

RESEARCH ARTICLE

Spatio-temporal variation in foodscapes modifies deer browsing impact on vegetation

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Abstract

Context Ungulate browsers often alter plant composition and reduce diversity in forests worldwide, yet our ability to predict browse impact on vegetation remains equivocal. Theory suggests, however, that ungulate distribution and foraging impacts are shaped by scale-dependent decisions based on variation in habitat composition and structure encountered within their home range.

Objective Examine how variation in habitat composition at landscape (259 ha) scales modulates browse impact on vegetation at local scales.

Methods We measured vegetation richness and abundance in plots with and without white-tailed deer (*Odocoileus virginianus*) at 23 northern hardwood

forest sites distributed across a 6500 km² area in Pennsylvania, USA. Experimental sites were embedded within landscapes with varying levels of habitat composition and deer densities.

Results Browsing reduced vegetation richness and cover by as much as 53 and 70%, respectively; however, we found browse impact was modulated by variation in the relative abundance of managed habitats that alter forage availability. Specifically, relative to fenced areas, browse impact weakened and ultimately disappeared as the proportion of forage-rich habitats (e.g., recent harvests) increased to $\geq 20\%$. Conversely, vegetation grew increasingly depauperate as landscapes contained greater proportions of forage-poor habitats (i.e., older harvests), particularly when browsed.

Conclusions Our results underscore how management actions that alter forage availability to ungulates throughout the landscape (i.e. the foodscape) can shape forest-ungulate interactions and suggest a new paradigm whereby managers evaluate and undertake actions at the appropriate spatio-temporal scales to proactively limit the deleterious impact of browsing on plant biodiversity.

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Introduction

Abundant empirical and theoretical evidence exists demonstrating that ungulate overbrowsing can undermine multiple ecosystem services provided by forests including biodiversity and sustainable wood production (Gill 1992; Russell et al. 2001; Rooney and Waller 2003; Côté et al. 2004). Consequently, research has focused on developing approaches to mitigate browse impacts including identifying population density thresholds compatible with sustaining diversity, population control, and fencing (Porter et al. 1991; Horsley et al. 2003; Vercauteren et al. 2006; Tremblay et al. 2007). While these approaches have merit, the fundamental question of predicting when and how ungulate foraging negatively affects plant biodiversity remains unanswered (Gordon et al. 2004; Wisdom et al. 2006). Thus, land managers are confronted with the dilemma of sustaining forest diversity within unpredictable and variable browsing regimes and often are forced to employ costly measures to maintain biodiversity (Waller and Alverson 1997).

Ecological theory, however, argues that ungulate distributions and foraging behavior are mediated by scale-dependent decisions based on habitat structure, resource availability, and predation risk (Senft et al. 1987; Kie et al. 2002; Hobbs 2003). In particular, spatio-temporal variation in the diversity, distribution, and abundance of habitat patches that provide forage or cover can shape population size, home range, and thus, browsing impacts across the landscape (e.g., Kie et al. 2002; Månsson 2009; Millington et al. 2010; Massé and Côté 2012). The growing awareness of scale-dependency has led to two differing views regarding how habitat diversity and abundance interact with resident ungulate herds to shape foraging impacts.

One view conjectures that variability in habitats at larger scales is critical in moderating ungulate foraging impacts at local scales (Johnson et al. 1995; Takada et al. 2002; Augustine and deCalesta 2003). This view suggests browse impact on vegetation may be weaker in forested landscapes containing a diverse configuration of habitat patch types and sizes, relative to large and relatively homogeneous forested landscapes. Consequently, from a forest management perspective, natural and anthropogenic disturbances that create a diversity of habitats, particularly those that increase forage, should mitigate browse impact

(deCalesta and Stout 1997; Månsson 2009; Miller et al. 2009; Hurley et al. 2012; Herfindal et al. 2015).

Alternatively, others hypothesize that ungulate populations will respond numerically via increased fecundity to increases in forest habitat and structural diversity (Cadenasso and Pickett 2000; Kie et al. 2002) and thereby, ultimately intensify browse impact on vegetation (Alverson et al. 1988; Augustine and Jordan 1998; Palmer et al. 2003; Reimoser et al. 2009). Hence, this viewpoint suggests that land-use decisions that minimize disturbance, such as maintaining large, contiguous forested blocks or low-intensity silvicultural systems (e.g., single-tree selection), may mitigate browse risk whereas more extensive and intensively managed areas would ultimately increase browse risk (Reimoser and Gossow 1996; Kramer et al. 2006; Faison et al. 2016).

To date, empirical evidence testing the degree to which browse impact on vegetation is scale-dependent on variation in ungulate densities and habitat composition remains limited and inconsistent. Existing findings suggest browse risk is mitigated (e.g., Hurley et al. 2012; Jarnemo et al. 2014), intensified (e.g., Reimoser and Gossow 1996; Faison et al. 2016), or even unaffected (e.g., Möst et al. 2015; Evans et al. 2016) by variation in landscape composition. Generalizing from existing work is problematic given that most existing studies offer limited replication, rely solely on existing variation in ungulate populations and habitat configuration, or utilize metrics that may inadequately capture the spatial complexities that shape foraging (e.g., one-dimensional metrics such as distance to edge). More importantly, existing studies lack vegetation surveys in paired exclosures. Consequently, it is difficult to separate browsing effects from site-to-site variation in plant diversity or additional, confounding factors (Côté et al. 2004).

Untangling these relationships is critically important to maintain diversity and productivity in forests where wide-ranging large ungulates exist at high density (Millington et al. 2010). Regrettably, Beguin and colleagues (2016) recently concluded that discerning how land management actions across scales shape browse risk remains equivocal. Here, we provide insight into this question using a hybrid experimental approach that incorporates a manipulative (i.e., fence/control) treatment to test how localized (i.e., stand-level) browse impact by white-tailed deer (*Odocoileus virginianus*) varies among multiple,

broadly distributed sites that vary in deer densities and habitat diversity. We hypothesized that variation in habitat types and abundance at the scale of a resident deer's home range shapes deer foraging behavior, thereby modulating browse impact on plant diversity at local scales. We predict that as the proportion of forage-producing habitat increases within the resident deer's home range, localized browse impact will decline, and vegetation cover, richness, and diversity will increase. Nonetheless, an alternative hypothesis is also possible wherein deer populations experience a numerical response as a function of habitat quality. If so, we predict increasing proportions of forage-producing habitats will cause a concomitant upsurge in deer populations, intensified browse impact, and decreases in vegetation cover, richness and diversity. In either case, we further predict the combination of habitat variables and deer density will predict browse impact on vegetation better than models containing deer densities alone.

