

# Predicting intensity of white-tailed deer herbivory in the Central Appalachian Mountains

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**Abstract** In eastern North America, white-tailed deer (*Odocoileus virginianus*) can have profound influences on forest biodiversity and forest successional processes. Moderate to high deer populations in the central Appalachians have resulted in lower forest biodiversity. Legacy effects in some areas persist even following deer population reductions or declines. This has prompted managers to consider deer population management goals in light of policies designed to support conservation of biodiversity and forest regeneration while continuing to support ample recreational hunting opportunities. However, despite known relationships between herbivory intensity and biodiversity impact, little information exists on the predictability of herbivory intensity across the varied and spatially diverse habitat conditions of the central Appalachians. We examined the predictability of browsing rates across central Appalachian landscapes at four

environmental scales: vegetative community characteristics, physical environment, habitat configuration, and local human and deer population demographics. In an *information-theoretic* approach, we found that a model fitting the number of stems browsed relative to local vegetation characteristics received most (62%) of the overall support of all tested models assessing herbivory impact. Our data suggest that deer herbivory responded most predictably to differences in vegetation quantity and type. No other spatial factors or demographic factors consistently affected browsing intensity. Because herbivory, vegetation communities, and productivity vary spatially, we suggest that effective broad-scale herbivory impact assessment should include spatially-balanced vegetation monitoring that accounts for regional differences in deer forage preference. Effective monitoring is necessary to avoid biodiversity impacts and deleterious changes in vegetation community composition that are difficult to reverse and/or may not be detected using traditional deer-density based management goals.

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## Introduction

Ungulates play a major role in forested ecosystems (Hobbs 1996; Russell et al. 2001; Rooney and Waller 2003) and, as a result of changes in habitat conditions and decreases in predator populations, ungulates exert increasingly negative effects on forest biodiversity and forest successional processes (Horsley et al. 2003; Côté et al. 2004; McShea 2005, 2012; DiTommaso et al. 2014). In eastern North

America, white-tailed deer (*Odocoileus virginianus*) (hereafter deer) affect forest ecosystems in many ways, including directly by browsing that changes growth rate, development, survival, and succession of plants as well as overall community composition (Russell et al. 2001), and indirectly through a cascade of impacts to other organisms affected by changes in the plant community. For example, impacts of deer affect bird communities, small mammals, and invertebrates (Côté et al. 2004).

Similar to other regions, deer populations in central Appalachian have fluctuated widely over the past century. Following widespread deer extirpation by the early twentieth century, reintroductions, harvest management, and habitat change, i.e., reforestation and farm abandonment since have led to relatively high deer populations (Halls 1984). Moderate to high deer populations over the past 20–30 years have reduced forest biodiversity and created legacy effects in some areas even where populations have been reduced (Royo et al. 2010; McShea 2012; Tanentzap et al. 2012). Changes in forest management practices, e.g., reductions in timber harvest on public lands, an increase in intensity of harvest on corporate lands, and changed hunter effort, also have contributed to changes in deer densities and forage availability (Campbell et al. 2006; Ford et al. 1993). In the central Appalachians portion of Virginia, wildland management is directed at biodiversity conservation, forest regeneration, and maintenance of sufficient deer numbers to satisfy recreational hunting demands (Virginia Department of Game and Inland Fisheries 2015). To be successful, these efforts require not only understanding of deer herbivory impacts but also of how herbivory varies regionally along environmental gradients and spatial scales. Generally, the effects of deer herbivory have been described well (Rooney 2001; Russell et al. 2001; Rooney and Waller 2003; Côté et al. 2004) and several metrics to assess the intensity of herbivory have been suggested, such as proportion of stems browsed and status of indicator species (Morellet et al. 2001, 2007; Koh et al. 2010; Frerker et al. 2013). Although these measures of herbivory impact might be valuable within appropriate contexts, some are difficult for managers to broadly apply across landscapes. For example, indicator species may not be present similarly across different habitat configurations and varied vegetation communities, or metrics may be validated only under certain habitat configurations (Morellet et al. 2007). Within a state or province, including Virginia, deer populations generally are managed on sub-regional or county scales. Yet, the effects of deer herbivory can vary substantially within local areas, such as within parks or other protected areas where hunting is not allowed or conversely within management areas where hunting occurs. Variations in deer harvest, predation, and land use further contribute to local variation in deer herbivory

effects. Because of this, predicting the relationship between deer herbivory intensity and spatial factors, such as landscape arrangement and land use, would provide valuable information for managers seeking to assess and monitor herbivory effects across landscapes.

