Broadening the ecological context of ungulate–ecosystem interactions: the importance of space, seasonality, and nitrogen

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Abstract. Spatial heterogeneity of soil resources, particularly nitrogen availability, affects herbaceous-layer cover and diversity in temperate forest ecosystems. Current hypotheses predict that ungulate herbivores influence nitrogen availability at the stand scale, but how ungulates affect nitrogen availability at finer spatial scales that are relevant to the herb layer is less understood. We tested the hypothesis that ungulate exclusion reduces the spatial complexity of nitrogen availability at neighborhood scales (1–26 m) apart from mean stand scale effects. This outcome was expected due to a lack of ungulate nitrogenous waste deposition within exclosures and seasonally variable ungulate habitat use. To test this hypothesis we examined spatial patterning of ammonium and nitrate availability, herb-layer cover and diversity, and under-canopy solar radiation using geostatistical models. Our study sites included six stands of eastern hemlock (*Tsuga canadensis*) forest: three where white-tailed deer (*Odocoileus virginianus*) were excluded and three that were accessible to deer. Where deer were present, patch sizes of ammonium availability, cover, and diversity were smaller compared to deer exclosures, whereas mean site-level effects were not significant. Within deer exclosures cover and solar radiation were more similar in patch size than were cover and nitrogen availability. Our results suggest that browsing ungulates affect spatial patterns of herb-layer cover and diversity through the excretion of nitrogenous wastes in small, discrete patches. Ungulate-excreted nitrogen deposition and herbivory were concentrated in the dormant season, allowing herb-layer plants a greater opportunity to benefit from nitrogen additions. Therefore, the impact of ungulates on nitrogen cycling in forest ecosystems varies with spatial scale and the seasonal timing of ungulate impacts. In this way, ungulates may function as a seasonally dependent link between fine-scale and landscape-level ecological processes.

Key words: context dependence; diversity; eastern hemlock; habitat use; herbaceous layer; heterogeneity; nitrogen; Odocoileus virginianus; *spatial patterning; temperate forest;* Tsuga canadensis; *white-tailed deer.*

Introduction

Determining what controls spatial and temporal patterns of nitrogen availability has important implications for understanding and maintaining key ecosystem functions (Gilliam 2006). Nitrogen is a limiting resource to primary production in many terrestrial ecosystems (Vitousek and Howarth 1991), and processes that influence spatial patterns in nitrogen availability influence plant biomass, competitive relationships, and thereby biodiversity (Vitousek et al. 1997, Gilliam 2006). Nitrogen availability is often homogenized by current human activities, especially via atmospheric deposition, which emphasizes the need to understand the mechanisms and context dependence (sensu Schmitz 2010) of processes that affect nitrogen heterogeneity. Such an understanding is important to address the homogenizing effects of human activities and develop a predictive understanding of ecosystem function.

The seasonal redistribution of nitrogen by animals such as ungulate herbivores is an important mechanism that tends to increase the spatial heterogeneity of nitrogen in terrestrial ecosystems (Steinauer and Collins 1995, Augustine and Frank 2001). Ungulate herbivores affect nitrogen availability through direct and indirect mechanisms. Direct effects occur by ungulates ingesting nitrogen from across the landscape and concentrating it into hotspots of excreta (Steinauer and Collins 1995, Augustine and Frank 2001, Peek and Forseth 2003) and carcasses (Bump et al. 2009*b*). Seasonal or diurnal habitat use patterns can facilitate a net transport of nitrogen across habitat boundaries (Seagle 2003, Abbas et al. 2012). Indirect effects occur due to preferential browsing of more palatable plant species, resulting in a plant community transition toward less nutritious species that produce lower quality leaf litter for decomposers. As a result, nitrogen availability to soil

biota and associated processes declines (Pastor et al. 1993, Bardgett and Wardle 2003, Bressette et al. 2012).

Although available evidence indicates that ungulates generally decelerate nitrogen cycling rates in forest ecosystems via indirect effects (Ritchie et al. 1998, reviewed in Pastor et al. 2006), few studies have addressed the importance of spatial heterogeneity at fine spatial scales of 1–20 m, which are influential in herbaceous-layer community dynamics (Frelich 2002, Gilliam 2007). In grasslands, ungulate excreta can increase heterogeneity of nitrogen availability at such fine scales (Steinauer and Collins 1995, Augustine and Frank 2001, Peek and Forseth 2003). Ungulate carcasses can generate nutrient hotspots for vegetation growth in grasslands (Towne 2000) and forest understories (Bump et al. 2009b). Modeling of ungulate habitat use patterns and nitrogen excretion rates suggests that impacts are expected to be heterogeneous at the landscape scale (Seagle 2003, Abbas et al. 2012). Ungulate effects on landscape- and local-scale nitrogen availability may link coarse- and fine-scale processes, as does ungulate herbivory (Hurley et al. 2012).