Methods

Study area

We conducted our study at 23 sites distributed across a 6500 km² area of Pennsylvania, USA (Fig. 1, Online Appendix 1). Major tree species include red maple (*Acer rubrum*), sugar maple (*A. saccharum*), black cherry (*Prunus serotina*), and American beech (*Fagus grandifolia*), with lesser abundances of hemlock (*Tsuga canadensis*), birches (*Betula alleghaniensis*, *B. lenta*), and white ash (*Fraxinus americana*) (Marquis 1975). Understory vegetation is dominated by unpalatable striped maple (*A. pensylvanicum*) and beech in the shrub layer, and ferns (e.g., *Dennstaedtia punctilobula*) in the herb layer (Royo et al. 2010b).

Deer populations within Pennsylvania, as throughout much of the USA, were excessively high for much of the 20th century (i.e., 15–23 deer/km²; Horsley et al. 2003). Beginning in 2003, changes in deer management policies, including additional antlerless licenses and concurrent buck-doe hunting seasons, allowed many of the public and private industrial landowners in the region to intensify hunting on their lands, resulting in deer herd reductions for over a decade (Royo et al. 2010b; Stout et al. 2013; see Online Appendix 1).

Experimental design

At each of the 23 sites, we selected one stand where managers initiated a regeneration sequence as the location of the experimental treatment. In all stands, managers conducted the initial cut of a shelterwood sequence to reduce stand relative density to levels appropriate for hardwood regeneration in mature Allegheny and northern hardwood forests (i.e., <75% relative density; Marquis et al. 1992). With the exception of one site (Regen134), shelterwood harvests occurred 0–5 years prior to fence construction (Online Appendix 1). The harvest reduced basal area across all sites from an average of 26.6–16.6 m²/ha. Additionally, 22 stands received broadcast herbicide treatments (glyphosate and sulfometuron methyl; Marquis et al. 1992) to control dense layers of interfering plant species within 4 years prior to fence construction (Online Appendix 1). By deploying our experiment within managed stands, we can (1) detect browse impacts on vegetation more rapidly and on a greater variety of species than in uncut areas (Horsley et al. 2003); (2) reduce the potential for lagged responses attributed to established recalcitrant layers (Royo et al. 2010b); and (3) directly link our results to common forest management actions.

Within each stand, we established paired 4200 m² (60 × 70 m²) plots and randomly assigned one plot a deer exclosure (fence) treatment while the other served as an unfenced control. Exclosure construction was completed by September 2013 except for one site (Rush) on which harvest occurred during winter of 2013/14. At this site, the exclosure was constructed in early spring 2014. Centered within each plot, we established a 2000 m² (40 × 50 m²) sampling area, divided into a 10 × 10 m² grid, leaving a ~10 m wide buffer between the perimeter of the plots and the sampling area.

Data collection

In summer 2015, two growing seasons after exclosure construction, we censused the plant community in 2 m radius (12.56 m²) subplots located at five randomly chosen nodes of the 10 × 10 m² grid. Vegetation was censused in the vertical dimension at 20 cm intervals from ground level to 2 m in each of the four cardinal directions (see Collins and Becker 2001; Rohleder 2013). We recorded vascular plant species richness of

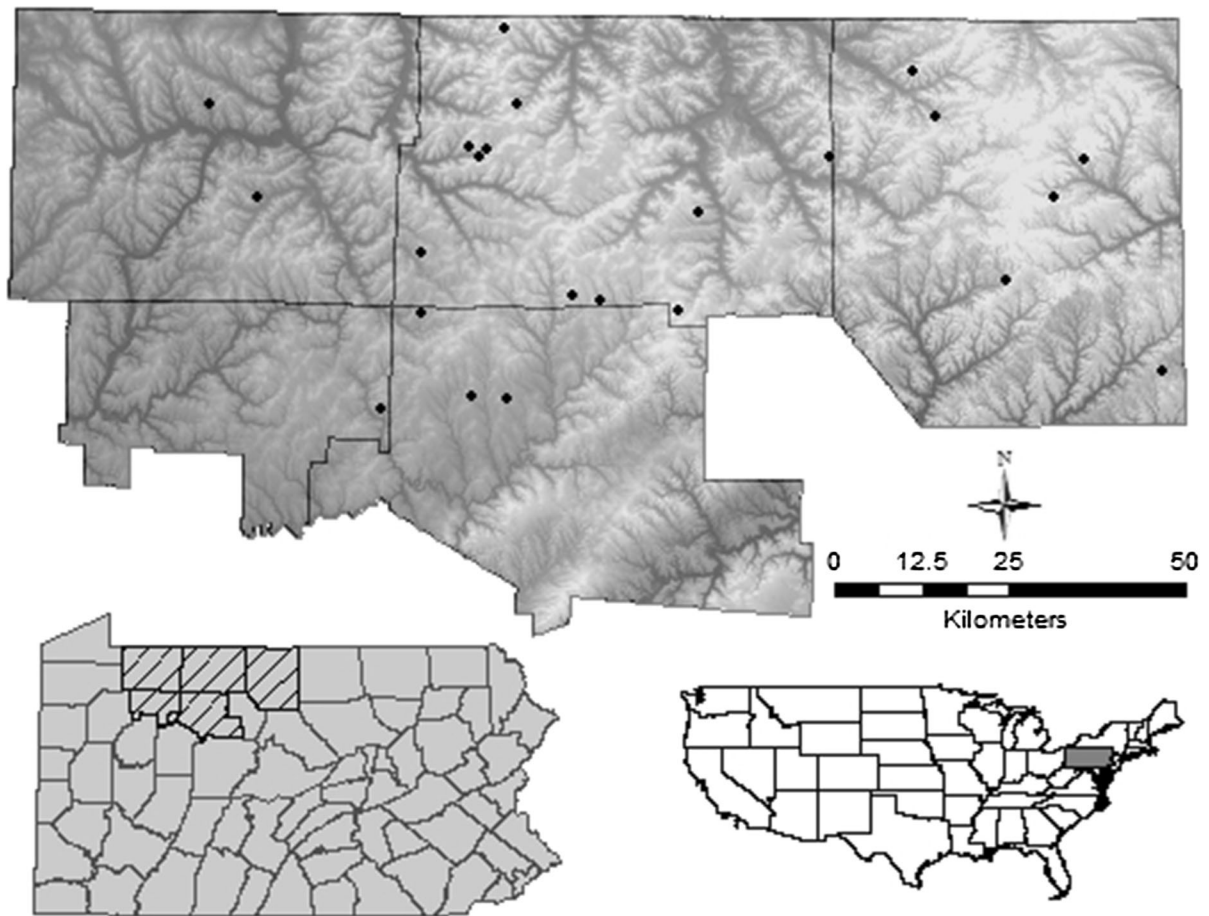


Fig. 1 Map showing the 23 study sites scattered throughout a four county region in northwest Pennsylvania, USA. Dots represent the approximate location of experimental stands and

the center of a 900 m radius (259 ha) buffer within which landscape metrics were calculated

the vegetation profile in each height interval along a 2-m line-intercept in each cardinal direction and species frequency by height class as the proportion of sample directions in which a species was tallied. Lastly, we estimated total vegetation cover along the vertical profile using a $20 \times 20 \text{ cm}^2$ cover template placed at the plot center viewed horizontally from a distance of 2 m in each cardinal direction (Online Appendix 2).

