



## Untangling the landscape of deer overabundance: Reserve size versus landscape context in the agricultural Midwest

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### ARTICLE INFO

#### Article history:

Received 3 February 2011

Received in revised form 5 October 2011

Accepted 18 October 2011

Available online 22 December 2011

#### Keywords:

Spatial heterogeneity

Landscape context

Protected area

Herbivory

*Odocoileus virginianus*

Cross-habitat interactions

Indiana state park

Herbaceous

### ABSTRACT

We investigated the potential for cross-habitat interactions to modulate per capita ungulate browse effects on forest herbaceous layers. Specifically, we examined how white-tailed deer (*Odocoileus virginianus*) abundance, reserve size, and landscape context at variable spatial scales interact to influence the impact of deer herbivory on forest understory communities in 16 Indiana state parks. We used native herb cover (NHC) as a proxy for deer impact to forest understories, and deer killed per unit hunter effort (DAI) as a proxy for deer abundance. Comparison of multiple regression models, using Akaike's Information Criterion, suggested that the per capita impact of deer herbivory to forest understories was strongly related to landscape configuration of deer habitat types at the scale of an individual deer's home range, whereas deer abundance was more strongly associated with landscape structure at broader spatial scales. Interspersion and juxtaposition of non-forested, perennial forage habitat with other habitat types (forest and agriculture) at the park plus a 0.5 km buffer scale, together with DAI, explained 84% of the variation in native herbaceous cover (NHC). A model with DAI alone as a predictor accounted for only 19% of the variation in NHC. Thus, although deer impact was related to deer abundance, habitat configuration in landscapes surrounding parks appeared to strongly modulate the level of impact associated with a particular abundance of deer. Our results underscore the importance of landscape context in determining foraging behavior and per capita impacts of ungulates on forest resources in protected areas.

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### 1. Introduction

Humans set aside natural areas with the intention of preserving biological diversity and ecological and evolutionary processes. As such, natural areas are progressively more important in a world where anthropogenic activity increasingly modifies habitats and compromises the ecological integrity of ecosystems. However, natural areas often resemble islands in hostile seas, too small to sustain important ecological processes (e.g., organism movements, natural disturbances) and surrounded by incompatible land uses. There are often, if not always, scale mismatches between the size of natural areas and the dynamics of “protected” populations and ecosystems (White et al., 2000), and cross-boundary issues have been an important theme related to the management of parks and wilderness for several decades (Landres et al., 1998; Schone-wald-Cox, 1988; Wright and Thompson, 1935). Pattern at a focal scale (e.g., plant diversity within a park or natural area) can be viewed as a consequence of constraints imposed by larger scale phenomena (e.g., climate, landscape structure, dispersal processes)

as well as the result of the additive effects of smaller scale phenomena (e.g., herbivory or competition) (Levin, 1992; Turner, 2005b). As such, the spatial heterogeneity in the surrounding landscape may be as important as the content of the natural area in its impact on biological diversity and ecosystem processes within the natural area (Hansen and DeFries, 2007; Schafer, 1994).

Because of their generally large size and wide-ranging movements, large herbivores potentially serve as cross-scale interactors, linking fine-scale processes operating at a local scale (e.g., within a natural area) to coarse-scale processes operating within the broader landscape. The effects of large herbivores on individual plants occur at fine scales (e.g., the selection of bites within patches) that are aggregated over time and space, whereas herbivores respond to vegetation pattern (and other elements of spatial heterogeneity) at the relatively coarse scales that characterize dispersal behavior, migratory movement, and seasonal habitat selection (Weisberg et al., 2006). For these reasons, the character of the broader-scale landscape surrounding a natural area may constrain how herbivores use forage and cover resources within a natural area. This could be especially important where natural areas are small relative to the size of an herbivore's home range or seasonal movement patterns (as is the case for many state parks and nature preserves).

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An important mechanism by which large terrestrial herbivores potentially link natural areas to the broader landscape is through cross-habitat interactions. Members of the deer family (Cervidae), for example, play important roles in the mediation of cross habitat interactions, by acting as biological vectors of nutrient or energy fluxes across ecosystem boundaries (Bump et al., 2009; Jensen et al., 2011; Polis et al., 1997; Seagle, 2003; Takimoto et al., 2009) or through aggregative and reproductive numerical responses associated with foraging behavior that involves movement across habitat boundaries (Polis et al., 1997; Takada et al., 2002; Takimoto et al., 2009). In the later case, herbivores may aggregate foraging activity in a preferred, highly productive habitat (e.g., a meadow or old-field) adjacent to a low productivity habitat (forest understory), resulting in diminished foraging pressure and improved plant performance in the low productivity habitat. Such an effect could be short-lived, however, depending on the relative strength and speed of an herbivore population's reproductive and aggregative numerical responses to the spatial and temporal scales of resource availability in the respective habitats (Takimoto et al., 2009).

In this paper, we explore how habitat heterogeneity in the landscapes surrounding Indiana state parks affects white-tailed deer (*Odocoileus virginianus*) abundance and foraging behavior, and as a consequence, has cascading effects that ultimately determine the distribution and abundance of herbaceous plant communities in forest understories within Indiana parks. These effects could be dramatic in Indiana state parks because of an overabundance of deer that has resulted from an absence of large mammalian predators in Indiana landscapes and, prior to the initiation of this study, a policy of no human hunting of deer within state park boundaries. According to our conceptual model, the expected effects of landscape spatial heterogeneity on native herb cover are indirect. Native herb cover will be directly affected by the rate and timing of herbivory, which in turn will be a function of deer abundance and herbivore foraging behavior. We expect that heterogeneity in landscape structure will affect foraging behavior directly (e.g., functional and aggregational responses), whereas its effects on herbivore abundance will operate primarily through its effects on individual fitness and population vital rates (i.e., reproductive numerical response).

