

Ungulate impacts on herbaceous-layer plant communities in even-aged and uneven-aged managed forests

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Abstract. Forest management and ungulate herbivory are extant drivers of herbaceous-layer community composition and diversity. We conducted a white-tailed deer (*Odocoileus virginianus*) exclosure experiment across a managed landscape to determine how deer impacts interact with the type of forest management system in influencing herb-layer (all vascular plants < 0.5 m tall) species richness and composition. Our study took place 3 yr after harvest in a deciduous forest landscape being managed through even-aged (~4.1 ha openings) and uneven-aged (~1.4 ha openings) silvicultural systems. We expected the severity of deer impacts on herb layer species richness and composition to vary according to opening position, opening size, and the spatial scale of inference. At forest stand and landscape scales, species richness within silvicultural openings was greater outside compared to inside deer exclosures, and did not differ according to deer access in edges or the forest matrix. However, greater levels of species richness associated with deer access were driven by infrequently occurring forbs, and overall species composition did not differ. Notably, these species were not exotics or ferns. Deer reduced the density of large saplings and blackberry (*Rubus* spp.) shrubs in the smaller openings characteristic of uneven-aged management stands, but had no effect on sapling density in the larger openings characteristic of even-aged management stands. This result extends the forage maturation hypothesis to silvicultural systems, and is consistent with predictions that plant tolerance and avoidance of herbivory increase with resource availability. Deer may have facilitated the establishment of forbs in recently created silvicultural openings by temporarily slowing sapling regeneration, creating establishment sites through physical disturbance, and seed dispersal via epizoochory and endozoochory. This outcome is contingent upon declining deer visitation rates as woody vegetation matures as well as distance from source populations of exotic species. We conclude that ecological context, such as local ungulate abundance, disturbance, and landscape factors, influence how ungulates interact with forest management systems.

Key words: Central Hardwood Forests; disturbance; exclosures; forage maturation hypothesis; herbaceous layer; *Odocoileus virginianus*; silviculture; spatial scale; species composition; species richness; white-tailed deer.

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INTRODUCTION

Disturbances are among the major factors that determine the species diversity and composition of herbaceous-layer plant communities in temperate forests (Roberts and Gilliam 2003, Royo et al. 2010, Burton et al. 2014). Historically, temperate forest disturbance regimes were driven by wind and fire, with herbivory influencing successional pathways (Frelich 2002). Stochastic disturbance regimes have been largely supplanted by planned forest management. Forest ungulates, which are a valuable wildlife resource, are often managed at population densities that exceed historic conditions. This results in complex and sometimes paradoxical impacts on plant populations and communities (Rooney and Waller 2003, Heckel et al. 2010, Royo et al. 2010, Rutherford and Schmitz 2010, Jensen et al. 2011) that may extend to other trophic levels (Nuttle et al. 2011, Lessard et al. 2012, Wheatall et al. 2013, Shelton et al. 2014). In this study, we examine how the presence of ungulates affects the species diversity and composition of herb-layer vegetation across the spectrum of environments created by silvicultural openings.

That forest ungulates can influence the species composition of herb-layer communities through selective herbivory is well known (Rooney and Waller 2003, Côté et al. 2004, Nuttle et al. 2014), but questions remain about how ecological context influences the degree of change. One factor that may influence the degree of change is how the severity of ungulate impacts varies across the spectrum of habitat types that are created by management openings. The species diversity and composition of the herb layer is driven by the combined availabilities of light, nutrients, and water, as well as interspecific competition with trees and other herbs (Gilliam and Roberts 2003). Low light and nutrient levels limit herb-layer biomass in closed-canopy forests, so that plant species that thrive in the understory tend to have high resource-use efficiencies, or the ability to capture ephemeral resource pulses (Grime 1977, Farley and Fitter 1999). Such plants have lower tolerance for herbivory, and ungulate herbivores reduce species diversity and shift composition toward non-palatable species (Rooney 2009, Nuttle et al. 2014; but see Heckel et al. 2010). In anthropogenic forest openings,

limiting resources become more available (Kimmins 2003), and the spatial variability in seedbed conditions increases through substrate disturbance. Consequently, herb-layer biomass and species diversity increase rapidly (Jenkins and Parker 1999, Kraft et al. 2004), and species composition shifts toward fast-growing ruderal species (Grime 1977). Forest ungulates congregate in such areas of high forage availability (Stewart et al. 2000, Kuijper et al. 2009), and selective herbivory can alter the outcome of competitive interactions among plant functional groups (Royo et al. 2010, Nuttle et al. 2013, 2014).

Another factor is that the severity of ungulate impacts varies with opening size. Ungulates are attracted to the flush of new growth immediately after an opening is created, but this effect may be short-lived in larger openings (Campbell et al. 2004). Maturing woody vegetation decreases in quality as the proportion of woody plant material increases along with the C:N ratio of the foliage (Bryant et al. 1983, Molvar et al. 1993, Hartley et al. 1997). Kuijper et al. (2009) and Tahtinen et al. (2014) have proposed that the “forage maturation hypothesis” (Fryxell 1991), which predicts that ungulate habitat-use patterns vary with the stage of maturing vegetation in time and space, suggests that ungulate use of smaller forest openings is elevated for a longer period of time compared to larger openings. This occurs because edge trees shade a larger portion of smaller openings, slowing the growth rate of saplings. The potential interaction between opening size and ungulate herbivory has clear significance for forest management, as managers use opening size to influence the species composition of forest regeneration.

Finally, the severity of ungulate impacts will depend on the scale of observation (Mladenoff and Stearns 1993). At the most fundamental level, herbivory affects individual plants (Brown and Allen 1989). The impact of herbivory scales up to plant communities when it influences competition among co-occurring individuals at the neighborhood scale, and the strength of this influence depends on the intensity of herbivory (Connell 1978). Intermediate levels of herbivory increase the spatial heterogeneity of community composition by suppressing dominant species. High levels of herbivory tend to homogenize community composition as only unpalatable and herbivore-tolerant species persist. At broader

spatial scales, differential impacts of herbivory in different habitat patches may increase plant species diversity across the landscape, even if it is homogenized in certain patches (Mladenoff and Stearns 1993). In complex forested landscapes, there is a need for studies that examine ungulate impacts across a range of spatial scales.

Our primary objective was to determine how ungulate access, position within an opening, and their interaction affect the species diversity, species composition, and spatial patterning of herb-layer plant communities under even-aged and uneven-aged forest management systems. To achieve this objective, we conducted a white-tailed deer (*Odocoileus virginianus*) enclosure experiment within a replicated, landscape-scale forest management study in south-central Indiana, USA. Deer enclosures were placed within silvicultural openings, in the edges of openings, and within the closed-canopy matrix prior to the first postharvest growing season. Half of the study sites were located in even-aged management areas where openings (hereafter referred to as “clearcuts”) were 4.1 ha on average, and half were located in uneven-aged management areas with an average opening size of 1.4 ha (hereafter referred to as “patch cuts”). Due to the well-known trend of increased resource availability after harvest (Kimmins 2003), we expected herb-layer species diversity to decrease along a gradient from the center of an opening to the closed-canopy matrix. The effect of deer access on herb-layer diversity will depend on ecological context and spatial scale. First, deer may cause lower levels of herb-layer diversity through herbivory. Second, deer may cause greater levels of herb-layer diversity by reducing the dominance of highly competitive plant species, as well as through non-consumptive impacts. Increased spatial patterning in species composition would support this mechanism. Third, early seral plant communities may be resistant to deer impacts, in which case diversity and composition will not vary according to deer access. We accounted for scale dependence by quantifying deer impacts on herb-layer diversity at the neighborhood, forest stand, and whole-experiment scales. In summary, this study explored how forest ungulates influence herb-layer diversity and species composition in even-aged and uneven-aged managed forests.

METHODS

Study sites

The experiment occurred on six forest management units in Morgan-Monroe and Yellowwood State Forests in south-central Indiana, USA (39°06′–39°21′ N, 86°17′–86°26′ W). These sites were located in the Brown County Section of the Highland Rim Natural Region of Indiana (Homoya et al. 1985), a landscape characterized by steep hills and valleys that has not been glaciated recently. Soils were bedrock-derived, fine-silty or loamy-skeletal, well-drained, and prone to erosion (Jenkins 2013). The dominant forest type was oak-hickory (*Quercus–Carya*) with chestnut oak (*Q. prinus*) dominant in xeric positions, and a mix of northern red oak (*Q. rubra*), American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and white ash (*Fraxinus americana*) in mesic positions. The understory on upper slopes was characterized by black huckleberry (*Gaylussacia bacata*), lowbush blueberry (*Vaccinium pallidum*), and greenbrier (*Smilax* spp.), with sugar maple saplings common in mesic areas (Jenkins 2013).

The study sites were part of the Hardwood Ecosystem Experiment (HEE), which is a replicated study of the ecological impacts of oak silviculture in the Central Hardwood Forest Region of North America (Kalb and Mycroft 2013). The HEE is composed of nine forest management units, and this study was located on the six units that were treated in the fall of 2008. These management units ranged in area from 78.3 to 110.4 ha and were contained within forested buffer areas that were approximately 300–400% larger in area. Three management units were treated according to an even-aged silvicultural prescription in which two 4.05 ha clearcuts and two 4.05 ha mid-story thinning treatments were created. The remainder of each even-aged management unit was not logged. The mid-story thinning treatments were not sampled as part of this study. Three management units were treated according to an uneven-aged silvicultural prescription which included eight patch cuts in three size classes: two 2.02 ha, two 1.20 ha, and four 0.40 ha. The remainder of each uneven-aged management unit was logged according to single-tree selection. These treatments were the initial harvest of a 100-yr rotation (Kalb and Mycroft 2013). The actual size

of the silvicultural openings varied based on local topography and forest composition. Forest structure and composition did not differ among forest management units prior to treatment in 2008 (Saunders and Arsenault 2013). We use the terms “even-aged” and “uneven-aged” to distinguish between management systems rather than the current age structure of the stands, which tends to be more even-aged.