We tested the hypothesis that stands with ungulate access would have more complex fine-scale spatial patterns of nitrogen availability and detectable nitrogen hotspots compared to exclosures, but exhibit no difference in mean nitrogen availability at the stand scale. If true, we also expected herb-layer cover and diversity to exhibit differences in spatial patterns at fine scales, but not necessarily mean differences at the stand scale. We expected greater complexity in spatial patterns of nitrogen availability due to deposition of ungulate excreta in discrete patches (Steinauer and Collins 1995, Augustine and Frank 2001). Increased nitrogen availability would increase plant growth rates (Peek and Forseth 2003) given that primary production in temperate forests is often nitrogen-limited (Vitousek and Howarth 1991) and temperate forest plants often possess adaptations to rapidly capitalize on ephemeral nitrogen pulses (Farley and Fitter 1999). We did not expect considerable consumptive effects because the seasonal timing of nitrogen inputs and herbivory are decoupled in our study system (Jensen et al. 2011, Witt et al. 2012). Ungulate use, and therefore nitrogen deposition and herbivory, occur mainly during the dormant season, allowing herbaceous plants increased nitrogen availability and reduced herbivory risk during the growing season. We tested this hypothesis using three large ungulate exclosures (up to 30 ha) and three nearby unexclosed sites located in winter ungulate habitat. Our within-site sampling design captured spatial variance at a scale of 1–26 m, which is relevant to herb-layer community interactions (Frelich 2002, Gilliam 2007). These analyses address the fundamental questions: at what spatial scales do ungulates affect nitrogen availability and what are the implications for herbaceous-layer vegetation?

METHODS

Study sites

Our study occurred in six stands dominated by eastern hemlock (*Tsuga canadensis*) in the western Upper Peninsula of Michigan, USA (Appendix A: Fig. A1). Three stands (Boneyard, Spree, and Walton Creek) were entirely enclosed by a 2 m tall fence that excluded white-tailed deer (*Odocoileus virginianus*), while allowing access to smaller animals. Three other stands (Ford Forestry Center, Silver River, and Sylvania) were accessible to deer. Deer exclosures were constructed in 2003 (Walton Creek) and 2007 (Boneyard and Spree). Deer access sites were selected from a set of 39 remnant hemlock stands in the western Upper Peninsula where winter deer use has been monitored since 2006 (see Appendix B and Witt and Webster 2010 for details). The deer access site selection criteria in the current study included high deer use during 2006–2010, intermediate size (10–30 ha), and similar soil type and forest structure to the previously constructed exclosures (see Appendix A: Table A1 for site information). Prior to the study year of 2011, the selected access sites experienced winter deer use well above the 39-site average. Growing season deer use was considerably less than winter deer use, and growing season deer herbivory was also less than expected based on winter deer use (Witt and Webster 2010, Jensen et al. 2011). The deer exclosures used in our study, at 4-ha and 30-ha area, were unusually large for temperate forest regions.

Sampling design

A cyclical sampling network was used to efficiently measure spatial patterning across a range of scales from single tree (1–10 m) to neighborhood (10–20 m; Frelich 2002). At each site, 1×1 m quadrants were placed in a repeating cycle of 0, 1, 3, and 9 m every 13 m along two intersecting 52-m transects. Transects intersected at the midpoint at a 60° angle (see Appendix B: Fig. B1 for a diagram). This sampling design maximized spatial information gained from as few sample points as possible (Clinger and Van Ness 1976, Scheller and Mladenoff 2002). Sample size was 33 quadrants at each site, or 99 quadrants per treatment, for a grand total of 198 quadrants.

Field data collection

Herb-layer vegetation was sampled by a visual survey of cover by species in each quadrant. We chose cover as a surrogate for biomass to reduce our impact on the forest, and because it is a reliable indicator of biomass (Hermy 1988). The same observer conducted all surveys to maintain consistency. Herb-layer vegetation was defined as all plants <1.0 m in height. Individual plants were grouped by species, with the exception of the Division Bryophyta, into the following cover classes: 0%, 1%, 5%, 10%, 25%, 50%, 75%, 90%, 95%, and 99% (McCune and Grace 2002). Early summer herb-layer

species were sampled on 6–11 June 2011, whereas late summer species were sampled on 25, 27, or 29 July. A nonmetric multidimensional scaling ordination procedure conducted in PC-ORD 5 (McCune and Mefford 2006) did not reveal a stable structure for herb-layer cover data (final stress, 37.7; instability, 0.046; 500 iterations).

The abundance of woody vegetation was measured in three size classes: seedlings (<0.25 m height), saplings (0.25–3.00 m height, <10.0 cm diameter at breast height [dbh, 1.37 m]), and trees (≥10.0 cm dbh). The number of seedlings was counted by species in each quadrant. Saplings were counted by species and height was recorded. Trees were quantified by five variable-radius plots (basal area factor, 2.3 m^2/ha) at each site. The center of a variable-radius plot was located at each transect terminus as well as the intersection of transects. Our sampling area for saplings and overstory trees was small and intended for descriptive purposes only.

Nitrogen ion availability was assessed by burying ion-exchange resin beads in situ, extracting the adsorbed ions in the laboratory, and colorimetrically measuring ammonium and nitrate concentrations of the extracts (described in Appendix B). Four resin bags were buried at 5–10 cm depth in each quadrant for 91 days (7–12 March through 6–11 June 2011). We chose this time period to capture nitrogen availability from spring snowmelt through establishment of the early summer understory flora.