We address four broad questions: (1) *Do characteristics of a park, such as size and shape, influence deer density and deer impact on forest herb communities?* Larger, more compact-shaped parks might have resident deer herds that are buffered from hunting pressures, and have home ranges that do not include alternative, healthy forage habitat (e.g., agricultural fields) found outside the park. Under this scenario, resident deer densities will be higher than in comparable landscapes outside of a park core area due to lower mortality rates, and fecundity will not drop until nutritionally compromised deer have already caused substantial damage to the forest understory. (2) *Does landscape structure in and around the park only impact native herb cover indirectly through its affect on deer density, or does it also influence deer foraging patterns in a manner that directly impacts native herbs as well?* More alternative habitat types for deer could lead to less pressure on forest habitats. Variability in the spatial distribution of habitat types could lead to variance in patterns of herbivory across habitat, irrespective of habitat amount. (3) *What is the interplay between deer density, landscape composition and landscape configuration that ultimately determines native herb cover in parks?* Landscape context might influence both deer density and deer foraging behavior, with the possibility of both direct and indirect effects of various landscape elements, either working in concert or competitively. (4) *How do these factors vary in their influence across spatial scales?* Per capita deer impact may be determined by factors operating at fairly local spatial scales (e.g., the scale of an individual deer's home range), whereas popu-

lation dynamics might be governed by processes operating across broader spatial scales.

A finding common to many landscape-level studies of large herbivore ecology is that increased spatial heterogeneity in resources can lead to improved habitat conditions, as reflected in reduced home range size (e.g., Kie et al., 2002; Anderson et al., 2005), and improved population performance and a stabilization of population dynamics (Hobbs and Gordon, 2010). Previous research suggests that, in forested ecosystems, deer prefer forest edge environments and constitute an edge effect on forest plants (Alverson et al., 1988; Cadenasso and Pickett, 2000; Côté et al., 2004; Miyashita et al., 2008). Deer reproductive fitness has been positively related to forest edge density, habitat diversity, and the presence of highly productive non-forest habitat interspersed with forest habitat (McLoughlin et al., 2007; Miyashita et al., 2008). Moreover, deer home range selection appears to be strongly biased toward areas with greater habitat diversity, small patch sizes, and a high level of interspersed and juxtaposition of cover and forage habitat types (Beier and McCullough, 1990; Fulbright and Ortega, 2006; Kie et al., 2002; Klaver, 2001; Nixon et al., 1991). Such spatial configuration of habitat types likely facilitates movement among the multiple habitat types that a deer needs to satisfy forage and cover requirements.

In light of this, we chose to emphasize the effects of four landscape variables in our analyses: (1) forest edge density, (2) the amount of perennial forage habitat (i.e., native or naturalized non-forest habitat, including wetland, shrubland, and successional habitat), (3) landscape level habitat interspersed, and (4) the interspersed and juxtaposition of perennial forage habitat. To limit the number of independent variables included in our analyses, we aggregated landcover types into three deer habitat classes – forest, perennial forage and agriculture. We placed special emphasis on perennial forage because of its demonstrated importance to overall deer biology and, of the three deer habitat types, it was consistently the rarest in the landscapes surrounding the 16 state parks included in this study. We hypothesized that parks in landscapes with greater habitat interspersed, greater edge density, and a greater abundance of perennial forage habitat will show less per capita impact of deer herbivory on the parks' forest herb communities. Our rationale is that deer in these parks will more readily have access to preferred forage and cover resources of higher productivity forest edge and non-forest environments, and as a consequence will show an aggregative numerical response (sensu Takimoto et al., 2009) to such spatial subsidies that will result in lower rates of herbivory within forest interior understories. Though deer abundance in state parks should respond positively to these same variables, we do not expect reproductive numerical responses to be fully realized due to human hunting in the landscapes surrounding state parks.

Finally, if there is a resident deer herd effect, then parks with large core areas should have greater herbivore impacts, and we should see increased impacts to native forest herb communities as distance between vegetation plots and either the park boundary or forest edge increases.

## 2. Methods

### 2.1. Study area

Indiana supports among the highest densities of white-tailed deer in North America (approx. 901 kg of deer per km<sup>2</sup>; Crête and Daigle, 1999), and ecological problems with deer overabundance have been evident since at least the mid-1970s (Mitchell et al., 1997). High deer densities can be attributed to a number of factors, including a mild climate and absence of heavy snow

cover during most winters, lack of large predators, a landscape composed of adequate cover habitat (e.g. forest, shrubland) and abundant, high quality forage, such as agricultural forage and row crop, pasture, successional habitat, and wetlands. In many areas, deer abundance levels appear to be higher than forest understory communities can withstand. Herbivory-associated damage to plant communities in state parks has been especially severe (Webster and Parker, 1997), primarily due to hunting prohibitions that were in place until the mid-1990s (Mitchell et al., 1997).

We chose 16 state parks for this study (Fig. 1). These parks represented a spectrum from small (<500 ha) to large (>6000 ha), and from parks nested in an entirely agricultural landscape, to parks nested in a primarily forested landscape (Table 1). The parks also varied substantially in shape, as reflected in shape indices computed with the program FRAGSTATS (McGarigal et al., 2002).

Condition of forest understories, as measured by native perennial herb cover (NHC) and deer relative abundance, varied considerably (Table 1). The Indiana Department of Natural Resources began annual public hunts in parks during the 1990s, and our estimates of deer abundance (deer abundance index or DAI) are based on the number of deer killed per unit hunter effort during the first annual hunt conducted for each state park (Webster and Parker, 2000). For first annual hunts, the average number of deer harvested per km<sup>2</sup> of park was 26.1 and ranged from a low of 6 per km<sup>2</sup> (Brown County) to a high of 60 per km<sup>2</sup> (Chain O'Lakes). These numbers underscore the magnitude of the overabundance problem but do not necessarily reflect densities within state parks for two reasons: (1) they include hunter killed deer that may have had substantial portions of their home ranges outside of park boundaries; and (2) hunter effort varied substantially across parks. Deer killed

per hunter effort, on the other hand, provides a relatively unbiased indicator of deer abundance (Webster and Parker, 2000). In analyses of Midwestern North American datasets, Roseberry and Woolf (1991) and Van Deelen and Etter (2003) both found that the relationship between deer density and deer killed per hunter effort was linear, at least over the range of data included in their analyses. This implied a linear functional response, but Van Deelen and Etter caution that a greater range in hunter kill and/or deer density data might show a curvilinear functional response. This consistently proportional relationship thus makes hunter kill per unit effort a reliable indicator of deer density and numerous studies have used it as such (Van Deelen and Etter, 2003). However, while functional responses appear to be linear, it is also apparent that the slope of the linear response varied substantially from region to region, so it is likely that there is some degree of spatial heterogeneity in the relationship between deer density and hunter effort among Indiana state parks as well.