Deer exclosures were constructed during the winter and spring of 2009, and were completed before the start of the first growing season in April. Each exclosure was 22 m wide, 22 m long, and 2.3 m in height, and was constructed of polypropylene fencing with a mesh size of 5.1 cm. Four clearcuts were selected for the exclosure study: two in management unit 9 and one in each of the other even-aged management units. Four patch cuts were also selected: two in management unit 8 and one in each of the other uneven-aged management units. The selected clearcuts ranged in size from 3.7 to 4.4 ha (mean = 4.1 ha) in area and the selected patch cuts ranged from 1.3 to 1.6 ha (mean = 1.4 ha). Four exclosures were associated with each clearcut: one each in the center, the midway (between the center and the forest edge), the forest edge, and within the closed-canopy matrix (Fig. 1). Three exclosures were associated with each patch cut and were placed in the center, along the forest edge, and within the closed-canopy matrix (Fig. 1). Therefore, there were 28 exclosures in total, 27 of which were sampled since one midway exclosure was skipped. The matrix exclosures were located > 40 m from the edge of the nearest opening. In uneven-aged management units, the matrix exclosures were not placed in single-tree openings.

Vegetation sampling

Herbaceous-layer vegetation (< 0.5 m height), seedlings (< 0.5 m height), and saplings (0.5–3.0 m height) were sampled within each deer exclosure and in an adjacent unfenced area that was accessible to deer (Fig. 1). Vegetation sampling occurred from late May through late July 2011, which was the third growing season after treatment and deer exclosure construction. For sampling the herb layer, we placed an array of 24 square sample plots of 0.25 m² area each. Each sampling array consisted of two transects

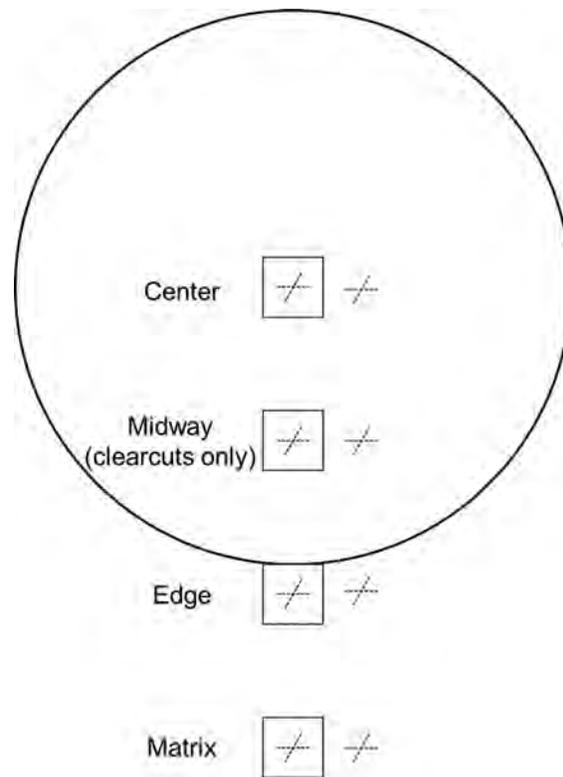


Fig. 1. Graphical schematic of our sampling design. Deer exclosures were 22 × 22 m in area and 2.3 m tall; vegetation sampling transects were 12 m in length and intersected at a 60° angle.

that were 12 m in length and intersected at an angle of 60°. Each transect was divided into four 3 m segments, and sample plots were placed at the 0, 0.5, and 2.0 m positions within each segment. The angle of the transects and the spacing of the plots maximized the sample size (number of plot pairs) per lag distance for spatial analysis (Clinger and Van Ness 1976, Scheller and Mladenoff 2002, Murray et al. 2013). Seedlings and saplings were sampled in the same location after increasing the plot size to 1 m² and placing plots every 0 and 1 m within each 3 m segment. The unfenced transects began 5 m from the exclosure fence, and extended to 17 m from the fence.

The herb-layer vegetation was quantified by ocularly estimating the percent cover class of each species. Cover class cutoffs included solitary or few individuals, 1%, 2%, 5%, 10%, 25%, 50%, 75%, 95%, and 100% (Peet et al. 1998).

Cover classes were converted to midpoints for analysis. The number of seedlings (< 0.5 m in height) and saplings (0.5–3.0 m in height) were counted by species in each sapling-layer plot. The importance of blackberry (*Rubus* spp.) shrubs was estimated by percent cover class at 1 m height in the herb-layer plots because they were very dense in some areas. Species nomenclature follows USDA Plants Database (USDA, NRCS 2013).

Herbaceous-layer species richness and cover

The effect of deer access on herb-layer species richness was assessed at the forest stand and whole-experiment scales by comparing the 95% confidence intervals of species rarefaction curves (Colwell et al. 2012). The rarefaction curves were based on species incidence per herb-layer plot, and separate curves were created for fenced and unfenced communities in each opening size by opening position treatment group. We concluded that deer access affects mean species richness significantly ($P \leq 0.05$) at a given spatial scale if the 95% confidence intervals of fenced and unfenced communities do not overlap at the corresponding sampled area on the rarefaction curves. This test is conservative in that non-overlap is a strong indication of statistical significance at $P \leq 0.05$, but some overlap does not necessarily indicate a lack of statistical significance (Colwell et al. 2012). Rarefaction curves were developed with EstimateS v.9.1.0 (Colwell 2013).

We used generalized linear mixed modeling (GLMM) to test the main effects of deer access, opening position, and their interaction, on species richness and cover at the neighborhood scale. Separate models were developed for clear-cuts ($n = 720$ plots) and patch cuts ($n = 576$ plots), and results were compared between the opening size classes qualitatively. First, we selected among four model types: Poisson, negative binomial, zero-inflated Poisson, and zero-inflated negative binomial; by considering the processes responsible for variation in the response variable, examining the untransformed distribution of the response variable, and comparing Akaike's information criterion among the full models. Each model included a random intercept parameter to account for differences among stands. We tested

the significance of the interaction effect, and then each of the main effects, by removing them one by one and comparing models with chi-squared likelihood ratio tests. The estimation of P -values in a likelihood ratio test among GLMMs is not conservative, therefore, we assessed statistical significance relative to $P < 0.01$ rather than $P < 0.05$ (Zuur et al. 2009). GLMMs were developed in the R package "glmmADMB" (Fournier et al. 2012, Skaug et al. 2014), and models were compared using the R packages "bbmle" (Bolker and R Team 2014) and "lme4" (Zeileis and Hothorn 2002), in R version 3.1.1 (R Core Team 2014).

The GLMM procedure described above was used to assess the species richness and cover of the total herb-layer community as well as for forbs, woody plants, and graminoids separately. Although ferns were sampled and were included in total, they were not sufficiently common to be analyzed separately. The Poisson and negative binomial distributions were well suited for modeling species richness because richness is a form of count data (Zuur et al. 2009). Although cover was measured as a proportional variable for each individual species, the Poisson and negative binomial distributions worked well for modeling the sums of cover midpoints across several species.

Herbaceous-layer species composition

To examine patterns in herb-layer species composition, we conducted a non-metric multidimensional scaling (NMS) ordination. The NMS was based on the mean of species cover midpoints within each treatment group combination by forest stand ($n_{\text{groups}} = 54$, $n_{\text{spp}} = 147$). Species in the genus *Carex* were pooled because many individuals were missing key species-specific structures at the time of sampling. The NMS ordination was run in PC-ORD v5.31 using the autopilot "slow and thorough" settings (Kruskal 1964, Mather 1976, McCune and Mefford 2006), Sørensen's dissimilarity (i.e., Bray-Curtis) as the distance measure, and random starting configurations. The slow and thorough option in PC-ORD v5.31 conducted 250 runs with real data and assessed dimensionality using a Monte Carlo test of 250 runs with randomized data and maximum of six dimensions. Stability was assessed based on a minimum criterion of <0.000001 within 500

iterations. We examined the Kendall's τ correlations between the final NMS scores and the environmental variables opening size, distance from edge (negative for interior positions, positive for exterior positions), aspect (sine and cosine), seedling density, and blackberry cover. We used multiple response permutation procedures (MRPP) to determine if composition differed according to opening size, opening position, and deer access (McCune and Grace 2002). MRPP tests the hypothesis of no difference between the sample groups. The outcome of the hypothesis test is evaluated based on a P -value, where $P < 0.05$ indicates that homogeneity is greater within sample groups than among sample groups. The effect size of MRPP is the chance-corrected within-group agreement, A , which describes within-group homogeneity compared to random expectation (McCune and Grace 2002). A Bonferroni correction for multiple comparisons was applied to the MRPP P -values.

Spatial patterning in the turnover of species composition at the herb-layer plot scale was assessed using Mantel correlograms (Legendre and Legendre 2012). Mantel's r was computed based on the Sørensen's dissimilarity among plot pairs at 0.5 m intervals up to an extent of 6.0 m. Plots were grouped according to opening size and treatment group, but plot pairs were limited to the same sampling array by setting the cutoff distance to 6.0 m. Plot pairs were determined to be significantly similar at a given lag distance if $P < 0.05$ and Mantel's r was positive, whereas a negative Mantel's r indicates dissimilarity. The sample size differed according to lag distance by the number of plot pairs as follows: 0.5 m, $n = 64$; 1.0 m, $n = 72$; 1.5 m, $n = 176$; 2.0 m, $n = 120$; 2.5 m, $n = 144$; 3.0 m, $n = 208$; 3.5 m, $n = 112$; 4.0 m, $n = 184$; 4.5 m, $n = 208$; 5.0 m, $n = 152$; 5.5 m, $n = 160$; 6.0 m, $n = 168$. Mantel correlograms were developed in R package "vegan" (Oksanen et al. 2013). All figures were created using the R package "ggplot2" (Wickham 2009).

Seedlings, saplings, and blackberry shrubs

The densities of seedlings, small and large saplings, and the cover of blackberry shrubs, were compared among treatments using GLMM as described above for herb-layer richness and cover.

RESULTS

Herbaceous-layer species richness and cover

We identified a total of 175 herb-layer species in 114 genera and 56 families across the study area (see Appendix S1: Tables S1 and S2, for a complete list). Deer access affected herb-layer species richness more strongly within management openings than in the edges or the matrix at the neighborhood, forest stand, and whole-experiment scale (Figs. 2 and 3). Within openings, our findings were consistent with the alternate prediction that deer access results in greater species richness. In these positions, more herb-layer species occurred outside compared to inside of deer enclosures (Tables 1 and 2). At the neighborhood scale, the effect of deer access transitioned from positive in opening centers to slightly negative in edges and the matrix. In patch cuts, deer access tended to have a positive effect on species richness in opening centers and edges, but no effect in the matrix (Table 3, Fig. 3). At the whole-experiment scale, species richness in clearcut centers was 25% greater in unfenced plots, and in patch cut centers, richness was 33% greater in unfenced plots (Fig. 2). In the edges and forest matrix, species richness did not differ according to deer access at any spatial scale (Table 3, Figs. 2 and 3).