The availability of light to herb-layer vegetation was estimated from digital hemispherical photographs of the canopy. Hemispherical photographs were taken from 1 m height during the 6–11 June sampling period. Direct and diffuse under-canopy radiation (mean photosynthetically active flux density, moles per square meter per day) was computed using the computer software WinSCANOPY (WinSCANOPY 2005) and a growing season length of 1 May through 30 September.

The location of deer excreta along transects was measured by visually searching for fecal pellet groups. A pellet group was counted if it was located within 1.5 m of the transect center, so that 321 m^2 was searched for pellet groups at each deer access site. Quadrants were visually inspected for earthworm middens, but none were observed.

Site-level comparisons

Site-level means of variables were computed as the mean of quadrant-level observations. We determined total percent cover as the sum of cover class midpoints of all species present in a quadrant. Seedling density was computed as the total number of seedlings per square meter. Sapling density was computed in the same manner. We determined species richness (S), Shannon's diversity index (H'), and evenness (E) for each quadrant.

We compared site-level means in nitrogen availability, under-canopy radiation, and vegetation attributes between deer access and exclosure sites. Monte Carlo randomization tests on absolute mean differences (Gotelli and Ellison 2004) were used because most variables did not approximate a normal distribution. The null distribution was generated with 1000 permutations. Site-level means were considered to be statistically significantly different if $P < 0.05$. Monte Carlo randomization tests were also performed on the 90th percentiles of ammonium, nitrate, and total nitrogen ion (sum of ammonium and nitrate by quadrant) to test the hypothesis of greater nitrogen hotspots in deer access sites. We chose the 90th percentile to test this hypothesis because it is more sensitive than the mean to extreme values.

Spatial analyses

Spatial patterning in nitrogen availability, under-canopy radiation, herb-layer cover, and diversity were compared using semivariance analysis (Goovaerts 1998). Semivariance ($\gamma(h)$) measures the spatial variance between sample points at variable separation distances (h).

Semivariance was standardized by dividing by the sample variance s^2 so that all semivariograms would be on the same scale for direct comparison. Also, a standardized semivariance less than 1 (semivariance < sample variance) indicates spatial dependence between sample points at a given separation distance. Standardized semivariance was computed for each h up to one-half the transect length (1–26 m) using the R statistical environment (R Development Core Team 2012) and the packages RGDAL (Keitt et al. 2012) and GSTAT (Pebesma 2004). We used the package GGPLOT2 (Wickham 2009) to generate empirical semivariograms by plotting observed $\gamma(h)$ by h. All variables except diversity required a Box-Cox transformation ($n = 198$ observations) to achieve normality prior to semivariance analysis.

We modeled spatial patterning in each variable by fitting five candidate models to each empirical semivariogram and selecting the most parsimonious model through an information-theoretic approach. We chose five models that are often useful for describing spatial patterning of variance: white noise (no systematic change in variance with increasing separation distance), linear (algebraic change in variance), spherical, exponential, and Gaussian (rapid change in variance at small separation distances that decreases at larger distances) (see Appendix B: Table B1 for model equations). The white noise model is a single-parameter model that represents random variation in variance with increasing h. The linear model contains slope (m) and y-intercept (γ_0) parameters and indicates a linear change in spatial dependence. The spherical, exponential, and Gaussian models each contain three parameters that represent the range of spatial dependence (a), the partial sill (C) that represents spatial variance explained by the model, and the nugget (ε) that represents spatial variance at distances shorter than the step size as well as sampling

TABLE 1.　Results of Monte Carlo randomization tests (1000 permutations; $\alpha = 0.05$) comparing site-level means grouped by access to white-tailed deer (*Odocoileus virginianus*) ($n = 3$ each).

Variable	Access mean (SE)	Exclosure mean (SE)	DIF_{obs}†	P‡
Ammonium (mg·L^{-1}·[g resin]$^{-1}$)	2.71 (0.36)	2.70 (0.40)	0.01	1.000
Nitrate (mg·L^{-1}·[g resin]$^{-1}$)	1.37 (0.46)	1.09 (0.35)	0.29	0.517
Total N ion (mg·L^{-1}·[g resin]$^{-1}$)	4.09 (0.63)	3.79 (0.30)	0.30	0.682
Direct UCR (mol·m^{-2}·d^{-1})	5.58 (0.49)	7.28 (0.39)	1.69	0.107
Diffuse UCR (mol·m^{-2}·d^{-1})	0.80 (0.10)	1.06 (0.08)	0.26	<0.001
Total UCR (mol·m^{-2}·d^{-1})	6.39 (0.54)	8.34 (0.43)	1.95	0.094
Herb cover (%)	15.4 (3.9)	36.0 (4.7)	20.6	0.097
S	4.26 (0.53)	5.97 (0.98)	1.71	0.084
H'	0.93 (0.091)	1.26 (0.15)	0.33	0.104
E	0.72 (0.03)	0.75 (0.01)	0.03	0.373
Seedling density (no. seedlings/m^2)	3.95 (1.40)	6.42 (1.81)	2.47	0.377
Sapling density (no. saplings/m^2)	0.01 (0.01)	1.13 (0.57)	1.12	<0.001

Notes: Data are from six eastern hemlock (*Tsuga canadensis*) stands in the Upper Peninsula of Michigan, USA. Total N ion equals the sum of ammonium concentration and nitrate concentration. UCR stands for under-canopy radiation. Total UCR equals the sum of direct UCR and diffuse UCR. Herb cover is the percent cover of herb-layer vegetation. S is species richness; H' is Shannon's diversity index; and E is evenness.