For each site, we assessed habitat composition at the landscape scale by developing 259 ha land cover maps centered on each experimental site. Following Putman and colleagues' (2011) advice, we scaled our assessment of habitat configuration to the typical home range size of the resident ungulate species. Hence, we chose a 259 ha buffer size because within the northern-hardwood region of the eastern U.S., this

area encompasses the typical deer mean home range size (range 64–223 ha; Tierson et al. 1985; Campbell et al. 2004). Maps were developed using the 2011 National Land Cover Database (Homer et al. 2015) as a basemap and augmented with aerial imagery, landowner spatial data, and on-the-ground verification. We identified 10 distinct habitats: *Mature Forest*, *Shelterwood*, *Recent Removal*, *Older Removals* (hereafter, stem exclusion stage), *Thinning/Salvage*, *Conifer*, *Herbaceous*, *Water*, *Developed Areas*, and *Agriculture*. We classified mature forest as any closed canopy hardwood stand that had not received recent timber harvest. Shelterwood was reserved for stands with a shelterwood harvest within the past 5 years. Recent removals were stands that had received a clear-cut ≤ 5 years prior to the year of classification, whereas areas entering stem exclusion stage were

clear-cut areas >5 years but ≤ 17 years prior to classification. Thinning and salvage timber areas were a distinct classification wherein a portion of the mature overstory was removed, but there were no immediate plans to proceed to a clearcut. Conifer areas contained $>90\%$ conifer (primarily hemlock) in the overstory. Herbaceous patches are dominated by non-woody vegetation (e.g., food plots, rights-of-ways, and failed regeneration harvests). Developed areas included roads, buildings, and other infrastructure. Agriculture included pastures and active or fallow cropland. Lastly, water represented areas where water is present during all or portions of the year (e.g., reservoirs, streams). We resampled the basemap to a higher resolution of 5 m following classification and used available landowner data to identify the timing of forest management treatments concluded prior to the start of winter 2015. Questionably classified areas were verified using aerial imagery from USGS National Agriculture Imagery Program (NAIP) and Google Earth for the summers of 2013, 2014, and 2015 and field visits in fall of 2015. Thus, our map captures the diversity and abundance of habitats within the home range of deer in the year vegetation data were sampled (see Online Appendix 1).

Finally, we estimated deer densities throughout each of the 259 areas surrounding each stand using fecal pellet surveys. Data were collected along five, 1.6 km transects spanning the site in spring (April to early May) of 2013–2015. Within each transect, deer pellet group counts were obtained on fifty-two, 4.67 m^2 plots spaced 30.5 m apart. Estimates derived from pellet group counts represent the average number of deer over winter for each site and therefore, the number of adult deer surviving into the spring and summer (see deCalesta 2013 for further details on methodology).

Statistical analyses

To avoid model overfitting our analyses proceeded hierarchically. We first screened potential analysis of covariance variables for collinearity using correlation analyses (Online Appendix 3). Additionally, as our hypotheses make specific predictions regarding available forage, we aggregated land cover classes capable of producing forage into a composite variable: *prop-forage*. These include recent forest management areas (i.e., shelterwood, recent removal, thinning, and

salvage harvests), agricultural areas, and herbaceous habitats. Stem exclusion patches generally lack abundant forage as sapling canopy closes and is increasingly out of reach of deer and the ensuing low-light conditions reduce herbaceous cover to very low levels (Johnson et al. 1995; Roberts 2004). Unmanaged, mature forest strongly covaried ($r = -0.75$) with propforage as it encompassed most of the habitat remaining across the landscape after accounting for managed forest habitats, and was therefore removed from further consideration.

Following preliminary variable screening, we used an exploratory model selection approach with model averaging to determine whether treatment (fence/control) and the landscape covariables of deer density and proportions of the landscape in forage, stem exclusion, and conifer cover were robust predictors to include in final models. We pooled the data and fit linear models to the mean species richness, total cover ($\log[\text{cover} + 0.1]$), and Shannon diversity (H') of each experimental unit (i.e., average of five subplots within each plot). For these models, treatment was converted to binary variable (0/1) and all possible variable combinations were examined the R function dredge (MuMIn package; Barton 2013). We compared competing models using AIC_C scores and weights and present AIC_C -weighted average parameter estimates across the top models ($\Delta\text{AIC}_C < 2$; Burnham and Anderson 2002).

We used a generalized linear mixed model to test how plant community responses varied as a function of deer browsing alone and interactions between deer browsing and selected landscape-level covariates. We modelled treatment (fence/control) and height as fixed effects. The model included one random effect for site and a second random effect of height nested within treatment(site) to account for the hierarchical nature of the design (Milliken 2006). We used an autoregressive first order covariance structure (AR(1)) in the G-matrix to model the dependence in samples between successive height strata. We initially tested the single treatment effect of fence to examine whether localized deer browsing affected vegetation across the entire 2 m profile, as established by Rohleder's (2013) methods. However, as our sites were fairly early in stand development, vegetation was almost uniformly low in stature with all of the species and 75% of the total plant cover contained in the first 60 cm of height. Hence, to examine whether localized deer browsing

impact on the plant community varied as a function of landscape-level covariates, we restricted our analyses to the lowermost 60 cm in height, corresponding to the three lowest height strata.

All analyses included a treatment $\times$ covariate term to test the homogeneity of slopes assumption. This interaction is central to our hypothesis testing whether landscape covariates modulate vegetation responses to browsing as a significant interaction would indicate treatment effects do not respond in a similar manner (i.e., non-parallel) to variation in the covariate. In cases where treatment was significant ($P < 0.10$), we utilized least-squared means to test pair-wise differences and, where treatment $\times$ covariate interactions were significant ($P < 0.10$), we tested for treatment differences along the entire range of the landscape covariate in 5% increments using least-squared means (Proc Glimmix; SAS Institute Inc. 2011). This approach allowed us to assess, for example, at which point along the landscape covariate, vegetation responses to browsing in control plots became indistinguishable from fenced plots.

