

SPATIAL PATTERNS IN THE MOOSE–FOREST–SOIL ECOSYSTEM ON ISLE ROYALE, MICHIGAN, USA

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Abstract. The effects of herbivores on landscape patterns and ecosystem processes have generally been inferred only from small-plot or enclosure experiments. However, it is important to directly determine the interactions between herbivores and landscape patterns, because herbivores range over large portions of the landscape to meet requirements for food and shelter. In two valleys on Isle Royale, Michigan, USA, soil nitrogen availability and its temporal variance decreased rapidly as consumption of browse by moose (*Alces alces*) increased up to $2 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$; with greater amounts of consumption, nitrogen availability was uniformly low and constant from year to year. We tested three geostatistical models of the spatial distribution of available browse, annual browse consumption, conifer basal area, and soil nitrogen availability across the landscape: (1) no spatial autocorrelation (random spatial distribution); (2) short-range spatial autocorrelation within a patch, but random distribution of patches at larger scales (spherical model); and (3) both short-range autocorrelation within a patch and regular arrangement of patches at larger scales (harmonic oscillator model). Conifer basal area and soil nitrogen availability fit the harmonic oscillator model in both valleys. Annual consumption and available browse showed oscillations in one of the valleys and only short-range autocorrelation in the other. In both valleys, however, the spatial pattern of annual consumption followed that of available browse. The predominance of spatially oscillatory patterns suggests that the interactions of moose with the forest ecosystem cause the development of both local patches of vegetation and associated nitrogen cycling rates, as well as the development of higher order patterns across the larger landscape. We suggest a coupled diffusion model of herbivore foraging and plant seed dispersal that may account for these patterns.

Key words: *Alces alces*; boreal forests; diffusion models; geostatistics; hardwood–conifer shift; herbivore–ecosystem interactions; Isle Royale; moose; nitrogen availability; spatial patterns.

INTRODUCTION

It has been suggested that large-scale landscape heterogeneity affects population dynamics and movements of animals (Kitching 1971, Wiens 1976, Kareiva and Shigesada 1983, Gardner et al. 1987, 1989, Senft et al. 1987, Urban and Smith 1989, Wiens and Milne 1989, Turner et al. 1994), and that animals alter ecosystem functioning and possibly landscape structure as they sample their environment for food and shelter (McNaughton 1985, Naiman et al. 1986, 1988, Huntly and Inouye 1988, Jefferies 1988, 1989, Pastor et al. 1988, Whicker and Detling 1988, Wiens and Milne 1989, Jefferies et al. 1994, Hobbs 1996, Pastor and Cohen 1997, Moen et al., *in press*).

Herbivore–ecosystem interactions are particularly interesting when we consider heavy grazing or browsing by ungulates (Senft et al. 1987, Whicker and Detling 1988, Wiens and Milne 1989, Milne 1991a, b). Because they have large home ranges, consume large

amounts of food, and forage selectively among plant parts and among plant species, large ungulates can affect species composition of communities, successional pathways, nutrient cycling, and ecosystem productivity (McNaughton 1985, Jefferies 1988, McNaughton et al. 1988, Pastor et al. 1988, *in press*, Whicker and Detling 1988, Pastor and Naiman 1992, Jefferies et al. 1994, Hobbs 1996). In northern ecosystems, herbivores alter nutrient cycles by shifting plant communities toward unbrowsed species (thereby controlling the arrays of plant litter returned to the soil) and by depositing urine, fecal material, and carcasses (McKendrick et al. 1980, Bryant and Chapin 1985, Reuss et al. 1989, Hobbs et al. 1991, Holland et al. 1992, McInnes et al. 1992, Pastor et al. 1993, Jefferies et al. 1994, Hobbs 1996).

Most previous field studies of herbivore–ecosystem interactions have been performed on small plots or enclosures a few tens or hundreds of square meters in area. The extent of herbivore-induced changes in ecosystem properties across the landscape and, therefore, their importance to large-scale patterns that are orders of magnitude larger in size than these experimental

plots, has only been inferred, not documented. Changes in ecosystem properties inside and outside exclosures clearly show that vertebrate herbivores can alter the local trajectory of ecosystem development (e.g., McKendrick et al. 1980, Jefferies 1988, McInnes et al. 1992, Pastor et al. 1993). At larger landscape scales corresponding to the size of an entire valley or even a substantial part of a home range, these changes in the local development of ecosystem properties may be overridden by other factors, such as topographic influences on microclimate or initial materials. In such a case, the distribution of ecosystem processes over the landscape would be correlated with other factors and only weakly, or even randomly, related to the influence of herbivores, even though the herbivores exert control at discrete points at smaller scales. Alternatively, the herbivores could be responsible for large-scale landscape patterns as they forage across their home range.

A simple example may illustrate how it is possible for properties to be correlated at local scales, but randomly distributed at larger scales. Assign the numbers 1 through 64 randomly to each square of a checkerboard. In this case, each square represents a local "ecosystem type" (for example, a particular combination of soil and vegetation) and the entire board represents the "landscape," or assemblage of ecosystem types (for example, a valley). Now, produce a second set of numbers by adding "1" to each number on its assigned square. The two sets of numbers might represent measurements of vegetation and soil properties, respectively. The two sets of numbers will be perfectly correlated across all plots (i.e., a "1" in the first set is associated with a "2" in the second, "2" is associated with "3," etc.), but each set, as well as particular pairs of points, will be randomly distributed in space. Therefore, local mechanisms that produce correlations between properties (in this case, "adding 1") do not necessarily produce higher order spatial patterns. However, higher order patterns might result if the assignment of the second set of numbers depends not only on the number in a given square, but also on the numbers in the adjacent squares. In this paper, we are interested in determining if local correlations between herbivory and ecosystem properties are randomly distributed at larger scales, or if higher order patterns (i.e., patchiness) also develop.

Boreal forests with their populations of large ungulates, are uniquely suited for investigating the role of scale in herbivore-ecosystem interactions. These forests are composed of a few tree species that differ greatly in life-form and have patchy distribution. Moreover, these different tree species are required by large herbivores for food and shelter (Stenseth 1977, Stenseth et al. 1977a, b, Hansson 1979, Telfer 1984). Finally, different tree species have very different tissue chemistries that determine both foraging preference by large ungulates (Bryant and Kuropat 1980, Bryant et

al. 1991) and decomposition of the plant's litter (Flanagan and Van Cleve 1983, Pastor et al. 1993).

Moose (*Alces alces*), in particular, preferentially forage on aspen (*Populus tremuloides*), hazel (*Corylus cornuta*), and other hardwoods, but avoid conifers such as spruce (*Picea mariana*, *P. glauca*); balsam fir (*Abies balsamea*) is eaten in winter but is not preferred (Telfer 1984, Risenhoover and Maass 1987, Brandner et al. 1990, McInnes et al. 1992). The high nutrient contents and low contents of lignin and secondary metabolites in hardwood tissues relative to conifer tissues are thought to be a primary reason both for their rapid decay as litter (Flanagan and Van Cleve 1983) and for the selective foraging behavior of moose (Bryant and Kuropat 1980). If moose browsing causes a shift in dominance from hardwoods to conifers across adjacent areas, then we should expect corresponding changes in soil nutrient availability over the landscape.

