

EFFECTS OF PAST LAND USE ON SPATIAL HETEROGENEITY OF SOIL NUTRIENTS IN SOUTHERN APPALACHIAN FORESTS

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Abstract. We examined patterns of nutrient heterogeneity in the mineral soil (0–15 cm depth) of 13 southern Appalachian forest stands in western North Carolina >60 yr after abandonment from pasture or timber harvest to investigate the long-term effects of land use on the spatial distribution and supply of soil resources. We measured soil carbon (C), nitrogen (N), acid-extractable phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) concentrations and pools, and potential net N mineralization and nitrification rates to evaluate differences in mean values, variance at multiple scales, and fine-scale spatial structure.

While comparisons of averaged values rarely indicated that historical land use had an enduring effect on mineral soil or N cycling, differences in variance and spatial structure suggested that former activities continue to influence nutrient distributions by altering their spatial heterogeneity. Patterns differed by element, but generally variance of soil C, N, and Ca decreased and variance of soil P, K, and Mg increased with intensive past land use. Changes in variance were most conspicuous and consistent locally (<28 m), but C, Ca, P, and Mg also exhibited appreciable differences in variance at coarser scales (>150 m). High variability in soil compaction resulted in some changes in scale-dependent patterns of nutrient pool variance compared with nutrient concentration variance. It also affected the variance of N cycling rates, such that mass-based rates varied less and area-based rates varied more in intensively used areas than in reference stands. Geostatistical analysis suggested that past land use homogenized the spatial structure of soil C, K, and P in former pastures. In contrast, logged stands had highly variable spatial patterning for Ca.

These results suggest that land use has persistent, multi-decadal effects on the spatial heterogeneity of soil resources, which may not be detectable when values are averaged across sites. By interacting with patterns of variability in the plant and heterotrophic biota, differences in nutrient distribution and supply could alter the composition and diversity of forest ecosystems. Scale-dependent changes in nutrient heterogeneity could also complicate efforts to determine biogeochemical budgets and cycling rates.

Key words: carbon; cations; forest ecosystem recovery; grazing; land-use history; logging; nitrogen; phosphorus; semivariograms.

INTRODUCTION

Land-use practices affect the distribution and supply of soil nutrients by directly altering soil properties and by influencing biological transformations in the rooting zone. Although its consequences vary, land conversion frequently leads to nutrient losses when it disrupts surface and mineral horizons (e.g., by mechanical disturbance) and reduces inputs of organic matter. Cultivation of forests, for example, diminishes soil carbon (C) within a few years of initial conversion (Davidson and Ackerman 1993, Murty et al. 2002) and substantially lowers mineralizable nitrogen (N) (Doran 1980, Richter et al. 2000). Conversion to pasture and logging gen-

erally leaves nutrient pools in the mineral soil unchanged but reduces forest floor stocks of C and N (Covington 1981, Federer 1984, Fearnside and Barbosa 1998). However, because accretion of aboveground and belowground nutrients resumes following cessation of these practices (Richter et al. 1999, Richter et al. 2000, Hooker and Compton 2003), it is expected that resources will eventually be recouped. Yet some nutrient patterns initiated by human activities have a surprisingly long duration. Comparative work in New England and European forests has demonstrated that plowing and applications of manure and lime lead to changes in N cycling rates and C, N, and phosphorus (P) stocks in the forest floor and mineral soil that last for at least a century after land abandonment (Koerner et al. 1999, Compton and Boone 2000, Dupouey et al. 2002, Jussy et al. 2002). Empirically based models predict that C and N pools in previously cultivated grasslands will remain diminished for well over 100 years (Knops and

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Tilman 2000), although active organic matter pools may recover more quickly (Burke et al. 1995).

The long-term effects of conversion to pasture and logging on soil nutrient pools and N cycling are more equivocal. Conversion of tropical forest to pasture appears to markedly enhance soil C, N, and organic P due to manure subsidies and the presence of C₄ grasses that recycle these nutrients rapidly enough to approximately balance losses of forest-derived nutrients (Reiners et al. 1994, Neill et al. 1997, Garcia-Montiel et al. 2000), but meta-analyses suggest that these changes may only persist a short time (McGrath et al. 2001, Guo and Gifford 2002, Murty et al. 2002). Other investigations indicate that the duration of impacts from logging are also short lived (Johnson and Curtis 2001, Guo and Gifford 2002), whereas Goodale and Aber (2001) found that differences in the relative accumulation of C and N following harvesting persistently affect nitrification rates.

