

# Spatial factors of white-tailed deer herbivory assessment in the central Appalachian Mountains

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**Abstract** Because moderate to over-abundant white-tailed deer (*Odocoileus virginianus*) herbivory impacts biodiversity and can alter community function, ecological benchmarks of herbivory impact are needed to assess deer impacts. We evaluated spatial patterns of deer herbivory and their relation to herbivory assessment by evaluating woody vegetation along 20 transects at each of 30 sites spread across a wide range of deer herd densities and vegetative condition throughout the biodiverse Appalachian Mountains of Virginia, USA. Surprisingly, herbivory patterns and the availability of woody forage generally were unchanged among physiographic regions and land use diversity classes. However, some relationships between browsing pattern and vegetation varied with scale. The total quantity of vegetation browsed on a given site and at the transect scale were related positively to the availability of forage, as the proportion of stems browsed decreased as stem density increased. However, this was only true when all stems were considered equally. When stem densities by species were weighted for deer preference, the

proportion of stems browsed had no relationship or increased with stem density. Compared to the value from all transects sampled, on average, the mean of  $\geq 3$  transects within a site was within 0.1 of the browsing ratio and stem densities were within  $0.5 \text{ stems m}^{-2}$ . Our results suggest that one transect per square kilometer with a minimum of three transects may be sufficient for most browsing intensity survey requirements to assess herbivory impacts in the Appalachian region of Virginia. Still, inclusion of spatial factors to help partition variation of deer herbivory potentially may allow for improved precision and accuracy in the design of field herbivory impact assessment methods and improve their application across various landscape contexts.

**Keywords** Appalachian Plateau · Blue Ridge · Forage availability · Herbivory · Impact assessment · *Odocoileus virginianus* · Ridge and Valley · White-tailed deer

## Introduction

Ungulates significantly modify ecosystem structure and biodiversity (Hobbs 1996; Rooney and Waller 2003; Royo et al. 2010a; Bressette et al. 2012). Deer (Cervidae) influence biodiversity in a variety of ways, including directly through herbivory, which changes growth rate, development, survival, and succession of plants and resulting community composition (Russell

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et al. 2001), and indirectly through a cascade of impacts to other organisms. For example, researchers have related impacts of deer to bird communities, small mammals, and invertebrates that respond to change in plant communities (reviewed by Côté et al. 2004). Further, through mechanical action (e.g., trampling and browsing), and fecal pellet deposition, deer can influence nutrient cycling and the soil environment (Hobbs 1996), leading to impacts on litter and below-ground processes and biota (Rearick et al. 2011).

Deer and other ungulates generally live within landscapes that are heterogeneous mosaics of vegetation types and conditions, land forms, and land uses (Urban et al. 1987). Ecologists have long had an interest in spatial patterns resulting from interactions between landscapes and ecological processes (Turner 1989). For example, many environmental factors of importance to plant communities (i.e., moisture, light, nutrients, and climate) correlate with topographic and geologic attributes of landscapes (Swanson et al. 1988; McNab 1993; Meilleur et al. 1994; Ford et al. 2000; Clinton 2003). White-tailed deer (*Odocoileus virginianus*) (hereafter deer) are the most common and widespread large herbivore in eastern North America. Deer selectively forage based on type and nutritional content of vegetation (Nixon et al. 1970; Vangilder et al. 1982; Berteaux et al. 1998; Dostaler et al. 2011). Furthermore, topographic, climatic, and other variables may influence, or restrict access by deer to landscape areas (Schmitz 1991; Rooney 1997; Comisky et al. 2005; Krueger and Peterson 2006; Chollet et al. 2013). Thus, deer herbivory may vary spatially in relation to landscape characteristics. Although research on deer herbivory has been substantial (Russell et al. 2001; Rooney and Waller 2003; Côté et al. 2004), most research has not evaluated underlying spatial factors (but see Augustine and Jordan 1998) or how the extent and pattern of observed herbivory impacts occur in landscapes broadly.

Because deer can cause substantial changes to biodiversity, efforts to include ecological benchmarks or measures of herbivory impact in deer population management have increased, particularly in light of real or perceived overabundance in the eastern USA (de Calesta and Stout 1997; Morellet et al. 2007; Tierney et al. 2009; McShea 2012). Nonetheless, how herbivory varies spatially across landscapes and among landscape scales typically is unknown to managers in most settings, particularly in the central Appalachians (Campbell et al. 2006). For example, managing deer

populations within limits that permit function of a biologically diverse ecosystem has been an objective of the Virginia, USA, state-wide deer management plan (Virginia Department of Game and Inland Fisheries 2015). However, there are few data or established protocols describing the sampling effort required to measure herbivory impact, the spatial variability of deer herbivory, or the applicability of suggested ecological measures across the varied habitats, landscapes, and surficial geology of Virginia or elsewhere (Côté et al. 2004; N. Lafon, Virginia Department of Game and Inland Fisheries, personal communication).

The development of broad-scale herbivory impact assessment methods requires an understanding of how deer browsing intensity or other measures of herbivory vary in relation to habitat productivity, topographic configuration, and other spatial factors. Additionally, understanding the variation of deer herbivory in relation to spatial factors potentially may improve the precision and accuracy of field assessment methods across various landscape contexts. Therefore, using a spatially balanced, multi-scale study design, our objectives were to examine (1) the relationship of deer herbivory patterns to geographical and land use configuration, (2) spatial patterns of deer herbivory, and (3) the influence of sampling effort on browsing intensity and forage availability estimates across the central Appalachian Mountains of Virginia, USA. Deer maintain small home-ranges (Campbell et al. 2004b) and herbivory impacts can be localized to widespread depending on herd density (Ford et al. 1993; Campbell et al. 2006). A priori, we hypothesized that various measures and characterizations of deer herbivory would vary across multiple spatial scales and that spatial patterns of herbivory would differ more among physiographic regions and habitat configurations than at local scales. Specifically, we hypothesized that sites with greater land use diversity would have greater spatial variation in herbivory intensity.