The purpose of this paper is to examine the large-scale landscape distribution of moose browsing intensity in relation to plant community composition and size structure, as well as soil nitrogen availability. Given that moose control plant community composition and, hence, soil nitrogen availability at scales of tens to hundreds of square meters (McInnes et al. 1992, Pastor et al. 1993), we are interested in determining whether these effects result in larger scale patterns across entire valleys.

STUDY AREA

We studied the spatial pattern of moose browsing and soil nitrogen availability in Isle Royale National Park, Michigan, United States. The landscape is rugged, composed of northeast-trending valleys with steep, north-facing slopes and gentle, south-facing slopes (Huber 1973). The bedrock geology of both valleys is uniformly Precambrian volcanic lava flows of the Portage Lake Formation (Huber 1973). Glacial deposits in these valleys are mainly kame moraines longitudinal to the valley strike along the valley walls, or recessional moraines across the valley floors (Huber 1973).

The upland vegetation includes plants typical of the southern boreal forest (Pastor and Mladenoff 1992), with quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and hazel (*Corylus cornuta*) being the principal food sources for moose. These shade-intolerant hardwoods eventually succeeded to balsam fir or white spruce. Browsing intensity on balsam fir varies across the island, ranging from light browsing in the northeast sector of the island, where these valleys are located, to heavy browsing in the southwest (Brandner et al. 1990). Spruce is not browsed at all. No fires have been recorded in these valleys since the turn of the century, although there have been fires elsewhere on Isle Royale (Hansen et al. 1973). Beaver ponds occupy riparian corridors in valley bottoms, and beaver have

harvested some of the adjacent aspen within ~ 50 m from the pond edge.

Winter moose densities in the study area average 3.7 moose/km² (Peterson 1991). It is not known exactly how many moose have affected our observational grids in these valleys during the three years of this study, but these densities are among the highest in the world.

METHODS

Establishment of sampling networks

We established a network of 100 points in each of two valleys in the northeast sector of Isle Royale. The valleys are 10 km apart; thus, they independently sample browsing by different individuals. The typical 500–1000 ha home range of moose (Telfer 1984, Peterson 1991) is small enough to make it unlikely that the same moose visited both valleys. However, we cannot entirely rule out the possibility that an individual moose occasionally used both valleys.

In each valley, 10 transects were randomly established by pacing uphill from the edge of the beaver meadows in the valley bottom. The distance between each transect was chosen from a uniform random distribution from 0 to 100 m, with an expected average distance of 50 m between transects. Depending on valley width, two to eight sampling points were then located randomly along each transect going upslope from the valley bottom, also by sampling from a uniform random distribution from 0 to 100 m.

The exact location of each sampling point was surveyed from one corner of the grid, using standard surveying procedures with tapes and compasses (Breed and Hosmer 1970). The compass direction between points was determined by two observers positioned at different sampling points (or intermediate turning points, where required) and sighting forward and backward on each other. The exact compass direction was taken as the average of these two sightings (correcting one, of course, by 180°). We closed ~ 10 smaller loops of the grids, as well as the entire grid, to maintain accuracy. (For readers not familiar with land surveying techniques, a loop is a complete circuit of a survey around a set of points back to the beginning point, taking measurements of distances and compass angles between each point. It allows one to “simulate” by trigonometry the entire traverse from the beginning point continuously around the “closed” polygon back to the starting point, using the measured distances and angles. The difference between the x and y coordinates of the simulated ending point around the polygon and the expected values on the ground yields an error measure, or “closure error,” for the entire loop).

The x , y coordinate data for each point were imported into ARC/INFO (Environmental Systems Research Institute 1992) for rectification and calculation of closure errors. The mapped grid was constructed by first entering locations of each point for each smaller loop,

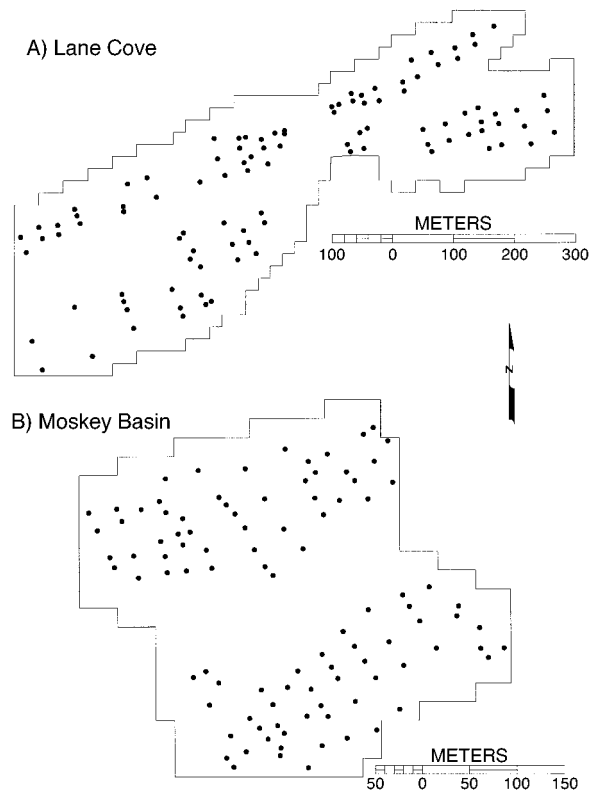


FIG. 1. Sampling grid point locations in Lane Cove and Moskey Basin. Streams and associated beaver ponds run through the center of the valleys from southwest to northeast; sampling points were not established in these areas, but only in adjacent upland areas.

going upslope on one transect, downslope on the next adjacent transect, and finally backsighting on the first point of the beginning transect in that loop. Closure error was then calculated for that loop. Locations of grid points of each successive loop were then corrected for the closure error of the previous loop. Closure error for the smaller loops was never >5 m and was usually within 1–2 m. By correcting for closure errors for each successive loop of the grid, we were able to maintain closure errors for the full grids to within 1:94 (nearly 1%) or better. (Cognoscenti of land surveying before the advent of portable global positioning system units will recognize that this is remarkable accuracy for compass and tape measurements). We now have a spatially explicit and accurate sampling network, with stratified randomization within a valley and replication between valleys (Fig. 1), upon which we can assess the spatial pattern of moose browsing in relation to ecosystem properties.