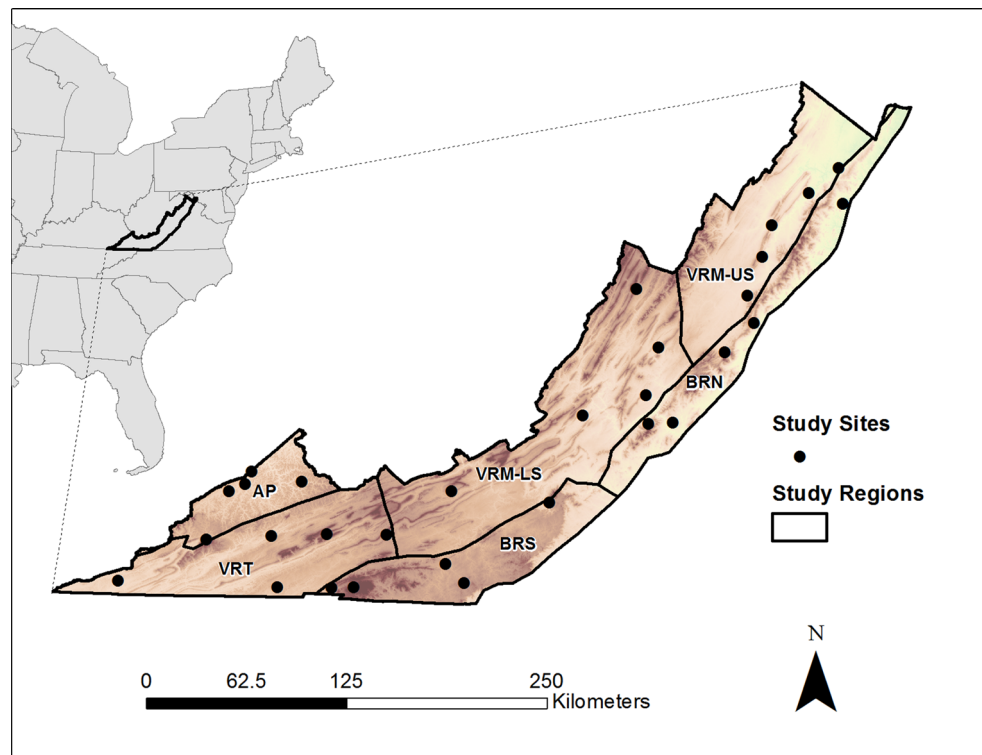
Frerker et al. (2013) reported that a more applicable metric, browsing rate or browsing ratios, provides a reliable indicator of ungulate impact in forest plant communities. Kniewski and Ford (2017) examined the spatial patterns of deer herbivory across central Appalachian forested landscapes and reported remarkable consistency across varied landscape contexts and large geographic areas. Nonetheless, little information exists regarding the predictability of herbivory intensity across most landscapes (but see Augustine and Jordan 1998; Campbell et al. 2006). Herein, we examine the predictability of browsing rates across central Appalachian landscapes regarding four distinct aspects of spatial location: vegetative condition, physical environment, habitat arrangement, and local demographics. A priori, we hypothesized that vegetative condition, i.e., composition and structure, would be the strongest predictor of browsing intensity. However, because deer often are most abundant near anthropogenically altered landscapes (Halls 1984; Augustine and Jordan 1998; Kilpatrick and Spohr 2000), we predicted that habitat configuration would be useful in predicting herbivory intensity and that habitat arrangement factors would have a stronger relationship with browsing intensity than physical environment. Knowledge of the role of these factors in deer herbivory could enable forest managers to plan for herbivory impacts on forest systems, particularly when planning harvest and regeneration or restoration actions.

## Methods

### Study area

Our study area was located in the central Appalachian Mountains of western Virginia, USA. We divided the study area into six sampling regions following physiographic divisions: Appalachian Plateau, Blue Ridge Northern, Blue Ridge Southern, Valley and Ridge within the Tennessee River drainage, and Valley and Ridge Middle (Fenneman 1938). We divided the Valley and Ridge Middle section into two sub-study regions because of its size and considerable latitudinal extent; the subdivision roughly followed the boundary of the Potomac and James River watersheds that separates the upper and lower portions of the Shenandoah Valley (Fig. 1). Throughout, elevations range from approximately 200–1700 m. Generally, Valley and Ridge and, to a lesser extent, the Blue Ridge regions are characterized by long mountain ridges with moderate to

**Fig. 1** White-tailed deer (*Odocoileus virginianus*) herbivory study regions and assessment sites in the central Appalachian Mountains, Virginia, USA, summer 2014. Regions are: Appalachian plateau, AP; Blue Ridge Northern, BRN; Blue Ridge Southern, BRS; Valley and Ridge Tennessee River Drainage, VRT; Valley and Ridge Middle-Upper Shenandoah, VRM-US; and Valley and Ridge Middle-Lower Shenandoah, VRM-LS



steep side slopes and narrow to moderately broad valleys. The Appalachian Plateau is characterized by rugged terrain with steep slopes and very narrow valleys. Landforms in the Appalachian Plateau generally display a dendritic pattern, although local relief generally is less than that of the Valley and Ridge or Blue Ridge. The entire study area predominately is forested (67%), intermixed with pasture or hay production in the valleys (22%), and limited areas of row-crop agriculture, residential, and urban development (Homer et al. 2015). However, the Appalachian Plateau is more forested (79%), has limited pasture or hay production (4%), and no row-crop agriculture. Dominant forest types are xeric oak (*Quercus* spp.) and mixed pine (*Pinus* spp.) with scattered, smaller patches of “cove” or other mesic hardwoods, and northern hardwoods depending on region, aspect, and elevation. Forests >1200 m in elevation in some locations support stands dominated by red spruce (*Picea rubens*) (Simon 2011, 2013).

### Field data collection

We selected five sites within each of the six sampling regions for a total of 30 sites where we sampled woody vegetation within forested areas along 20 transects at each site. We distributed sites across a range of habitat and land use configurations using a combination of landscape diversity metrics. To facilitate the site distribution, we calculated a measure of local forest diversity by creating a

30 × 30 m grid where values were the sum of the number of forest types defined by the Northeastern Terrestrial Wildlife Habitat Classification System (NETWHCS; Gawler 2008) within a 1 km radius surrounding each grid cell. Forest types were reclassified into 8 types prior to diversity calculation to allow better comparability across sampling regions: cove hardwood, xeric oak, floodplain, mesic hardwood, mixed pine, northern hardwood, pine, and spruce-fir (*Abies* spp.). We ranked locations with forest diversity values  $\geq 4$  as high forest diversity; locations with a diversity value of 3 as average forest diversity; and areas with diversity values of 1 or 2 as low forest diversity. Similarly, we used the National Land Cover Dataset (NLCD; Fry et al. 2011) to calculate a measure of land use diversity by creating a 30 × 30 m grid where values were the number of different land use classes within a 1 km radius surrounding each grid cell. Land use classes were reclassified prior to diversity calculation into 7 land cover types: water, residential, urban, forest, grass or swampland, pasture, and row-crop. We ranked areas with land use diversity values  $\geq 6$  as high land use diversity; areas with diversity values of 4 or 5 as average; and areas with diversity values  $\leq 3$  as low. We identified and categorized possible assessment sites within each region based on their combination of forest and land use diversity values. Within available locations, we selected one site in each of the following combinations of forest and land use diversity: high forest and high land use; high forest and low land use;

low forest and high land use; low forest and low land use; and average land use, average forest diversity. We defined or limited herbivory assessment site boundaries to a  $\leq 3$  km<sup>2</sup> circular area to limit intra-site variation in browsing intensity due to variations in local deer population density; sites of this size approximate the home range of an adult deer in the central Appalachians and an individual deer present on a site could access all areas of the site assuming normal movement patterns (Halls 1984; Tierson et al. 1985; Campbell et al. 2004).