These apparently inconsistent patterns may in fact reflect another consequence of human land use that is less often considered, namely its effects on the spatial heterogeneity of soil nutrients. Human activities have the potential to modify the spatial distribution of nutrients at multiple scales. Land use may alter the local patchiness of soil nutrients by decoupling interactions between microclimate, microtopography, vegetation, and soil biota. Mechanical soil mixing and maintenance of monocultures, for instance, result in the fine-scale homogenization of soil resources in cultivated systems (Robertson et al. 1993, Paz-Gonzalez and Taboada 2000, Paz-Gonzalez et al. 2000). In grazed and logged systems, nutrient redistribution and changes in vegetation-mediated soil dynamics may likewise lead to localized shifts in soil heterogeneity. Extensive tree removal, for example, may homogenize both pastures and cut-overs at fine scales by integrating soil horizons and eliminating organic matter sources (Huntington and Ryan 1990, Yanai et al. 2003). Nutrient heterogeneity in pastures may be further reduced by the maintenance of forage grasses, which provide spatially homogenous litter inputs (Lavado et al. 1996). However, the deposition of excreta may enhance the heterogeneity of those nutrients that are abundant in manure, such as P, K, and Mg (Afzal and Adams 1992, Augustine and Frank 2001, Augustine 2003). Changes in tree community composition following land abandonment may also influence the spatial distribution of soil nutrients, especially those such as C, N, and calcium (Ca), which are closely associated with litter inputs (Melillo et al. 1982, Kalisz 1986, Dijkstra and Smits 2002). Pastures and logged stands may consequently exhibit similar levels of C, N, and Ca variability and different levels of P, potassium (K), and magnesium (Mg) variability. The distribution of nutrients at broad scales may be more strongly related to regional land use patterns. Because historically, human activities were both diverse and changeable (Foster 1992), there may be an

overall increase in nutrient heterogeneity at landscape scales. Broad-scale differences in the vegetation communities that establish on abandoned lands may further enhance heterogeneity (Foster et al. 1998, Lovett et al. 2000, Ollinger et al. 2002).

Whether such land-use driven changes in nutrient heterogeneity might persist over time is poorly understood. Robertson et al. (1988, 1993) found that nutrient stocks in formerly cultivated soils remained less spatially variable than those in untilled soils 40 years after abandonment, and a more recent study in the same area showed that microbial communities of abandoned farms remain similar to those of presently cultivated fields (Buckley and Schmidt 2001). Yet Gross et al. (1995) suggested that successional processes, specifically turnover in species composition, could erase or obscure spatial patterns produced by prior human activities. However, they found little support for this hypothesis among N availability patterns in plant communities at different stages of succession.

Regardless, there is strong justification for investigating spatial distributions of soil resources in addition to mean values. Understanding current ecosystem states and forecasting how they will change may rely on knowing the spatial distribution of several ecosystem components. For example, Bergelson et al. (1993) found that the vulnerability of a perennial ryegrass community to invasion by weeds depended more on the heterogeneity of bare ground than on its mean amount; Jurena and Archer (2003) found a similar relationship for woody plant establishment in Texas grasslands. The spatial distribution of soil nutrients may be equally influential in recovering forests, where environmental sorting continues to shape plant populations and communities (Verheyen et al. 2003). For instance, low resource heterogeneity may favor species that are able to withstand uniformly high levels of competition (Day et al. 2003a, b, Hutchings et al. 2003) or may impede the survival of species that require unique regeneration niches (Beckage and Clark 2003, Maestre et al. 2003), whereas high resource heterogeneity may promote species diversity (Bakker et al. 2003). The implications of changes in nutrient distributions for other taxa have not yet been examined closely, but there is evidence that ants and other soil biota may respond to differences in resource heterogeneity that influence plant community composition (Blomqvist et al. 2000, Ribas et al. 2003). Nutrient budgets and estimates of regional and local cycling rates may also be influenced by patterns of nutrient distribution, although this relationship has not been widely investigated.

Here we examine patterns of soil nutrient distributions as a function of former land use in forests of the southern Appalachian Mountains. We evaluate how mean mineral soil properties and N turnover rates vary among sites with different land use histories, but focus primarily on how past land use influences nutrient heterogeneity. Specifically, we address: (Question 1) How