Vegetation and browse sampling

At each sampling point, annual consumption by moose was estimated from 1989 to 1992 inclusive by counting the number of newly browsed twigs each spring and fall in 2-m² circular plots concentric to each

grid point. The spring sampling determined the amount of browse removed over the previous winter, whereas the fall sampling determined the amount of browse removed during summer. Winter browsing removes twigs (with needles attached, in the case of conifers). During summer, moose strip leaves from the twigs of hardwoods without browsing the woody tissue; such leaf stripping is easily noted by the remnants of attached petioles. Thus, we noted whether a twig was browsed or stripped of leaves during the fall sampling. We multiplied the number of browsed or stripped twigs by average bite size for each species during winter and summer removals (0.5–1.5 g; Miquelle 1983, Risenhoover 1987). We also counted the totaled number of twigs in the plots and multiplied this number by bite size for each species to estimate available browse. A 0.01 ha circular plot was established concentric to the browse plot, within which the diameter and species of all trees were inventoried in 1991. The transects and grid points were far enough apart so that no two plots established at adjacent grid points overlapped.

Soil nitrogen availability

To sample nitrogen availability, three resin bags, each containing 10 g of Rexyn I-300 (Fisher Scientific, Fairlawn, New Jersey, USA) mixed-bed, cation–anion exchange resin (Binkley 1984), were buried in the Oh or A1 horizon of the soil (5–10 cm deep) immediately outside the 2-m² plot within one or two days of 19 July, and were retrieved in the following year during the period 1989–1992 inclusive. These bags sample plant-available ammonium and nitrate released during the decomposition of humus throughout the year and, thus, provide an index of nitrogen availability to plants that correlates with productivity (Binkley et al. 1984). Ammonium and nitrate were extracted from 2-g subsamples of resin composited by plot with 100 mL of 1 mol/L KCl; the resins were shaken for 15 min in 25 mL KCl, decanted, shaken again in another 25 mL aliquot, poured into small Buchner funnels (5.5 cm diameter) equipped with pre-washed #1 Whatman filters, and washed several times with additional KCl before the filtrate was brought to 100 mL volume. The extracts were analyzed by standard methods for NH₄-N and NO₃-N on a Lachat autoanalyzer (Lachat Instruments, Milwaukee, Wisconsin, USA).

Statistical analyses

Prior to examining spatial variances for various properties, we undertook exploratory data analysis of trends and correlations between properties of interest (Rossi et al. 1992). Specific statistical procedures were chosen to elucidate various observed patterns and will be discussed, where appropriate, in *Results*.

Geostatistical methods of data analysis have become popular in ecological investigations in recent years (Robertson 1987, Rossi et al. 1992). These methods seek to determine the existence and scale of patterns

of a property across the landscape. The central idea is to identify patches of low variance of a property between sampling points, and to examine how the variance changes with increasing distance between sampling points. All such methods rely on calculating some measure of variance, covariance, or correlation between a property at pairs of points separated by increasingly larger distances. These distances are known as “lags.” Various models derived from assumptions about the underlying nature of the spatial variance are fit to the trends in variance plotted against lag, or distance between points.

The estimated semivariance, $\hat{\gamma}$, is one-half of the mean square differences between measurements at points separated by a set of distances \mathbf{h} :

$$\hat{\gamma}(\mathbf{h}) = \frac{1}{2N(\mathbf{h})} \sum_{i=1}^{N(\mathbf{h})} [z(x_i) - z(x_i + \mathbf{h})]^2 \quad (1)$$

where $N(\mathbf{h})$ is the number of pairs of points separated by distances \mathbf{h} , $z(x_i)$ is a measured property at point x_i , and $z(x_i + \mathbf{h})$ are measurements of the same property at various distances.

The semivariance is a statistical estimate of variance of a property across the space demarcated by the grid of sample points. Its relationship to the “true” variance across continuous space is analogous to the relationship between the sample variance, s , and the population variance, σ , in univariate statistics. We calculated the semivariance for mean annual browse availability, mean annual consumption, conifer basal area, and mean annual soil nitrogen availability across 4626 pairs of points in Lane Cove and 4876 pairs of points in Moskey Basin. Semivariances were calculated between approximately 20 m and 600 m in all compass directions for 21 lag distances in Lane Cove and 16 lag distances in Moskey Basin. There were >100 pairs ($N(\mathbf{h})$), usually >200 pairs, and occasionally >400 pairs of points for each lag distance in each valley, except for 20 m and 600 m in Moskey Basin, for which $N(\mathbf{h}) = 64$ and 68 pairs of points, respectively. The total number of pairs of points and the number of pairs at each distance differed between the two valleys because of their different shapes (Fig. 1). Data were log-transformed when necessary to conform to normal distributions. A normal distribution insures that the differences between $z(x_i)$ and $z(x_i + \mathbf{h})$ are symmetrically distributed about the mean.

We then fit three models, representing different spatial patterns, to these semivariances:

Model 1.—A property is randomly distributed with no spatial autocorrelation. This model assumes that the semivariance values are randomly distributed around a mean semivariance that is stationary (i.e., does not exhibit any trends with increasing distance between sample points).

Model 2.—A property exhibits short-range autocorrelation evidenced by low variance between points separated by short distances, but the variance increases

asymptotically with increasing distance between sampling points. This model suggests the existence of homogeneous patches that, themselves, are randomly distributed across the landscape. The equation most often used to describe such a pattern is the so-called "spherical" model (Robertson 1987, Rossi et al. 1992):

$$\gamma(\mathbf{h}) = C[1.5 \mathbf{h}/a - (\mathbf{h}/a)^3] + \varepsilon \quad \mathbf{h} \leq a \quad (2a)$$

and

$$\gamma(\mathbf{h}) = C, \quad \mathbf{h} \geq a \quad (2b)$$

where C is the asymptote of $\gamma(\mathbf{h})$, otherwise known as the sill; a is the value of \mathbf{h} at C , otherwise known as the range; and ε , otherwise known as the nugget, is the y -intercept or unaccounted for spatial variation at intervals smaller than the shortest distance between sample points. The range can be interpreted as the mean radius of a patch of low variance between sampling points. Beyond the range, variance between points is high and stationary, suggesting no higher order patterns.

Model 3.—Higher order spatial patterns could emerge when patches are regularly arranged across the landscape. As one moves from the center out of a patch, the variance of a property between two points should increase, as in Model 2. However, as one moves farther (\mathbf{h} increases) and begins to enter patches similar to that where one started, the difference between $z(x_i)$ and $z(x_i + \mathbf{h})$, and, therefore, also $\gamma(\mathbf{h})$, should begin to decrease. If such patches are regularly arranged in the landscape, one should expect a sinusoidal trend in semivariance between sample points with increasing distance, as one moves into and out of patches of similar measured values for that property.