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 six topographic and landform criteria; further subdividing the criteria into two aspect classes for a total of 12 strata classes (Table 1). Where strata were not present within a site, we assigned transect locations to an available alternate stratum. We defined low to moderate slope as slopes  $\leq 20^\circ$ , and steep slopes as slopes  $> 20^\circ$  and we used deviation from mean elevation (DEV) within a 500 m radius (De Reu et al. 2013) as a measure of topographic exposure; positive values indicate the location is higher and negative values indicate the location is lower than the mean elevation of the area (McNab 1993; Wilson and Gallant 2000; De Reu et al. 2013). We defined sheltered landforms as locations with a DEV  $< -0.7$ , and exposed landforms as those with a DEV  $> 0.7$  with average landforms as those not strongly exposed or sheltered ( $-0.7 \leq \text{DEV} \leq 0.7$ ). We defined southeast aspects as aspects between  $45^\circ$  and  $225^\circ$  and northwest aspects as aspects between  $0^\circ$  and  $45^\circ$  or

between  $225^\circ$  and  $359^\circ$ . These aspect categories typically split along ridgelines in the study area resulting in an aspect category for each dominant slope face. We oversampled random transect locations within each stratum and, as needed, selected alternate random locations within the strata to maintain a minimum distance of 100 m between any two transects.

We oriented transects perpendicular to the terrain slope to minimize elevation changes along transects or in a random direction if the location had no obvious slope. At each transect location, forest age was categorized visually by estimating the average diameter at breast height (dbh) of the largest trees within the stand as young, approximately  $< 20$  cm dbh; intermediate, approximately  $\geq 20$  to  $\leq 50$  cm dbh; and mature, approximately  $> 50$  cm dbh (DeGraaf et al. 1992). Likewise, we visually classified overstory density at each transect location as: open, moderate, or closed (Young et al. 1967). We recorded recent (within the past year) forest management activities encompassing transects as burned, harvested, burned and harvested, or none. We categorized forest type at each transect broadly as one of the following types (modified from Braun 1974): spruce-fir, dominated by red spruce and/or Fraser fir (*Abies fraseri*); northern hardwood, dominated by American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*) and black cherry (*Prunus serotina*); upland oak or mixed hardwood, dominated by oak species, and other hardwoods such as hickory (*Carya* spp.), red maple (*Acer rubrum*) and blackgum (*Nyssa sylvatica*); cove hardwood dominated by yellow poplar (*Liriodendron tulipifera*), American basswood (*Tilia americana*), and northern red oak (*Q. rubra*); pine-hemlock, dominated by eastern hemlock (*Tsuga canadensis*) and white pine (*Pinus strobus*); mixed pine-hardwood, dominated by various yellow pines and white pine along with hardwood associates from the upland hardwood community; valley white oak, dominated by white oak (*Q. alba*) but often with other oaks, black walnut (*Juglans nigra*), and blackgum; riparian/floodplain, dominated by American sycamore (*Platanus occidentalis*) and black walnut (*Juglans nigra*).

We evaluated the browsing intensity of deer along each transect by assessing woody vegetation within 1 m<sup>2</sup> subplots by only evaluating woody stems because these display persistent and conspicuous evidence of browsing whereas herbaceous vegetation is ephemeral, the whole plant can be consumed, and plants more easily are damaged by non-browsing events (Frerker et al. 2013). We distributed subplots evenly (every 5 m) along 50 m transects (10 per transect) and then counted and identified the total number of woody stems between 0.2 and 1.8 m in height within each subplot by vegetation species and also recorded the number of stems that had been browsed by deer. Although browsing by species other than deer rarely

**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, average landform, SE aspect	1
High slope, average landform, NW aspect	1
Total	20

SE southeast, NW northwest



was encountered, we were careful to differentiate between the coarse browse scars resulting from the browsing of deer from clean cut stems resulting from the browsing of rabbits (*Sylvilagus* spp.) or rodents (Morellet et al. 2001).