Although we do not have data that allow us to predict deer density from DAI, Swihart (1998) provide pre-first-harvest density estimates for two state parks, Pokagon in the fall of 1995 with a density of 30.6 deer km<sup>-2</sup> and Brown County in the fall of 1993 with 21.7 deer km<sup>-2</sup>. Deer killed per hunter effort for the first annual hunt at these parks was 1.34 and 0.85, respectively. Control areas located near each state park (see Webster and Parker, 2000), which have been hunted for several decades, had substantially lower deer killed per hunter effort (mean 0.22) than any of the state parks (mean 0.9, range 0.42–1.39).

As a measure of deer impact and understory condition, we measured percent cover of native herbaceous plants (NHC) in mature, mesic hardwood forest. This forest type generally has a closed canopy, a densely shaded understory and moist, nutrient rich soils. According to the carbon-nutrient balance hypothesis of Graves et al. (2006), perennial herbs should form a continuous, tall layer in temperate deciduous forests where light is limited but nutrients and moisture are abundant, whereas woody plant abundance should be favored where the supply of carbon is high relative to

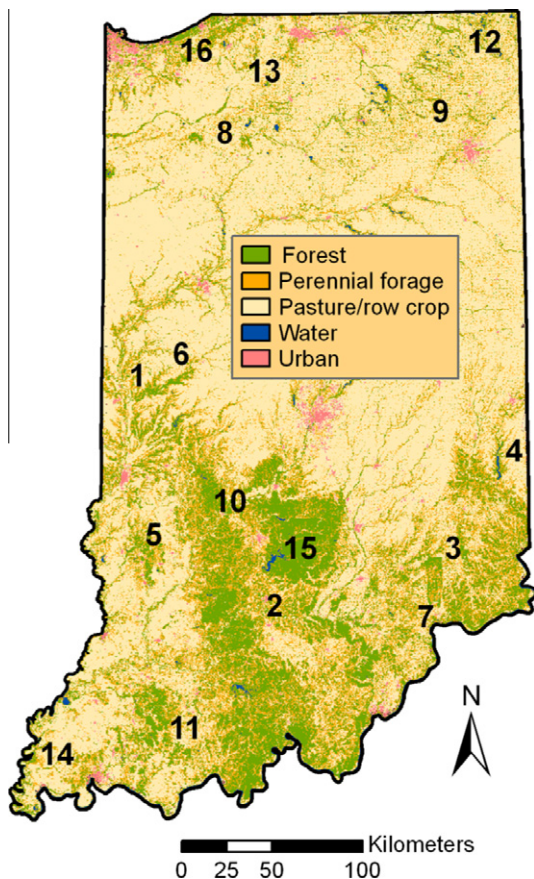


Fig. 1. Locations of sampled Indiana state parks. Numbers indicate park rank, from highest to lowest, in native herb cover. See Table 1 for park names.

Table 1

Park characteristics, including landscape context, deer abundance index (DAI), and native herb cover (NHC) in mature, mesic deciduous forest. Parks are sorted from highest to lowest NHC.

State Park Name	Landscape context	Area (ha)	Shape index <sup>a</sup>	% Forest (in park)	DAI	NHC
Turkey Run SP	Forest	952	1.46	90.2	0.49	42.12
Spring Mill SP	Mixed	542	1.29	92.4	0.43	41.47
Versailles SP	Forest	2368	2.64	92.4	0.69	40.61
Whitewater SP	Agriculture	612	1.71	75.8	0.94	35.84
Shakamak SP	Agriculture	720	1.24	69.6	0.52	35.69
Shades SP	Mixed	1248	1.78	91.7	0.64	34.63
Clifty Falls SP	Urban	560	1.58	87.9	0.42	32.31
Tippecanoe River SP	Agriculture	1169	2.24	61.0	1.23	27.97
Chain O'Lakes SP	Agriculture	1194	1.70	54.3	0.90	27.27
McCormick's Creek SP	Forest	731	1.27	94.4	0.63	25.55
Lincoln SP	Forest	762	1.94	93.7	0.47	21.83
Pokagon SP	Agriculture	477	1.03	71.9	1.34	18.91
Potato Creek SP	Agriculture	1514	1.71	35.5	1.27	14.85
Harmonie SP	Agriculture	1392	1.79	89.5	1.39	6.80
Brown County SP	Forest	6473	2.01	98.6	0.85	6.26
Indiana Dunes SP	Mixed	887	1.54	79.6	0.67	4.73

<sup>a</sup> Shape index = 1 when the patch is maximally compact and increases without limit as patch shape becomes more irregular.

**Table 2**

Variable abbreviations and descriptions, including: (1) plot and park-level variables; and (2) class-level metrics used to quantify landscape structure in and around 16 Indiana state parks.

Code	Variable name	Description <sup>a</sup>
DAI	Deer abundance index	An index of deer abundance based on number of deer killed per hunter effort
NHC	Native herb cover	Percent cover of native herbaceous plants
DistBndy	Distance to park boundary	Distance in km from plot centers to park boundary
DistEdge	Distance to forest edge	Distance in km from plot centers to forest edge
%LAND <sub>pr</sub>	Percentage of landscape (%)	Percent of landscape composed of the perennial forage habitat type
ED <sub>r</sub>	Forest edge density (m/ha)	Edge length per unit area associated with a particular with forest habitat type
IJI	Interspersion and juxtaposition index (%) (for all habitats)	A measure of the extent to which habitat types are intermixed with other habitat types, with high values indicating an even distribution of adjacencies
IJI <sub>pr</sub>	Interspersion and juxtaposition index (%) (for perennial forage habitat)	A measure of the extent to which perennial forage habitat is intermixed with other habitat types, with high values indicating an even distribution of adjacencies
PCORE	Park core area	The area in the park greater than the specified depth-of-edge distance (500 m) from the perimeter

<sup>a</sup> See McGarigal et al. (2002) for a complete description and mathematical definition of each landscape metric.

moisture or nutrient levels. Thus, absence of an abundant and rich herb layer suggests unsustainable rates of herbivory (or other chronic disturbance), low moisture, or low nutrient availability. By restricting our sampling to closed canopy forests with high soil moisture and nutrient levels and flat to moderately sloping topography, we have substantially reduced variability in conditions other than herbivory that can reasonably account for differences in NHC among parks. Previous work at these same sites by Webster and Parker (2000) and Webster et al. (2001) also supports the utility of NHC as an indicator of deer overabundance, because NHC was highly correlated with the mean heights of several plant species whose population size structures have been successfully used as predictors of browsing intensity.