Accordingly, we fit to our data equations for a harmonic oscillator similar to that proposed by Thiébaux (1985) and Shapiro and Botha (1991) to test for conformance to Model 3:

$$\gamma(\mathbf{h}) = \bar{\gamma} + Ae^{k\mathbf{h}}\sin(\omega\mathbf{h} + \beta) \quad (3)$$

where A is the amplitude of variance about $\bar{\gamma}$, k is the rate by which the amplitude changes with distance \mathbf{h} , ω is the frequency (radians/m), and β is the phase. A useful feature of this model is that the "wavelength" or period of oscillation (T) of variance with distance is

$$T = 2\pi/\omega. \quad (4)$$

Linear regressions of Eqs. 2 and 3 against the data are not possible. Eq. 2 is a discontinuous function; all regression techniques assume that the candidate function can be integrated at every point within the range of the data, but the derivative of the spherical model is undefined at a . Nonlinear parameter estimation by the Simplex or Quasi-Newton methods resulted in unrealistic values for the parameters of Eq. 3, because the techniques reduced the frequency to such small values that the equation went through every point, with multiple oscillations between points. Therefore, initial

estimates of the parameters of Eqs. 2 and 3 were made by inspection and then adjusted by manual iterations to minimize residuals. These secondary adjustments were minor and involved only the third or fourth significant figure of each parameter value.

We then tested for goodness-of-fit between each model and the data by calculating the residual mean square (RMS) difference between model predictions of variance for each lag distance and the measured values. Because these models are nonlinear, it is not possible to assign statistical significance for the RMS of each. We therefore present the RMS of each model for each property and discuss the emergence of higher order spatial patterns based on decreases in RMS from Model 1 (random distribution of a property) to Model 3 (regularly arranged patches).

RESULTS

Local scale bivariate relationships between moose consumption, vegetation, and soil N

Frequency distributions of diameters of aspen and balsam fir differ in relation to browse consumption (Fig. 2). In both valleys, the smaller size classes of aspen that are still accessible to moose are present only where consumption is $<4 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. These smaller size classes are depleted of aspen where consumption is higher. Frequency distributions for diameters of paper birch (*Betula papyrifera*) and other preferred species follow the same pattern with increasing browse consumption as do aspen. In contrast, the number of individuals in the smaller diameter classes of fir increases with increasing browse consumption on its competitors. White spruce (not preferred) shows diameter distributions similar to those of fir.

Curiously, the larger size classes of aspen are sometimes depleted or absent with increasing browsing intensity, even though leaves or twigs of such large trees are not accessible to moose. Trees of these larger size classes appear to date back to the 1930s, when moose populations were at their highest and before wolves had arrived on the island (Allen 1976, Peterson 1991). It is possible that the depletion of aspen in the larger, and therefore older, size classes is an artifact of historically high browsing levels (Hansen et al. 1973, Krefting 1974). The depletion of larger size classes coincident with current depletion of smaller size classes in areas of high consumption suggests that moose repeatedly visit previously browsed areas.

High N availability occurs only in the absence of significant plant consumption by moose, regardless of position in valley or topographic aspect (Fig. 3). High soil N availability was never associated with high browse consumption by moose. Both average annual N availability and its annual variance decline rapidly with increases of mean consumption to $2 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ and remain uniformly low with greater annual consumption. Inverse power functions fit to these data with

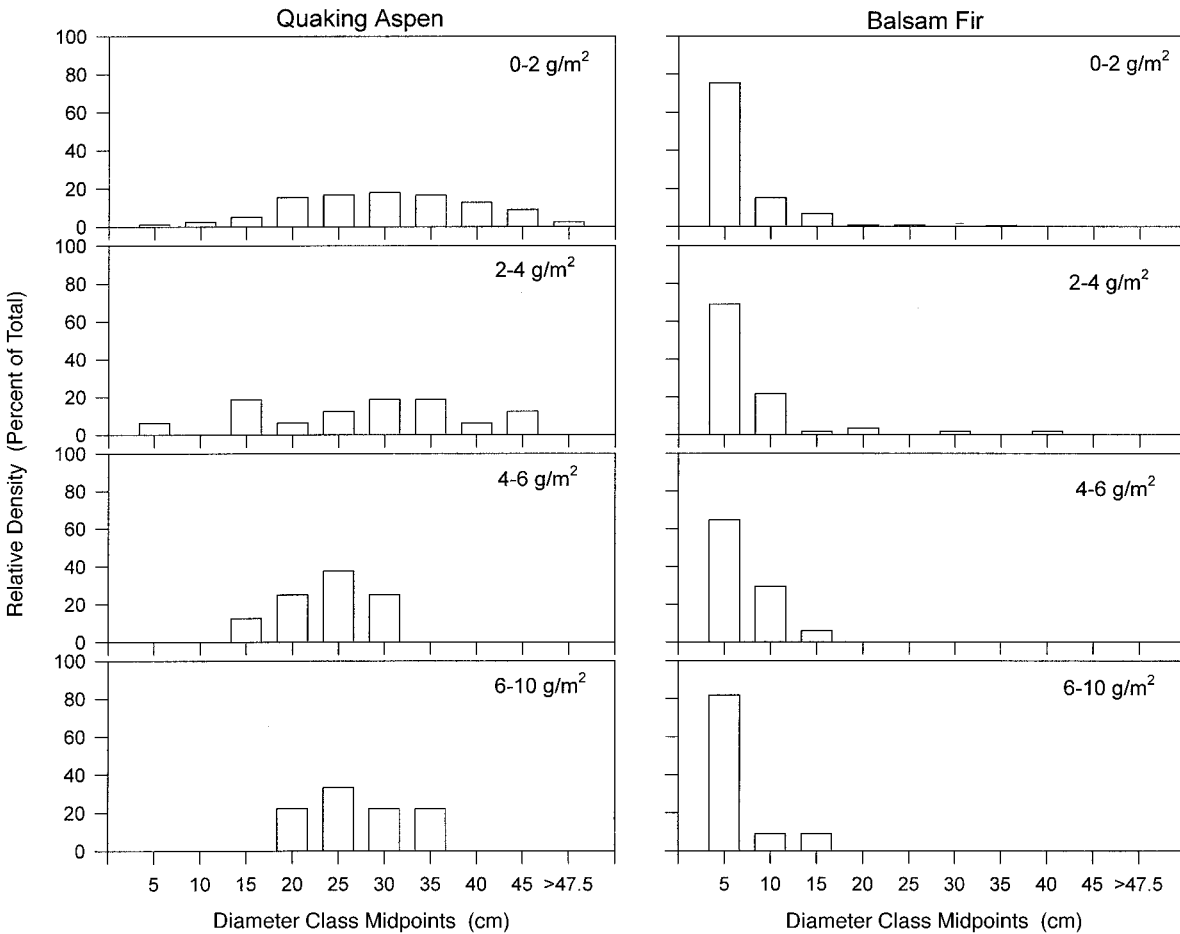


FIG. 2. Frequency distributions of diameters of aspen and fir in Lane Cove relative to annual browse consumption by moose (ranges are in the upper right corner of each graph). Frequency distributions of diameters of spruce are similar to those of fir, and those of paper birch are similar to those of aspen. Frequency distributions of diameters of all species in Moskey Basin are similar to those in Lane Cove. Notice the depletion of smaller size classes of aspen, but not fir, as browse consumption increases.

nonlinear regression by the Quasi-Newton method (Wilkinson 1990) yielded the following:

$$\bar{N} = 191.2 + \frac{1}{(\bar{C} + 0.005)^{1.33}} \quad (5)$$

$$N_{SE} = 45.1 + \frac{1}{(\bar{C} + 0.005)^{1.12}} \quad (6)$$

where \bar{N} and \bar{C} are mean annual nitrogen availability and consumption, respectively, and N_{SE} is the standard error of mean annual nitrogen availability. These equations describe a very rapid decline in N availability and its temporal variation with any increase in moose consumption up to 2–4 g·m⁻²·yr⁻¹, and slower declines with further increases in moose consumption to an asymptote of 191.2 ± 45.1 μg N/g resin (mean ± 1 SE). It is noteworthy that the same general equation (with different parameter values) describes both the spatial and temporal relationships between moose consumption and soil N availability. This suggests that the same

processes may be controlling both spatial and temporal variation of the association between low soil N availability and high moose consumption.