## Materials and methods

### Study area

Our study area was the central Appalachian Mountain region of western Virginia, USA, comprising the Blue Ridge, Valley and Ridge, and Appalachian Plateau physiographic regions. Though variable across the wide

ranges of elevations (200–1700 m), aspects, terrain shape/sheltering, surficial geology, and past land use, the region primarily is forested and largely dominated by (*Quercus* spp.) oak-hickory (*Carya* spp.), oak-pine (*Pinus* spp.), or mesic cove hardwood types. Wider valley bottoms in the Ridge and Valley and Blue Ridge contain a mix of pastoral grazing lands and limited row-crop agriculture, residences, and urbanized areas (Kniewski and Ford 2017). Other than early-successional habitat derived from forest harvesting and regeneration, nonforested habitats in the Appalachian Plateau primarily are reclaimed coal-production surface mines (Oliphant et al. 2016). Deer densities also varied across the region from high ( $> 20 \text{ km}^2$ ) to low ( $< 2 \text{ km}^2$ ). Generally, deer abundance was greater on private land than public land, and numbers in the Appalachian Plateaus were significantly less than either the Valley and Ridge or Blue Ridge (Virginia Department of Game and Inland Fisheries 2015).

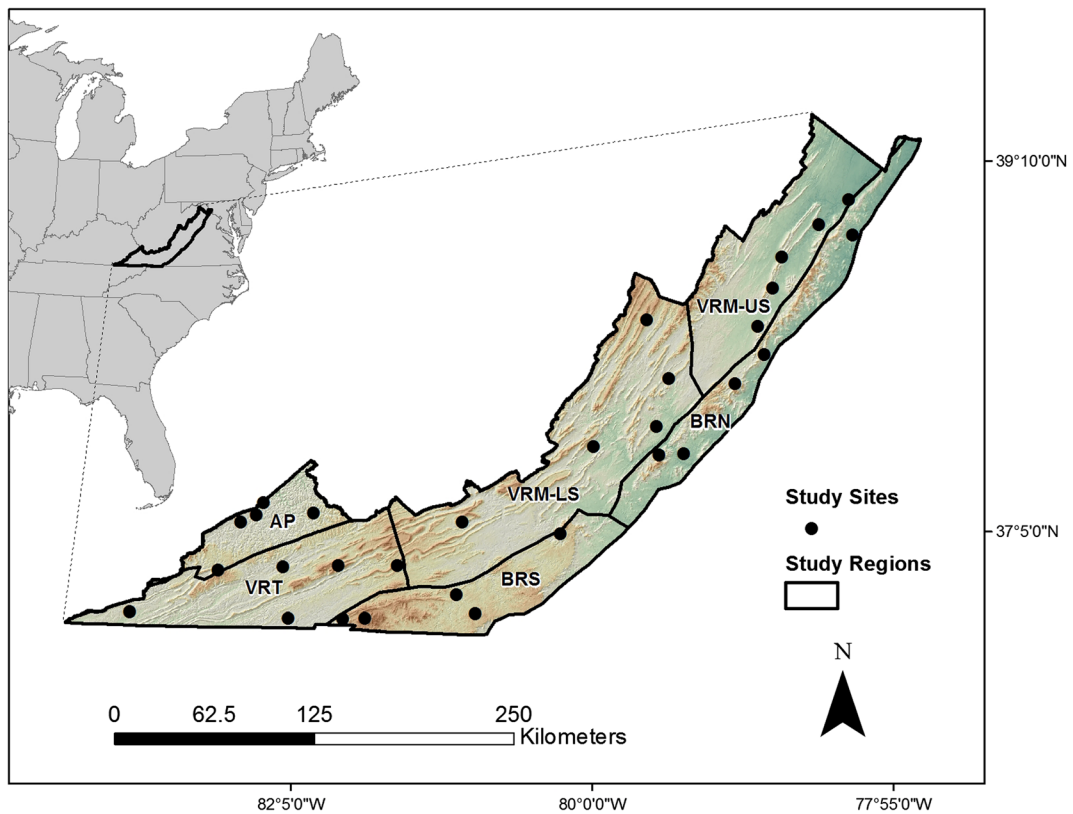
#### Data collection

We divided the study area into six sampling regions following the physiographic divisions of Fenneman (1938) within the Appalachian Mountains of Virginia: Appalachian Plateau, Blue Ridge Northern, Blue Ridge Southern, Valley and Ridge Tennessee, and Valley and Ridge Middle. We divided the Valley and Ridge Middle section into two study regions due to its size; the subdivision roughly followed the boundary of the Potomac and James River watersheds, which separate the upper and lower portions of the Shenandoah Valley (Fig. 1). We selected 30 sites, five sites within each of the six sampling regions, and sampled woody vegetation within forested areas along 20 transects at each site. We distributed sites across forest types and land use with forest and land use diversity metrics. We calculated a measure of local forest diversity by creating a  $30 \times 30$ -m grid where values were the sum of the number of forest types defined by the Northeastern Terrestrial Wildlife Habitat Classification (Gawler 2008) within a 1-km radius surrounding each grid cell. To improve comparability among regions, we reclassified forest types into the following groups prior to diversity calculations: floodplain, cove hardwood, mesic hardwood, oak-hickory, mixed pine-oak, pine, northern hardwood, and red spruce (*Picea rubens*)-Fraser fir (*Abies fraseri*). Based on the distribution of our derived cover types, we ranked locations with forest diversity

values  $\geq 4$  as high forest diversity, locations with a diversity value of 3 as moderate forest diversity, and areas with diversity values of  $\leq 2$  as low forest diversity (Kniewski and Ford 2017).