## 2.2. Field sampling methods

In each state park, we sampled either three (two parks) or six (14 parks) randomly selected, closed canopy mesic forest stands during the summer of 1997 (for additional detail, see Webster and Parker, 1997). Approximate plot locations within each stand were randomly determined except that plot centers were located midslope, depending on local topography, and at least 30 m from forest/non-forest edge. Three, 10 m line transects were established at each plot, with the center line at the middle of and running parallel to the slope. The other transects were placed above and below, at random distances from (3 to 5 m), and parallel to the center transect. Linear coverage along each transect of all woody (<50 cm tall) and herbaceous plant species was recorded in cm, and percent coverage was calculated as the distance covered by each species divided by the total distance (3000 cm) per plot.

## 2.3. Landscape structure and spatial scale

We used the Indiana GAP landcover map derived from Landsat Thematic Mapper (TM) data (Indiana Gap Analysis Project, 1995) to quantify landscape structure at multiple spatial scales. Scales include the park only and the park plus one of five buffer areas (1 km, 5 km, 1 km, 3 km, or 7 km buffer). Scale thus refers to the specific area for which we derived measurements of landscape structure, and is referenced in tables and figures by the following as subscripts:  $p$  (the park only),  $p + 0.1$  (the park plus 0.1 km buffer),  $p + 0.5$  (the park plus 0.5 km buffer),  $p + 1$  (the park plus 1 km buffer),  $p + 3$  (the park plus 3 km buffer),  $p + 7$  (the park plus 7 km buffer). The minimum scale is constrained by the area of each park, while the maximum scale is large enough to encompass the home range of most or all deer that seasonally utilize park resources.

TM data has a pixel size of  $30 \times 30$  m, but the final Indiana GAP land cover classification used a rule-based aggregation procedure

to yield minimum mapping units equal to 1 ha zones. Using ArcGIS (ESRI, 2002), we reclassified landcover classes into either background or one of three deer habitat types: (1) forest ( $f$ ), composed of deciduous, evergreen and mixed terrestrial forest, and palustrine deciduous forest; (2) perennial forage ( $pf$ ), composed of terrestrial shrubland, terrestrial woodland, palustrine herbaceous, palustrine shrubland and palustrine woodland; and (3) pasture/row crop ( $p/rc$ ), composed of row crop and pasture/grassland within 200 m of either perennial forage or forest. Pasture and row crop greater than 200 m from forest or perennial forage was classified as background; previous work suggests that agricultural forage located >200 m from cover habitat is either suboptimal or unsuitable deer habitat (Roseberry and Woolf, 1998). Other background cover types included developed non-vegetated, developed high density urban, developed low density urban, palustrine sparsely vegetated, and water. Combining cover types improved overall classification accuracy from 71.0% to 87.7%.

For each of the three composite habitat types not incorporated as background, we calculated landscape composition and configuration metrics with the program FRAGSTATS (McGarigal et al., 2002). We chose two class-level (forest edge density and perennial forage habitat interspersion/juxtaposition) and one landscape (overall habitat interspersion/juxtaposition) configuration metrics that describe different elements of landscape spatial pattern (Table 2). In the GIS, we also measured state park core area and the linear distance from sampling plot midpoints to park boundary (DistBndy) and forest/non-forest edge (DistEdge).

## 2.4. Analyses

### 2.4.1. Quantile regression on plot-level variables

For plot-level variables (DistBndy, DistEdge), we performed nonlinear quantile regression (Cade and Noon, 2003) to assess whether deer impact to forest herbs increased with greater distance from park boundary or forest edge. Specifically, we used a nonlinear negative exponential function ( $y = \beta_0 e^{-\beta_2 x}$ ) to model the relationships between NHC and DistBndy, and NHC and DistEdge, for the 0.5 and 0.8 regression quantiles of NHC. We used quantile regression because, for the pooled data (plot data from all parks combined), scatter plots of the relationships between NHC and the distance measures revealed substantial heteroscedasticity and a lack of normality in the error distribution. In addition, both the mean and variance in NHC appear to decline at increasing plot distances from the park boundary and from forest edge. Thus deer herbivory may impose an upper limit to native herb cover that decreases as distance from either park boundary or forest edge increases, and this trend may only be apparent for upper quantiles of the conditional distribution of the response variable (see Cade and Noon, 2003). Finally, we chose a negative exponential model

because we expect that NHC will decline at a decreasing rate as distance increases and NHC asymptotically approaches zero.

#### 2.4.2. Multiple regression on landscape-level variables

For park-level variables, we performed multiple linear regression analyses to examine the relationship between NHC, DAI, and the landscape structure variables. We constructed two sets of models, one with NHC as the response variable, the other with DAI as the response variable. Within each model set, we used Akaike's Information Criterion for small sample sizes (AICc) to compare models with different combinations of predictor variables. AICc protects against model 'overfitting' (Gotelli and Ellison, 2004), and represents a parsimonious compromise between variance explained and model complexity. We also computed Akaike weights ( $w_i$ ) and evidence ratios to aid in the evaluation of different models, including an intercept only null model. The  $w_i$  indicates the probability that, given the data, a particular model is the best model of the set of models that have been evaluated with AICc. The evidence ratio indicates the relative support of a model relative to another model; for example, if we take the 'best' model (the one with lowest AICc) as the reference, then the evidence ratio tells you how many times greater the weight of evidence favors the best model over the model in question.

For multiple regression models with NHC as the response variable, possible predictor variables included DAI, PCORE, IJIp<sub>f</sub>, IJI, and ED<sub>f</sub> (see Table 2 for variable descriptions). DAI was included in all NHC models because we wanted to assess an affect of landscape structure that represented a per capita impact of deer on forest herbs. For models with DAI as the response variable, predictor variables included %LAND<sub>pf</sub>, IJI, and ED<sub>f</sub>. IJIp<sub>f</sub> was not included as a predictor for DAI because of low variability at the 7 km scale. We first assessed the best scale of analysis by comparing AICc values of the 'best' models (those with the lowest AICc values) at each spatial scale, both to each other and to an intercept only null model. We then compared multiple models with different combinations of predictors, with the constraint that the scale of measurement for the landscape variables was that of the previously defined 'best' spatial scale.

#### 2.4.3. Path analysis

We used path analysis to illustrate the possible strength and direction of causal relationships among NHC, DAI and the various landscape variables describing the composition and configuration of landscape elements. Our purpose here was illustrative rather

than confirmatory hypothesis testing. We chose as landscape variables those that were incorporated into the multiple regression models that had the highest Akaike weights ( $w_i$ ). The resultant path diagram and magnitude and direction of path coefficients represent mechanistic hypotheses about the interrelationships among the variables (Gotelli and Ellison, 2004).