We did not include the simple main effects of the landscape covariates as these were collinear with the blocking term Site (i.e., each site has unique values for landscape covariates) and were applied to responses in both the fence and control plots. Instead, we examined whether responses against landscape covariates had non-zero slopes. For all analyses, we utilized the Kenward-Rogers denominator degrees of freedom method. Compliance to the ANOVA assumptions of homoscedasticity and normality of the residuals was assessed using boxplots and Levene's test. Species richness was modelled using a Poisson distribution, percent cover was modelled using a gamma distribution, and diversity (H') was modelled using a normal distribution.

To examine whether species composition differed across treatments, and treatments $\times$ landscape covariate interactions, we ran partial redundancy analyses (RDA) using the Jaccard distance metric on the mean frequency of species throughout 0–60 cm stratum. Redundancy analyses are the canonical extension of principal component analysis (PCA) and have the flexibility of allowing the effects of known covariables, such as spatial blocking effects, to be accounted for (i.e., 'partialled out'; ter Braak 1988). Species present on <3 plots (42% of species) were culled from the analyses as rare species exert unduly large

influence in multivariate analyses and distort interpretation (McCune and Grace 2002). Species frequencies were standardized using the Hellinger standardization following Legendre and Gallagher (2001). To account for the paired nature of the design, site was included as a conditional covariable in the RDA and permuted tests of significance (999 permutations) were constrained within sites using the *strata* option in the *vegan* package in R version 3.1.2 (Oksanen et al. 2015). Species associations with the constraining variables were visualized using RDA biplots. Community composition analyses were run using the *rda* and *anova* functions in the *vegan* package.

Results

General patterns

We censused vegetation in plots covering a two-dimensional footprint of $\sim 3141 \text{ m}^2$ and a total volume across the entire vegetation profile of 6282 m^3 . We surveyed 61 taxa of which 16 were tree species. Across the entire 2-m height, deer browsing reduced overall plant species richness by 53% (Richness_{Trt}: $F_{1,73.3} = 6.31$; $P = 0.01$; Fig. 2a) and overall cover by 70% (Cover_{Trt}: $F_{1,34.4} = 41.73$; $P < 0.0001$; Fig. 2b, see also Table 2 for similar results on lower strata). Progressively taller strata grew increasingly depauperate, exhibiting both fewer species and less cover (Richness_{Ht}: $F_{9,389.3} = 47.6$; $P < 0.0001$ and Cover_{Ht}: $F_{9,370.2} = 85.23$; $P < 0.0001$; Fig. 2) and browsing exacerbated this decline for cover (Cover_{Trt $\times$ Ht}: $F_{9,370.2} = 6.85$; $P < 0.0001$). Across all strata, the most abundant species were *Rubus allegheniensis* (16% relative frequency), *Dennstaedtia punctilobula* (9%) and various grasses and sedges (17% combined). Among the tree species, *Prunus pensylvanica* (8%), *Acer rubrum* (8%), and *Betula* spp. (*B. allegheniensis* and *B. lenta*; 4.8%) were the most frequently tallied.

Habitat composition modulates browse impact

The most plausible (i.e., lowest AIC_C) models predicting species richness, cover, and diversity all included treatment (fence vs control), forage-producing habitats, and stem exclusion stands as essential landscape variables (Table 1A). In fact, stem

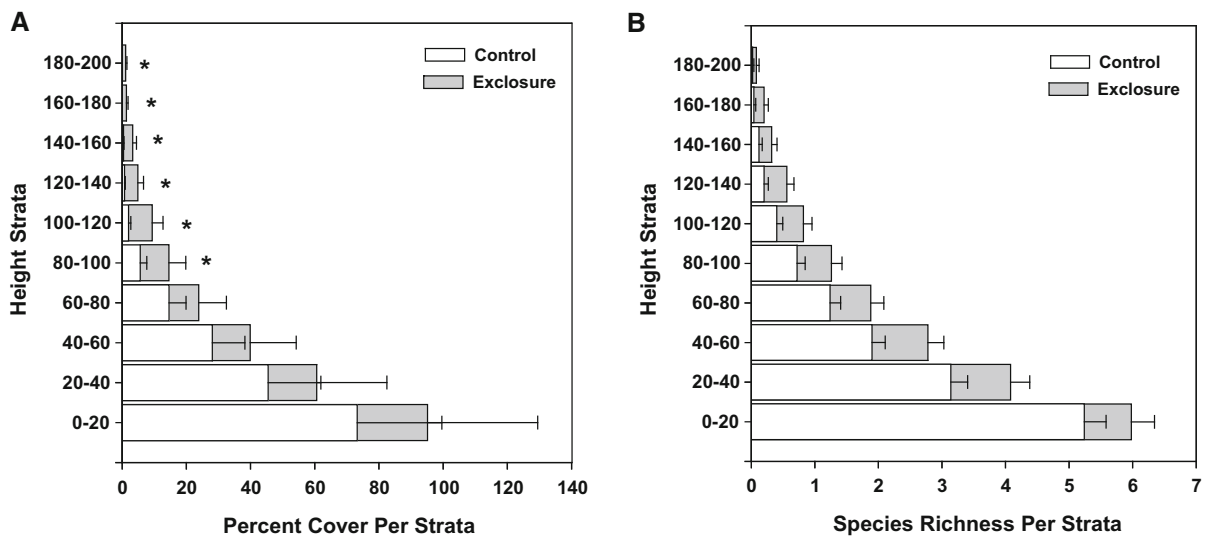


Fig. 2 Mean overall ($\pm$ 1SE) percent cover (a) and species richness (b), by 20 cm interval height strata, with and without ambient browsing. In both responses there were significant ($P < 0.05$) treatment and height main effects. Percent cover also

had a significant treatment $\times$ height interaction and therefore we further examined treatment differences within height strata. Asterisks (*) denote a significant pair-wise difference in treatment within a height strata

exclusion stands were selected in all models receiving competitive support ($\Delta AIC_C < 2$). Forage-producing habitats were selected in 78% of all alternative, competitive models. None of the remaining landscape variables, including average deer density, were identified in the most plausible (lowest AICc) model. While average deer density and proportion conifer appeared in the confidence set of models, confidence intervals crossed zero. Additionally, models without any landscape variables (i.e., intercept only or an intercept + treatment models) were not identified as competitive or plausible models (e.g., high AICc values, low R^2 values, low weights). Excluding deer and increasing proportions of forage habitat were associated with greater richness, cover, and diversity whereas increasing the proportion of stands in stem exclusion diminished these metrics (Table 1B).