### Spatial data and modeling

We extracted spatial factors for each transect from geographical information system (GIS) layers using *ArcMap*<sup>1</sup> (Version 10.3.1, Environmental Systems Research Institute, Redlands, CA). Physical environment factors, including elevation, DEV, slope (in degrees), and aspect (linearized using the transformation  $[1 - \cos(\text{aspect})] + [1 - \sin(\text{aspect})]$ ), were obtained or derived from the United States Geological Survey (USGS) National Elevation Dataset (<http://nationalmap.gov/>; accessed 9 September 2015) at 1/3 arc-second resolution. We used the Virginia geologic map dataset from the USGS Mineral Resources spatial data repository (<http://mrddata.usgs.gov/geology/state/>; accessed 29 August 2015) to obtain bedrock type. To calculate landscape and habitat arrangement factors for each transect, we used *FRAGSTATS* (version 4.2, <http://www.umass.edu/landeco/research/fragstats/fragstats.html>). We calculated three metrics for land use types, including edge density, mean radius of gyration (a measure of patch extent), and Simpson's diversity index (diversity of land use), and three metrics exclusively for forest land use, including edge density, mean radius of gyration, and patch cohesion index (a measure of the physical connectedness of patches; patch cohesion increases as the patch type becomes more clumped or aggregated in its distribution) (McGarigal et al. 2012). We calculated all landscape and habitat arrangement factors at two spatial scales, 1 and 5 km radius circular areas surrounding each transect. Additionally, for each transect, we calculated the distance to the nearest forest edge (defined as any non-forest land use type by the NLCD) for a total of 13 landscape and habitat arrangement factors. Demographic factors included human population density estimates for 2014 by county or city from U.S. Census Bureau data and 2014 deer harvest density by county or city (Virginia Department of Game and Inland Fisheries 2015). We considered including the decadal average deer harvest density and the coefficient of variation (Zar 1984) of the decadal deer harvest density in models; however, both factors highly were correlated ( $>0.82$ ) with either the 2014 human population density or the 2014 harvest density. In addition to the vegetation characteristics recorded in the field, we used tree canopy cover from the NLCD tree cover dataset to provide further

description of forest condition (Homer et al. 2015). Because deer browse vegetation preferentially (Nixon et al. 1970; Vangilder et al. 1982; Crimmins et al. 2010; Dostaler et al. 2011), we calculated a measure of average vegetation preference for each transect. To do so, we multiplied stem counts for each vegetation species by the regional browsing ratio for that species. This resulted in stems of plant species browsed frequently by deer being more heavily weighted while those of vegetation species rarely browsed were less weighted in count totals. Using the weighted counts, we calculated the mean stem weight (hereafter forage preference) for each transect.

The proportion of stems browsed, or browsing ratio, has been shown to be a reliable indicator of herbivory intensity and impacts to forest plant communities (Castleberry et al. 1999; Morellet et al. 2001; Frerker et al. 2013). However, modeling ratios directly can be problematic and lead to spurious correlations and difficulty interpreting model coefficients (Kronmal 1993). Because of this, we developed candidate models of herbivory intensity using the number of stems browsed as an independent variable and included the number of stems available and the mean stem preference as dependent variables in all models (Kronmal 1993). Our developed candidate models included additional dependent variables in groups representing the vegetative condition, physical environment, and demographics as defined above. We included a model for each group of dependent variables separately and all possible pair-wise combinations of the variable groups. The same methodology for the factors of landscape and habitat arrangement was used; because factors were correlated strongly with each other, we created models for each factor individually.

Initially, we fit models with the number of stems browsed as an independent variable and the number of stems available and the mean forage preference as dependent variables in all models as described above. However, we predicted that the relationship between the number of stems browsed and the number of stems available would be non-linear; likewise, the preference of the available stems could influence the proportion of stems browsed, a relationship that might change with forage availability. Accordingly, we included a model with the square of the number of stems available and the interaction between forage preference and stems available as a candidate model. Because the model including the square and interactive terms for the local vegetation characteristics greatly outranked the other candidate models, we used this as a base model and then refit all candidate models including the square and interactive terms and selected spatial factors. We also included a reduced base model that did not include the interaction and squared terms and a null model in the candidate model list for a total of 61 models (Supplementary Appendix A: Table SA.1).

<sup>1</sup> The use of any trade, product or firm names does not imply endorsement by the US government.

Our transects were nested within sites and sites within sampling regions, therefore we used a linear mixed model approach and included random intercepts for site and region (Snijders 2011). Stems available and stems browsed were  $\log + 1$  transformed prior to model fitting. We centered and scaled all other independent continuous variables so that we directly could assess effect sizes (Schielezeth 2010). As there were multiple transects per county, we included a random intercept for county in each model where demographic factors were present. We ranked models using Akaike's information criterion corrected for small sample size ( $AIC_c$ ), the difference between the model with the lowest  $AIC_c$  and the  $AIC_c$  of the  $i$ th model ( $\Delta_i$ ), and Akaike's weights ( $w_i$ ) (Burnham and Anderson 2002). We assessed the variance explained by the top model using marginal and conditional  $r^2$  for linear mixed models as described by Nakagawa and Schielzeth (2013). To assess the ability of the top model to predict herbivory intensity, we randomly selected 70% of the dataset to use for model fitting and used the remaining 30% to test the model. We used the top supported model to predict the number of stems browsed on transects for the data retained for model testing and then back-transformed the values to the original scale and compared the predicted to the observed values. We predicted values both including and excluding information regarding the random variables to simulate field observations where broader site conditions were and were not known. Predicted values were rounded to the nearest whole number and we evaluated predictive accuracy by calculating mean error, and root mean square error (RMSE) of the predicted values (Chai and Draxler 2014). We used R (Version 3.2.3, [www.r-project.org](http://www.r-project.org)) and packages "lme4" (Version 1.1-10, <https://cran.r-project.org/package=lme4>), "MuMIn" (Version 1.15-6, <https://cran.r-project.org/package=MuMIn>), and "multcomp" (Version 1.4-1, <https://cran.r-project.org/package=multcomp>) to fit and rank models.

## Results

Between 2 June 2014 and 7 August 2014, we counted and identified 11,137 woody plant stems or  $1.86 \text{ stems m}^{-2}$  of 82 species or species groups across all 30 sites and 600 transects. Mean browsing ratio study-wide was 0.28, whereas mean regionally-weighted browsing ratio was 0.46. Browsing ratios varied considerably among vegetation species study-wide, but ratios were similar among regions (Supplementary Appendix A: Table SA.2). The number of stems per-transect was lowest in the Appalachian Plateau and highest in the Southern Ridge and Valley region (Table 2). Conversely, edge density was greater in the Appalachian Plateau and Southern Ridge and

Valley regions compared with other regions to the northeast.