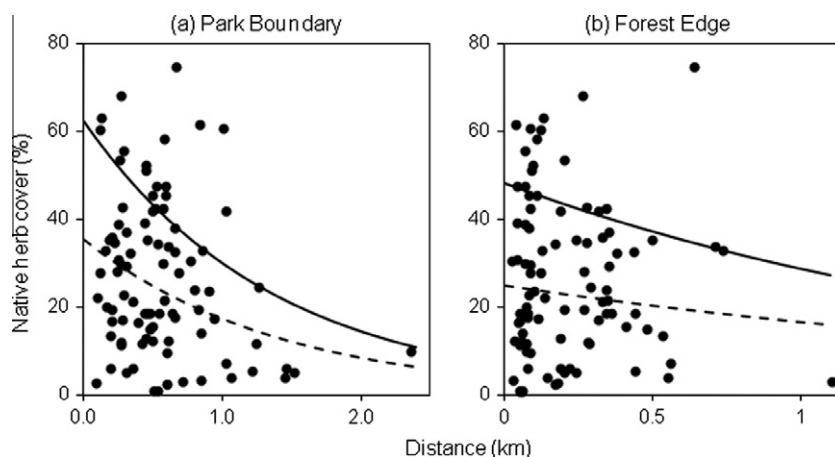
### 3. Results

#### 3.1. Quantile regression on plot-level variables

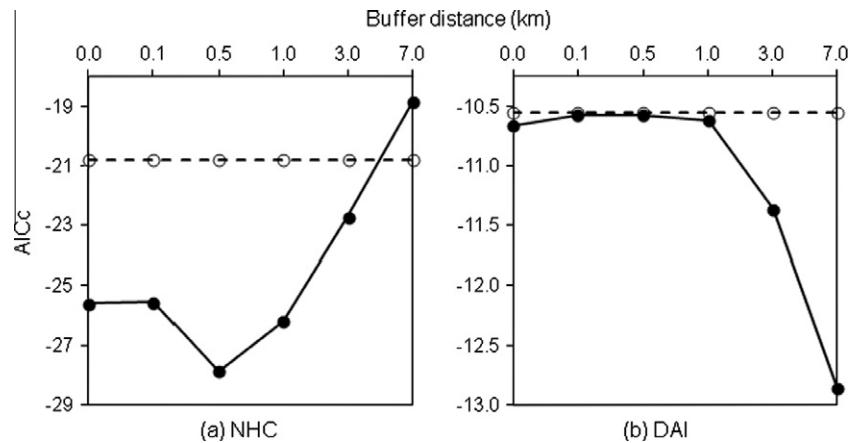
Correlations between NHC and plot-level variables were weak. While distance to park boundary had a marginally significant, negative effect on NHC for the 50th regression quantile when plots were pooled (Fig. 2), there was no consistent trend evident when we examined each park individually. The correlation between DistBndy and NHC was positive for seven and negative for nine of the 16 parks. However, the range of distances for the pooled data set was much greater than for individual parks, and the larger data set potentially allowed for a more rigorous test of the resident deer herd hypothesis. Using pooled data, a first order negative exponential model did reveal statistically significant effects of DistBndy for the 50th ( $\tau = 0.5$ ) regression quantile (Fig. 2;  $\beta_1 = -0.67$ ,  $se = 0.33$ ,  $t = -2.05$ ,  $p = 0.043$ ); results for the 80th ( $\tau = 0.8$ ) regression quantile are suggestive but do not lend strong support to the resident deer herd hypothesis ( $\beta_1 = -0.73$ ,  $se = 0.48$ ,  $t = -1.54$ ,  $p = 0.13$ ). For DistEdge, slope parameter estimates ( $\beta_1$ ) were not statistically significant.

#### 3.2. Multiple linear regressions of landscape-level variables

Based on AICc values, the best scale of analysis for predicting NHC was the park plus 0.5 km scale (Fig. 3a). However, all scales defined by buffer distances  $\leq 1$  km had AICc values substantially lower than that of the null model. After 1 km there was an abrupt increase in the AICc values, suggesting that landscape structure at distances greater than 1 km from park boundaries had little or no effect on per capita rates of herbivory in forest understories within state parks. We saw a reverse pattern in AICc values across spatial scales for models with DAI as the response variable, however (Fig. 3b). In this case, the best scale of analysis was the broadest spatial scale considered (the park plus the 7 km buffer), and AICc values for scales defined by buffer distances  $< 3$  km were essentially no different than that for the null model.



**Fig. 2.** Relationship between native forest herb cover (NHC) within plots and (a) distance from plot centers to state park boundary (DistBndy), and (b) distance from plot centers to nearest forest edge (DistEdge). Dashed lines indicates negative exponential model ( $y = \beta_0 e^{-\beta_2 x}$ ) results for 0.5 quantile regression; solid lines indicate results for the 0.8 quantile regression.



**Fig. 3.** AICc values for the best model at each spatial scale (solid line) compared to AICc for the null model (dashed line), with NHC as the response variable in (a) and DAI as the response variable in (b).

**Table 3**

Rankings and information theoretic statistics for candidate multiple linear regression models. Response variables include native herb cover for models shown in (a) and deer abundance index (DAI) for those in (b). Note that DAI is both a predictor of native herb cover (the first model set) and the response variable in the second model set. For (a), landscape variables were measured at the park plus 0.5 km buffer scale, and for (b) they were measured at the park plus 7 km buffer scale. Parameter estimates and their 95% confidence limits for the “best” models are provided in Table 4.

Model Rank	Model predictors <sup>a</sup>	<i>k</i>	AICc	<i>w<sub>i</sub></i>	Evidence ratio
<i>(a) Native herb cover (0.5 km buffer scale)</i>					
1	DAI + IJI <sub>pf</sub>	4	-27.88	0.787	1.00
2	DAI + IJI <sub>pf</sub> + ED <sub>f</sub>	5	-24.36	0.136	5.80
3	DAI + IJI	4	-20.62	0.021	37.63
4	DAI + ED <sub>f</sub>	4	-20.43	0.019	41.53
5	DAI	3	-19.59	0.012	63.20
6	DAI + PCORE	4	-17.01	0.003	232.54
7	DAI + %LAND <sub>pf</sub>	4	-16.42	0.003	307.75
Null		2	-20.78	0.023	34.77
<i>(b) Deer abundance index (7 km buffer scale)</i>					
1	%LAND <sub>pf</sub>	3	12.86	0.368	1.00
2	IJI	3	12.81	0.358	1.03
3	%LAND <sub>pf</sub> + ED <sub>f</sub>	4	10.49	0.113	3.27
4	ED <sub>f</sub>	3	-8.68	0.045	8.10
Null		2	10.55	0.116	3.17

<sup>a</sup> See Table 2 for descriptions of variables.