† Observed difference $= |mean_{access} - mean_{exclosure}|$.

‡ Proportion of $DIF_{sim} \geq DIF_{obs}$, where DIF_{sim} are from a randomized distribution.

error. For the spherical model the partial sill C is the limit of $\gamma(h)$ as $h \to a$. The exponential and Gaussian models also reach C asymptotically, but the practical range a must be estimated from the range parameter b. The practical range is reached when $\gamma(h) = 0.95(C)$, which can be computed by $a = 3b$ for the exponential model and $a = \sqrt{3}b$ for the Gaussian model (Goovaerts 1998). Models were fit by the Gauss-Newton nonlinear minimization algorithm in the R statistical environment (R Development Core Team 2012). The weights N_j/h_j^2 were used in the sum of squares function.

From the set of five candidate models, we selected the most parsimonious using Akaike's Information Criterion corrected for small sample sizes (AIC$_c$; Burnham and Anderson 2004), computed in the R statistical environment (R Development Core Team 2012). We defined the most parsimonious model as having the lowest AIC$_c$ and where the next model has ΔAIC$_c > 2$ (Burnham and Anderson 2002). The most parsimonious model was used to compute the appropriate geostatistical parameters for each variable.

RESULTS

Deer use

Stand-level deer use during the winter of 2010–2011 did not show a consistent trend across sites relative to the previous five winters (Appendix A: Table A1). Pellet group density at Silver River (610.0 groups/ha) was similar to previous winters (545.5 ± 99.8 groups/ha, mean ± SE, $n = 5$). Pellet group density was greater than any of the previous five years at Sylvania (1130.2 groups/ha vs. 366.0 ± 105.5 groups/ha), and lower than the previous five years at Ford Forestry Center (107.6 groups/ha vs. 355.2 ± 62.8 groups/ha). We estimated the proportion of each stand that was directly affected by deer excreta using the observed stand-level pellet count

densities. We made the conservative assumptions that one excretion event affects a 0.25-m^2 area (Steinauer and Collins 1995) and that deer urinate and defecate simultaneously (Wallmo 1981). Deer excretion affected 1.5% of the sampled area at Silver River, 2.8% of the Sylvania site, and 0.3% of the Ford Forestry Center site. Transect fecal pellet group counts followed the same pattern. Pellet group density was 93 groups/ha at Silver River, 280 groups/ha at Sylvania, and no pellet groups were observed at the Ford Forestry Center.

Site-level comparisons

Ammonium, nitrate, and total nitrogen ion availability did not differ according to deer access at the site level based on Monte Carlo randomization tests of the mean (Table 1, Fig. 1). Direct and total under-canopy radiation did not differ, while diffuse under-canopy radiation was significantly greater at exclosure sites (observed mean difference, $DIF_{obs} = 0.26$ mol·m^{-2}·d^{-1}, $P < 0.001$). Herb-layer vegetation attributes did not differ statistically at the site level (Table 1, Fig. 1), although mean cover was more than 50% greater in exclosures. Sapling density was significantly greater in exclosures ($DIF_{obs} = 1.12$ m^2, $P < 0.001$; see Appendix C: Table C1). A complete list of species including mean cover by site can be found in Appendix C: Table C2.

Monte Carlo randomization tests of the 90th percentile were not significantly different for ammonium ($DIF_{obs} = 0.31$ mg·L^{-1}·[g resin]$^{-1}$, $P = 0.895$), nitrate ($DIF_{obs} = 0.28$ mg·L^{-1}·[g resin]$^{-1}$, $P = 1$), or total nitrogen ion availability ($DIF_{obs} = 0.49$ mg·L^{-1}·[g resin]$^{-1}$, $P = 0.807$).