The base model fitting the number of stems browsed exclusively by local vegetation characteristics received the greatest percentage (62%) of overall support (Table 3). Because no other model had  $\Delta_i < 2$ , we used estimates directly from the best supported model. There was no evidence that models containing factors of the physical environment, habitat arrangement, local demographics, or expanded vegetative conditions were improved over the model containing only those factors relating to local vegetative conditions. Our top model explained 56% of the variation in the number of stems browsed not accounting for the random factors and 63% of the variation after accounting for random factors. The mean error of predictions by the top model not accounting for random factors was 2.41 stems per transect or 18.0% of the number of available stems; the RMSE was 3.17 stems. The mean error of predictions by the top model accounting for random factors was 2.34 stems per transect or 17.5% of the number of available stems; the RMSE was 3.17 stems.

## Discussion

Contrary to our predictions, we did not find that spatial factors relating to the physical environment, habitat arrangement, or demographics improved models of deer herbivory intensity. Although deer are known to prefer habitat edges and often are abundant in fragmented landscapes in the Appalachians and elsewhere (Alverson et al. 1988; Ford et al. 1993; Campbell et al. 2006), they also are present in large contiguous forests and highly agricultural areas as well. Because deer adapt well to many habitat types and configurations, as demonstrated by their rapid population growth over the last several decades, deer are ubiquitous across the core of their distribution in North America. In the mixed forest and agriculture of southcentral Minnesota, for example, Augustine and Jordan (1998) found that browsing intensity was strongly correlated with the availability of row crops and alfalfa (*Medicago sativa*) fields within 1.5 km of herbivory sampling locations. Our study area had only a limited and moderate acreage of row crops or improved pasture, respectively, providing supplemental food for deer outside largely forested habitats. As a result, we were not able to examine the influence of row crops and other potential alternative food sources directly. Lacking strong potential associations between forest edge and alternate, available food resources, edge did not appear to influence browsing intensity in our study. Furthermore, our top supported model suggests that measurements of the type and abundance of available forage were sufficient to predict the intensity of deer herbivory

**Table 2** Mean  $\pm$  standard deviation of model factors for white-tailed deer (*Odocoileus virginianus*) herbivory assessment transects in the central Appalachian Mountains of Virginia, USA, summer 2014

	Appalachian Plateau	Blue Ridge Northern	Blue Ridge Southern	Ridge and Valley Middle	Ridge and Valley, Tennessee	Upper Shenandoah Valley
Woody stems ( <i>n</i> )	13.47 $\pm$ 8.87	21.23 $\pm$ 13.22	18.19 $\pm$ 9.18	16.84 $\pm$ 13.23	22.94 $\pm$ 13.88	20.21 $\pm$ 13.17
Stems browsed ( <i>n</i> )	4.788 $\pm$ 4.415	5.620 $\pm$ 6.665	5.440 $\pm$ 5.008	4.151 $\pm$ 4.265	5.310 $\pm$ 4.603	6.717 $\pm$ 6.641
Stem preference	0.375 $\pm$ 0.144	0.268 $\pm$ 0.105	0.301 $\pm$ 0.146	0.3 $\pm$ 0.191	0.244 $\pm$ 0.123	0.354 $\pm$ 0.141
Browsing ratio	0.395 $\pm$ 0.287	0.253 $\pm$ 0.183	0.321 $\pm$ 0.238	0.352 $\pm$ 0.317	0.274 $\pm$ 0.226	0.395 $\pm$ 0.285
Distance to forest edge (m)	137.5 $\pm$ 100.6	251.9 $\pm$ 212.6	355.7 $\pm$ 330.6	294.5 $\pm$ 304.1	222.1 $\pm$ 318.5	282.9 $\pm$ 231.3
Tree cover (%)	91.7 $\pm$ 15.07	95.88 $\pm$ 8.5	95.76 $\pm$ 7.68	91.28 $\pm$ 14.66	96.92 $\pm$ 5.08	92.12 $\pm$ 11.72
Slope (°)	20.08 $\pm$ 9.98	14.55 $\pm$ 8.05	20.36 $\pm$ 9.25	16.00 $\pm$ 8.68	18.51 $\pm$ 9.31	13.49 $\pm$ 9.78
DEV	-0.026 $\pm$ 1.046	-0.011 $\pm$ 0.914	-0.005 $\pm$ 0.957	0.030 $\pm$ 0.949	0.010 $\pm$ 1.019	-0.126 $\pm$ 0.852
Transformed aspect	1.953 $\pm$ 0.929	1.895 $\pm$ 0.989	2.213 $\pm$ 0.904	2.12 $\pm$ 1.065	2.017 $\pm$ 1.002	1.885 $\pm$ 0.93
Edge density 1 km (m ha <sup>-1</sup> )	81.15 $\pm$ 27.77	52.38 $\pm$ 30.83	41.54 $\pm$ 29.36	50.5 $\pm$ 43.12	69.74 $\pm$ 37.58	36.28 $\pm$ 26.71
Radius of gyration 1 km (m)	110.5 $\pm$ 36.9	142.8 $\pm$ 57.6	188.8 $\pm$ 161.3	182.9 $\pm$ 136.7	139.7 $\pm$ 143.5	222.2 $\pm$ 139.6
Simpson's diversity index 1 km	0.331 $\pm$ 0.156	0.246 $\pm$ 0.164	0.201 $\pm$ 0.162	0.219 $\pm$ 0.201	0.384 $\pm$ 0.224	0.22 $\pm$ 0.217
Edge density 5 km (m ha <sup>-1</sup> )	83 $\pm$ 18.62	47.66 $\pm$ 17.62	59.66 $\pm$ 25.42	49.44 $\pm$ 14.63	89.32 $\pm$ 39.46	59.53 $\pm$ 14.3
Radius of gyration 5 km (m)	92.3 $\pm$ 7.66	142.6 $\pm$ 16.9	99.16 $\pm$ 12.59	130.2 $\pm$ 12.2	97.24 $\pm$ 8.07	129.7 $\pm$ 13.5
Simpson's diversity index 5 km	0.365 $\pm$ 0.092	0.276 $\pm$ 0.143	0.31 $\pm$ 0.141	0.321 $\pm$ 0.104	0.527 $\pm$ 0.171	0.468 $\pm$ 0.094
Forest edge density 1 km (m ha <sup>-1</sup> )	64.73 $\pm$ 18.8	46.16 $\pm$ 27.86	31.13 $\pm$ 22.62	42.64 $\pm$ 33.2	51.35 $\pm$ 27.55	28 $\pm$ 17.95
Forest radius of gyration 1 km (m)	257 $\pm$ 188.7	341.1 $\pm$ 195	467.8 $\pm$ 206.9	446.1 $\pm$ 244.5	308 $\pm$ 203.6	446.7 $\pm$ 248
Forest patch cohesion index 1 km	99.07 $\pm$ 0.86	99.62 $\pm$ 0.36	99.75 $\pm$ 0.33	99.72 $\pm$ 0.43	99.42 $\pm$ 0.47	99.44 $\pm$ 0.85
Forest edge density 5 km (m ha <sup>-1</sup> )	65.18 $\pm$ 12.08	39.85 $\pm$ 12.47	45.72 $\pm$ 17.72	39.03 $\pm$ 11.06	52.61 $\pm$ 15.49	40.46 $\pm$ 12.24
Forest radius of gyration 5 km (m)	169.5 $\pm$ 47.3	266.8 $\pm$ 109.4	161.8 $\pm$ 43.4	171.3 $\pm$ 40.4	112.6 $\pm$ 16.7	121.2 $\pm$ 13.3
Forest patch cohesion index 5 km	99.87 $\pm$ 0.08	99.75 $\pm$ 0.18	99.86 $\pm$ 0.1	99.83 $\pm$ 0.13	98.66 $\pm$ 1.39	99.42 $\pm$ 0.4
Deer harvest density (n km <sup>-2</sup> )	0.824 $\pm$ 0.207	1.792 $\pm$ 0.357	1.736 $\pm$ 0.474	1.669 $\pm$ 0.326	1.152 $\pm$ 0.496	1.797 $\pm$ 0.368
Human population density (n km <sup>-2</sup> )	26.74 $\pm$ 32.92	27.17 $\pm$ 15.88	40.59 $\pm$ 28.74	14.56 $\pm$ 6.97	115.4 $\pm$ 189.4	47.76 $\pm$ 17.82