The greater level of species richness associated with deer access was primarily driven by forbs (Table 3, Fig. 3). Although these species contributed to species richness, they occurred infrequently and contributed little to total herb-layer cover (Table 4, Fig. 4). Forbs were more species-rich in deer access plots in the centers of clearcuts and patch cuts, as well as the edges of patch cuts (Table 3, Fig. 3). In clearcuts only, woody plants were slightly more species-rich in fenced plots in the edge and matrix positions (Table 3, Fig. 3). Graminoids were more species-rich in unfenced plots in the edge and matrix positions of patch cuts, but did not influence total species richness due to their low species numbers compared to forbs and woody plants (Table 3, Fig. 3). Total herb-layer cover in clearcuts flipped from being greater in unfenced plots in the center and midway, to being greater in fenced plots in the edges and forest matrix (Table 4, Fig. 4). Woody plants, which

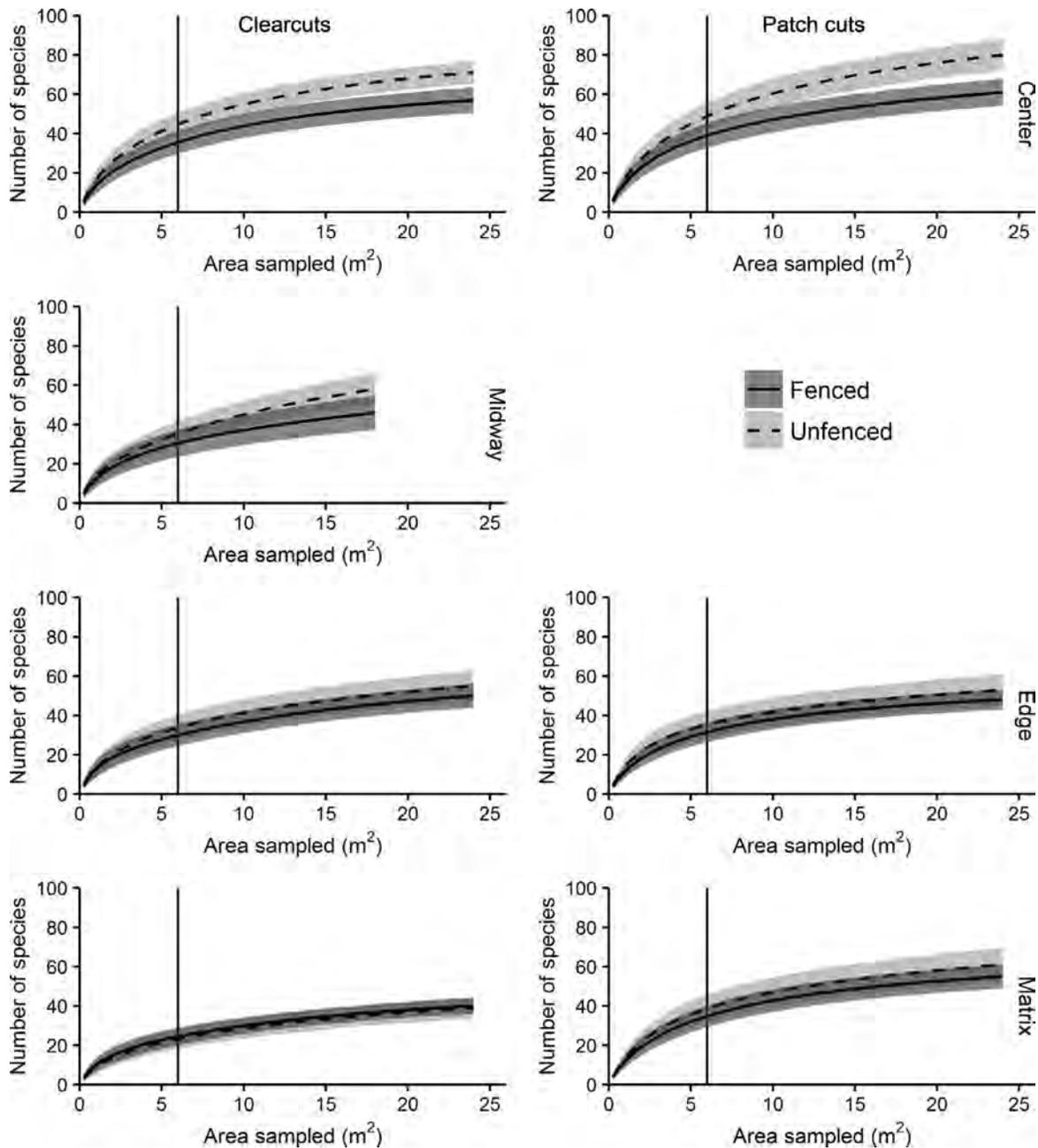


Fig. 2. Sample-based rarefaction curves based on plot-level herbaceous-layer (< 0.5 m tall) species incidence data in four clearcuts (~4.1 ha) and four patch cuts (~1.4 ha). The gray ribbons represent 95% confidence intervals. The vertical lines at $x = 6.0 \text{ m}^2$ indicate the area sampled within a single sampling array. Non-overlap in 95% confidence intervals indicates a significant difference ($P < 0.05$) in species richness (Colwell et al. 2012).

were greater in cover than graminoids or forbs, followed this pattern. Forbs and graminoids exhibited a reciprocal pattern, suggesting a negative relationship between the cover of woody and

herbaceous plants. In patch cuts, the position by deer access interaction was not significant in total or for any of the functional groups individually. Woody plants and graminoids were the

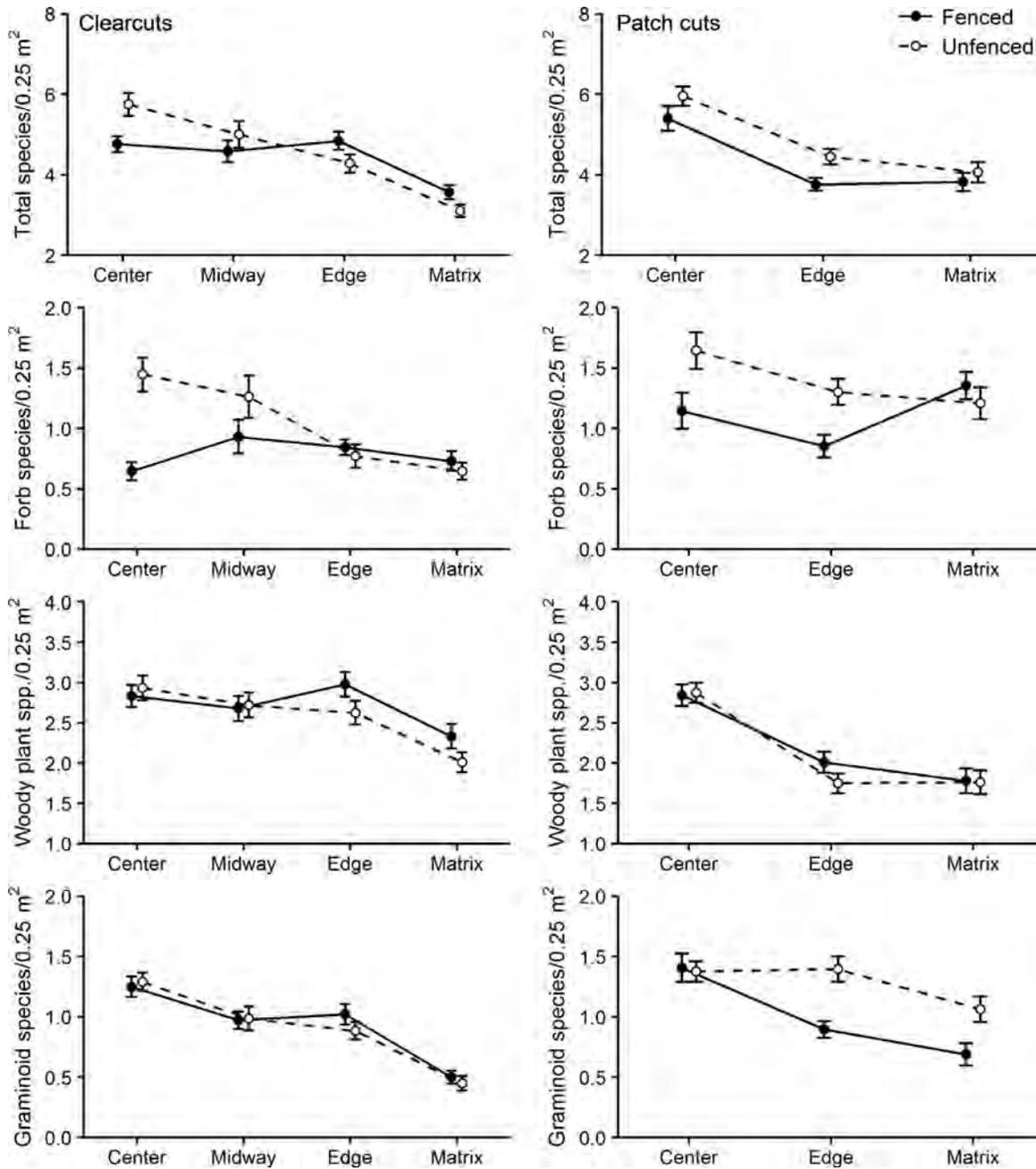


Fig. 3. Mean (\pm standard error) species richness of the herbaceous-layer vegetation (< 0.5 m tall) at the sample plot scale of 0.25 m² in silvicultural openings within Central Hardwood forests of south-central Indiana, USA. Clearcut openings were located in even-aged managed forests and were 4.1 ha in size on average. Patch cut openings were located in uneven-aged managed forests and were 1.4 ha in size on average. There were 24, 0.25 m² sample plots per sampling array, for a total $n = 96$ plots per treatment group combination, except for midway positions where $n = 72$ plots per treatment group (global $N = 720$ plots over four clearcuts and 576 plots over four patch cuts).