In Fig. 3, points of particular aspects or positions do not segregate along gradients of moose consumption or nitrogen availability, but are evenly arranged throughout the graph. This suggests that nitrogen availability and moose consumption are both independent of aspect or topographic position. This conclusion is supported by ANOVAs of nitrogen availability and consumption against aspect or topographic position: neither the main effects of these topographic variables nor their interaction were significant predictors of nitrogen availability.

Geostatistical analyses of landscape patterns

The spatial variances of browse availability, browse consumption, conifer basal area, and nitrogen availability were distinctly sinusoidal in Moskey Basin (Fig. 4), as were conifer basal area and nitrogen availability

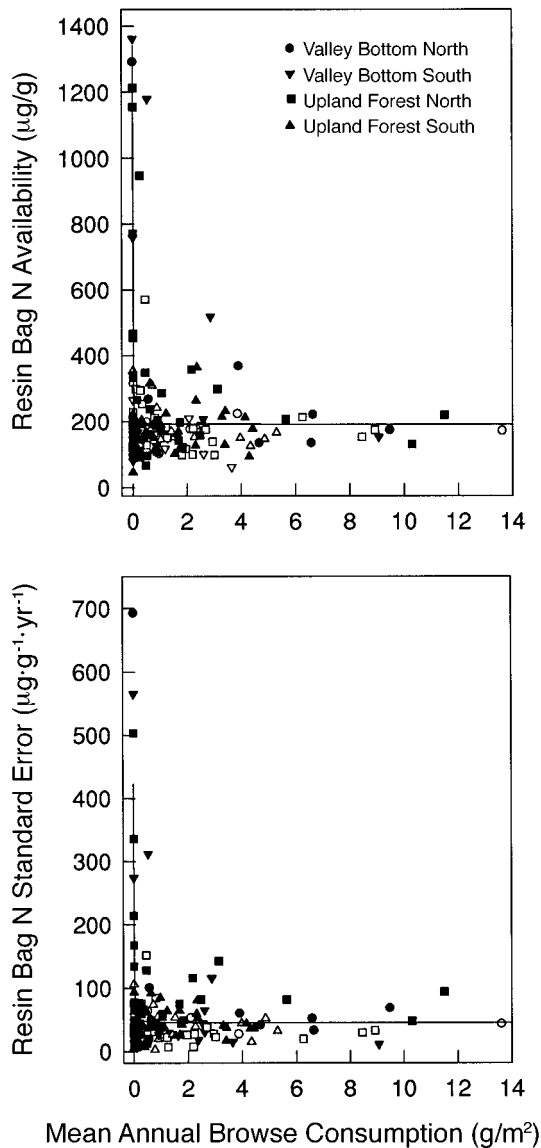


FIG. 3. Relationship between mean annual nitrogen availability, the standard error of annual nitrogen availability over three years, and mean annual browse consumption. Open symbols represent data for Lane Cove; closed symbols represent Moskey Basin data. Lines are best fits of Eqs. 5 and 6.

in Lane Cove (Fig. 5), although the patterns sometimes weakened at longer distances. The sinusoidal patterns of semivariance are similar to those reported by Cohen et al. (1990), but unlike most others reported previously for terrestrial ecosystems, where behavior conforming to a spherical model is most commonly observed (Burrough 1983, Robertson et al. 1988). The residual mean square was lowest for the harmonic oscillator model in all cases except for browse availability and mean annual browse consumption in Lane Cove, where the spherical model fit the data better (Table 1).

In those properties described by the harmonic oscillator model, there is a regular, recurring pattern of

decreasing and then increasing semivariance as the points become further separated. Because the semivariance is a measure of similarity between measured values at points h meters apart, this means that one is moving through a landscape in which homogeneous patches are regularly arranged. Local homogeneity of a property is therefore repeated in a higher order pattern for these properties. Wavelengths for conifer basal area and nitrogen availability are shorter than the wavelengths for browse availability and annual consumption in Moskey Basin. This requires that patches of similar conifer basal area and nitrogen availability repeat themselves more frequently across the landscape than patches of similar browse availability and consumption. Thus, patches of similar conifer basal area and soil nitrogen availability are embedded within somewhat larger patches of available browse and browse consumption.

The spatial patterns of browse availability and consumption fit the harmonic oscillator model in Moskey Basin but not in Lane Cove, where these properties showed only short-range spatial autocorrelation described by the spherical model, but no higher order pattern described by the harmonic oscillator model. However, the shape of Lane Cove may have prevented the detection of long-range oscillations in these properties. Wavelengths for spatial variation of available browse and browse consumption in Moskey Basin were 300 m. This is approximately equal to the width of Lane Cove (Fig. 1). Therefore, it would only be possible to detect a wave pattern of these properties in Lane Cove travelling along the trend of the valley. This would constrain the harmonic oscillator model to operate only in a NE–SW direction in Lane Cove, reducing its descriptive power accordingly.

DISCUSSION

Factors other than moose–ecosystem interactions

There were no differences in nitrogen availability or browse consumption due to slope or aspect across our two sampling grids. Thus, the spatial patterns are not caused by topographic relief alone, nor can they be explained by any underlying pattern in bedrock or glacial geology (Huber 1973) or by recent fire history (Hansen et al. 1973). Beaver also impose spatial patterns on vegetation by cutting trees, particularly aspen in valley bottoms (*personal observations* of the authors on Isle Royale; see also Johnston and Naiman 1990). However, our sampling grids extend well beyond the area of beaver cutting, which is almost always confined to a narrow band ≤ 80 m from the stream course (Johnston and Naiman 1990). The sinusoidal patterns in the semivariograms extend well beyond the valley bottoms, and position in the valley did not account for the relationship between nitrogen availability and browse consumption (Fig. 2). Therefore, these alternative factors do not appear to fully account for our observed