Habitat arrangement metrics were calculated over 1 and 5 km radius areas as indicated. Deer harvest density and human population density reflect the mean density of the city or county of the transect locations not the mean density for the study region

DEV deviation from mean elevation

across the variety of landscape characteristics found in this portion of the central Appalachians.

Our predictive herbivory intensity models accounted for both the amount of and average preference for the available forage. These factors can change substantially across the landscape and in relationship to landscape attributes. For

example, McNab (1989, 1993) found strong relationships between tree growth and landform indices, suggesting a predictable difference in forest productivity and species/community composition across landforms in the Appalachians. In spite of this, we did not find any improvement in models of herbivory intensity by including

**Table 3** Three best supported linear mixed models of number of woody plant stems browsed by white-tailed deer (*Odocoileus virginianus*) on herbivory assessment transects in the central Appalachian Mountains, Virginia, USA, summer 2014

Model	<i>df</i>	logLik	AIC <sub>c</sub>	$\Delta_i$	$w_i$
Base model	8	−340.89	698.1	0	0.618
Base model + Simpson's diversity index 5 km	9	−342.39	703.2	5.10	0.048
Base model + Forest edge density 5 km	9	−342.47	703.4	5.24	0.045

Model parameters are given as well as the degrees of freedom (*df*), log likelihoods (logLik), Akaike's information criterion corrected for small sample size (AIC<sub>c</sub>), difference in AIC<sub>c</sub> value between top model and *i*th model ( $\Delta_i$ ), and model support ( $w_i$ ). All models contained a random intercept for site and study region; the base model included the number of available stems, the square of the number of available stems, forage preference, and the interaction between the number of stems available and forage preference

factors relating to landform or other physical attributes of location. One reason for this lack of relationship may be the scale differences between the measurement of physical attributes and how deer browse landscapes or other confounding factors of herbivory. Landforms vary in size, availability and configuration on the landscape. Also, deer establish relatively stable home range areas that generally encompass different landforms and foraging opportunities (Campbell et al. 2004). Although understory vegetation community type and productivity in the Appalachians is influenced by a suite of factors including landform and site quality (Ford et al. 2000), previous attempts to link deer physiological metrics such as harvest weight to potential vegetation productivity as measured by site index were largely equivocal (Ford et al. 1997). If deer herbivory is influenced to a greater degree by vegetation type than factors such as vegetation quantity, measures of forest productivity, for example, may not necessarily be related directly to browsing intensity. A lack of relationship between landscape attributes and herbivory intensity also could result from very productive areas providing greater amounts of herbaceous forage that might change or mask herbivory pressure on woody species evaluated in this study.

The lack of relationship between spatial factors and deer herbivory intensity highlights both the simplicity of the best supported model and the difficulty of predicting browsing intensity across complex, multi-faceted landscapes. Although our research suggests that herbivory intensity can be predicted with relatively simple models, no physical or demographic attributes or set of attributes were identified that might prove useful for identifying landscape areas prone to increased levels of browsing intensity over this large portion of the central Appalachians. As a result, without measurement of or obtaining data on local vegetative conditions, broad-scale prediction of herbivory intensity remains difficult. Likewise, understanding forest vegetative condition across landscapes undoubtedly will remain a critical component for continued development of herbivory impact assessment methods. New and emerging

methods, such as remote sensing of understory conditions (Latifi et al. 2016), or modifying existing data collection programs, such as the U.S. Forest Service, Forest Inventory and Analysis program that provide more details of understory conditions might enhance the assessment of herbivory intensity across landscapes.