Similarly, we used the National Land Cover Dataset (Fry et al. 2011) to calculate land use diversity by creating a  $30 \times 30$ -m grid where values were the number of different land use classes within a 1-km radius surrounding each grid cell. Prior to the diversity calculation, we reclassified land use as water, residential, urban, forest, grassland, pasture, and row-crop. We ranked areas with land use diversity values of  $\geq 6$  as high, 4 or 5 as moderate, and areas  $\leq 3$  as low land use diversity. We categorized possible assessment sites within each region based on forest type and land use diversity values, selecting one site with each of the following combinations of forest and land use diversity: high forest, high land use; high forest, low land use; low forest, high land use; low forest, low land use; and moderate land use, moderate forest diversity. We defined or limited site boundaries to a circular area  $\leq 3 \text{ km}^2$  to limit intra-site variation in browsing intensity due to potential variations in local deer population density. Therefore, our sites were approximately the home range size of an individual deer or female (doe) group in the region (Halls 1984; Tierson et al. 1985; Campbell et al. 2004a).

To provide a topographically representative and spatially balanced herbivory sample, within each site, we randomly selected 20 transect locations within forested areas using a generalized random tessellation-stratified design (Stevens and Olsen 2004). We stratified locations among 12 topographic and landform criteria representing combinations of slope, topographic exposure, and aspect (Swanson et al. 1988; McNab 1993; Meilleur et al. 1994; Ford et al. 2000; Clinton 2003) (Table 1). We defined slopes  $\leq 20^\circ$  as low to moderate and those  $> 20^\circ$  as high. To assess topographic exposure, we used deviation from mean elevation (DEV) within a 500-m radius (De Reu et al. 2013) as the metric; positive values were higher than the surrounding mean elevation whereas negative values were lower than the surrounding mean (McNab 1993; Wilson and Gallant 2000; De Reu et al. 2013). We defined sheltered areas as those with a DEV  $< -0.7$  and exposed areas as those with a DEV  $> 0.7$ . We defined areas with DEV  $-0.7$  to  $0.7$  as moderately exposed. We defined aspects  $45^\circ$ – $225^\circ$  as southeast and aspects  $0^\circ$ – $45^\circ$  or  $225^\circ$ – $359^\circ$  as northwest. Due to the long, linear alignment of most ridges in the region, these



**Fig. 1** White-tailed deer (*Odocoileus virginianus*) herbivory study regions and assessment sites in the central Appalachian Mountains of Virginia, USA, summer 2014. Regions include Appalachian Plateau (AP), Blue Ridge Northern (BRN), Blue

Ridge Southern (BRS), Valley and Ridge Tennessee (VRT), Valley and Ridge Middle-Upper Shenandoah (VRM-US), and Valley and Ridge Middle-Lower Shenandoah (VRM-LS)

categories resulted in an aspect category for each dominant slope face. We oversampled random

transect locations within each strata and maintaining at least 100 m between any two transects.

**Table 1** Distribution of transects among topographic and landform criteria on white-tailed deer (*Odocoileus virginianus*) herbivory assessment sites in the central Appalachian Mountains of Virginia, USA, summer 2014

Strata criteria	N transects
Low to moderate slope, exposed landform, SE aspect	2
Low to moderate slope, exposed landform, NW aspect	2
Low to moderate slope, sheltered landform, SE aspect	2
Low to moderate slope, sheltered landform, NW aspect	2
High slope, exposed landform, SE aspect	2
High slope, exposed landform, NW aspect	2
High slope, sheltered landform, SE aspect	2
High slope, sheltered landform, NW aspect	2
Low to moderate slope, average landform, SE aspect	1
Low to moderate slope, average landform, NW aspect	1
High slope, moderate landform, SE aspect	1
High slope, moderate landform, NW aspect	1
Total	20

To minimize elevation changes along transects, we oriented transects perpendicular to the grade or randomly in more flat locations. Along each transect at each location, we measured browsing intensity assessing woody vegetation within 1-m<sup>2</sup> subplots. We only examined and tallied woody stems because these leave persistent evidence of browsing unlike herbaceous plant growth (Morellet et al. 2001; Frerker et al. 2013). Across evenly distributed subplots (every 5 m) along 50-m transects (10 per transect), we counted and identified to species the total number of woody stems between 0.2 and 1.8 m in height within each subplot and recorded the number of stems browsed. We used rough versus clipped browse scar patterns to distinguish between that of deer versus the few instances when we observed browsing by cottontail rabbits (*Sylvilagus* spp.; Morellet et al. 2001).

#### Data analysis

We calculated two factors for each transect and site that were used as dependent variables in analyses. These included the number or density of woody stems (stems m<sup>-2</sup>) as an estimate of woody forage availability and the proportion of stems browsed by deer as a measure of deer browsing intensity (browsed stems/total number of stems; browsing ratio; Castleberry et al. 1999; Frerker et al. 2013). Because deer browse vegetation preferentially (Nixon et al. 1970; Vangilder et al. 1982; Dostaler et al. 2011), we calculated the browsing ratio of each vegetation species within the study area and by region to provide an estimate of deer forage preference. As vegetation changes from deer herbivory may be affected by browsing preference, we also calculated browsing ratios and stem densities weighted by deer forage preference. To do so, we multiplied the vegetation stem count by the study-wide or regional browsing ratio for each vegetation species as provided by (Kniowski and Ford 2017) before calculation of the site or transect browsing ratio. This resulted in stems of plant species browsed frequently by deer being weighted more and those of vegetation species rarely browsed weighted less in stem count totals.