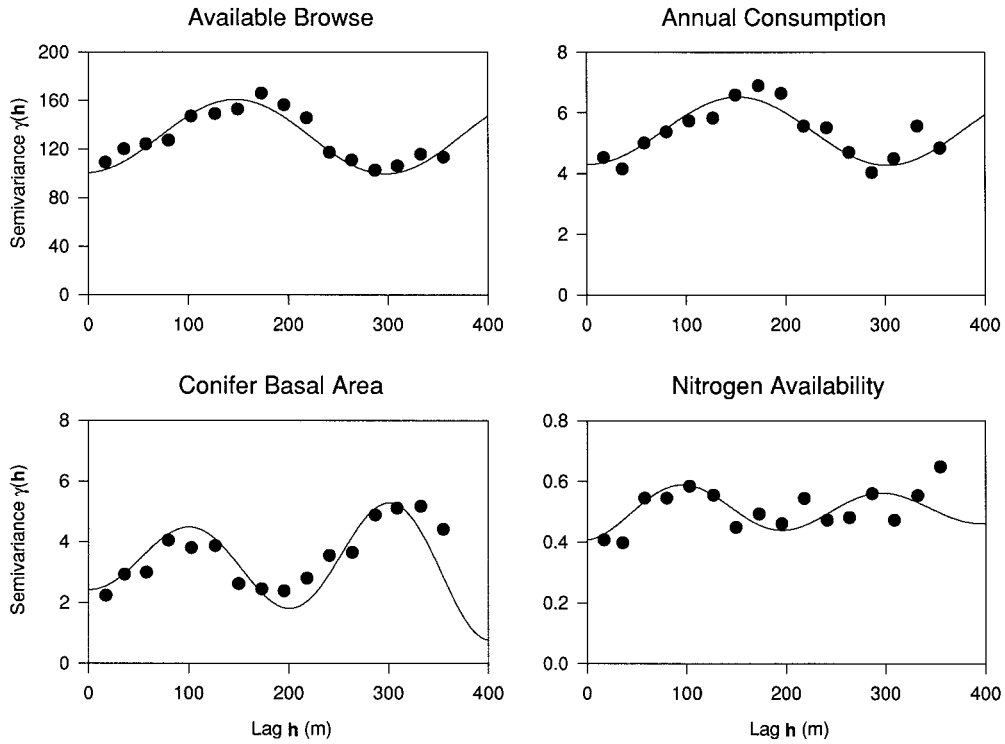


FIG. 4. Semivariograms of available browse, annual browse consumption, conifer basal area, and nitrogen availability in Moskey Basin. Data are points, and lines are best fits of Eq. 3. Each semivariance is calculated from >200 pairs of points, except for those at the shortest and longest lag distances, which are calculated from 64 and 68 pairs of points, respectively.

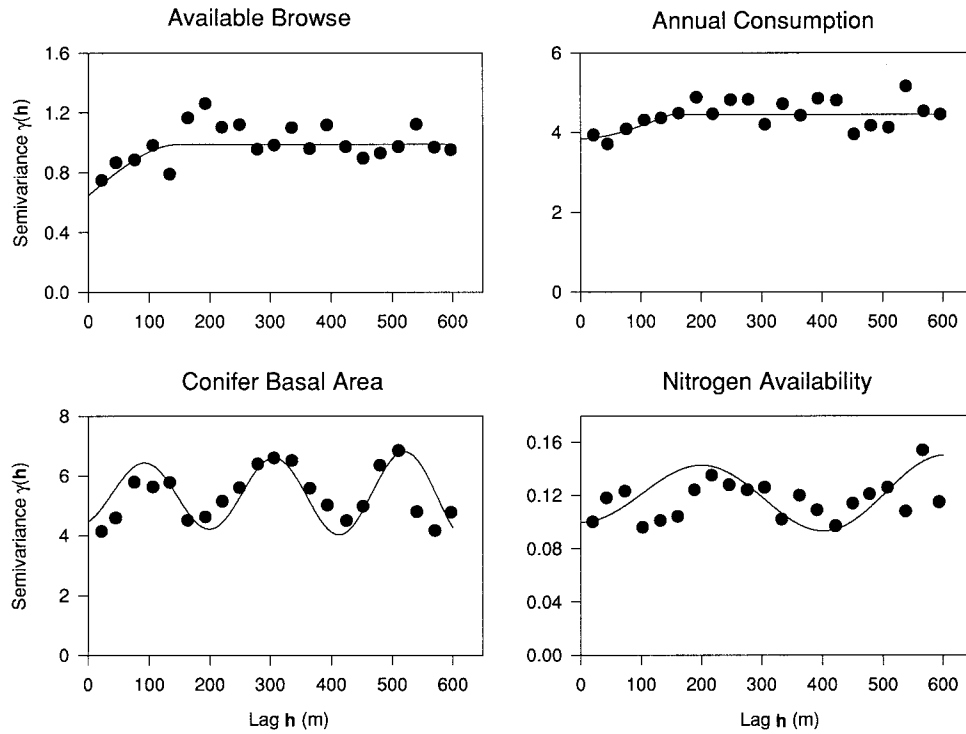


FIG. 5. Semivariograms as in Fig. 4, but for Lane Cove. Data are points, and lines are best fits of Eq. 2 or Eq. 3, whichever had the lowest residual mean square for each property. Each semivariance is calculated from >100 pairs of points.

TABLE 1. Residual mean squares of the fit of three models to the semivariance data. See Figs. 4 and 5 for graphs of the model with the best fit in each case (lowest RMS). The models are explained in *Methods: Statistical analyses*.

Property	Model		
	Random	Spherical	Harmonic
Lane Cove			
Available browse	0.0169	0.0116	0.0132
Browse consumption	0.145	0.0928	0.172
Conifer basal area	0.745	0.643	0.493
Nitrogen availability	0.000214	0.000364	0.000200
Moskey Basin			
Available browse	448.1	480.0	72.6
Browse consumption	0.815	0.766	0.203
Conifer basal area	1.12	0.846	0.452
Nitrogen availability	0.0048	0.0061	0.0039

patterns of vegetation, moose browsing, and soil nitrogen availability.

Dynamic mechanisms that may account for these patterns

In the absence of any other overriding factors such as topography, bedrock geology, fire history, or other herbivores, we suggest that the correlations of moose browsing and vegetation and soil properties (Figs. 2 and 3), as well as their spatial patterns (Figs. 4 and 5) emerge from the dynamic interactions between moose foraging and plant communities. Elsewhere, we have experimentally shown, using four exclosures on Isle Royale, that moose depress nitrogen availability by shifting plant community composition toward unbrowsed spruce and lightly browsed balsam fir (McInnes et al. 1992, Pastor et al. 1993). These species are not preferred because their leaves have high lignin and resin contents, properties that also slow their decay and nitrogen release when they are returned to the soil as litter. With time, the small-diameter balsam fir and spruce, which are not killed by moose browsing (Fig. 2), will grow and enter the larger diameter size classes in both valleys. In contrast, a few small-diameter aspen will remain in places where moose browsing is $<4 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (Fig. 2).