Spatial analyses

Complexity of spatial variance structure, as determined by model complexity and type, differed according to deer access for cover and diversity but not for
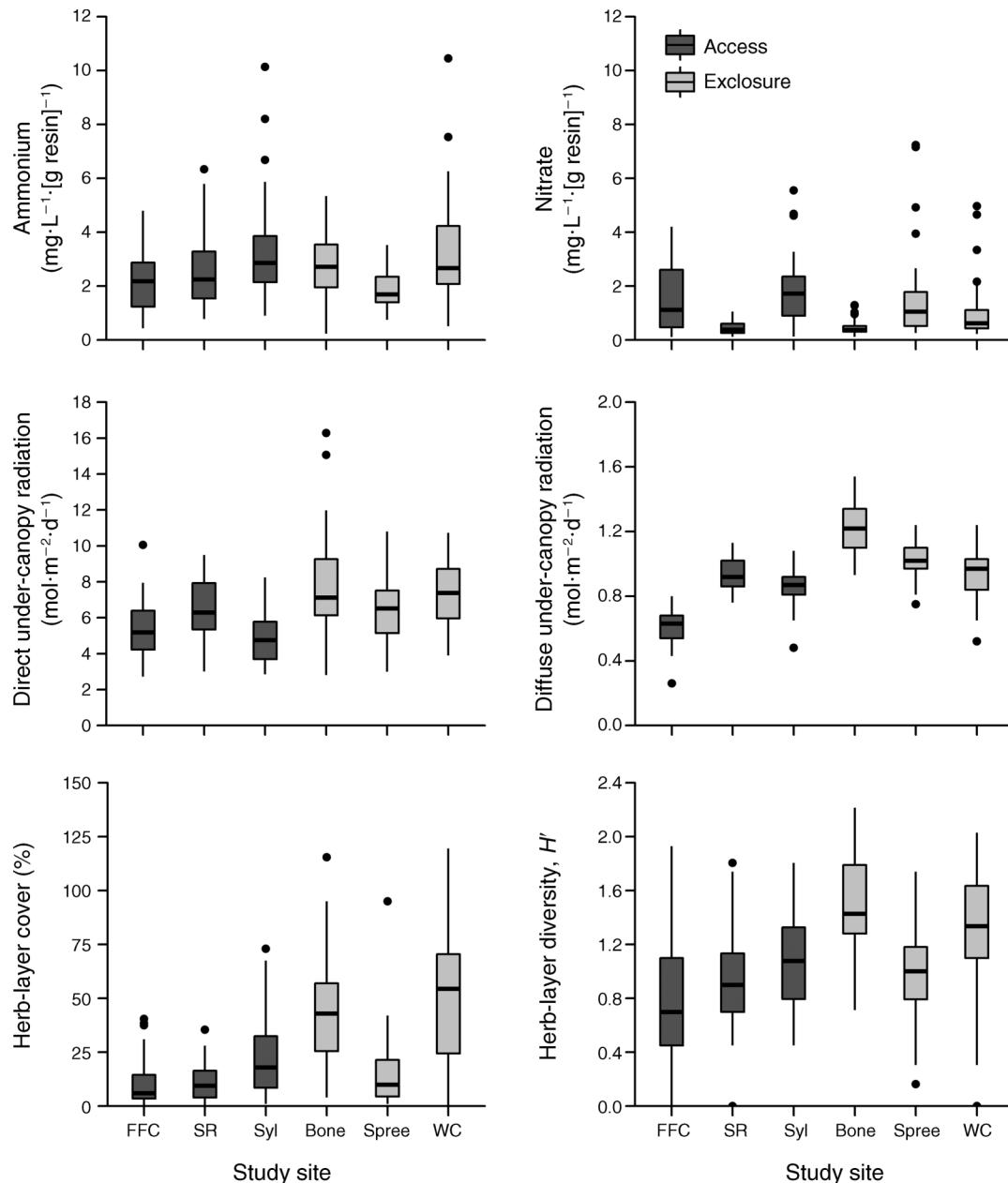
FIG. 1. Boxplots of each variable by site in eastern hemlock (*Tsuga canadensis*) stands in the Upper Peninsula of Michigan, USA. In each box, the dark middle line represents the median, and the upper and lower extents of the box represent the 75th and 25th percentiles, respectively. Lines extend to 1.5 times the interquartile range (difference of 75th and 25th percentiles). Black circles indicate outliers. Site name abbreviations: FFC, Ford Forestry Center; SR, Silver River; Syl, Sylvania; Bone, Boneyard; WC, Walton Creek.

nitrogen availability or under-canopy radiation (Table 2). Cover exhibited a nonlinear, exponential spatial variance structure at deer access and exclosure sites, although the inclusion of a nugget parameter significantly improved the model in deer exclosures (Table 2). A nugget parameter represents unexplained variance either due to significant spatial variance at separation distances smaller than the sampling grain (1 m in our study) or sampling error (Goovaerts 1998). Assuming

equal sampling error at each site, this finding suggests significant spatial variance at very fine (<1 m) scales in deer exclosures, but not at deer access sites. Spatial variance structure of diversity was more complex in access sites compared to exclosures (Table 2, Fig. 2). Direct under-canopy radiation was best represented by nonlinear, Gaussian models with a nugget in deer access and exclosure sites, with little difference in parameter estimates according to deer access. Other variables were

TABLE 2. Parameter estimates for the most parsimonious (based on ΔAIC_c) semivariogram models.

Variable	Access model	Range† (m)	Sill‡ (γ)	Nug.§ (γ)	RSE	df	Exclosure model	Range (m)	Sill (γ)	Nug. (γ)	RSE	df
Ammonium	exponential	3.30	0.91	NA	0.363	24	exponential	7.47	0.86	NA	0.115	24
Nitrate	linear¶	NA	NA	0.81	0.136	24	exponential	2.80	0.66	NA	0.144	24
Direct UCR	Gaussian	2.57	0.84	0.18	0.092	23	Gaussian	3.45	0.94	0.10	0.158	23
Diffuse UCR	linear#	NA	NA	0.15	0.051	24	exponential	18.84	0.69	NA	0.100	24
Herb cover	exponential	5.98	0.89	NA	0.123	24	exponential	16.49	0.84	0.13	0.093	23
Herb diversity	exponential	5.70	0.87	NA	0.124	24	white noise	NA	NA	0.51	0.149	25

Notes: Key to abbreviations: RSE is residual standard error; NA indicates "not applicable to selected model"; UCR is under-canopy (solar) radiation; γ, semivariance/sample variance; h, distance (m) between sample plots. Semivariogram model parameters are: b, range parameter; C, partial sill; and ε, residual variance.