Table 1. List of the species that occurred only in fenced or unfenced areas within the centers of clearcuts (~4.1 ha openings).

Fenced			Unfenced		
Species	Cover (%)	Habit†	Species	Cover (%)	Habit
<i>Carex umbellata</i>	0.7	Gram.	<i>Panicum flexile</i>	1.4	Gram.
<i>Lespedeza intermedia</i>	0.6	Forb	<i>Carya glabra</i>	0.9	WP
<i>Symphytotrichum lateriflorum</i>	0.4	Forb	<i>Poa</i> spp.	0.9	Gram.
<i>Amelanchier arborea</i>	0.2	WP	<i>Carex hirtifolia</i>	0.8	Gram.
<i>Carya ovata</i>	0.2	WP	<i>Solidago caesia</i>	0.7	Forb
<i>Prunus serotina</i>	0.2	WP	<i>Carex grisea</i>	0.4	Gram.
<i>Polygonum virginianum</i>	0.1	Forb	<i>Hydrangea arborescens</i>	0.4	WP
<i>Prenanthes altissima‡</i>	0.1	Forb	<i>Aralia spinosa</i>	0.3	WP
<i>Quercus coccinea</i>	0.1	WP	<i>Carex willdenowii</i>	0.3	Gram.
<i>Carex rosea</i>	0.1	Gram.	<i>Hieracium</i> spp.	0.3	Forb
<i>Amphicarpaea bracteata</i>	T§	Forb	<i>Carex blanda</i>	0.2	Gram.
<i>Heuchera americana</i>	T	Forb	<i>Medeola virginiana</i>	0.1	Forb
<i>Platanus occidentalis</i>	T	WP	<i>Polygonum</i> spp.	0.1	Forb
<i>Smilax</i> spp.	T	WP	<i>Eupatorium</i> spp.	0.1	Forb
<i>Solidago altissima</i>	T	Forb	<i>Ageratina altissima</i>	T	Forb
			<i>Andropogon virginicus</i>	T	Gram.
			<i>Aster</i> spp.	T	Forb
			<i>Carex brevior</i>	T	Gram.
			<i>Carex plantaginea</i>	T	Gram.
			<i>Erechtites hieracifolia</i>	T	Forb
			<i>Lactuca canadensis</i>	T	Forb
			<i>Maianthemum racemosum</i>	T	Forb
			<i>Oenothera biennis</i>	T	Forb
			<i>Polygonatum biflorum</i>	T	Forb
			<i>Rosa carolina</i>	T	WP

† Gram., graminoid; WP, woody plant.

‡ Exotic species (Rothrock 2004).

§ T trace amounts (<0.1% cover).

dominant groups in opening centers, whereas greater evenness among groups occurred in matrix positions (Fig. 4, Table 4).

Herbaceous-layer species composition

The NMS ordination explained 83.2% of the compositional variance, with a three-dimensional solution of stress 12.63 and instability < 0.00001 in 85 iterations. Axis 2 represented 42.5% of the variance, and was correlated with environmental variables that affect light availability to the herb layer, including distance from edge ($\tau = -0.501$), sapling density ($\tau = 0.487$), blackberry cover ($\tau = 0.406$), and opening size ($\tau = 0.393$). Axis 1 represented 24.3% of the variance and was not correlated with any environmental variable. Axis 3 represented 16.3% of the variance and was moderately correlated with sapling density ($\tau = 0.255$).

Herb-layer species composition differed according to position, although the effect size (A , chance-corrected within-group agreement) was not large (MRPP results: $T = -9.37$, $A = 0.075$, $P < 0.001$). Composition did not differ according to opening size ($T = -0.95$, $A = 0.004$, $P = 0.157$) or deer access ($T = 1.22$, $A = -0.005$, $P = 0.943$). Due to the small but significant effect size of opening position, and the significant correlation of the NMS with distance from edge, we conducted additional MRPPs to compare opening positions in each opening size class separately. There were significant differences in composition among positions in clearcuts ($T = -4.98$, $A = 0.080$, $P < 0.001$) and patch cuts ($T = -4.88$, $A = 0.076$, $P < 0.001$). In clearcuts, the interior positions differed from the matrix (center: $T = -7.89$, $A = 0.141$, $P < 0.001$; midway: $T = -5.23$, $A = 0.102$, $P = 0.001$), but other positions did not differ from one another. In patch cuts, the centers differed from the edges ($T = -3.57$, $A = 0.059$,

Table 2. List of the species that occurred only in fenced or unfenced areas within the centers of patch cuts (~1.4 ha openings).

Fenced			Unfenced		
Species	Cover (%)	Habit†	Species	Cover (%)	Habit
<i>Symphyotrichum lateriflorum</i>	0.7	Forb	<i>Carex picta</i>	17.8	Gram.
<i>Carya glabra</i>	0.4	WP	<i>Carex laxiflora</i>	6.1	Gram.
<i>Platanus occidentalis</i>	0.3	WP	<i>Amelanchier arborea</i>	0.7	WP
<i>Carya tomentosa</i>	0.2	WP	<i>Vaccinium pallidum</i>	0.6	WP
<i>Solidago caesia</i>	0.2	Forb	<i>Lactuca canadensis</i>	0.5	Forb
<i>Carex vulpinoidea</i>	0.1	Gram.	<i>Dryopteris carthusiana</i>	0.4	Fern
<i>Carya ovata</i>	0.1	WP	<i>Lespedeza hirta</i>	0.4	Forb
<i>Hydrangea arborescens</i>	0.1	WP	<i>Andropogon virginicus</i>	0.2	Gram.
<i>Microstegium vimineum</i> ‡	0.1	Gram.	<i>Mentha spicata</i> ‡	0.2	Forb
<i>Arisaema triphyllum</i>	T§	Forb	<i>Quercus velutina</i>	0.2	WP
<i>Aristolochia serpentaria</i>	T	Forb	<i>Symphyotrichum</i> spp.	0.2	Forb
<i>Aster</i> spp.	T	Forb	<i>Thelypteris noveboracensis</i>	0.2	Fern
<i>Carex frankii</i>	T	Gram.	<i>Ageratina altissima</i>	0.1	Forb
<i>Erigeron annuus</i>	T	Forb	<i>Carya cordiformis</i>	0.1	WP
<i>Kummerowia striata</i> ‡	T	Forb	<i>Chamaecrista nictitans</i>	0.1	Forb
<i>Maianthemum racemosum</i>	T	Forb	<i>Euthamia graminifolia</i>	0.1	Forb
<i>Polygonum sagittatum</i>	T	Forb	<i>Galium circaeans</i>	0.1	Forb
<i>Solidago</i> spp.	T	Forb	<i>Ipomoea purpurea</i> ‡	0.1	Forb
			<i>Juniperus virginiana</i>	0.1	WP
			<i>Polystichum acrostichoides</i>	0.1	Fern
			<i>Smallanthus uvedalia</i>	0.1	Forb
			<i>Ambrosia artemisiifolia</i>	T	Forb
			<i>Carex grayi</i>	T	Gram.
			<i>Carex plantaginea</i>	T	Gram.
			<i>Cirsium</i> spp.‡	T	Forb
			<i>Dioscorea villosa</i>	T	Forb
			<i>Gaylussacia baccata</i>	T	WP
			<i>Hieracium</i> spp.	T	Forb
			<i>Juncus effusus</i>	T	Gram.
			<i>Lespedeza</i> spp.	T	Forb
			<i>Oxalis</i> spp.	T	Forb
			<i>Polygonum sagittatum</i>	T	Forb
			<i>Senecio</i> spp.	T	Forb
			<i>Ulmus rubra</i>	T	WP
			<i>Verbascum thapsus</i> ‡	T	Forb
			<i>Verbena urticifolia</i>	T	Forb

† Gram., graminoid; WP, woody plant.

‡ Exotic species (Rothrock 2004).

§ T trace amounts (< 0.1% cover).

$P = 0.010$) and the matrix ($T = -5.90$, $A = 0.100$, $P < 0.001$). However, the edges did not differ from the matrix ($T = -1.09$, $A = 0.020$, $P = 0.410$).

The Mantel correlograms revealed that the lag distance of significantly similar species composition did not differ according to deer access in clearcut centers, but was smaller for fenced herb-layer communities in patch cut centers (Fig. 5). Therefore, the patch size of similar species composition was greater outside of deer fences in

patch cuts. The spatial patterning of composition did not vary according to deer access at any other position (see Appendix S2: Fig. S1).

Seedlings, saplings, and blackberry shrubs

Patterns of seedling and sapling density, and blackberry shrub cover, suggest that deer browsing influenced competition among vegetation strata differently in clearcuts and patch cuts. Overall, seedlings were more abundant where

Table 3. Results of GLMM likelihood ratio tests for the effects of deer access and position (relative to the silvicultural opening) on the species richness of the herbaceous layer (all vegetation < 0.5 m in height).

Source	Clearcuts				Patch cuts			
	χ^2 †	df‡	N§	Model¶	χ^2	df	N	Model
Total								
Deer	0.220	1	720	P	7.76*	1	576	P
Position	88.1***	3	720	P	74.6***	2	576	P
Deer × position	16.4**	3	720	P	1.16	2	576	P
Forbs								
Deer	11.3**	1	720	ZIP	11.3**	1	576	ZINB
Position	17.4**	3	720	ZIP	17.4**	2	576	ZINB
Deer × position	23.1***	3	720	ZIP	9.73*	2	576	ZINB
Woody plants								
Deer	8.24*	1	720	P	0.460	1	576	P
Position	8.06	3	720	P	61.0***	2	576	P
Deer × position	10.2*	3	720	P	1.30	2	576	P
Graminoids								
Deer	0.258	1	720	P	10.0*	1	576	P
Position	74.2***	3	720	P	22.7***	2	576	P
Deer × position	1.01	3	720	P	8.32	2	576	P

Notes: Clearcuts (~4.1 ha) and patch cuts (~1.4 ha) were analyzed separately. Each model included a random intercept parameter for site, and four sites were sampled in each opening size group. Model testing proceeded by first selecting the appropriate distribution, and then conducting χ^2 likelihood ratio tests on the parameters (Zuur et al. 2009). Each model was estimated using maximum likelihood.