Environmental change occurs temporarily and spatially, therefore periodic assessment of herbivory intensity unfortunately will be necessary to identify locations at risk from excessive deer herbivory to provide managers sufficient time to implement management changes before substantial or long-term degradations occur. However, landscapes likely already contain areas previously degraded by high levels of deer herbivory. For example, large areas of the central Appalachians of Pennsylvania currently display substantial reductions in forest biodiversity (Goetsch et al. 2011; Schumacher and Carson 2013) and recovery of these degraded systems can be slow (Royo et al. 2010; Tanentzap et al. 2012). As a result, any broad-scale assessment of herbivory intensity will need to incorporate measures of ecosystem health that encompass current, past, and future conditions and goals to aid in establishing and maintaining healthy and sustainable ecosystems.

## Conclusions

Our results suggest that herbivory impact assessment should include spatially-balanced vegetation monitoring and account for regional differences in deer forage preference. Traditional deer density based management goals might not adequately incorporate ecological factors that affect biodiversity maintenance or recovery (McShea 2012). Because of this, developing effective monitoring of herbivory impacts is essential for the central Appalachian region to document if negative impacts to forest biodiversity are occurring from herbivory. In turn, that provides managers with threshold or decision points where



management actions can be evaluated or implemented in terms of deer harvest or additional habitat manipulations.

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## References

- Alverson WS, Waller DM, Solheim SL (1988) Forests too deer: edge effects in northern Wisconsin. *Conserv Biol* 2:348–358
- Augustine DJ, Jordan PA (1998) Predictors of white-tailed deer grazing intensity in fragmented deciduous forests. *J Wildl Manag* 62:1076–1085
- Braun EL (1974) Deciduous forests of eastern North America. Hafner Press, New York, p 596
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference a practical information-theoretic approach. Springer, New York, p 488
- Campbell TA, Laseter BR, Ford WM, Miller KV (2004) Movements of female white-tailed deer (*Odocoileus virginianus*) in relation to timber harvests in the central Appalachians. *For Ecol Manag* 199:371–378
- Campbell TA, Laseter BR, Ford WM, Odom RH, Miller KV (2006) Abiotic factors influencing deer browsing in West Virginia. *North J Appl For* 23:20–26
- Castleberry SB, Ford WM, Miller KV, Smith WP (1999) White-tailed deer browse preferences in a southern bottomland hardwood forest. *South J Appl For* 23:78–82
- Chai T, Draxler RR (2014) Root mean square error (RMSE) or mean absolute error (MAE)? Arguments against avoiding RMSE in the literature. *Geosci Model Dev* 7:1247–1250
- Côté SD, Rooney TP, Tremblay JP, Dussault C, Waller DM (2004) Ecological impacts of deer overabundance. *Annu Rev Ecol Evol Syst* 35:113–147
- Crimmins SM, Edwards JW, Ford WM, Keyser PD, Crum JM (2010) Browsing patterns of white-tailed deer following increased timber harvest and a decline in population density. *Int J For Res* 2010:1–7
- De Reu J, Bourgeois J, Bats M, Zwervaegher A, Gelorini V, De Smedt P, Chu W, Antrop M, De Maeyer P, Finke P, Van Meirvenne M, Verniers J, Crombé P (2013) Application of the topographic position index to heterogeneous landscapes. *Geomorphology* 186:39–49
- DeGraaf RM, Yamasaki M, Leak WB, Lanier JW (1992) New England wildlife: management forested habitats. In: General technical report NE-144. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Radnor, Pennsylvania, p 271
- DiTommaso A, Morris SH, Parker J, Cone CL, Agrawal AA (2014) Deer browsing delays succession by altering aboveground vegetation and belowground seed banks. *PLoS ONE* 9:e91155
- Dostaler S, Ouellet JP, Therrien JF, Côté SD (2011) Are feeding preferences of white-tailed deer related to plant constituents? *J Wildl Manag* 75:913–918
- Fenneman NM (1938) Physiography of eastern United States. McGraw-Hill, New York, p 714
- Ford WM, Johnson AS, Hale PE, Wentworth JM (1993) Availability and use of spring and summer woody browse by deer in clearcut and uncut forests of the southern Appalachians. *South J Appl For* 17:116–119
- Ford WM, Johnson AS, Hale PE, Wentworth JM (1997) Influences of forest type, stand age, and weather on deer weights and antler size in the southern Appalachians. *South J Appl For* 21:11–18
- Ford WM, Odom RH, Hale PE, Chapman BR (2000) Stand-age, stand characteristics, and landform effects on understory herbaceous communities in southern Appalachian cove-hardwoods. *Biol Conserv* 93:237–246
- Frerker K, Sonnier G, Waller DM (2013) Browsing rates and ratios provide reliable indices of ungulate impacts on forest plant communities. *For Ecol Manag* 291:55–64
- Fry JA, Xian G, Jin SM, Dewitz J, Homer CG, Yang LM, Barnes CA, Herold ND, Wickham J (2011) Completion of the 2006 national land cover database for the conterminous United States. *Photogramm Eng Remote Sens* 77:858–864
- Gawler SC (2008) Northeastern terrestrial wildlife habitat classification. Report to the Virginia Department of Game and Inland Fisheries on behalf of the Northeast Association of Fish and Wildlife Agencies and the National Fish and Wildlife Foundation, Boston, Massachusetts, p 102
- Goetsch C, Wigg J, Royo AA, Ristau T, Carson WP (2011) Chronic over browsing and biodiversity collapse in a forest understory in Pennsylvania: results from a 60 year-old deer exclusion plot. *J Torrey Bot Soc* 138:220–224
- Halls LK (1984) White-tailed deer: ecology and management. Stackpole Books, Harrisburg, p 864
- Hobbs NT (1996) Modification of ecosystems by ungulates. *J Wildl Manag* 60:695–713
- Homer C, Dewitz JA, Yang L, Jin S, Danielson P, Xian G, Coulston J, Herold ND, Wickham JD, Megown K (2015) Completion of the 2011 national land cover database for the conterminous United States—representing a decade of land cover change information. *Photogramm Eng Remote Sens* 81:345–354
- Horsley SB, Stout SL, DeCalesta DS (2003) White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecol Appl* 13:98–118
- Kilpatrick HJ, Spohr SM (2000) Spatial and temporal use of a suburban landscape by female white-tailed deer. *Wildl Soc Bull* 28:1023–1029
- Kniowski AB, Ford WM (2017) Spatial patterns of white-tailed deer herbivory in the central appalachian mountains. *For Ecol Manage* (in review)
- Koh S, Bazely DR, Tanentzap AJ, Voigt DR, Da Silva E (2010) *Trillium grandiflorum* height is an indicator of white-tailed deer density at local and regional scales. *For Ecol Manag* 259:1472–1479
- Kronmal RA (1993) Spurious correlation and the fallacy of the ratio standard revisited. *J R Stat Soc Ser A* 156:379–392
- Latifi H, Heurich M, Hartig F, Müller J, Krzystek P, Jehl H, Dech S (2016) Estimating over- and understory canopy density of temperate mixed stands by airborne LiDAR data. *Forestry* 89:69–81
- McGarigal K, Cushman SA, Ene E (2012) FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. University of Massachusetts, Amherst. <http://www.umass.edu/landeco/research/fragstats/fragstats.html>
- McNab H (1989) Terrain shape index: quantifying effect of minor landforms on tree height. *For Sci* 35:91–104
- McNab WH (1993) A topographic index to quantify the effect of mesoscale landform on site productivity. *Can J For Res* 23:1100–1107
- McShea WJ (2005) When ungulates rule the world. In: Ray JC, Redford KH, Steneck RS, Berger J (eds) Large carnivores and the conservation of biodiversity. Island Press, Washington, pp 138–153
- McShea WJ (2012) Ecology and management of white-tailed deer in a changing world. *Ann N Y Acad Sci* 1249:45–56