Land cover covariates consistently modulated browse impact across the lowermost strata of the vegetation profile (Table 2). Specifically, we found the negative impacts of deer browsing on richness and abundance weakened as the proportion of forage-producing habitats increased across the landscape (significant treatment $\times$ propforage interaction; Table 2; Fig. 3). This relationship was not observed within areas where deer were excluded. Comparisons

of the two treatments along the propforage covariate found that when landscapes contained $\geq 20\%$ in forage-producing habitats, the plant community richness cover became indistinguishable from that found within exclosures (Online Appendix 4). Overall species richness, abundance, and diversity grew increasingly depauperate in landscapes with greater proportions of stem exclusion stands, and particularly so in areas with ambient browsing (significant treatment $\times$ stmex interaction; Table 2; Fig. 4). However, even within exclosures, we detected richness and diversity declines in sites embedded in landscapes with more area in stem exclusion stands.

Deer browsing significantly altered species composition (RDA_{Trt} : $F_{1,20} = 2.19$, $P = 0.004$; Online Appendix 5). The RDA indicated that in areas with ambient browsing, ferns and graminoids (*D. punctilobula*, *Carex* spp., *T. noveboracensis*) were 20, 37, and 300% more frequent, respectively. In contrast, eliminating browsing increased the frequency of *P. pennsylvanica*, *F. grandifolia*, *Magnolia acuminata*, and *Sambucus* spp. by 177, 192, 358 and 204%, respectively. Additionally, in areas with ambient browsing, stands embedded in landscapes with greater proportions of forage-producing habitats resulted in greater frequencies of some species including

Table 1 Linear model selection results for the overall cover ($\ln[\text{Cover} + 0.1]$), species richness ($\ln[\text{richness} + 0.1]$), and diversity (Shannon H') of the vegetation in the 0–60 cm stratum. (A) Models with $\Delta\text{AIC}_C < 2$ are presented as well as an intercept-only model and a intercept + treatment only

model. For all models we present the degrees of freedom (df), the second-order Akaike information criterion (AIC_C), the distance from the best model (ΔAIC_C), likelihood ratio based R^2 , and Akaike weight (w_i). (B) Model averaged results averaged across top models ($\Delta\text{AIC}_C < 2$)

A							
Response	Model	df	Log-likelihood	AIC_C	ΔAIC_C	R^2	w_i
Cover	Int + Trt + StmEx + PropFor	5	−137.1	284.7	0.00	0.26	0.21
	Int + Trt + StmEx + PropFor + DeerDens	6	−136.4	285.5	0.74	0.27	0.15
	Int + Trt + StmEx + PropFor + Conif	6	−137.0	286.7	1.98	0.26	0.11
	Int	2	−157.8	319.9	35.20	0.03	0.00
	Int + Trt	3	−155.5	317.2	32.50	0.03	0.00
Richness	Int + Trt + StmEx + PropFor	5	−272.9	556.3	0.00	0.17	0.21
	Int + Trt + StmEx	4	−274.3	556.9	0.59	0.15	0.16
	Int + Trt + StmEx + PropFor + DeerDens	6	−272.8	558.2	1.92	0.17	0.08
	Int + Trt + StmEx + PropFor + Conif	6	−272.8	558.3	1.99	0.17	0.08
	Int	2	−285.8	575.7	19.42	0.00	0.00
Diversity	Int + Trt	3	−282.5	571.3	14.97	0.05	0.00
	Int + Trt + StmEx + PropFor	5	−73.9	158.2	0.00	0.19	0.21
	Int + Trt + StmEx	4	−75.1	158.5	0.39	0.18	0.17
	Int + Trt + StmEx + PropFor + Conif	6	−73.7	160.1	1.96	0.19	0.08
	Int	2	−88.4	180.9	22.73	0	0.00
	Int + Trt	3	−84.8	175.7	17.55	0.05	0.00

B									
	Cover			Richness			Diversity		
	Est.	SE	Pr(> z)	Est.	SE	Pr(> z)	Est.	SE	Pr(> z)
Intercept	3.84	0.19	<0.0001	3.82	0.43	<0.0001	1.17	0.09	<0.0001
Stem Exclusion	−0.04	0.01	<0.0001	−0.08	0.02	<0.0001	−0.02	0.00	<0.0001
PropForage	1.10	0.52	0.04	2.29	1.38	0.10	0.52	0.32	0.12
Treatment	0.27	0.11	0.02	0.83	0.30	<0.01	0.21	0.07	<0.01
Deer density	0.03	0.02	0.24	0.03	0.06	0.62	–	–	–
Conifer	0.00	0.00	0.66	0.00	0.02	0.66	0.00	0.00	0.64

Int intercept, Trt treatment (i.e., enclosure versus control), PF proportion of landscape in forage, StmEx proportion of landscape in stem exclusion, DeerDens 3 year average deer density (2013–2014), Conif proportion of stands in conifer

Polygonum cilinode, *Fragaria virginiana*, and *Eurybia divaricata* ($\text{RDA}_{\text{Trt} \times \text{PF}}$: $F_{1, 20} = 1.60$, $P = 0.057$).

Discussion

Dynamic foodscapes

Our experiment demonstrates that variation in the relative abundance of key habitats at large spatial scales modulates localized browse impact in two

diametrically opposed ways: disturbances that open up forest canopies and create early-successional habitats initially mitigate browse impact whereas expanding mid-successional habitats intensify browsing. In the largely forested landscapes where we conducted our study, land cover changes are mainly created by harvesting, although herbaceous areas and agricultural patches occur and natural disturbances are common (Online Appendix 1, Royo et al. 2016b). Overstory tree harvests, coupled with the herbicide applications, increased light availability and disturbed the soil

Table 2 Results of analyses of covariance on overall cover, species richness, and diversity (H') for vegetation in the 0–60 cm height stratum