We assessed the relationships of deer herbivory patterns to geographical and land use configuration using linear mixed models with a random factor for

site to account for our nested study design (Bolker et al. 2009; Zuur et al. 2009). We centered coordinates and square-root transformed scale, stem densities, and browsing ratios prior to the analyses. We tested for a difference in forage availability between study regions and between site habitat diversity categories using Kruskal-Wallis rank sum tests (Zar 1984). We used nonparametric tests for comparisons between regions and habitat diversity categories because data were not normally distributed. We evaluated the relationship between the quantity of forage browsed and forage availability and browsing ratio and forage availability using least square regression at the site scale and linear mixed models at the transect scale with site as a random factor. We log-transformed the number of stems, number of browsed stems, and number of available stems prior to analyses whereas the browsing ratio was square-root transformed. We used  $R^1$  (Version 3.2.3, [www.r-project.org](http://www.r-project.org), accessed 12 Dec 2015) to calculate statistical tests; packages “lme4” (Version 1.1-10, <https://cran.r-project.org/package=lme4>, accessed 10 Oct 2015), “MuMIn” (Version 1.15.6, <https://cran.r-project.org/package=MuMIn>, accessed 12 Dec 2015), and “multcomp” (Version 1.4-1, <https://cran.r-project.org/package=multcomp>, accessed 23 Aug 2015) were used in mixed model calculations. Pseudo r-squared values were calculated using the methods of Nakagawa and Schielzeth (2013).

To assess spatial patterns of deer herbivory, we estimated the variability of deer browsing intensity and the variability of foraging within each site by computing the coefficient of variation (CV; Zar 1984) of the browsing ratio, the weighted browsing ratio and number of stems and weighted stems, respectively, on transects. We compared site browsing intensity variation and vegetation density variation between study regions and between categories of site habitat diversity using Kruskal-Wallis rank sum tests. We used least square regression to evaluate the relationship between the variability of site browsing intensity and site forage availability, forage availability variation and site browsing ratio, browsing intensity variability and site browsing ratio, forage availability variation and site forage

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availability, and forage availability variation and browsing intensity variation.

To evaluate the extent of spatial relatedness of transect stem densities and browsing ratios, we calculated spatial autocorrelation and semi-variance statistics (Isaaks and Srivastava 1989; Fortin and Dale 2009). We used correlograms and semi-variograms to visualize how autocorrelation and semi-variance change with separation distance. We used package “nfcf” (Version 1.1-6, <https://cran.r-project.org/package=nfcf>, accessed 7 Dec 2015) in *R* to calculate autocorrelation statistics and assess correlation significance in 250 m distance class increments for separation distances 0–2 km and in 10 km distance class increments for separation distances 5–200 km. We used package “gstat” (Version 1.1-0, <https://cran.r-project.org/package=gstat>, accessed 18 Oct 2015) in *R* to calculate and fit semi-variance models.

To evaluate the influence of sampling effort on site browsing ratio and stem density estimates, we used Monte Carlo simulations to mimic different amounts of sampling effort. For each simulation, we computed the absolute difference of the mean browsing ratio of a random subset of transects to the mean browsing ratio of all 20 transects on a site. We varied the number of transects in the subset from 2 to 19 to simulate different levels of sampling effort resulting in 18 simulations per site. We iterated each simulation 1000 times and recorded the standard deviation and mean difference for each level of sampling effort for all sites.