- Morellet N, Champely S, Gaillard JM, Ballon P, Boscardin Y (2001) The browsing index: new tool uses browsing pressure to monitor deer populations. *Wildl Soc Bull* 29:1243–1252
- Morellet N, Gaillard JM, Hewison AJM, Ballon P, Boscardin Y, Duncan P, Klein F, Maillard D (2007) Indicators of ecological change: new tools for managing populations of large herbivores. *J Appl Ecol* 44:634–643
- Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining  $R^2$  from generalized linear mixed-effects models. *Methods Ecol Evol* 4:133–142
- Nixon CM, McClain MW, Russell KR (1970) Deer food habits and range characteristics in Ohio. *J Wildl Manag* 34:870–886
- Rooney TP (2001) Deer impacts on forest ecosystems: a North American perspective. *Forestry* 74:201–208
- Rooney TP, Waller DM (2003) Direct and indirect effects of white-tailed deer in forest ecosystems. *For Ecol Manag* 181:165–176
- Royo AA, Stout SL, deCalesta DS, Pierson TG (2010) Restoring forest herb communities through landscape-level deer herd reductions: is recovery limited by legacy effects? *Biol Conserv* 143:2425–2434
- Russell FL, Zippin DB, Fowler NL (2001) Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. *Am Midl Nat* 146:1–26
- Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. *Methods Ecol Evol* 1:103–113
- Schumacher HB, Carson WP (2013) Biotic homogenization of the sapling layer in 19 late-successional and old-growth forest stands in Pennsylvania. *J Torrey Bot Soc* 140:313–328
- Simon SA (2011) Ecological zones on the George Washington National Forest: first approximation mapping. Final Report to The Nature Conservancy, Virginia Field Office, Charlottesville, VA, p 23
- Simon SA (2013) Ecological zones on the Jefferson National Forest Study Area: first approximation. Final Report to The Nature Conservancy, Virginia Field Office, Charlottesville, VA, p 28
- Snijders TAB (2011) Multilevel analysis. In: Lovric M (ed) *International encyclopedia of statistical science*. Springer, Berlin, pp 879–882
- Stevens DLJ, Olsen AR (2004) Spatially balanced sampling of natural resources. *J Am Stat Assoc* 99:262–278
- Tanentzap AJ, Kirby KJ, Goldberg E (2012) Slow responses of ecosystems to reductions in deer (*Cervidae*) populations and strategies for achieving recovery. *For Ecol Manag* 264:159–166
- Tierson WC, Mattfeld GF, Sage RW, Behrend DF (1985) Seasonal movements and home ranges of white-tailed deer in the Adirondacks. *J Wildl Manag* 49:760–769
- Vangilder LD, Torgerson O, Porath WR (1982) Factors influencing diet selection by white-tailed deer. *J Wildl Manag* 46:711–718
- Virginia Department of Game and Inland Fisheries (2015) Virginia deer management plan 2015–2024. Richmond, Virginia, p 137
- Wilson JP, Gallant JC (2000) *Terrain analysis: principles and applications*. Wiley, New York, p 520
- Young JA, Hedrick DW, Keniston RF (1967) Forest cover and logging–herbage and browse production in the mixed coniferous forest of northeastern Oregon. *J For* 65:807–813
- Zar JH (1984) *Biostatistical analysis*. Prentice-Hall Inc, Englewood Cliffs, p 718