**Table 4**

Parameter estimates and their 95% confidence limits for the “best” models (those with the lowest AICc values) shown in Table 3a and b.

Model response variable and spatial scale	Parameter	Estimate	95% Confidence limit
(a) Native herb cover (0.5 km buffer scale)	Intercept	0.3850	0.1301
	DAI	-0.2738	0.1075
	IJI <sub>pf</sub>	0.0134	0.0038
(b) Deer abundance index (7 km buffer scale)	Intercept	0.6583	0.1519
	%LAND <sub>pf</sub>	0.1135	0.0611

The best model for predicting NHC, at the 0.5 km scale, included DAI and IJI<sub>pf</sub> as predictors (Table 3a, Fig. 4). The probability that this is the best model, given the data and the set of models considered, is 0.787. Only one other model in the set considered, that with DAI, IJI<sub>pf</sub>, and ED<sub>f</sub> as predictors, has a moderately high model probability (*w<sub>i</sub>* = 0.136). These two models had adjusted *R*<sup>2</sup>s of 0.84 and 0.85, respectively, so both represent good models in terms of

explanatory power. All other models perform poorly, with model probabilities as low as or lower than that of the null model.

For DAI as the response variable at the 7 km scale, two models, each with a single predictor, performed better than the null model. One model had %LAND<sub>pf</sub> and the other had IJI as the sole predictor, but neither can unambiguously be considered the best model because they had indistinguishable model probabilities (Table 3b). In addition, due to collinearity, combining these two variables into a single model was not possible and we therefore cannot ascertain whether only one or both of these variables are useful predictors of DAI. Evidence ratios indicate that the weight of evidence for these models was three times greater than that for the null model.

### 3.3. Path analysis

In Fig. 5, we depict path diagrams of potential causal relationships that ultimately determine level of impact. To illustrate possible strengths of direct and indirect effects, we used the current data set to estimate path coefficients, and considered the effect of %LAND<sub>pf</sub> and IJI at the park plus 7 km buffer scale and IJI<sub>pf</sub> at the park plus 0.5 km buffer scale. The amount of perennial forage

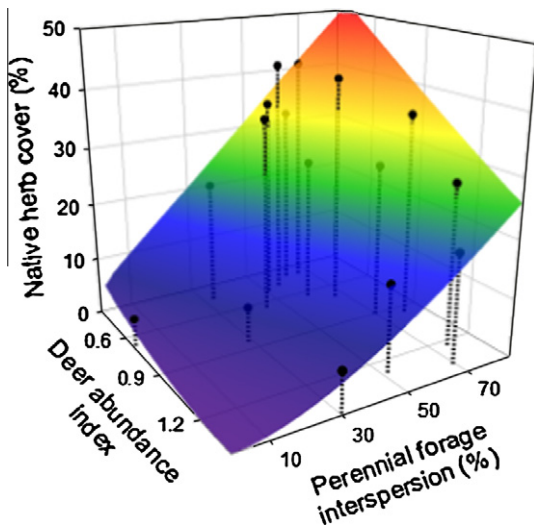


Fig. 4. Scatter plot and response surface relating native herb cover to deer abundance (DAI) and the interspersions/juxtaposition of perennial forage habitat ( $IJ_{pf,p+0.5}$ ). See Table 4 for parameter estimates and their 95% confidence limits.

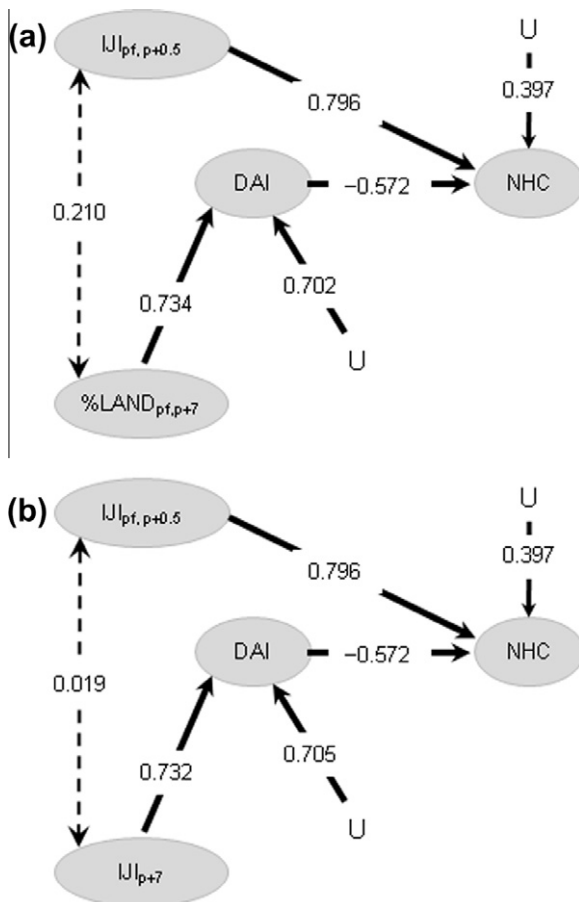


Fig. 5. Path diagrams showing possible causal relationships among native herb cover (NHC), deer abundance (DAI) and landscape variables. Thickness of lines is proportion to magnitude of estimated direct effects. Both (a) and (b) consider the effect of  $IJ_{pf}$  at a local scale (the park plus a 0.5 km buffer). However, at the at a broader 7 km scale, (a) considers the effect  $\%LAND_{pf}$  whereas (b) considers the effect of  $IJ$ . The path identified by U represents unexplained effects.

habitat at the broader spatial scale had a strongly negative, indirect effect on NHC. At a local scale, the interspersions of perennial forage had a positive effect on NHC, whereas at a broader spatial scale the

effects of overall habitat interspersions (Fig. 4b) may be substantially negative. The impacts of landscape variables at the broader spatial scale are primarily driven by indirect effects working through deer abundance (DAI). However, we cannot differentiate between the possible indirect negative effects of  $IJ_{p+7000}$  and  $\%LAND_{pf,p+7000}$  because of the high correlation ( $r = 0.933$ ) between these two variables.