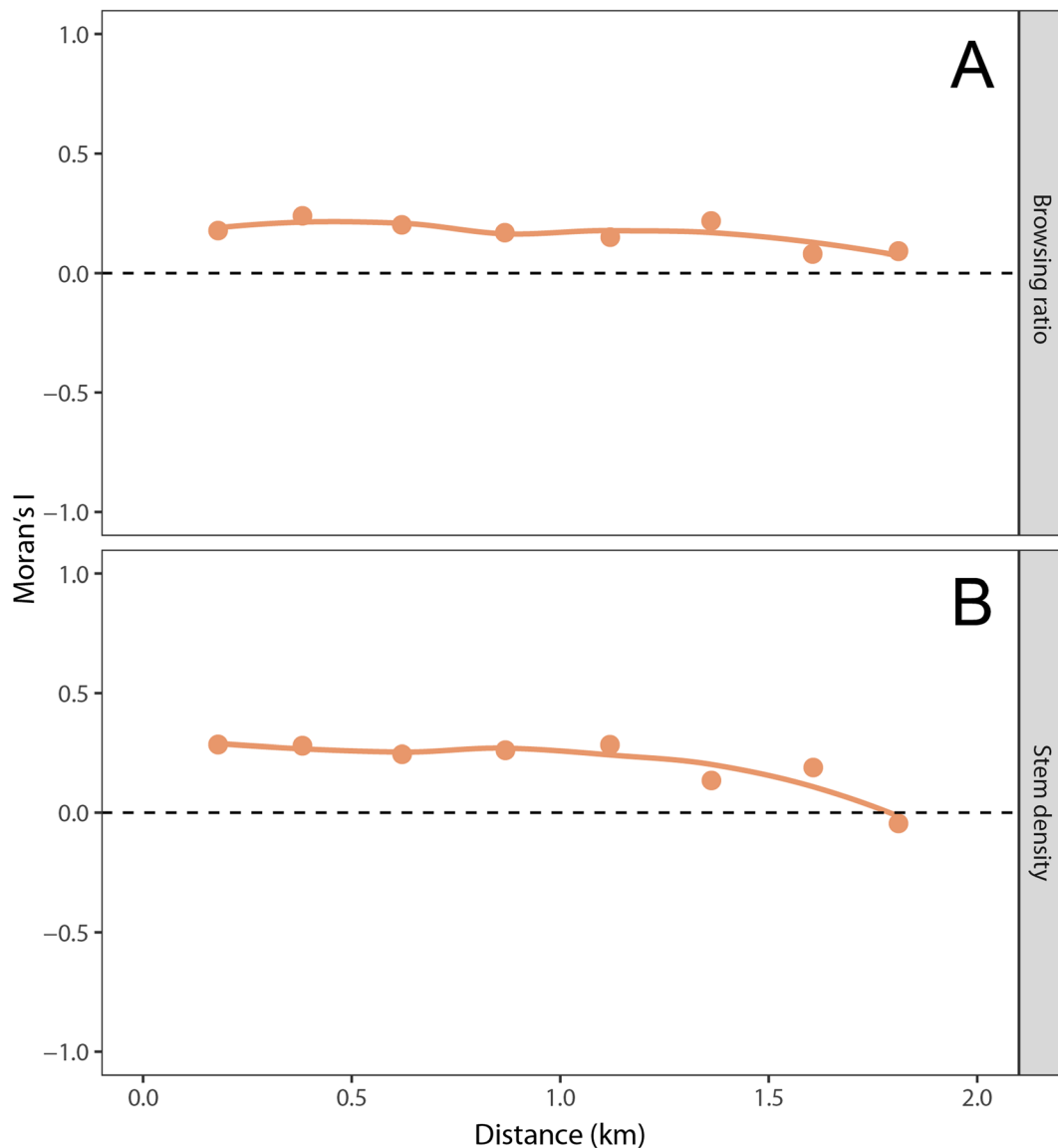
## Results and discussion

### Results

Overall, browsing ratios varied considerably among the 82 individual woody plant species and/or species groups as well as overall totals we documented study-wide. There were no significant differences between the number of woody stems on sites among regions or diversity categories ( $P \geq 0.177$ ). There was a positive relationship between the number of stems that were browsed on a site and the total number of stems available on the site ( $r^2_{\text{adjusted}} = 0.24$ ,  $\beta = 0.52$ ,  $F_{1, 28} = 10.39$ ,  $P = 0.003$ ). The relationship increased in strength for weighted

stems ( $r^2_{\text{adjusted}} = 0.42$ ,  $\beta = 0.61$ ,  $F_{1, 28} = 21.99$ ,  $P < 0.001$ ;  $r^2_{\text{adjusted}} = 0.64$ ,  $\beta = 0.87$ ,  $F_{1, 28} = 53.41$ ,  $P < 0.001$ ; for study-weighted and regionally weighted stem counts, respectively). There was a positive relationship between the number of browsed stems on individual transects and the total number of stems on transects (pseudo- $r^2_{\text{marginal}} = 0.29$ ,  $\beta = 0.61$ , 95% CI = 0.53 to 0.69). The relationship between the number of browsed stems on an individual transect and weighted stem counts was stronger than unweighted stems (pseudo- $r^2_{\text{marginal}} = 0.50$ ,  $\beta = 0.98$ , 95% CI = 0.90 to 1.06; pseudo- $r^2_{\text{marginal}} = 0.56$ ,  $\beta = 0.98$ , 95% CI = 0.90 to 1.05, for study-wide and regionally weighted stem counts, respectively). There was a negative relationship between the site browsing ratio and the total number of stems available on a site for unweighted stems ( $r^2_{\text{adjusted}} = 0.24$ ,  $F_{1, 28} = 10.24$ ,  $P = 0.003$ ,  $\beta = -0.13$ ), but no relationship with weighted stem counts ( $P \geq 0.108$ ). There was a weak negative relationship between the browsing ratio on an individual transect and total number of stems on a transect (pseudo- $r^2_{\text{marginal}} = 0.01$ ,  $\beta = -0.03$ , 95% CI = -0.06 to -0.01). We observed a positive relationship between the transect browsing ratio and weighted stem counts (pseudo- $r^2_{\text{marginal}} = 0.05$ ,  $\beta = 0.09$ , 95% CI = 0.06 to 0.13; pseudo- $r^2_{\text{marginal}} = 0.07$ ,  $\beta = 0.11$ , 95% CI = 0.08 to 0.14) for study-wide and regionally weighted stem counts, respectively.

There was no difference in intra-site browsing intensity variation among study regions or site diversity categories ( $P \geq 0.15$ ). Likewise, there was no difference in study-wide or regionally weighted intra-site browsing variation across study regions or site diversity categories ( $P \geq 0.35$ ). Intra-site stem density variation and intra-site weighted stem density variation also did not vary among study regions or site diversity categories ( $P \geq 0.08$ ). There was no relationship between site browsing variation and stem density ( $P = 0.68$ ) or site stem density variation and site browsing ratio ( $P = 0.23$ ). However, there was a negative relationship between site browsing variation and site browsing ratio ( $r^2_{\text{adjusted}} = 0.50$ ,  $F_{1, 28} = 29.5$ ,  $P < 0.001$ ) and site stem density variation and site stem density ( $r^2_{\text{adjusted}} = 0.30$ ,  $F_{1, 28} = 14.2$ ,  $P < 0.001$ ). That is, sites with high intensities of herbivory were browsed more uniformly and sites