† Range = $3b$ for exponential models; range = $\sqrt{3b}$ for Gaussian models.

‡ Sill = $C + \varepsilon$.

§ Nugget = ε for spherical, exponential, and Gaussian models; nugget = mean$[(\varepsilon(h)]$ for white noise and linear models.

¶ Slope parameter $m = -0.01$.
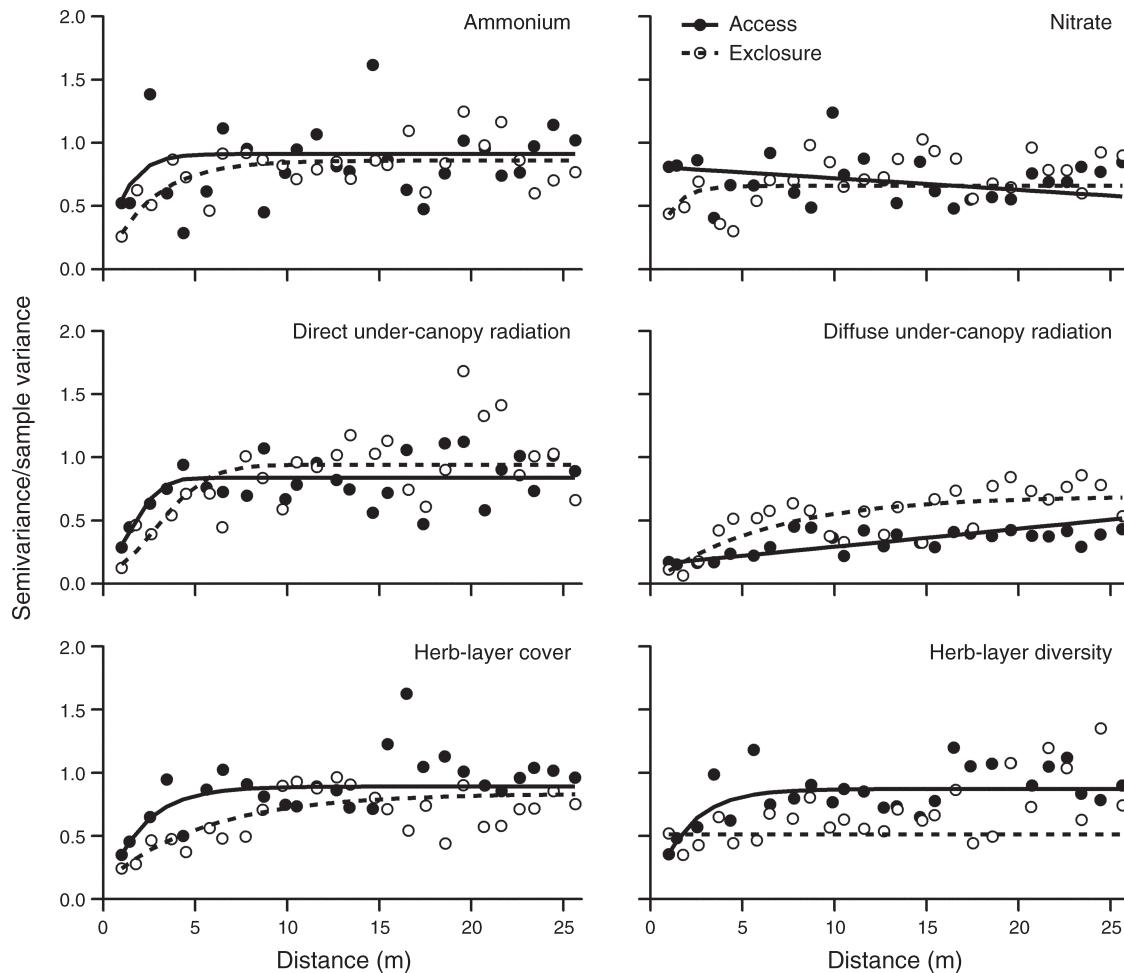
Slope parameter $m = 0.01$.

FIG. 2. Empirical semivariograms (circles) and modeled semivariograms (lines), grouped according to white-tailed deer (*Odocoileus virginianus*) access (open circles, deer have access; solid circles, exclosures prevent deer access). A semivariogram displays changes in semivariance (*y*-axis) over increasing separation distances between sample plots (*x*-axis). See Table 2 for model identification and parameter estimates.

best represented by two-parameter exponential models (Table 2). No semivariogram model estimated a sill >1 (Table 2), indicating spatial dependence even at the largest separation distance.