This mechanism may result in low soil nitrogen availability in these valleys wherever moose browsing exceeds $2\text{--}4 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (Fig. 3). Where browsing on regenerating aspen and other hardwoods is high, conifers dominate the forest and depress nitrogen availability by their slowly decomposing litter. The altering of ecosystem nutrient cycles by selective foraging by moose, suggested theoretically (Bryant and Chapin 1985, Pastor and Naiman 1992, Pastor and Cohen 1997) and confirmed experimentally in small plots (McInnes et al. 1992, Pastor et al. 1993), appears to apply across the larger landscape. Therefore, moose alter nitrogen availability in these two valleys by controlling the distribution of vegetation, one of the important state factors of ecosystem development in boreal regions (Van Cleve et al. 1991).

This strong effect of an herbivore on the distribution and variance of the rate of nitrogen cycling across the landscape (Fig. 3) is surprising, especially for a solitary animal in a forested ecosystem, and particularly at such an apparently low level of browse consumption ($2\text{--}4 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$; Fig. 3). Historic high browse consumption (Krefting 1974) may have resulted in conifer invasion and subsequent depression of nitrogen availability, and only $2\text{--}4 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ may now be required to maintain conifer dominance and low N availability by suppressing hardwood growth.

In addition, the effects of moose on vegetation and nitrogen cycling could be expressed at very low levels of browsing because their browsing is concentrated on photosynthetic and meristemic tissues of a few target species. It is interesting to note that $2\text{--}4 \text{ g}$ is approximately the size of one to two bites by free-ranging moose (Miquelle 1983, Risenhoover 1987; J. Pastor, K. Standke, K. Farnsworth, R. Moen, and Y. Cohen, *unpublished manuscript*). Repeated browsing at such a low level on aspen saplings or hazel shrubs can slow their height growth (Danell and Huss-Danell 1985, Bergstrom and Danell 1987, 1995, Danell et al. 1994, Ouellet et al. 1994) and thereby alter the competitive balance between them and the adjacent lightly browsed or unbrowsed fir or spruce (Krefting 1974, McInnes et al. 1992). The unbrowsed spruce or fir grows in height and eventually overtops the browsed plant whose photosynthetic and apical meristemic tissues have been removed, thereby outcompeting the generally less shade-tolerant browsed species for light.

Moose arrived on Isle Royale around the start of the 20th century (Allen 1976). Therefore, the correspondence of patterns of moose browsing with available browse, conifer cover, and soil nitrogen availability must have developed within the past century. This is relatively rapid, occurring within 50 generations of resident moose, starting from a small initial population, and within only one or two generations of trees. This is additional, albeit circumstantial, evidence for the strong effect that moose can exert over successional and ecosystem processes.

It might be objected that the patterns between moose browsing and nitrogen availability reflect a preference of moose for areas of low nitrogen availability. This does not seem likely, because ungulates must meet energy and protein requirements from their diet (Wallmo et al. 1977, Hobbs et al. 1982). It would make no sense for moose to forage heavily in areas where the cycling of nitrogen needed for protein is low, particularly when this low nitrogen availability is associated with a preponderance of unpreferred conifers. Because consumption is high in areas of low nitrogen availability, unbrowsed or lightly browsed conifers can invade these areas as the intense browsing on the few remaining hardwoods in these spots depresses their competitive abilities (Fig. 3).

Populations of moose and wolves and tree growth rates on Isle Royale oscillate through time (McLaren and Peterson 1994); these results indicate that some properties of the system exhibit spatial periodicity as well. Interactions between herbivores and vegetation in other terrestrial ecosystems may also result in such spatial patterns. Andrew (1988) observed the development of ring-like patterns of vegetation away from water sources in grazed rangelands. Ring et al. (1985) also report what appear to be wave-like patterns in grazed rangelands, and Hobbs et al. (1991) show the formation of regular patterns of grazing intensity in rangelands that are affected by both grazing pressure and fire. These patterns may be wave-like in form and are reminiscent of those observed and modeled in grazed phytoplankton systems (Dubois 1975, Segal and Levin 1976, Steele 1974).

Is there a biologically plausible and mathematically rigorous model for the development of patches of browse abundance, browsing intensity, and conifer abundance (Figs. 4 and 5) from the mechanism of selective foraging on hardwood species? Recall the checkerboard example in the *Introduction* where a mechanism may produce correlations between two properties locally (i.e., at discrete points) but may still result in random distribution at larger scales. The local mechanism proposed here is selective foraging and the plant responses to it at a given point. For higher order patterns ("patchiness" or "periodicity") to develop, another mechanism is needed to correlate a given property between adjacent squares. We seek, therefore, a dynamic model that can incorporate the local effects of selective foraging on plant communities with a mechanism of spatial spread of organisms to correlate adjacent points, thereby producing patches and even periodicities.

It is well known that coupled reaction-diffusion models of biological systems can produce patchy distributions of properties and even wave form patterns analogous to those seen here (Murray 1980, Okubo 1980, Kareiva 1982, Kareiva and Shigesada 1983). Such systems are usually modeled with coupled Lotka-Volterra equations for interacting components, each

component having a diffusion term (Levin 1976). In these models, the Lotka-Volterra equations provide the mechanisms of interaction at local scales and the diffusion term is the mechanism of spatial spread. For patchiness to develop, these models require that the diffusion rates of a predator (in this case, moose) be greater than those of the prey (the plants), and that the growth of patches of at least one of the prey species be self-enhancing (an autocatalytic mechanism; Okubo 1980).

The moose-forest system may have the essential features of this type of mechanism; if so, then Lotka-Volterra models with diffusion terms may be useful tools to describe its dynamics. Seed dispersal is a plausible mechanism of diffusion of plant species; spatially dynamic foraging strategies (Turner et al. 1994, Moen et al. 1997) would create a similar diffusion gradient for moose foraging pressure and its effect on deciduous browse. If so, then the Lotka-Volterra equations (Levin 1976, Okubo 1980) coupling moose foraging pressure with the growth of deciduous and conifer biomass at position x , along with the diffusion of these organisms would be

$$\frac{\partial S_1}{\partial t} = r_1 S_1 (1 - a_{11} S_1) + a_{12} S_1 S_2 + a_{13} S_1 S_3 + D_1 \frac{\partial^2 S_2}{\partial x^2} \quad (7a)$$

$$\frac{\partial S_2}{\partial t} = r_2 S_2 (1 - a_{22} S_2) + a_{21} S_1 S_2 - a_{23} S_3 + D_2 \frac{\partial^2 S_2}{\partial x^2} \quad (7b)$$

$$\frac{\partial S_3}{\partial t} = r_3 S_3 (1 + a_{33} S_3) - a_{31} S_1 S_3 - a_{32} S_2 + D_3 \frac{\partial^2 S_3}{\partial x^2} \quad (7c)$$