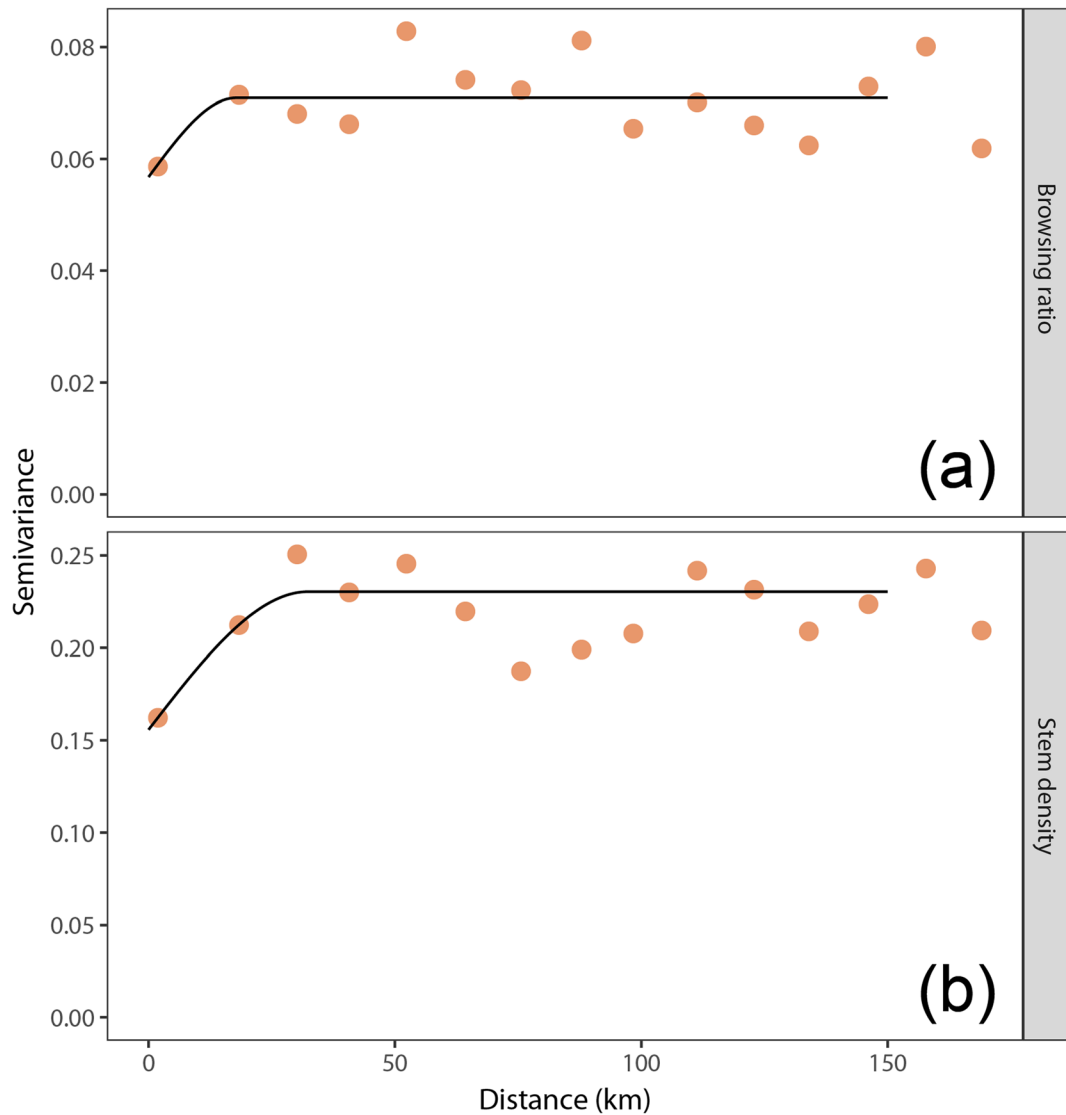
**Fig. 2** Correlograms of woody vegetation browsing ratios (a) and stem densities (b) among transects at white-tailed deer (*Odocoileus virginianus*) herbivory assessment sites in the central

Appalachian Mountains of Virginia, USA, summer 2014. Trend lines are loess smoothed fit of the autocorrelation values

with higher densities of woody stems had less intra-site variation in woody stem density. There was no relationship between the variation in the number of woody stems and the variation in browsing intensity ( $P = 0.97$ ).

Transect stem densities were autocorrelated ( $P < 0.05$ ) at separation distances  $< 1800$  m (Fig. 2a). We found stem density autocorrelation near zero across separation distances  $\geq 5$  km, although scattered classes

statistically were significant. Similarly, browsing ratios were autocorrelated at separation distances  $< 1600$  m (Fig. 2b), but were near zero at separation distances  $\geq 5$  km, although scattered classes statistically were significant. There was little spatial dependence in stem counts or browsing ratios beyond the site scale (Fig. 3). Large nugget variance and small sill for both stem counts and browsing ratios suggested that spatial dependence was low across all distance classes and



**Fig. 3** Semi-variograms for woody vegetation browsing ratios (a) and stem densities (b) among transects at white-tailed deer (*Odocoileus virginianus*) herbivory assessment sites in the central Appalachian Mountains of Virginia, USA, summer 2014

accounted for only 32 and 21% of the variation at the shortest distance class (approximately 1900 m), respectively (Table 2). There was little spatial

dependence beyond separation distances of approximately 29 and 16 km for stem counts and browsing ratios, respectively.