† P -value classes of χ^2 likelihood ratio tests: * < 0.01, ** < 0.001, *** < 0.0001.

‡ Degrees of freedom for the χ^2 likelihood ratio test.

§ The number of sample plots.

¶ Potential model types: P, Poisson; NB, negative binomial; ZIP, zero-inflated Poisson; ZINB, zero-inflated negative binomial.

small and large sapling densities were lower; differences that were associated with deer access and overstory cover (Fig. 6). Opening position had a significant effect on seedling and small sapling density in both clearcuts and patch cuts (Table 5). Seedlings transitioned from greater abundance outside exclosures to greater abundance inside exclosures from opening centers to the matrix (Fig. 6), however, the interaction between deer access and position was statistically significant only in patch cuts (Table 5). In patch cuts, deer fencing was associated with lower seedling density while deer access was associated with lower small sapling density (Fig. 6). Blackberry shrubs were high in cover in opening centers, but exhibited greater cover outside of deer fences in clearcuts, and greater cover inside of deer fences in patch cuts (Fig. 6).

DISCUSSION

Our study suggests that forest management systems influence the impact of ungulate browsers on the species richness and spatial patterning

of herb-layer plant communities, and in our study this impact was mediated by the sapling layer. This finding illustrates that the forage maturation hypothesis (Fryxell 1991) is helpful in understanding how forest ungulates utilize forest openings of various sizes (Kuijper et al. 2009, Tahtinen et al. 2014) in managed forest landscapes. Second, it demonstrates how deer impacts on one vegetation strata, the sapling layer, can have indirect effects on other strata, such as the herb layer. Overall, our study demonstrates how factors, such as landscape context and the presence of mast-producing tree species set the ecological stage for ungulate impacts on forest vegetation (Royo et al. 2010, Rutherford and Schmitz 2010). Understanding these factors can help forest managers integrate forestry and wildlife interests into strategies for long-term sustainable management.

The influence of opening size on ungulate impacts

The density of larger saplings was reduced outside of deer exclosures in smaller openings, but not in larger openings. This result is

Table 4. Results of GLMM likelihood ratio tests for the effects of deer access and position (relative to the silvicultural opening) on the cover of the herbaceous layer (all vegetation < 0.5 m in height).

Source	Clearcuts				Patch cuts			
	χ^2 †	df‡	N§	Model¶	χ^2	df	N	Model
Total								
Deer	0.860	1	720	NB	10.0*	1	576	P
Position	262***	3	720	NB	22.7***	2	576	P
Deer × position	18.8**	3	720	NB	8.32	2	576	P
Forbs								
Deer	0.880	1	720	ZINB	7.38*	1	576	ZINB
Position	16.1*	3	720	ZINB	26.2***	2	576	ZINB
Deer × position	9.90	3	720	ZINB	1.78	2	576	ZINB
Woody plants								
Deer	0.440	1	720	NB	0.100	1	576	ZINB
Position	174***	3	720	NB	197***	2	576	ZINB
Deer × position	18.4**	3	720	NB	4.86	2	576	ZINB
Graminoids								
Deer	3.12	1	720	ZINB	9.70*	1	576	ZINB
Position	165***	3	720	ZINB	125***	2	576	ZINB
Deer × position	6.48	3	720	ZINB	6.04	2	576	ZINB

Notes: Clearcuts (~4.1 ha) and patch cuts (~1.4 ha) were analyzed separately. Each model included a random intercept parameter for site, and four sites were sampled in each opening size group. Model testing proceeded by first selecting the appropriate distribution, and then conducting χ^2 likelihood ratio tests on the parameters (Zuur et al. 2009). Each model was estimated using maximum likelihood.

† P-value classes of χ^2 likelihood ratio tests: * < 0.01, ** < 0.001, *** < 0.0001.

‡ Degrees of freedom for the χ^2 likelihood ratio test.

§ The number of sample plots.

¶ Potential model types: P, Poisson; NB, negative binomial; ZIP, zero-inflated Poisson; ZINB, zero-inflated negative binomial.

consistent with three non-mutually exclusive mechanisms: the forage maturation hypothesis (Fryxell 1991, Kuijper et al. 2009, Tahtinen et al. 2014), the influence of resource availability on plant tolerance to herbivory (Maschinski and Whitham 1989, Strauss and Agrawal 1999), and plant avoidance of herbivory due to chance. These mechanisms are based on the fact that forest openings create a resource pulse of light, water, and nutrient availability (Kimmins 2003), producing a pulse of vegetation growth that lies within reach of ungulates.

When applied to forest ecosystems, the forage maturation hypothesis suggests that browsers delay forest regeneration in smaller openings to a greater extent than in larger openings, assuming that other factors like ungulate abundance are similar. Early seral plant species growing in high-light intensity conditions tend to develop tissues with a greater C:N ratio, which are less palatable to ungulates, compared to shade-grown plant tissues with a lower ratio of C:N (Molvar et al. 1993, Hartley et al. 1997). Browsing ungulates

face a trade-off between foraging in the closed-canopy forest, where vegetation is more digestible and nutritious, but more dispersed, and foraging in openings where vegetation is abundant but less palatable on average. In central Europe, forest ungulates forage at higher densities in openings compared to closed-canopy forests, suggesting a preference for quantity over quality (Kuijper et al. 2009). The same trend seems to be true for white-tailed deer in North America. For example, deer use of canopy gaps (up to 450 m²) in a Michigan eastern hemlock (*Tsuga canadensis*) forest was greatest in gaps < 100 m² in area (Tahtinen et al. 2014). In our study, deer browsing reduced the rate of forest regeneration in patch cuts (~1.4 ha) associated with uneven-aged silviculture, but had little effect on the rate of regeneration in clearcuts (~4.1 ha) associated with even-aged silviculture.

Besides the forage maturation hypothesis, the lower impact of ungulate browsing in larger openings may be explained through plant tolerance and avoidance of herbivory. Plant

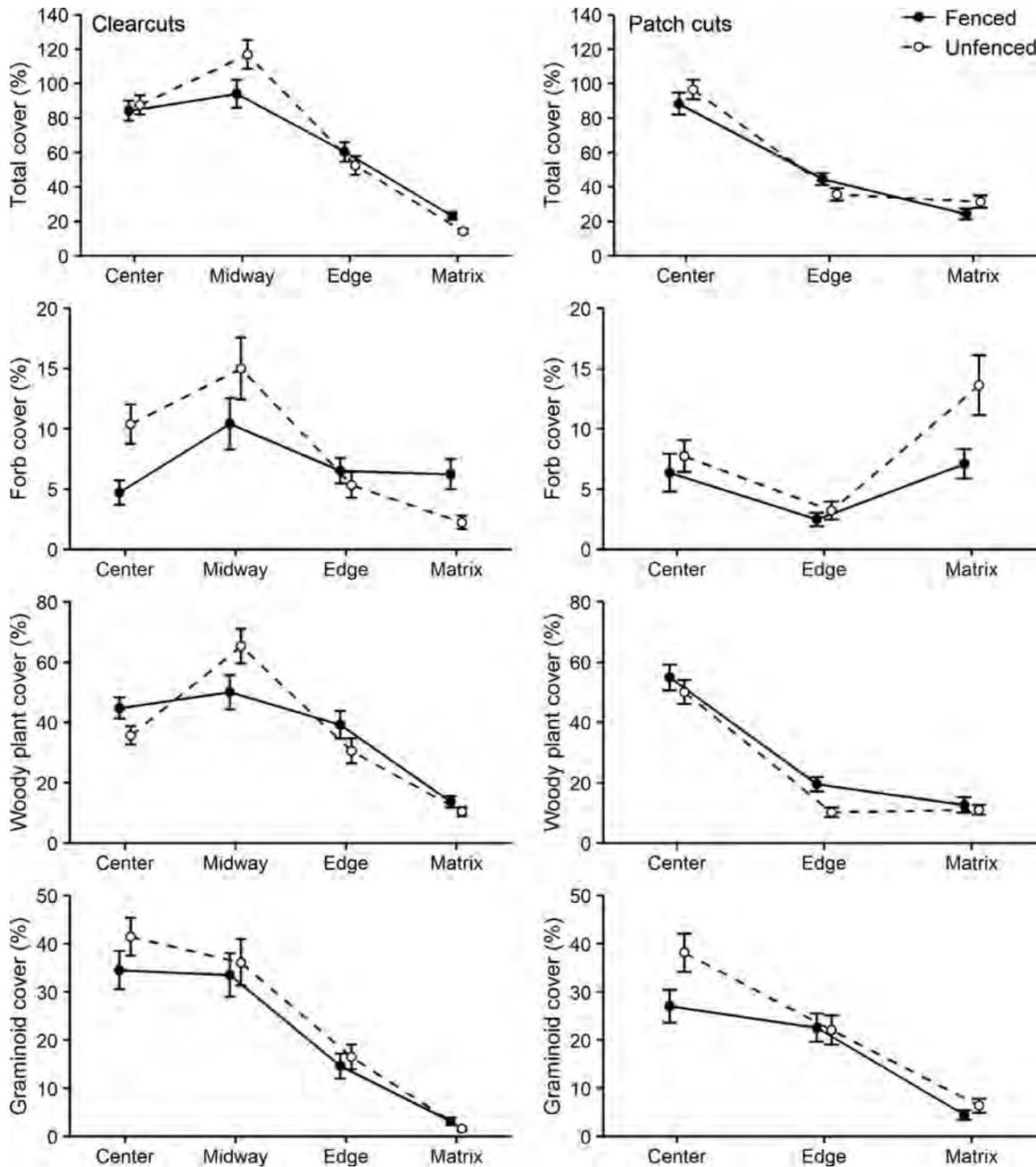


Fig. 4. Mean (\pm standard error) percent cover of the herbaceous-layer vegetation (< 0.5 m tall) at the sample plot scale of 0.25 m² in silvicultural openings within Central Hardwood forests of south-central Indiana, USA. Sampling intensity was as described in the caption of Fig. 3.

tolerance to herbivory is positively associated with light, nutrient, and water resource availability (Maschinski and Whitham 1989, Strauss and Agrawal 1999), so that woody plants in clearcuts may be more tolerant of herbivory than

those growing in patch cuts. Second, in clearcuts, a larger portion of woody stems escape herbivory or trampling due to chance. This mechanism would be more prevalent where the local deer density is not too high, and where deer have