Source	Cover	Richness	Diversity
Treatment	$F_{1,30.0} = 3.67$; $P = 0.07$	$F_{1,45.6} = 6.76$; $P = 0.01$	$F_{1,44.1} = 4.25$; $P = 0.05$
Height	$F_{2,23.4} = 40.23$; $P < 0.0001$	$F_{2,56.1} = 125.66$; $P < 0.0001$	$F_{2,45.9} = 111.21$; $P < 0.0001$
Trt*Height	$F_{2,46.5} = 3.89$; $P = 0.03$	$F_{2,63.5} = 63.49$; $P = 0.09$	$F_{2,77.1} = 1.08$; $P = 0.34$
Trt*PF	$F_{2,35.9} = 3.42$; $P = 0.04$	$F_{2,43.3} = 2.90$; $P = 0.07$	$F_{2,45.0} = 2.30$; $P = 0.11$
Control _{Trt×PF}	$\beta = 1.43 \pm 0.56$; $t = 2.55^*$	$\beta = 1.30 \pm 0.54$; $t = 2.41^*$	–
Exclosure _{Trt×PF}	$\beta = -0.16 \pm 0.56$; $t = -0.28$	$\beta = 0.05 \pm 0.51$; $t = 0.11$	–
Trt*StmEx	$F_{2,35.9} = 11.10$; $P < 0.001$	$F_{2,44.2} = 3.68$; $P = 0.03$	$F_{2,45.1} = 8.17$; $P = 0.01$
Control _{Trt×StmEx}	$\beta = -3.59 \pm 0.77$; $t = -4.64^*$	$\beta = -1.69 \pm 0.80$; $t = -2.11^*$	$\beta = -1.91 \pm 0.65$; $t = -2.93^*$
Exclosure _{Trt×StmEx}	$\beta = -1.06 \pm 0.77$; $t = -1.37$	$\beta = -1.29 \pm 0.72$; $t = -1.79^*$	$\beta = -1.18 \pm 0.65$; $t = -2.80^*$

Where a significant ($P < 0.10$) treatment $\times$ covariate effect exists, we present the regression equations for each treatment to test whether their slopes are significantly different (*) from zero. Vegetation cover was tested using a gamma distribution, species richness was modelled with a Poisson distribution, and diversity was modelled using a normal distribution

Trt treatment, PF proportion of landscape in forage, StmEx proportion of landscape in stem exclusion

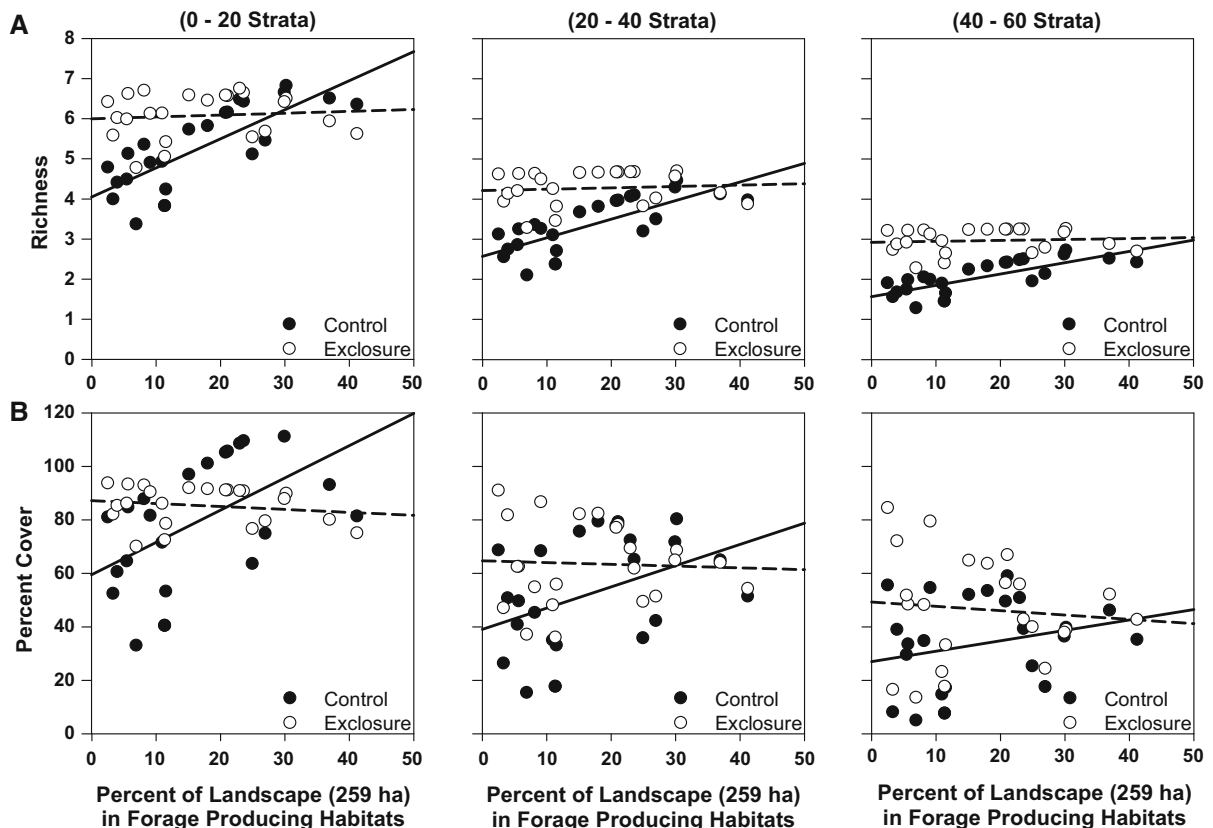


Fig. 3 Relationships between percent of landscape (259 ha) in forage-producing habitats and overall **a** species richness and **b** cover, in the 0–60 cm strata with (filled circle) and without (open circle) ambient browsing. For richness and cover data plotted are back-transformed values of the Poisson and gamma distributions, respectively. Data analysis was based on a

hierarchically nested approach wherein each height strata within a plot was a unit of observation and the nestedness and covariance structure among successive heights within plot were accounted for in the model. For convenience, data are presented separately for each height strata (0–20; 20–40; 40–60 cm). See Table 2 for analyses