**Table 2** Statistics for semi-variogram model fits for woody stem density and browsing ratios on white-tailed deer (*Odocoileus virginianus*) herbivory assessment sites in the central Appalachian Mountains of Virginia, USA, summer 2014. The proportion

spatially structured (PSS) is the proportion of the sample variance that is explained by spatial structure (Isaaks and Srivastava 1989; Didier and Porter 2003)

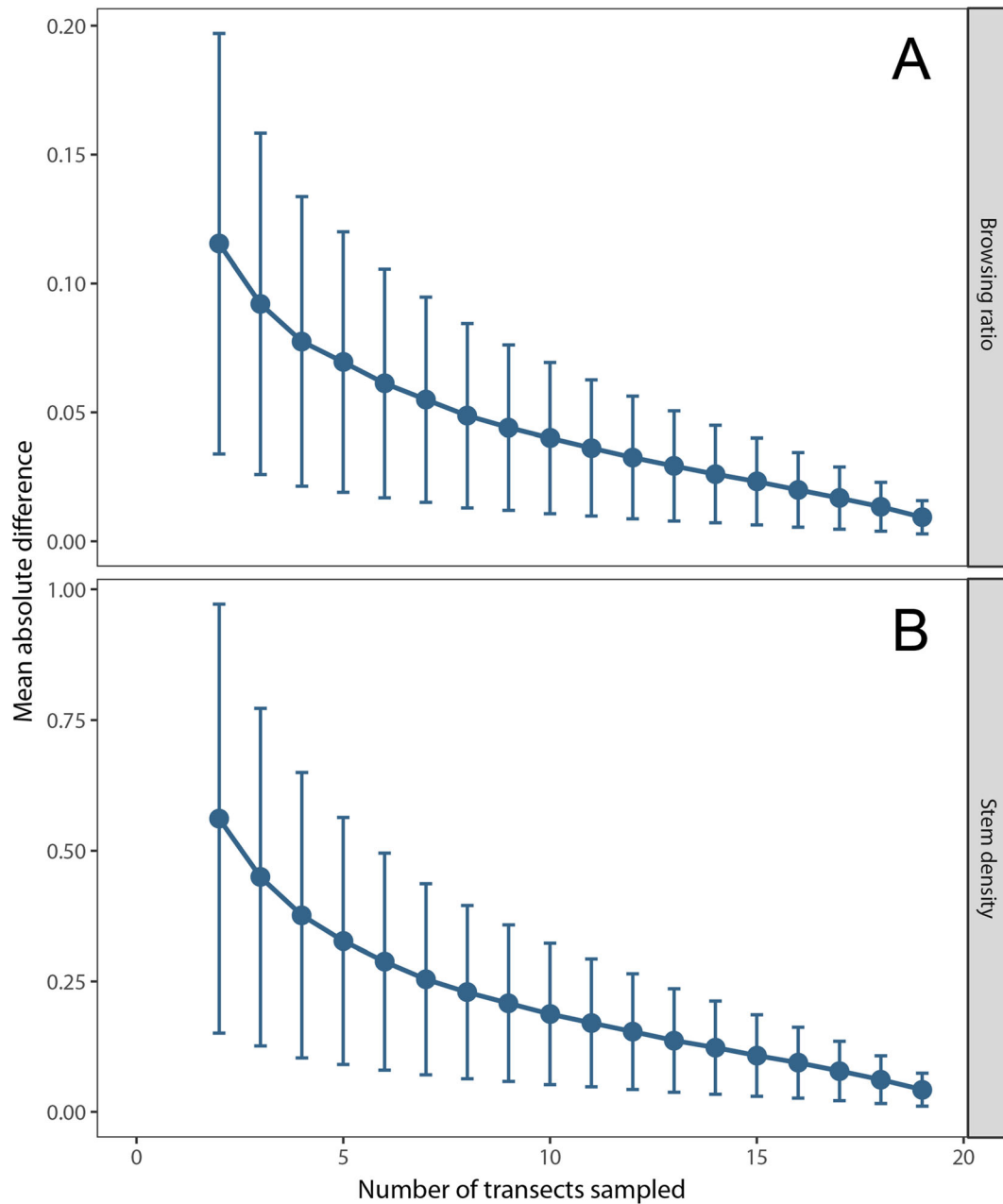
Dataset	Model	Nugget	Sill	PSS	Range (m)
Woody density	Spherical	0.156	0.229	0.322	28,913
Browsing ratio	Spherical	0.056	0.071	0.212	16,371



Although browsing intensity and stem densities were variable across sites, on average, the mean of  $\geq 3$  transects within a site was within 0.1 of the site mean browsing ratio and 0.5 stems  $m^{-2}$  (Fig. 4). All regions followed a similar sampling effort trend for both browsing ratios and stem densities. Accordingly, estimate accuracy was similar among regions.

Discussion

Spatial patterns of deer herbivory unexpectedly were consistent across our large study area. Herbivory patterns and the availability of woody forage generally were unchanged among physiographic regions and land use diversity classes. Contrary to our hypothesis, we



**Fig. 4** Mean ( $\pm$  SD) absolute difference of woody vegetation browsing ratios (a) or woody vegetation stem densities (b) from Monte Carlo simulations of reduced sampling on sites compared

to the mean calculated from all 20 transects on white-tailed deer (*Odocoileus virginianus*) herbivory assessment sites in the central Appalachian Mountains, Virginia, USA, summer 2014

found no evidence that deer in different physiographic provinces and sub-divisions or habitat conditions use different browsing strategies or display alternate herbivory patterns. Deer are highly adaptable herbivores, yet they browse selectively, choosing some vegetation species preferentially within local areas (Nixon et al. 1970; Vangilder et al. 1982; Dostaler et al. 2011). Although the availability of particular vegetation species and understory communities change substantially across the study area, deer appear to switch among available forage species in their local area to maintain a “consistent” herbivory pattern spatially which may simplify assessment protocols.

The spatially consistent herbivory patterns we observed study-wide included some relationships that do and some that do not change with scale. The total quantity (not proportion) of vegetation browsed on a site and on the transect scale were related positively to the availability of forage. For decades regionally, forage management strategies, such as forest harvesting and food plot establishment, have been used to move or concentrate deer herbivory within the landscape by creating patches of available, high-density browse in the Appalachians (e.g., Johnson et al. 1995; Campbell et al. 2004a; Miller et al. 2009; Crimmins et al. 2010). Optimal foraging theory suggests that deer may consume more vegetation at these locations if it is energetically or nutritionally beneficial (Schoener 1971; Senft et al. 1987). Our study supports the observation that deer will consume more vegetation in areas with greater amounts of browse available. Notably, our results suggest this relationship is stronger where the available browse is a type preferred by deer. As a result, how vegetation succession could develop over time under the anticipated herbivory intensity may provide additional considerations relative to management goals and habitat needs of deer and other wildlife (Johnson et al. 1995; Belote et al. 2012).