where S_1 , S_2 , and S_3 are moose, deciduous, and conifer biomass density, respectively; r_n are the respective growth rates; a_{ij} are the effects of species j on i for each two-way interaction; and D_1 , D_2 , D_3 are the diffusion coefficients of moose, deciduous, and conifer species, respectively. Because moose are solitary, the diffusion of moose foraging pressure depends on the gradient of food supply ($\partial^2 S_2 / \partial x^2$) rather than on gradients of its own population density. Plant diffusion is from areas of high biomass to areas of low biomass, reflecting the dispersal of seeds away from seed sources. In contrast, the diffusion of moose foraging pressure would be from areas of reduced forage biomass to areas of greater forage biomass. Notice that both plant species have a positive effect on moose biomass ($a_{12} S_2$ and $a_{13} S_3$), that moose consumption has a reciprocal negative effect on both plant species ($-a_{21} S_1$ and $-a_{31} S_1$), and that moose prefer deciduous over conifer species ($a_{12} > a_{13}$). The positive, autocatalytic term ($a_{33} S_3$) for the growth of conifer biomass describes an increase in seedling establishment with increasing biomass and, hence, seed supply of shade-tolerant co-

nifers. In contrast, the corresponding term for shade-intolerant deciduous species is negative ($-a_{22}S_2$), reflecting self-suppression of seedling establishment beneath their own canopies. This model is similar to a model that couples herbivore population dynamics and diffusion to spatial changes in overall plant "quality" (Morris and Dwyer 1997). In our model, the ratio of preferred (S_2) to unpreferred (S_3) plant species is an explicit measure of forage quality.

Notice that this system of equations does not imply inherent spatial periodicity in the underlying processes: the diffusion term in the equations is linear and reflects simple Brownian motion. The spatial patchiness arises from the differential rates of diffusion and the magnitudes, signs, and asymmetries of the interaction terms $a_{i,j}$ for the effects of species j on i (Okubo 1980). Often, such models yield periodic patterns from certain values of these parameters (Murray 1980, Okubo 1980) that are qualitatively similar to those described here by harmonic oscillators (Figs. 4 and 5). It remains to be seen whether such a reaction-diffusion model for this moose-forest system meets required underlying mathematical assumptions (Murray 1980, Okubo 1980) and whether the equations themselves are tractable. An additional complication not considered in these equations is that conifer and deciduous species consumption by moose are seasonally out of phase: deciduous species are consumed almost exclusively in summer, but some balsam fir is mixed into the diet in winter (Miquelle 1983, Risenhoover 1987, Peterson 1991).

Nonetheless, the model does provide some insight into the origin of the spatial patterns described here. The 500–1000 ha home range size of moose (Peterson 1955) is much greater than the seed dispersal distances of boreal tree species (generally <200 m; Burns and Honkala 1990). Therefore, $D_1 > D_2, D_3$, and the model would exhibit diffusive instability that would, in turn, result in patch formation (Okubo 1980) that may correspond to the sinusoidal patterns in the semivariograms (Figs. 4 and 5). Such a spatially dynamic ecosystem model could also prove useful in the analysis of other ecosystems dominated by mobile herbivores (McNaughton 1985, Jefferies 1988, 1989).

Management implications

Sizes of patches of habitat elements and their proportions in the landscape are often prescribed in management recommendations (Allen et al. 1987). However, the basis for the sizes and proportions of patches to be maintained through timber harvesting or other techniques is often anecdotal. For example, Peek et al. (1976) suggested that, because large wildfires have historically generated aspen browse for moose populations in northern Minnesota, wildlife managers might be justified in employing large clearcuts to increase moose populations. This suggestion forms the sole justification for the employment of large (>16.2 ha, or 40 acre) clearcuts in northern Minnesota's moose management

zones (W. Russ, U.S. Forest Service, *personal communication*), despite other findings that moose almost never venture >80 m into clearcuts away from cover (Hamilton et al. 1980). This anecdotal basis for management decisions is due, in part, to the lack of spatially explicit data on animal-habitat relationships. The need to consider spatial relationships in landscape management has been emphasized in recent years by the growing field of conservation biology (Harris 1984), but specific examples and techniques to formulate management recommendations based on these theories have been lacking. The applied sciences of wildlife management and conservation biology recognize the effect of high herbivore densities on plant communities, but are only beginning to recognize that the functional relationships between foraging animals, the plant community, and the chemistry of the plant tissues can at least partly control the development of ecosystem properties (Pastor et al. 1997).

The data here indicate that there are characteristic scales of browse distribution and utilization, conifer cover, and soil nutrient availability in moose-dominated boreal ecosystems of Isle Royale. These scales (200–550 m) are smaller than the sizes of large disturbances often prescribed for moose management in the Lake Superior region. The Isle Royale moose population has survived without active management for almost a century, although population levels have been highly cyclic (McLaren and Peterson 1994). Furthermore, there have been no natural large-scale disturbances such as wildfire in these two valleys (disturbance regimes that managers sometimes invoke to justify large clearcuts) and there has been only one episode of large wildfires on Isle Royale in the 1930s (Hansen et al. 1973). Although the Isle Royale moose population grew rapidly after this period of large fires (Peterson 1991), the aspen and birch that regenerated in these areas have grown beyond the reach of moose, and the historic wildfires cannot account for the high densities during the current study period. This would suggest that large clearcuts, which supposedly mimic large wildfires, are not as important to moose populations as are particular patterns of interspersed browse and conifer cover. If these findings are to be used as a first approximation, then they suggest that managers might seek to establish a landscape of conifer patches 200–300 m from each other and embedded within larger patches of browse 300–550 m from each other (Figs. 4 and 5) for the benefit of moose simultaneously seeking food from browse and shelter from conifer patches. Alternatively, and perhaps even better, the manager might seek natural areas within his or her region, determine the spatial patterns of browsing, forage, and conifer cover by methods similar to those here, and base his or her management decisions on them.

Both Hansson (1979) and Rosenzweig and Abramsky (1980) argue that population cycles inevitably result from heterogeneities in resource distribution, re-

source quality, or animal foraging behaviors. The data here suggest that such a temporally cyclic population may be associated with spatial patchiness and even periodicities of ecosystem properties across the landscape, through the animals' foraging decisions. Such population cycles and associated spatial patterns may, therefore, be an intrinsic property of an intact, properly functioning ecosystem or landscape. A characteristic of such oscillating systems is not some particular population level, or rate of ecosystem process, or even a particular static pattern in the landscape, but rather a spatial and temporal variance structure of all components of the landscape.

This research raises the following unanswered questions. How does a moose move through landscapes that it, other moose, and other herbivores have previously modified? How does the landscape respond to movement patterns and resource acquisition by moose? How stable is the spatial patchiness of browse availability, browse intensity, conifer basal area, and soil nitrogen availability? If these patches grow or shrink, as implied by the reaction-diffusion model (Eq. 7), what sequence of events accompanies these changes? How do these patterns change with population cycles of moose (McLaren and Peterson 1994)? Identification of existing spatial patterns using spatially explicit field sampling, data analysis using geostatistics, and theoretical analysis using solutions to the diffusion model previously suggested, or spatially explicit simulation models (Turner et al. 1994, Moen et al. 1997, *in press*), should prove useful in answering these questions, in designing new management techniques, and in clarifying and quantifying the concept of sustainability in both managed and unmanaged populations.

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