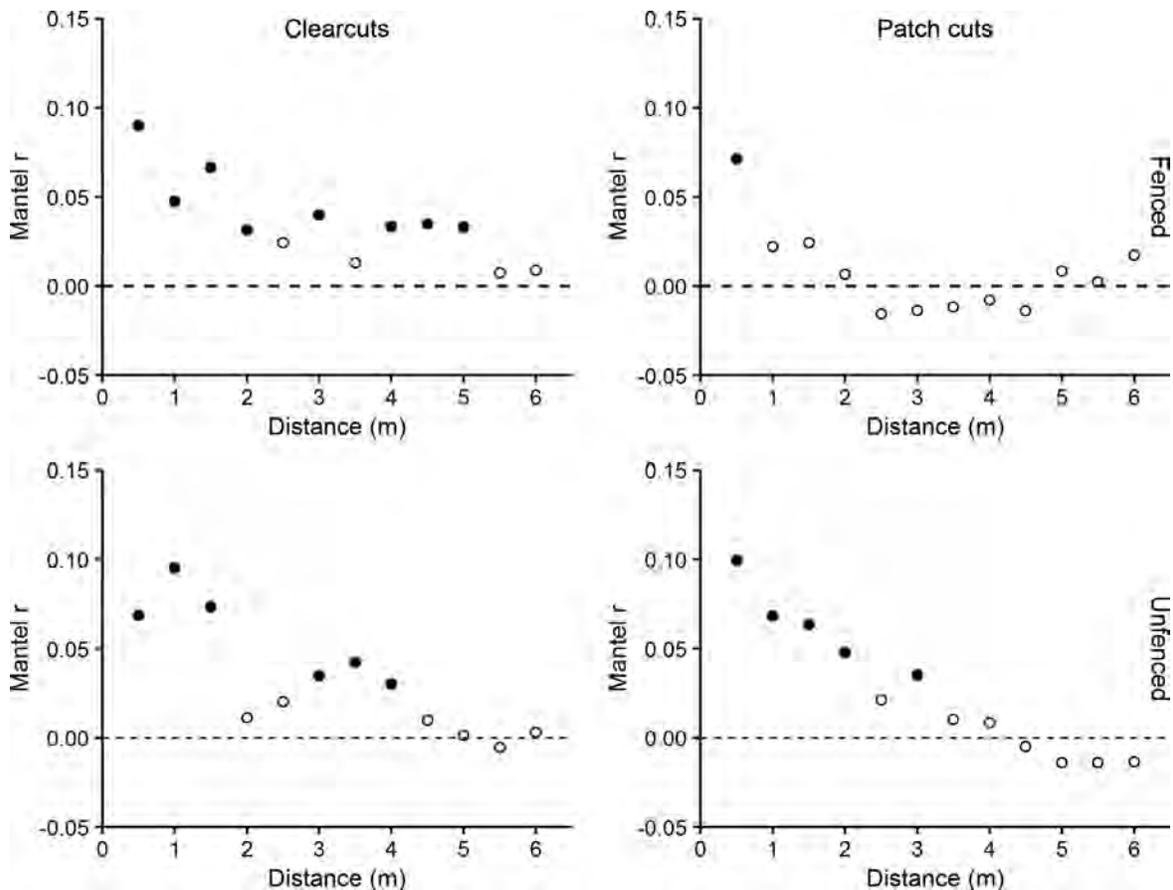


Fig. 5. Mantel correlograms depicting spatial correlation among sample plots based on the Sørensen index in the center positions of clearcuts (~4.1 ha) and patch cuts (~1.4 ha). Filled circles represent significant correlation ($P < 0.05$) in species composition among plots at a given distance, whereas open circles indicate no correlation. Samples were pooled within treatment groups, but the cutoff distance was set to 6.0 m so that only plots within the same sampling array could compose a pair. Sample sizes varied by lag distance according to the number of plot pairs as follows: 0.5 m, $n = 64$; 1.0 m, $n = 72$; 1.5 m, $n = 176$; 2.0 m, $n = 120$; 2.5 m, $n = 144$; 3.0 m, $n = 208$; 3.5 m, $n = 112$; 4.0 m, $n = 184$; 4.5 m, $n = 208$; 5.0 m, $n = 152$; 5.5 m, $n = 160$; 6.0 m, $n = 168$.

a variety of food sources ranging from woody plants, herbaceous plants, and mast (Royo et al. 2010). Both of these contingencies are true for our study area. Deer harvest per hunter effort in Morgan, Monroe, and Brown Counties is lower than the Indiana state average (Appendix S3: Table S1). The region does not have a history of deer overabundance outside of areas where hunting was restricted for several decades, such as Indiana State Parks (Webster and Parker 1997, Jenkins et al. 2014, 2015). The landscape that was chosen for the HEE is currently dominated by mast-producing species of oak and hickory (Saunders and Arsenault 2013), creating an

alternative to woody stems as a dormant-season food source.

Other studies have reported that deer impacts tend to be pervasive and persistent in single-tree-fall gaps and small canopy openings (Royo et al. 2010, Holmes and Webster 2011, Forrester et al. 2014), but deer use of larger management openings diminishes rapidly. For instance, deer use of logged clearcuts (11.3–21.9 ha) in Virginia decreased across a chronosequence of 2–7 yr since harvest (Blymyer and Mosby 1977). Blymyer and Mosby (1977) noted that moderate-sized management openings seemed to provide the best possible balance between forestry and wildlife

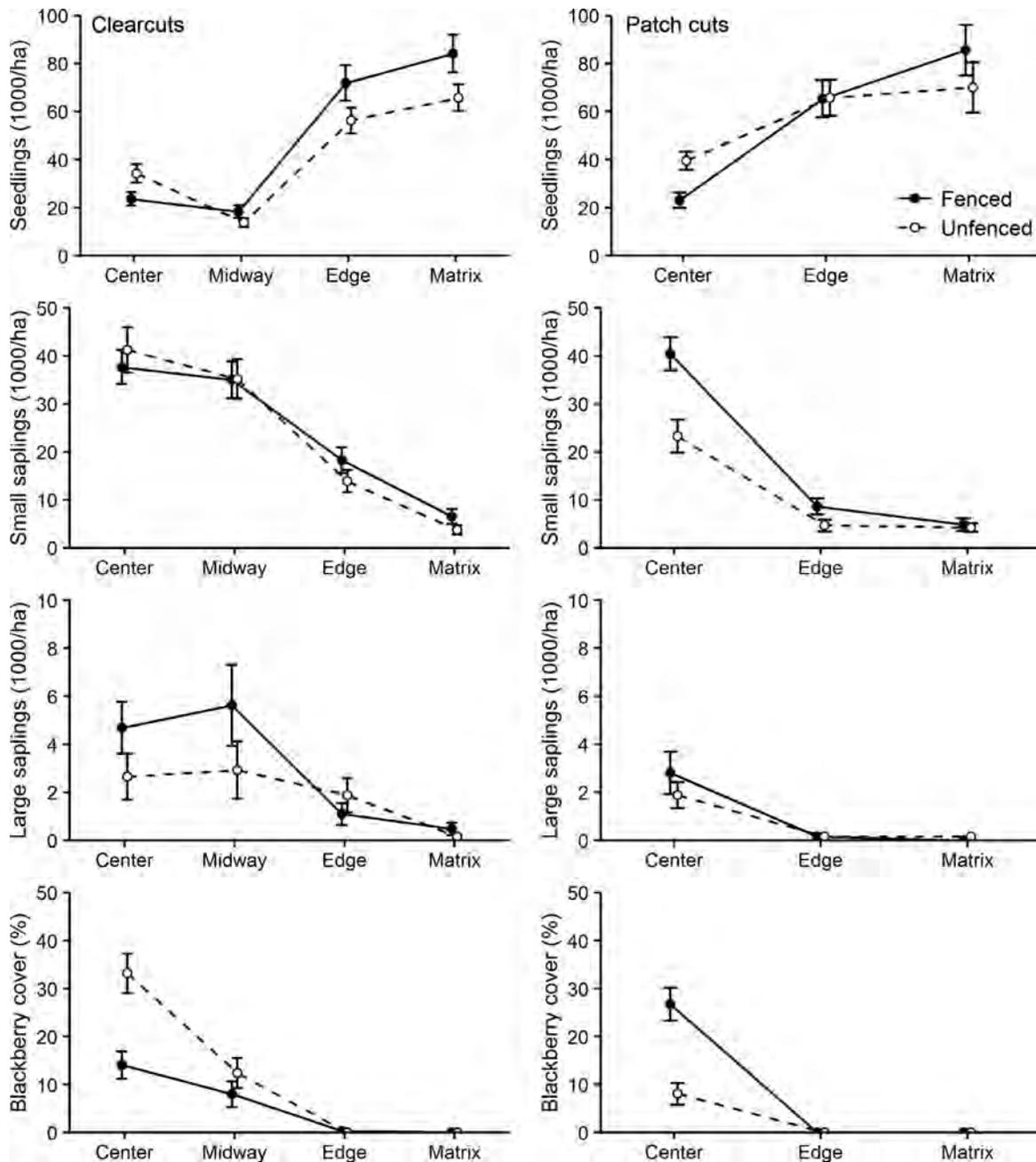


Fig. 6. Mean (\pm standard error) densities of seedlings (< 0.5 m tall), small saplings ($0.5\text{--}2.0$ m tall), and large saplings ($2.0\text{--}3.0$ m tall), and mean percent cover of blackberry shrubs (≤ 1.0 m tall) in silvicultural openings within Central Hardwood forests of south-central Indiana, USA. Clearcut openings were located in even-aged managed forests and were 4.1 ha in size on average. Patch cut openings were located in uneven-aged managed forests and were 1.4 ha in size on average. There were 16, 1.0 m^2 sample plots per sampling array, for a total $n = 64$ plots per treatment group combination, except for midway positions where $n = 48$ plots per treatment group (global $N = 480$ plots over four clearcuts and 384 plots over four patch cuts).

Table 5. Results of GLMM likelihood ratio tests for the effects of deer access and position (relative to the silvicultural opening) on density of seedlings (< 0.5 m tall) and small saplings (0.5–2.0 m tall).