The proportion of stems browsed suggests an alternate and scale-dependent relationship with stem density. Although the proportion of stems browsed decreased as stem density increased at both the site and transect scales, this was true only when all stems were considered equally as seen elsewhere in the central Appalachians (Campbell et al. 2006). Where stem densities were weighted for deer preference, the browsing ratio had no relationship with stem density at the site scale and increased with density at the transect scale. This highlights the scale-dependent and selective nature of deer browsing and the complexity of evaluating

herbivory impacts (Ford et al. 1993). Our data are consistent with the supposition that increasing forage availability would result in a smaller proportion of the vegetation browsed in general (Johnson et al. 1995; Crimmins et al. 2010). However, when the forage preference of deer also is considered, our data suggest that increasing the density of a preferred browse species would not necessarily reduce the proportion of that species consumed on a site and actually may lead to an increase of the proportion browsed at smaller scales. As a result, attempts to reduce browsing rates on a preferred browse species by increasing its availability may not be viable without careful consideration of the relationship between herbivory of the browse species and the local to perhaps the county-level deer density.

Intra-site spatial browsing uniformity was consistent across the study area. For example, intra-site variation in browsing intensity did not change across land use diversity classes. This is in contrast to our hypothesis that sites with more uniform habitats are browsed more uniformly than sites with diverse habitats and land use classes. Secondly, we found no relationship between deer browsing intensity variation and stem density variation. That is, patchy distribution of stems did not result in patchy distribution of browsing. This reflects small-scale browsing selectivity by deer suggesting that there may not be a correlation between factors that affect browsing variation and those that affect the variation in stem densities. Because there is a strong relationship between site browsing variation and browsing intensity, our data suggest that the spatial pattern of deer herbivory may be associated more directly with the relative deer population density than environmental or vegetative conditions as noted by others (deCalesta and Stout 1997; Augustine et al. 1998; Royo et al. 2010a; Royo et al. 2010b).

Deer herbivory has direct effects on particular vegetation species, forest communities, and understories, and indirect effects on many other plants and organisms (Augustine and Frelich 1998; Russell et al. 2001; Rooney and Waller 2003; Côté et al. 2004; Koh et al. 2010). The spatial patterns of herbivory observed in our study suggest that these effects require consideration of spatial context to be understood fully. Deer are spatially as well as vegetatively selective browsers, but observations and assessments are scale-dependent, reflecting in part deer biology in addition to habitat conditions. Koda and Fujita (2011) found that there is a nonlinear relationship between deer density and herbivory of forest vegetation, a result of switching diet and browse species

at different population densities. That is, deer may exhibit density-dependent forage selectivity such that less-preferred food being consumed at greater rates due to availability at that moment of consumption or because interactions with conspecifics alter how and where deer forage. Our data suggest that preferred browse species would not escape herbivory by deer even in areas with ample quantities of alternate browse. Frerker et al. (2013) found that browsing ratios provide reliable indices of ungulate impacts in the Great Lakes region; however, our data suggest conservation of particular plant species may need special, direct attention where deer are present. Despite these complexities and although our study does not examine causal factors, the spatial uniformity of browsing in areas with low stem densities found in our study posits a mechanism to explain the herbivory pattern whereby areas become steady-state, species depauperate “deer savannas” or “fern parks” (Stromayer and Warren 1997; Augustine et al. 1998; Rooney 2001).

There is ample evidence that vegetation in areas that experience high levels of browsing intensity over long periods can be altered significantly, reducing plant diversity (Stromayer and Warren 1997; Côté et al. 2004; Royo et al. 2010b). Because of this and because deer are spatially selective browsers, management seeking to preserve biodiversity must address the browsing intensity of the present deer herd regardless of the adequacy of available food sources in maintaining herd health. Vegetative communities shaped by high levels of herbivory can be slow to recover even if herbivory intensity is reduced, thereby resulting in legacy impact to biodiversity (Stromayer and Warren 1997; Augustine et al. 1998; Baiser et al. 2008; Royo et al. 2010b). As a result, deer management focused solely on maintaining deer health or herd density likely will not address preservation of biodiversity (McShea 2012).

## Conclusion

Our results have several implications for deer herbivory impact assessments and understanding and applying them to deer management. First, our results provide one of the first examinations of the spatial variability of deer herbivory across landscapes. Particularly, our results reflect a landscape more complex in topography and associated spatial variability in vegetation communities not present in many other studies of deer herbivory

(e.g., Augustine and Frelich 1998; Castleberry et al. 1999; Horsley et al. 2003; Wiegmann and Waller 2006; Goetsch et al. 2011). With improved spatial information, managers have improved capacity to assess the usefulness of available herbivory metrics based on the management scale at question, which for managing deer harvest in the Appalachian Mountains of Virginia, as well as surrounding states, occurs at the county to sub-region level. Understanding both the management scale and the variability of herbivory can inform decisions on sampling intensity needed at the local to county-level to meet management needs and goals. Managers increasingly are called upon to manage holistically for biodiversity and ecosystems rather than one or a few species. By employing an informed, multi-scale approach to the assessment and understanding of deer herbivory and resulting environmental effects, managers will have improved ability to manage for the diverse desires of stakeholders, such as hunters who desire more deer versus foresters or agriculturalists who desire fewer deer.

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