#### 4. Discussion

Our results strongly suggest that the spatial heterogeneity in forage and cover resources within landscapes surrounding Indiana state parks have substantial effects on both white-tailed deer abundance and per-capita level of deer impact on forest understories within state parks (Table 3, Fig. 5). Unsurprisingly, deer impact was in part associated with deer density, but the configuration of landscape elements appeared to strongly modulate the level of impact associated with a particular deer density. These effects were scale dependent. The interspersions (but not the amount) of perennial forage habitat (e.g., wetlands, shrubland, early successional habitat) at the scale of a deer's home range appeared to strongly modulate per capita rates of deer herbivory, as reflected in the higher native herb cover associated with higher levels of perennial forage habitat interspersions (Fig. 4). We also found that the amount of perennial forage habitat may have played an important role in determining deer abundance in state parks, but this effect was only evident at the largest spatial scales considered. This effect was also confounded because of a high positive correlation between the amount of perennial forage habitat and overall habitat interspersions at the larger spatial scales. Thus, habitat interspersions may have had competing effects operating at different spatial scales, with a positive direct effect on native herb cover at a local scale being partially offset by a negative indirect effect at a broader spatial scale (Fig. 5).

The lack of an association between landscape structure variables and deer abundance at the smaller spatial local scales was somewhat surprising (Fig. 3). The implication would seem to be that local spatial heterogeneity did not affect deer abundance, or that local population dynamics were simply overwhelmed by stronger, regional-scale dynamics. We also did not find a substantive effect of forest edge density or park core area on either deer abundance or the per capita level of deer impact. Forest edges are widely thought to provide favorable habitat conditions for deer (Alverson et al., 1988; Anderson, 1997; Augustine and deCalesta, 2003; Beier and McCullough, 1990; McLoughlin et al., 2007; Miyashita et al., 2008; Nixon et al., 1991; Waller and Alverson, 1997), but in many cases it is not clear whether forest edge environments *per se* provide critical deer habitat, or whether the correlation is merely incidental to the fact that forest edges abut highly productive non-forest habitats that supply deer with superior forage and cover resources. For example, Miyashita et al. (2008) found that higher reproductive fitness of female sika deer (*Cervus nippon*) was positively related to forest edge density, and suggested that this could be due to either higher productivity of forest edges when compared to forest interior, or to the high productivity of agricultural lands in the more fragmented landscapes associated with high edge density.

The poor performance of park core area (PCORE) as a model predictor suggests the absence of an obvious 'resident deer herd' effect (Table 3). A resident deer herd would not be exposed to landscape influences outside of park boundaries except through long distance immigration and emigration processes, and as such should cause more damage to forest understories than deer that forage at least part-time on extra-park resources and experience some mortality due to human hunting. The lack of a park core area effect on

percent native herb cover, however, may have been due to a rather limited number of parks with large core areas that would have experienced a substantial resident deer herd effect. Only two parks had greater than 50% of their total area within the core area, and only one park had a core area > 1000 ha (Brown County State Park, core area = 4950 ha). When plotting percent native herb cover against distance to park boundary, however, we do see the hint of a resident deer herd effect in that there appears to be an upper limit to native herb cover that declines with distance from the park boundary (Fig. 2). A dataset that includes more large parks and a greater abundance of plots distant from park boundary or forest edge would be needed to more adequately test our hypothesis about the impact of a resident deer herd.

Why is the amount and interspersed of perennial forage habitat so important? There are a number of possible reasons, including: (1) provision of substantially more primary productivity within a foraging deer's reach (approx. 1.8 m) than an equivalent area of forest; (2) provision of an alternate food source during spring and summer when forest herbs are both most vulnerable (Alverson et al., 1988; Anderson, 1997; Augustine and deCalesta, 2003; Augustine and Jordan, 1998; Garcia and Ehrlen, 2002; Knight, 2003; Whigham and Chapa, 1999) and a large component of the white-tailed deer diet (Johnson et al., 1995; McCullough, 1985; Nixon et al., 1991); and (3) provision of alternate hiding cover proximate to agricultural fields, which decreases time spent in forest. Shrubland, early successional forest, and some wetlands probably provide better forage and escape/bedding cover than mature forest (McCullough, 1984; Nixon et al., 1991). Moreover, deer with access to seasonally abundant food resources within agricultural fields are probably less likely to deplete forage within non-forested cover habitats, reducing the need to utilize forage available within forest understories during spring and early summer when crop subsidies are less abundant (Nixon et al., 1991).

The temporal/spatial pattern in plant phenology across a landscape likely plays an important role in determining the impact of deer herbivory to forest understories. The nutritional quality of forage often tracks phenological progression, with early growth being of higher quality, if less abundant, than later growth, and there is growing evidence that behavioral tracking of spatial heterogeneity in plant phenology can improve the physiological and reproductive performance of large herbivores, which in turn leads to improved population performance (Hobbs and Gordon, 2010). While we cannot ascertain the role that heterogeneity in forage phenology played at our study sites, it seems likely that such behavioral tracking would lead to increased impacts to forest herbs if different deer habitats differed in the timing of peak forage nutritional quality. Homogeneity in plant phenology, on the other hand, might lead to reduced deer impacts, as Augustine and Jordan (1998) found for spring and early summer forest herbs in woodlots adjacent to alfalfa fields that provide quality forage in early summer as opposed to those adjacent to row crops that do not. As such, impacts to non-preferred habitats or resources depend strongly on their spatial and temporal proximity to preferred habitats/resources (Augustine and Jordan, 1998; Gordon et al., 2004), and it is thus critical to know not only the herbivore abundance and resource composition of a landscape but also the spatial patterning and temporal availability of resources within a landscape if we hope to understand and manage herbivore impacts to vegetation.