Source	Clearcuts				Patch cuts			
	χ^2 †	df‡	N§	Model¶	χ^2	df	N	Model
Seedlings								
Deer	2.52	1	480	ZINB	0.200	1	384	NB
Position	161***	3	480	ZINB	49.3***	2	384	NB
Deer × position	6.78	3	480	ZINB	13.0*	2	384	NB
Small saplings								
Deer	1.13	1	480	ZINB	15.8***	1	384	ZINB
Position	202***	3	480	ZINB	153***	2	384	ZINB
Deer × position	4.30	3	480	ZINB	4.55	2	384	ZINB

Notes: Large saplings (2.0–3.0 m tall) occurred too infrequently for analysis. Clearcuts (~4.1 ha) and patch cuts (~1.4 ha) were analyzed separately. Each model included a random intercept parameter for site, and four sites were sampled in each opening size group. Model testing proceeded by first selecting the appropriate distribution, and then conducting χ^2 likelihood ratio tests on the parameters (Zuur et al. 2009). Each model was estimated using maximum likelihood.

† P-value classes of χ^2 likelihood ratio tests: * < 0.01, *** < 0.0001.

‡ Degrees of freedom for the χ^2 likelihood ratio tests.

§ The number of sample plots.

¶ Potential model types: P, Poisson; NB, negative binomial; ZIP, zero-inflated Poisson; ZINB, zero-inflated negative binomial.

habitat interests. In the central Appalachians, deer foraged in dense aggregations within large clearcuts (13–25 ha) shortly after harvest, but the intensity of deer use subsided within months (Campbell et al. 2004). Although our results support the prediction that the severity of ungulate impacts increases as opening size decreases, our experiment did not include openings smaller than 1.3 ha.

Ungulate browsing and herb-layer diversity and composition

Our data suggest that, under the right ecological context, ungulates can facilitate the establishment of herb-layer species into recently created silvicultural openings. Forest ungulates are rarely associated with greater species richness, and when they are, it is through complex interactions with other disturbances (Royo et al. 2010). Ungulates could facilitate species establishment in early seral communities through three non-exclusive pathways. In new openings that are not too large, ungulate browsing slows the development of the sapling layer and increases spatial heterogeneity in sapling density by repeatedly cropping woody plants (Pedersen and Wallis 2004, Royo and Carson 2006, Tremblay et al. 2007). Such an impact would increase the availability and heterogeneity of solar radiation reaching plants at ground level,

potentially increasing the species richness and spatial complexity of plant communities. Our results support this pathway in patch cuts, where sapling density was lower, and spatial heterogeneity was higher, outside of deer exclosures. Although sapling density did not differ according to deer access in clearcuts, this pathway may have played a role if concentrated deer use briefly suppressed regeneration in the first months to a year after harvest and the established plant populations persisted after deer visitation declined. Second, trampling and other physical disturbances caused by ungulates create new establishment sites (Hobbs 1996). Where deer visitation rates are high for a few months and then decline, the physical disturbance may facilitate the establishment of a variety of species that were otherwise excluded by competition. Third, deer may increase dispersal rates into openings through epizoochory and endozoochory (Vellend et al. 2003, Myers et al. 2004). In the case of endozoochory, fecal pellets and urine would supply N and Ca to newly established plants (Karberg and Lilleskov 2008, Jensen et al. 2011, Murray et al. 2013).

Comparing our results with those of the numerous studies that report negative ungulate impacts in forest understories emphasizes the importance of ecological context. Herbivory, physical disturbance, and seed dispersal are

well-known pathways through which ungulates can facilitate plant establishment, but they often benefit exotic species, or ferns and graminoids, over endemic forbs (Vavra et al. 2007, Webster et al. 2008, Knight et al. 2009). The traits that increase the invasiveness of exotic species favor establishment in more disturbed habitats, and invasive species tend to be unpalatable to ungulates. Ferns and graminoids are also unpalatable, and increase in dominance in forest understories with a history of chronic ungulate overabundance (de la Cretaz and Kelty 1999, Webster et al. 2005, Rooney 2009, Nuttle et al. 2014). Our findings illustrate that ungulates can have a net positive effect on herb-layer diversity in recently created silvicultural openings, particularly at the forest stand and landscape scales, where exotic species invasion is not a major concern and ungulate visitation rates decline quickly with forest maturation. Finally, our study occurred in a complex forested landscape containing a variety of habitat types and food sources, including mast-producing species, which may ameliorate the impact of ungulates on understory plant communities (Royo et al. 2010).

We found little indication of deer impacts in the edge or closed-canopy forest. The herb-layer communities of these locations were not directly impacted by harvesting, therefore, deer impacts would only be detected by the recovery of vegetation within the exclosures. These changes are likely to occur over a longer period of time than the 3-yr duration of this study. However, seedling and small sapling densities suggest that a pattern may be developing where deer impacts are generally positive within opening centers, and negative in the understories of closed-canopy forests (Fig. 6).

CONCLUSIONS

The diversity and composition of understory plant communities is strongly influenced by disturbance (Roberts and Gilliam 2003, Royo et al. 2010), which includes forest management systems and ungulates across many modern forested landscapes. In this study, we set out to determine if even-aged or uneven-aged management systems reduce the negative impacts of white-tailed deer on herb-layer plant communities, and we expected the conclusion to

be scale dependent. However, we found that deer were associated with greater herb-layer species richness, and this result occurred across spatial scales. This suggests that in resource-rich environments, such as the interiors of silvicultural openings, ungulates may facilitate the establishment of new species in the herb-layer by temporarily slowing sapling regeneration, creating establishment sites through physical disturbance, and seed dispersal via epizoochory and endozoochory. The identity of the recolonizing species will vary from site to site according to the seed bank as well as stochastic processes. Ungulate impacts are likely to be greatest in forest openings that are smaller than those in our study area. Smaller openings also experience a flush of forest regrowth, but ungulates will suppress regeneration over a longer period of time.

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LITERATURE CITED

- Blymyer, M. J., and H. S. Mosby. 1977. Deer utilization of clearcuts in southwestern Virginia. *Southern Journal of Applied Forestry* 1:10–13.
- Bolker, B., and R Development Core Team. 2014. *bbmle: Tools for general maximum likelihood estimation*. R package version 1.0.17. <http://CRAN.R-project.org/package=bbmle>
- Brown, B. J., and T. F. H. Allen. 1989. The importance of scale in evaluating herbivory impacts. *Oikos* 54:189–194.
- Bryant, J. P., F. S. Chapin III, and D. R. Klein. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40:357–368.
- Burton, J. I., D. J. Mladenoff, J. A. Forrester, and M. K. Clayton. 2014. Experimentally linking disturbance, resources and productivity to diversity in forest ground-layer plant communities. *Journal of Ecology* 102:1634–1648.
- Campbell, T. A., B. R. Laseter, W. M. Ford, and K. V. Miller. 2004. Movements of female white-tailed

- deer (*Odocoileus virginianus*) in relation to timber harvests in the central Appalachians. *Forest Ecology and Management* 199:371–378.
- Clinger, W., and J. W. Van Ness. 1976. On unequally spaced time points in time series. *Annals of Statistics* 4:736–745.
- Colwell, R. K. 2013. *EstimateS*: Statistical estimation of species richness and shared species from samples. Version 9. <http://www.purl.oclc.org/estimates>
- Colwell, R. K., A. Chao, N. J. Gotelli, S.-Y. Lin, C. X. Mao, R. L. Chazdon, and J. T. Longino. 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology* 5:3–21.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310.
- Côté, S. D., T. P. Rooney, J.-P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics* 35:113–147.
- de la Cretaz, A. L., and M. J. Kelty. 1999. Establishment and control of hay-scented fern: a native invasive species. *Biological Invasions* 1:223–236.
- Farley, R. A., and A. H. Fitter. 1999. Temporal and spatial variation in soil resources in a deciduous woodland. *Journal of Ecology* 87:688–696.
- Forrester, J. A., C. G. Lorimer, J. H. Dyer, S. T. Gower, and D. J. Mladenoff. 2014. Response of tree regeneration to experimental gap creation and deer herbivory in north temperate forests. *Forest Ecology and Management* 329:137–147.
- Fournier, D. A., H. J. Skaug, J. Ancheta, J. Ianneli, A. Magnusson, M. Maunder, A. Nielsen, and J. Sibert. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software* 27:233–249.
- Frelich, L. E. 2002. *Forest dynamics and disturbance regimes*. Cambridge University Press, Cambridge, UK.
- Fryxell, J. M. 1991. Forage quality and aggregation by large herbivores. *American Naturalist* 138:478–498.
- Gilliam, F. S., and M. R. Roberts. 2003. Introduction: conceptual framework for studies of the herbaceous layer. Pages 3–14 in F. S. Gilliam and M. R. Roberts, editors. *The herbaceous layer of forests in eastern North America*. Oxford University Press, Oxford, UK.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111:1169–1194.
- Hartley, S. E., G. R. Iason, A. J. Duncan, and D. Hitchcock. 1997. Feeding behaviour of red deer (*Cervus elaphus*) offered Sitka spruce (*Picea sitchensis*) grown under different light and nutrient regimes. *Functional Ecology* 11:348–357.
- Heckel, C. D., N. A. Bourg, W. J. McShea, and S. Kalisz. 2010. Nonconsumptive effects of a generalist ungulate herbivore drive decline of unpalatable forest herbs. *Ecology* 91:319–326.
- Hobbs, N. T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* 60:695–713.
- Holmes, S. A., and C. R. Webster. 2011. Herbivore-induced expansion of generalist species as a driver of homogenization in post-disturbance plant communities. *Plant Ecology* 212:753–768.
- Homoya, M. A., D. B. Abrell, J. R. Aldrich, and T. W. Post. 1985. The natural regions of Indiana. *Proceedings of the Indiana Academy of Science* 94:245–268.
- Jenkins, M. A. 2013. The history of human disturbance in forest ecosystems of southern Indiana. Pages 2–11 in R. Swihart, M. Saunders, R. Kalb, S. Haulton, and C. Michler, editors. *The hardwood ecosystem experiment: a framework for studying responses to forest management*. United States Department of Agriculture Forest Service General Technical Report NRS-P-108. Northern Research Station, Newtown Square, Pennsylvania, USA.
- Jenkins, M. A., and G. R. Parker. 1999. Composition and diversity of ground-layer vegetation in silvicultural openings of southern Indiana forests. *American Midland Naturalist* 142:1–16.
- Jenkins, L. H., M. A. Jenkins, C. R. Webster, P. A. Zollner, and J. M. Shields. 2014. Herbaceous layer response to 17 years of controlled deer hunting in forested natural areas. *Biological Conservation* 175:119–128.
- Jenkins, L. H., B. D. Murray, M. A. Jenkins, and C. R. Webster. 2015. Woody regeneration response to over a decade of deer population reductions in Indiana state parks. *Journal of the Torrey Botanical Society* 142:205–219.
- Jensen, N. R., C. R. Webster, J. C. Witt, and J. B. Grant. 2011. Ungulate winter habitat selection as a driver of herbaceous-layer heterogeneity in northern temperate forests. *Ecosphere* 2:67.
- Kalb, R. A., and C. J. Mycroft. 2013. The hardwood ecosystem experiment: goals, design, and implementation. Pages 36–59 in R. Swihart, M. Saunders, R. Kalb, S. Haulton, and C. Michler, editors. *The hardwood ecosystem experiment: a framework for studying responses to forest management*. United States Department of Agriculture Forest Service General Technical Report NRS-P-108. Northern Research Station, Newtown Square, Pennsylvania, USA.
- Karberg, N. J., and E. A. Lilleskov. 2008. White-tailed deer (*Odocoileus virginianus*) fecal pellet decomposition is accelerated by the invasive