Differences in patch size associated with deer access can be examined by comparing the range of spatial dependence (Table 2, Fig. 2). The patch size of ammonium availability was 66% smaller in deer access sites compared to deer exclosures (range = 7.47 vs. 3.30 m; Table 2, Fig. 2). Cover patch size was 64% smaller in deer access sites (range, 16.49 vs. 5.98 m; Table 2, Fig. 2). Nitrate availability and diffuse under-canopy radiation exhibited weaker spatial variance structure at deer access sites compared to exclosures as evidenced by the selection of simpler, linear models for access sites (Table 2). The patch size of these variables likely exceeds the maximum distance of our models because their nugget parameters (y-intercept) are less than 1 and their slopes are small. Diversity patch size in deer exclosures may also exceed the maximum distance for the same reason. The patch size of direct under-canopy radiation was 26% smaller in access sites compared to exclosures (Table 2, Fig. 2), which is less of a difference compared to ammonium and cover.

In comparing patch size among variables, cover and diversity were similar to ammonium availability and direct under-canopy radiation at deer access sites. Within deer exclosures the patch size of cover was similar to diffuse under-canopy radiation. Direct under-canopy radiation and nitrate availability patch sizes were similar, and smaller, than ammonium (Table 2, Fig. 2).

DISCUSSION

Our results support the hypothesis that ungulate excreta maintain more complex spatial patterns in soil nitrogen resources and herb-layer cover at a spatial extent of 1–20 m. Where deer are present, the spatial pattern of nitrogen availability may be patchier despite a lack of difference in mean stand-level nitrogen availability. Although many studies have documented the growth-stimulating effects of ungulate excreta, particularly urea nitrogen (e.g., Steinauer and Collins 1995, Peek and Forseth 2003), our study demonstrates that it can affect spatial heterogeneity in resource availability and herb-layer cover at spatial scales relevant to herb-layer communities of temperate forests.

In forest ecosystems light availability is another resource, in addition to nutrient availability, that limits herb-layer growth (Gilliam and Roberts 2003) and influences the spatial patterning of herb-layer communities (Scheller and Mladenoff 2002). In our study light seemed to have a greater influence on the spatial patterning of cover where deer were absent, but not where they were present. At deer access sites the sapling layer was greatly reduced compared to exclosures, presumably due to dormant season browsing (Frelich and Lorimer 1985, Rooney et al. 2000, Witt and

Webster 2010). Consequently, the spatial patterning of diffuse under-canopy radiation was less complex. However, spatial patterning of herb-layer cover and diversity exhibited smaller patch sizes despite less complex spatial patterning in diffuse radiation. In deer exclosures the sapling layer and spatial pattern of diffuse radiation were more complex, and the patch size of cover closely resembled that of diffuse radiation. Deer have been known to homogenize plant communities across spatial gradients of resource availability via browsing (e.g., Holmes and Webster 2011), but in our study deer appear to have increased heterogeneity in understory cover.

Although deer and other ungulates are generally regarded as homogenizers of plant communities (e.g., Rooney et al. 2004, Webster et al. 2005, Rooney 2009), deer effects on vegetation operate within a broader ecological context (Schmitz and Sinclair 1997). Until recently studies of deer impacts were limited to case studies where a problem was perceived a priori, making them susceptible to pseudoreplication (Côté et al. 2004). Several recent studies have highlighted the broader ecological function of deer in forest ecosystems. For example, Royo et al. (2010) found that at intermediate deer densities browsing interacts with other disturbances, such as fire and gap creation, to increase plant diversity. Deer exclusion reduced diversity by allowing fast-growing, palatable plant species to dominate the community following disturbance. Long-term exclusion of browsing ungulates can lead to a similar outcome even in the absence of disturbance (Perrin et al. 2011). Deer abundance is often thought of as an indicator of deer impacts; however, deer impacts also depend on the abundance of palatable plants (Schmitz and Sinclair 1997) and landscape context (Rutherford and Schmitz 2010, Hurley et al. 2012). At the landscape scale deer may function as vectors for nutrient transport from ecosystems of greater nutrient availability to those of lower nutrient availability (Seagle 2003, Bump et al. 2009a, Abbas et al. 2012). At finer scales ungulate carcasses can create nutrient hotspots that affect forest and prairie plant community composition (Towne 2000, Bump et al. 2009b).

Our results likely apply to other deer populations and ungulate species because of seasonally (or diurnally) dynamic aggregations, dispersals, and migrations common to these species. Consequently, our study highlights the importance of seasonal timing in both resource inputs and herbivory to the outcome of complex feedbacks between herbivores and the spatial distribution of resources. A plant's ability to compensate for herbivory depends on the timing of herbivory and nutrient availability, in addition to competition with other plants (Maschinski and Whitham 1989). Hemlock forests are used by deer primarily for winter cover rather than food. Deer migrate from hemlock stands to more productive habitats as severe winter weather subsides (Verme 1973), so that most deer herbivory occurs during

the dormant season (Frelich and Lorimer 1985, Rooney et al. 2000, Witt and Webster 2010). Due to seasonal deer use, much of the deer-source nitrogen inputs occur during winter and enter the soil pool as a pulse during spring snowmelt. Spring ephemerals and soil microorganisms would benefit directly from these nitrogen pulses, and capture nitrogen for later uptake by summer vegetation (Zak et al. 1990). Plant community heterogeneity has previously been linked to deer use in remnant hemlock stands (Jensen et al. 2011). Therefore, we hypothesize that the seasonal decoupling of ungulate habitat use and plant growth has allowed understory plants the opportunity to respond to ungulate-excreted nitrogen additions without greater risk of being consumed by ungulates. The patchy spatial distribution of deer excreta results in patches of increased vegetation growth, increasing the spatial heterogeneity of vegetation cover.

