overabundant ungulate populations elsewhere where chronic herbivory has degraded vegetation communities.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2014.04.022>.

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