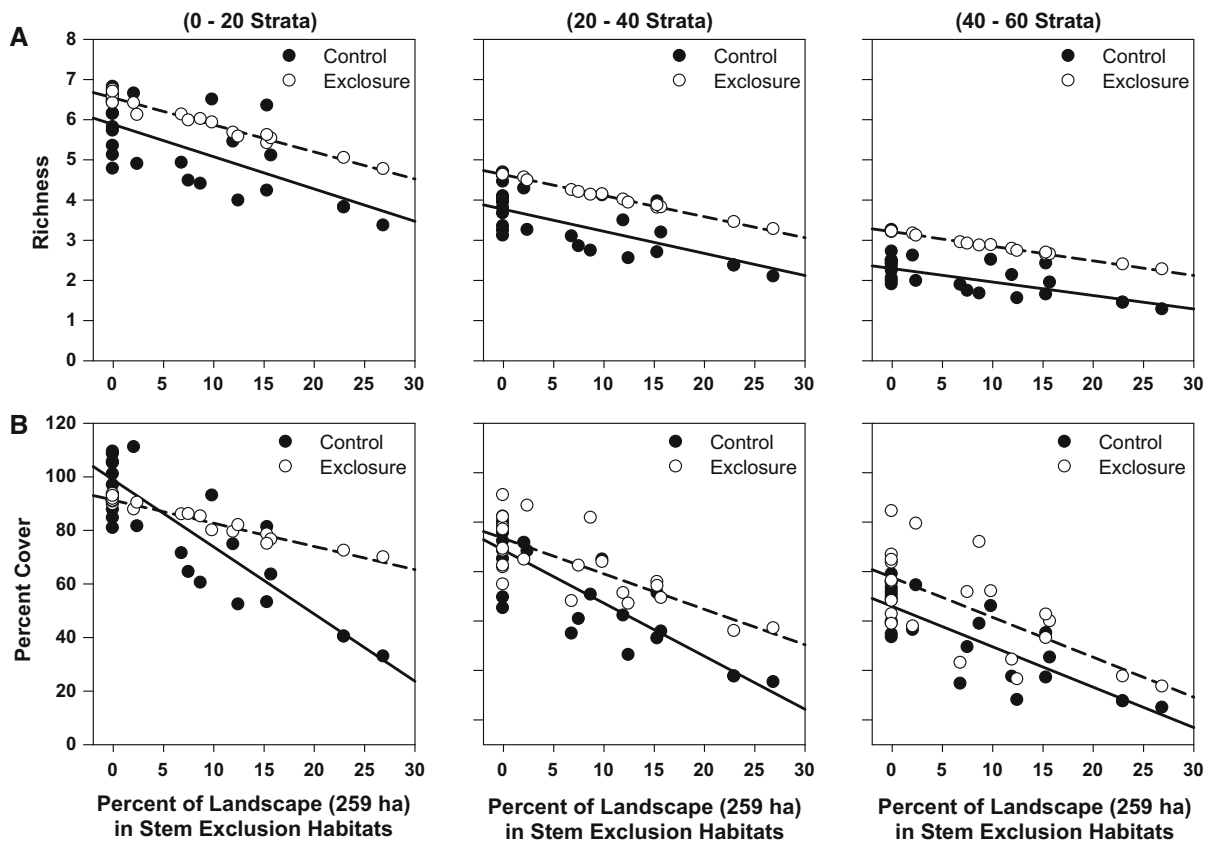


Fig. 4 Relationships between percent of landscape (259 ha) in stem exclusion habitat and overall **a** species richness and **b** cover, in the 0–60 cm strata with (filled circle) and without (open circle) ambient browsing. For richness and cover data plotted are back-transformed values of the Poisson and gamma distributions, respectively. Data analysis was based on a

hierarchically nested approach wherein each height strata within a plot was a unit of observation and the nestedness and covariance structure among successive heights within plot were accounted for in the model. For convenience, data are presented separately for each height strata (0–20; 20–40; 40–60 cm). See Table 2 for analyses

surface thereby promoting plant germination, growth, flowering, and fruiting within the lower vegetation strata. The concomitant changes in composition and structure caused by harvesting creates high quality forage patches favored by wildlife (reviewed by Greenberg et al. 2011) and mitigate localized browse impact in the short term (deCalesta and Stout 1997; Månsson 2009; Miller et al. 2009; reviewed by Hurley et al. 2012; Gerhardt et al. 2013; Herfindal et al. 2015). Our study extends and enhances these prior findings by unequivocally isolating deer impact across nearly two dozen sites that vary greatly in habitat composition and deer densities. Moreover, our study identifies target levels of area under forest management beyond which negative effects of browsing on plant community richness, diversity, and abundance are completely mitigated. Our analyses indicate that, under the range

of deer densities observed in our study, when approximately 20% of the landscape (52/259 ha) is in forage-producing habitats (e.g., forest harvests, agriculture, herbaceous openings), browse impact on cover and diversity of the plant community is indistinguishable from that found within a fence.

Our findings also indicate that interactions between browsing and variation in relative abundance of forage-producing habitats create communities with contrasting plant composition. Excluding deer benefited fast-growing, highly preferred species trees, particularly *P. pensylvanica* (Horsley et al. 2003). Under ambient browsing, however, species composition in areas embedded in landscapes with high amounts of alternative forage did not mirror that found within a fence. Instead, the habitat-mediated reductions in browse impact allowed moderately

preferred species, including *Polygonum cilinode*, *Fragaria virginiana*, and *Eurybia divaricata* (Atwood 1941) to persist. In contrast, as forage became less available to resident deer herds, browsing intensified and constricted species composition toward the least nutritious, browse tolerant and highly recalcitrant species, including ferns and sedges (Royo and Carson 2006). These findings suggest that deer may suppress or promote species coexistence, depending on landscape context. Although herbivory and stand-level disturbances are known to promote coexistence where they co-occur (Royo et al. 2010a; Faison et al. 2016), such interactions occurring at larger spatial scales remain largely unexplored.

Our findings also suggest the role of disturbance in modulating browsing is temporally dynamic as changes to vegetation structure, composition, and abundance that occur during succession eventually reverse and intensify browse impact. We found plant communities became increasingly depauperate when embedded in landscapes with higher proportions of stem exclusion stands. We suggest this effect is caused by both historic and present intensification of browse pressure. During stem exclusion, plant biomass becomes increasingly concentrated in the competing tree canopy and, concomitantly, woody and herbaceous biomass available to deer in lower strata declines (Christensen and Peet 1984; Johnson et al. 1995; Howard and Lee 2003; Roberts 2004). Hence, from an ungulate browser's perspective, stem exclusion stands present a tradeoff between suboptimal, forage-poor habitat and dense hiding cover, both of which will concentrate foraging activity in forage hotspots created by harvesting (Partl et al. 2002; Vospernik and Reimoser 2008; Månsson 2009). Within our study areas, stem exclusion stands predate the building of the exclosures. Hence, we suggest our sites experienced past browse pressure that intensified in landscapes with abundant stem exclusion stands which may have negatively impacted plant richness, cover and diversity, even in areas that were ultimately fenced.

Considered in their entirety, our findings suggest habitat-mediated effects on foraging activity and browse pressure are both scale-dependent and dynamic. Our findings indicate that in largely forested areas, the application of even-aged forest management practices that stimulate vegetation establishment and growth in hardwoods initially mitigates and ultimately

intensifies browse impacts on vegetation as successional changes to forage availability cause deer to concentrate browsing. Hence, the modulating effect of disturbance-driven habitat heterogeneity on browsing changes as the 'foodscape' (sensu Searle et al. 2007) throughout the home range of the ungulate population may wax and wane both spatially and temporally.