The impact of deer on neighborhood scale heterogeneity in nitrogen availability and herb-layer cover suggests a link between fine-scale and landscape-scale processes. Ungulates select habitat patches at coarse landscape-level scales, whereas impacts on vegetation occur at the scale of individual plants (Weisberg et al. 2006). Consequently, landscape configuration can modulate the impact of ungulate herbivory on vegetation at a given ungulate density (Hurley et al. 2012). In the northern hardwood–hemlock forest mosaic of our study, deer selection of conifer-dominated winter habitat is influenced by landscape context in addition to stand-level variables (Witt et al. 2012). In our study seasonal patterns in deer habitat selection reduced cover of large seedlings and saplings that grow above the snowpack. Growing season herbivory may be reducing cover in access sites relative to exclosures, although the reduction was not statistically significant. Moderate levels of growing season herbivory may result in greater diversity even if cover is reduced (Royo et al. 2010). If moderate growing season herbivory reduces total cover, deer may still increase heterogeneity through patchy nitrogenous waste deposition (Steinauer and Collins 1995, Augustine and Frank 2001), trampling (Heckel et al. 2010), and selective herbivory (Augustine and McNaughton 1998). Similarly, the patch size of nitrogen and cover may vary over the landscape with changes in deer use, linking fine-scale and coarse-scale processes. This question could be explored further by incorporating deer access sites across a gradient of deer densities.

Our failure to detect nitrogen hotspots at deer access sites does not compromise our conclusion that ungulate excreta increase spatial heterogeneity in nitrogen availability. First, most of the deer-excreted nitrogen measured by ion-exchange resin bags was deposited during winter and passed through the snowpack before reaching the soil. This process is likely to have increased the area affected by an excretion event while making its patch boundary more diffuse and difficult to detect.

Second, resin bags were buried for several weeks after snowmelt. Other nitrogen inputs during this time may have masked deer-excreted nitrogen. We retrieved resin bags during the vegetation survey to ensure that we measured the nitrogen available to the observed vegetation community. Third, it is highly unlikely that we placed a resin bag in the exact location that a deer urinated or defecated during winter 2010–2011 given that fecal pellets occurred in <3% of the sampled area. The observed differences in spatial patterns may be the cumulative result of deer-excreted nitrogen inputs over multiple seasons.

Browsing ungulates may be an important source of spatial heterogeneity in forest ecosystems. Human activities are greatly altering nitrogen cycling in many temperate forest ecosystems, and one outcome is the homogenization of nitrogen availability (Gilliam 2006). Atmospheric nitrogen deposition levels are less elevated in the northern Great Lakes region where our study took place compared to more industrialized areas (e.g., Gilliam 2006, 2007), although they are greater than annual nitrogen sequestration by plants (Talhelm et al. 2012). Herb-layer communities contain much of the biodiversity in temperate forests (Gilliam 2007), but biodiversity declines as a result of nitrogen saturation and homogenization (Gilliam 2006). Therefore, ecological processes that increase spatial heterogeneity of nitrogen availability and are scale dependent are important to maintaining biodiversity. Ungulates may increase or decrease heterogeneity of these processes depending on ecological context, and may be an important component of unaltered forest nitrogen cycles as they are in grasslands (e.g., McNaughton 1985, Augustine et al. 2003). Although ungulate exclosures are useful for restoring vegetation in many cases, they may not be effective at restoring spatial patterns of resource availability.

Our results demonstrate that forest ungulates can create complex spatial patterns in soil nitrogen, a critical and limiting terrestrial resource. The ecological importance of this effect is contingent upon the scale of inference and the seasonal timing of ungulate impacts relative to ecosystem response. Ungulates are common in forest ecosystems, and may be an important ecological link between fine-scale and landscape-scale processes that are further modulated by seasonally dynamic habitat selection. Our main results highlight the general need to examine (and reexamine) the dynamic role of ungulate species in affecting ecosystem processes. Questions of scale and heterogeneity are prominent in ecology because they provide a link between ecosystem and animal ecology that advances conservation science (Levin 1992, Loreau 2010, Ritchie 2010). Forest ungulate ecology may be better understood when viewed within a broad ecological context that includes scale, heterogeneity, and ecosystem processes.

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Supplemental Material

Appendix A

Ottawa National Forest and Ford Forestry Center study site information (*Ecological Archives* E094-117-A1).

Appendix B

Detailed description of deer use survey, ion-exchange resin bag, and spatial variance modeling methodologies (*Ecological Archives* E094-117-A2).

Appendix C

Data tables describing understory tree height class distributions and mean cover of herb-layer species by site (*Ecological Archives* E094-117-A3).