- earthworm *Lumbricus terrestris*. *Biological Invasions* 11:761–767.
- Kimmins, J. P. 2003. *Forest ecology*. Third edition. Benjamin Cummings, San Francisco, California, USA.
- Knight, T. M., J. L. Dunn, L. A. Smith, J. Davis, and S. Kalisz. 2009. Deer facilitate invasive plant success in a Pennsylvania forest understory. *Natural Areas Journal* 29:110–116.
- Kraft, L. S., T. R. Crow, D. S. Buckley, E. A. Nauertz, and J. C. Zasada. 2004. Effects of harvesting and deer browsing on attributes of understory plants in northern hardwood forests, Upper Michigan, USA. *Forest Ecology and Management* 199:219–230.
- Kruskal, J. B. 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29:115–129.
- Kuijper, D. P. J., J. P. G. M. Cromsigt, M. Churski, B. Adam, B. Jędrzejewska, and W. Jędrzejewska. 2009. Do ungulates preferentially feed in forest gaps in European temperate forest? *Forest Ecology and Management* 258:1528–1535.
- Legendre, P., and L. F. J. Legendre. 2012. *Numerical ecology*. Third English edition. Elsevier, Amsterdam, the Netherlands.
- Lessard, J.-P., et al. 2012. Equivalence in the strength of deer herbivory on above and below ground communities. *Basic and Applied Ecology* 13:59–66.
- Maschinski, J., and T. G. Whitham. 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. *American Naturalist* 134:1–19.
- Mather, P. M. 1976. *Computational methods of multivariate analysis in physical geography*. John Wiley and Sons, London, UK.
- McCune, B., and J. B. Grace. 2002. *Analysis of ecological communities*. MjM Software, Gleneden Beach, Oregon, USA.
- McCune, B., and M. J. Mefford. 2006. *PC-ORD. Multivariate analysis of ecological data*. Version 5.31. MjM Software, Gleneden Beach, Oregon, USA.
- Mladenoff, D. J., and F. Stearns. 1993. Eastern hemlock regeneration and deer browsing in the northern Great Lakes region: a re-examination and model simulation. *Conservation Biology* 7:889–900.
- Molvar, E. M., R. T. Bowyer, V. Van Ballenberghe, and V. Van Braunenberone. 1993. Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community. *Oecologia* 94:472–479.
- Murray, B. D., C. R. Webster, and J. K. Bump. 2013. Broadening the ecological context of ungulate-ecosystem interactions: the importance of space, seasonality, and nitrogen. *Ecology* 94:1317–1326.
- Myers, J. A., M. Vellend, S. Gardescu, and P. L. Marks. 2004. Seed dispersal by white-tailed deer: implications for long-distance dispersal, invasion, and migration of plants in eastern North America. *Oecologia* 139:35–44.
- Nuttle, T., E. H. Yerger, S. H. Stoleson, and T. E. Ristau. 2011. Legacy of top-down herbivore pressure ricochets back up multiple trophic levels in forest canopies over 30 years. *Ecosphere* 2:4.
- Nuttle, T., A. A. Royo, M. B. Adams, and W. P. Carson. 2013. Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. *Ecological Monographs* 83:3–17.
- Nuttle, T., T. E. Ristau, and A. A. Royo. 2014. Long-term biological legacies of herbivore density in a landscape-scale experiment: forest understoreys reflect past deer density treatments for at least 20 years. *Journal of Ecology* 102:221–228.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2013. *vegan: community ecology package*. R package version 2.0-10. <http://CRAN.R-project.org/package=vegan>
- Pedersen, B. S., and A. M. Wallis. 2004. Effects of white-tailed deer herbivory on forest gap dynamics in a wildlife preserve, Pennsylvania, USA. *Natural Areas Journal* 24:82–94.
- Peet, R. K., T. R. Wentworth, and P. S. White. 1998. A flexible, multipurpose method for recording vegetation composition and structure. *Castanea* 63:262–274.
- R Core Team. 2014. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Roberts, M. R., and F. S. Gilliam. 2003. Response of the herbaceous layer to disturbance in eastern forests. Pages 302–322 *in* F. S. Gilliam and M. R. Roberts, editors. *The herbaceous layer in forests of eastern North America*. Oxford University Press, Oxford, UK.
- Rooney, T. P. 2009. High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. *Plant Ecology* 202:103–111.
- Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* 181:165–176.
- Rothrock, P. E. 2004. Floristic quality assessment in Indiana: the concept, use, and development of coefficients of conservatism. Final Report ARN A305-4-5. www.in.gov/idem/files/fqaindianarprt.doc
- Royo, A. A., and W. P. Carson. 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Canadian Journal of Forest Research* 36:1345–1362.

- Royo, A. A., R. Collins, M. B. Adams, C. Kirschbaum, and W. P. Carson. 2010. Pervasive interactions between ungulate browsers and disturbance regimes promotes temperate forest herbaceous diversity. *Ecology* 91:93–105.
- Rutherford, A. C., and O. J. Schmitz. 2010. Regional-scale assessment of deer impacts on vegetation within western Connecticut, USA. *Journal of Wildlife Management* 74:1257–1263.
- Saunders, M. R., and J. E. Arsenault. 2013. Pre-treatment analysis of woody vegetation composition and structure on the Hardwood Ecosystem Experiment research units. Pages 96–125 in R. Swihart, M. Saunders, R. Kalb, S. Haulton, and C. Michler, editors. *The hardwood ecosystem experiment: a framework for studying responses to forest management*. United States Department of Agriculture Forest Service General Technical Report NRS-P-108. Northern Research Station, Newtown Square, Pennsylvania, USA.
- Scheller, R. M., and D. J. Mladenoff. 2002. Understory species patterns and diversity in old-growth and managed northern hardwood forests. *Ecological Applications* 12:1329–1343.
- Shelton, A. L., J. A. Henning, P. Schultz, and K. Clay. 2014. Effects of abundant white-tailed deer on vegetation, animals, mycorrhizal fungi, and soil. *Forest Ecology and Management* 320:39–49.
- Skaug, H., D. Fournier, B. Bolker, A. Magnusson, and A. Nielsen. 2014. Generalized linear mixed models using AD builder software. R package version 8. <http://glmmadmb.r-forge.r-project.org>
- Stewart, K. M., T. E. Fulbright, and D. L. Drawe. 2000. White-tailed deer use of clearings relative to forage availability. *Journal of Wildlife Management* 64:733–741.
- Strauss, S. Y., and A. A. Agrawal. 1999. The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology & the Environment* 14:179–185.
- Tahtinen, B., B. D. Murray, C. R. Webster, C. S. Tarsoff, and A. J. Burton. 2014. Does ungulate foraging behavior in forest canopy gaps produce a spatial subsidy with cascading effects on vegetation? *Forest Science* 60:819–829.
- Tremblay, J.-P., J. Huot, and F. Potvin. 2007. Density-related effects of deer browsing on the regeneration dynamics of boreal forests. *Journal of Applied Ecology* 44:552–562.
- USDA, NRCS. 2013. The PLANTS database. National Plant Data Team, Greensboro, North Carolina, USA. <http://plants.usda.gov>
- Vavra, M., C. G. Parks, and M. J. Wisdom. 2007. Biodiversity, exotic plant species, and herbivory: the good, the bad, and the ungulate. *Forest Ecology and Management* 246:66–72.
- Vellend, M., J. A. Myers, S. Gardescu, and P. L. Marks. 2003. Dispersal of *Trillium* seeds by deer: implications for long-distance migration of forest herbs. *Ecology* 84:1067–1072.
- Webster, C. R., and G. R. Parker. 1997. The effects of white-tailed deer on plant communities within Indiana state parks. *Proceedings of the Indiana Academy of Science* 106:213–231.
- Webster, C. R., M. A. Jenkins, and J. H. Rock. 2005. Long-term response of spring flora to chronic herbivory and deer exclusion in Great Smoky Mountains National Park, USA. *Biological Conservation* 125:297–307.
- Webster, C. R., J. H. Rock, R. E. Froese, and M. A. Jenkins. 2008. Drought-herbivory interaction disrupts competitive displacement of native plants by *Microstegium vimineum*, 10 year results. *Oecologia* 157:497–508.
- Wheatall, L., T. Nuttle, and E. Yerger. 2013. Indirect effects of pandemic deer overabundance inferred from caterpillar-host relations. *Conservation Biology* 27:1107–1116.
- Wickham, H. 2009. *ggplot2: elegant graphics for data analysis*. Springer, New York, New York, USA.
- Zeileis, A., and T. Hothorn. 2002. Diagnostic checking in regression relationships. *R News* 2: 7–10. <http://CRAN.R-project.org/doc/Rnews/>
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. Springer, New York, New York, USA.

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