Reconciling opposing predictions

Our experimental findings support the hypothesis that variation in habitat composition, and particularly the relative abundance of forage patches, mitigates the negative effect of browsing on plant cover and species richness. This modulating effect assumes deer populations are relatively stable throughout the landscape. However, natural or anthropogenic disturbance that increases productivity and forage availability increase carrying capacity and, thereby, may eventually increase deer populations (Gill et al. 1996; Kramer et al. 2006) and, thereby, ultimately intensify browse impacts (Alverson et al. 1988; Augustine and Jordan 1998; Reimoser et al. 2009). Moreover, some have argued that any modulating effects of increasing forage throughout a landscape may be overwhelmed at high deer densities (Augustine and Jordan 1998; Beguin et al. 2016). Our findings cannot refute these alternative predictions as our experiment was carried out under conditions where landowners and game management policies encouraged strong top-down control over deer population growth by increasing hunting opportunities and courting hunter participation (Stout et al. 2013). In fact, although average deer densities in our study were higher than precolonial estimates (<4 deer/km²; McCabe and McCabe 1997), they are intermediate between thresholds identified to maintain overall plant biodiversity (~ 4 deer/km²; Alverson et al. 1988; deCalesta and Stout 1997) and negative thresholds identified for tree regeneration (~ 8 deer/km²; Horsley et al. 2003; Tremblay et al. 2007). Moreover, within our study areas, deer populations remained stable over time, even in areas with high forage (see Online Appendix 1 and 3). Thus, our results apply to managed forests in which deer densities are moderately high (median = 6.3 deer/km²; range 3.2–12.3 deer/km²) and which are largely open to seasonal hunting pressure. Therefore, it is not clear the degree to which our conclusions would apply in landscapes with weak top-down control (i.e., lax

hunting, absence of predators) where deer populations would be free to respond positively to increasing forage availability. Nonetheless, even under those conditions, populations may build over a few years as a result of lags in juvenile recruitment and low emigration from nearby social groups (Fryxell et al. 1991; Miller et al. 2010). Understanding spatiotemporal dynamics and interplay between vegetation development and ungulate populations should be a focus of future studies.

Deer matter, but density estimates lack precision

Contrary to expectations, we found estimated deer densities were not a robust predictor of vegetation responses, even when coupled with landscape predictors. However, we do not conclude deer are unimportant in driving vegetation dynamics in this system. Indeed, our results demonstrate that browsing limited species richness, abundance, diversity, restricted recruitment of species into taller strata, and altered species composition. We suggest the reason average deer densities fail to consistently emerge as a robust predictor in this and other studies may lie in the precision of the variable itself relative to the response (Royo et al. 2010b). Indeed, although fecal surveys provide a comparative population density index at the scale critical to our analyses (Forsyth et al. 2007), variability in fecal deposition and persistence rates may render them unreliable as predictors of localized impact (Putman et al. 2011). Indeed, estimates based on standing crop (i.e., without removing prior year's pellets) may be biased because pellets may take years to disappear (Alves et al. 2013). Moreover, indices based on over winter fecal deposition rates reflect deer habitat use during a time when deer limit their movement and seek thermal cover (e.g., conifer stands). Thus, the temporal disconnect between winter thermoregulation needs and summer browse foraging in harvested areas may limit the utility of these estimates. Additionally, although we used a 3-year average density estimate in our models, observed browsing impacts at individual sites may be highly idiosyncratic, resulting from foraging bouts that occurred in the past, present, or both, hence further complicating interpretation. Finally, efforts to relate aggregate plant community metrics (e.g., richness, abundance) to densities of selective foragers like deer is problematic as variation in the composition and

abundance of the plant community may mask interpretation. Given these complications, it is not surprising that studies that detect relationships between deer density and vegetation are generally focused on highly palatable species (e.g., Augustine and Jordan 1998), specific growth forms (e.g., woody sprouts; Royo et al. 2016a), subsets of the plant community (e.g., native herb cover; Hurley et al. 2012), or analyses that are sensitive to changes in species composition (Bachand et al. 2015).

Proactive management of deer impact

Our work provides empirical evidence to substantiate a paradigm shift in how land managers can sustainably manage their forests under resident ungulate herds (Reimoser and Gossow 1996). Currently, management options to sustain and promote plant diversity are reactive and costly, including the removal of matriarchal social groups from localized areas, localized culls using sharpshooters, or the widespread use of fencing (Porter et al. 1991; Vercauteren et al. 2006; Miller et al. 2010). Our findings inform guidelines for a distinct alternative whereby managers manipulate the landscape on the appropriate temporal and spatial scales to mitigate deer impacts on plant biodiversity at the stand level. Specifically, we suggest that in forested landscapes managed under even-aged silviculture in which deer are hunted, land managers might consider entering approximately 20% of the area within the average home range of deer into a regeneration sequence within 5 years in order to buffer plant communities from browsing. This proportion may be adjusted downward, according to the degree to which alternative forage patches already exist within the landscape (e.g., agriculture). Following these initial entries, we recommend managers limit any additional harvesting within the area as browse risk will increase over the next couple decades as stands transition into stem exclusion. Indeed, stem exclusion patches are an important consideration, as we show browse risk intensifies as the relative abundance of this habitat type increases. Harvests in landscapes containing abundant stem exclusion stands may require increased deer harvest pressure or fencing to mitigate potential risks to biodiversity.

Our recommendation regarding the proportion of the landscape in forage producing habitats is higher than Miller and colleagues' (2009) recommendation

of 14% in <10 year old stands and Stout and colleagues' (2013) finding that 15% of early successional forests are sufficient to ensure diverse regeneration without fencing and enhance growth and reproduction of browse sensitive herbs. The lower proportions identified by Miller et al. (2009) and Stout et al. (2013) relative to ours may arise as a consequence of their harvests all being recent removals which stimulate abundant regeneration, whereas our classification combines recent removals with partial harvests containing a more subdued regeneration response, and hence, less forage (Horsley et al. 2003).

Our findings are applicable to forests across the eastern United States and elsewhere where forest managers practice even-aged silviculture and contend with browse impact from white-tailed deer. Collectively, our results underscore the importance of understanding how management practices exert scale-dependent influences on ungulate foraging which may intensify or mitigate conflicts between deer and forest management (Jarnemo et al. 2014; Beguin et al. 2016). More broadly, our results support the growing consensus of the benefits of early successional forest habit to biodiversity conservation (Swanson et al. 2011) and demonstrate that forest management may mitigate deer impact and maintain biodiversity while circumventing the contentious socioeconomic-political debates that often surround ungulate management in forests.

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