The relationship between white-tailed deer impact to forest plant communities and landscape structure has been considered previously by Alverson et al. (1988), Anderson (1997), Augustine and Jordan (1998), and Augustine and deCalesta (2003). A clear understanding of these relationships has yet to emerge, as much of the thinking to date has been speculative and lacks a firm theoretical foundation. One recurrent theme is the idea of a 'dilution effect,' whereby the per capita deer impact to understory plants of

old growth forest is spread out over large areas of largely contiguous mature forest. Alverson et al. (1988) and Anderson (1997) argued that in contiguously forested landscapes where remnants of old growth forest exist in a multiple-use landscape managed primarily for timber harvest, an abundance of highly productive early successional habitat supports higher densities of deer than historical landscapes that were dominated by old growth forest. In this case, the forest herbs of the old growth forest apparently represent a form of luxury consumption, whereby they are preferred forage whose depletion does not result in density dependent negative feedbacks to deer population growth because of over-abundance of accessible and assimilable primary productivity in a matrix of early successional forest. As such, the restoration of large contiguous blocks of mature and old-growth forest would be necessary to reduce deer densities to the point where they no longer threaten recruitment of browse-sensitive tree species (e.g., *Tsuga canadensis*) and population viability of understory herbs (e.g., *Panax quinquefolius* and *Trillium grandiflorum*). A similar mechanism has been suggested for forest fragments in agricultural landscapes, whereby woodland herbs represent a form of luxury consumption that does not result in negative feedback as they become depleted due to an abundance of agricultural subsidies that sustain unnaturally high deer densities (Anderson, 1997; Augustine and deCalesta (2003). In support of these predictions, Rouleau et al. (2002) found that biomass of preferred understory plant species was six times higher for forest stands located in a forested landscape compared to an agricultural landscape. In both cases, increasing old-growth forest cover should lead to lower per capita deer impact as negative feedbacks between forest understory condition and deer population growth strengthen and foraging on understory plants is spread out over larger areas.

Whether such proposals for increasing the abundance of old-growth forest within a landscape would be successful in ameliorating deer impacts to forest understories is not clear. Augustine and deCalesta (2003) argue that creation of large, contiguous blocks of old-growth forest in areas that lack predators and experience mild winters could lead to especially severe problems of white-tailed deer overabundance, because there is no alternative forage and hunter access may be limited. They suggest that judicious management of forest openings, in combination with hunting, can be used as a tool to alleviate deer impacts on forest understories, assuming deer concentrate their foraging in openings and selective foraging on the forest floor is spread over a large area. In this case, the assumption appears to be that the proportional consumption of old growth forage plants will be less than their proportional availability, which is the opposite of the underlying assumptions of the 'dilution effect' discussed previously.

Our results do not support the 'dilution effect' hypothesis, in that parks in the most heavily forested landscapes tended to suffer greater impact than parks in agricultural landscapes that contained a diversity of highly interspersed anthropogenic and natural (or semi-natural) habitat types. What we appear to be observing are the results of indirect effects associated with cross-habitat resource subsidies that result in aggregative numerical responses that are of greater magnitude than concomitant reproductive numerical responses.

Mathematical modeling by Takimoto et al. (2009) indicates that such effects should be short term unless the cross-habitat resource subsidies fluctuate rapidly relative to the timescale required for a reproductive numerical response, but not so rapidly as to preclude an aggregative numerical response. Given that the habitats in question are relatively permanent landscape features that provide deer with abundant food and cover resources, it seems likely that the negative impact of a reproductive numerical response should have canceled any positive effects of an aggregational response. However, if recreational hunting in the landscapes surrounding



the parks kept deer populations below the landscape carrying capacity, then we might expect that park deer populations, outside of a core area where only resident deer reside, were also below carrying capacity. It is also possible that emigration rates were more than high enough to offset immigration rates, as might be expected if resource conditions in landscapes surrounding parks were in substantially better condition than those within parks. Testing this hypotheses would require further empirical study, as well as a better theoretical understanding (than that currently available; see Takimoto et al., 2009) of how the distribution of resources at multiple scales across a landscape mediates the interactions between local and regional deer populations.

In many areas where white-tailed deer are considered overabundant, simply increasing the areal coverage of old-growth forest within a landscape is not always a politically viable option. And even where politically feasible, such a strategy will likely not be sufficient, by itself, to restore rates of deer herbivory that are compatible with the ecological integrity of native forest understories, except in cases where natural predator communities are still intact or deer populations frequently pass through population bottlenecks due to severe abiotic conditions (e.g., severe cold, drought). In the absence of natural predators or severe winters, the preservation or restoration of the ecological integrity of forest understories in protected areas may require a combination of habitat management and human hunting. The relationship between deer density and hunter effort per deer killed is hyperbolic (Van Deelen and Etter, 2003), such that as deer density declines, the rate of increase in hunter effort accelerates rapidly at moderate deer densities before leveling off at low densities. Therefore, recreational hunting is likely to be most effective in cases where landscapes can sustainably support moderately high densities of deer. Paradoxically, this likely means that deer impacts to forest understories may be more difficult to manage in forested landscapes that are largely intact and where conservation status precludes habitat management. Restoration of large predator communities or hiring professional hunters may be the only viable options in such cases.

## 5. Conclusion

This study further clarifies the relationship between landscape context and deer overabundance within mixed forest–agricultural landscapes. Management that focuses on limiting deer abundance and optimizing the interspersed/juxtaposition of non-forested permanent cover habitat with agricultural and forested habitat immediately surrounding protected areas may be successful in ameliorating some impacts to understory plant communities. Landscape management alone will likely not be sufficient in most cases, and should be coupled with deer population reduction programs. Increased habitat diversity and interspersed habitat types around protected areas might help to alleviate problems of deer overabundance in a mixed forest–agricultural context; however, in largely forested landscapes, habitat conversion may not always be compatible with other conservation goals and other measures such as restoration of natural predator communities may sometimes be necessary.

Leopold (1933) made explicit mention of the benefits of habitat diversity and interspersed habitat to many game species (including deer) almost 80 years ago, so the basic questions addressed by this and other recent studies (cited above) are not new. However, questions regarding how broad-scale spatial heterogeneity can have cascading ecological effects on local-scale species interactions have not been explicitly made until more recently (Turner, 2005a). Such “spatial cascades” are an important cross-boundary issue for managers of natural areas, and may necessitate cooperation across administrative and/or ownership boundaries. Because they are

strong interactors in terrestrial food web dynamics (Paine, 2000), large herbivores may play an especially important role in this regard, especially in cases where humans have eliminated large predators and have otherwise altered the spatial and temporal dynamics of landscapes.

## Acknowledgements

Jason Meyer and Scott Lawler assisted with field work and data entry during the field data collection phases of the study. Forest Clark of the USFWS provided unpublished Indiana GAP landcover data, and Mike Hyslop provided invaluable assistance with spatial data processing. Casey Huckins, Linda Nagel, and Andrew Storer provided helpful comments on earlier drafts of the manuscript. Support for this project was provided by the Indiana Department of Natural Resources, Martin Foundation, and the School of Forest Resources and Environmental Science at Michigan Technological University.

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