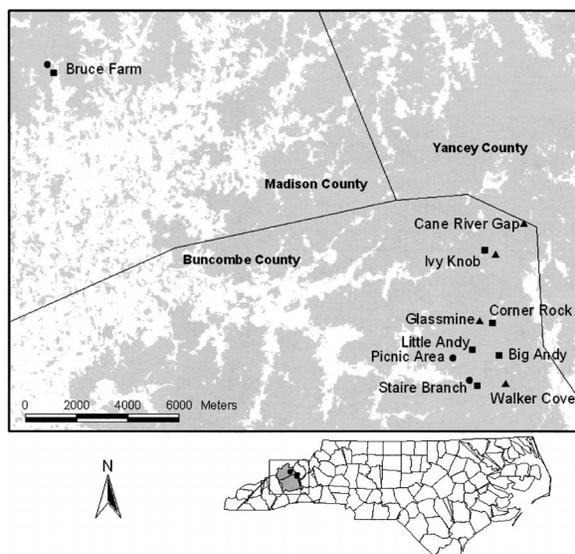


FIG. 1. Site locations in Madison and Buncombe counties, western North Carolina, USA, land-use history (pasturing, solid circles; logging, solid squares; reference, solid triangles) and land cover (gray, forest; white, non-forest).

is the variability of soil properties and N turnover and the scale at which that variability is expressed influenced by past land use? and (Question 2) How does the explicit spatial structure of soil properties change with former land use? We hypothesized that sites historically subjected to intensive use would have reduced concentrations and stocks of soil nutrients and reduced rates of N turnover due to legacies of organic matter depletion and slow accumulation following abandonment. We further expected that effects of former practices on nutrient heterogeneity would be detectable in

both the magnitude and scale of variance, and in the spatial distribution of nutrients at local scales, but that these patterns would depend on the nutrient being considered.

METHODS

Study area and history

Land use throughout the last 150 years has transformed the landscape of the southeastern United States. The Southern Blue Ridge Province of the southern Appalachian Mountains in particular has experienced extensive changes in dominant land use and forest cover (Wear and Bolstad 1998). While most forests in the southern Appalachian region were farmed or logged by the early 1900s, low yields, resource depletion, and increased opportunities for nonfarm income led to widespread land abandonment and natural reforestation during the early and mid-1900s (Yarnell 1998, Davis 2000). Today, forests span ~70% of the landscape (SAMAB 1996) and cover more area than at the turn of the last century (Pearson et al. 1998).

Our study was conducted in primary and secondary cove-hardwood forests located in three watersheds (Dillingham Creek, North Fork, and Gabriel's Creek) of the French Broad River Basin in Madison and Buncombe counties, western North Carolina (Fig. 1). Soils are both colluvial and residual and possess mixed mineralogy, but all are well-drained, upland mountain soils derived predominately from granite, gneiss, and mica-schist (Table 1). Of the six mapped soil series (three complexes), five are classified as Typic Dystrudepts, acidic Inceptisols with humid moisture regimes. Soils in the Toecane series are classified as Humic Hapludults (USDA NRCS). The vegetation is representative of the mixed mesophytic communities of the Southern Blue

TABLE 1. Characteristics of the study sites and details of the sampling design.

Site	Watershed and elevation group†	Historical land use	Period used‡	Elevation (m)	Soil series§	Area (ha)	Year sampled	No. plots	No. cores
Big Andy	DC-H	logged	1950–1970	1160	P-U	6.7	2002	3	15
Corner Rock	DC-H	logged	1950–1970	1040	T-T	2.5	2002	1	5
Glassmine	DC-H	reference	no record	1060	P-U	3.7	2002	1	5
Walker Cove ,¶	DC-H	reference	no record	1150	P-U	12.9	2001/2002	3/4	39/55
Little Andy ,¶	DC-L	logged	1950–1970	915	P-U	6.4	2001/2002	3/3	66/15
Staire Branch	DC-L	logged	1950–1970	915	P-U	3.1	2002	1	5
Picnic Area ,¶	DC-L	pasture	1850–1930	860	P-U, T-T	11.4	2001/2002	2/3	53/15
Staire Branch ,¶	DC-L	pasture	1850–1930	870	T-T	4.0	2001/2002	2/1	53/5
Bruce Farm¶	GC	logged	1977–1978	860	B-C	2.1	2001	3	66
Bruce Farm¶	GC	pasture	1890–1975	860	B-C	4.2	2001	2	53
Ivy Knob¶	NF	logged	1960–1970	1040	T-T	3.3	2001	3	66
Cane River Gap¶	NF	reference	no record	1230	T-T	6.9	2001/2002	3/1	39/40
Ivy Knob¶	NF	reference	no record	1060	T-T	5.7	2001/2002	3/1	39/40

† Watersheds: DC-H, Dillingham Creek, high elevation; DC-L, Dillingham Creek, low elevation; GC, Gabriel's Creek; NF, North Fork.

‡ Sources: Haile (1979), the Keith family genealogy (Mars Hill College Appalachian Room Archives), and data from the USFS Continuous Inventory of Stand Conditions (CISC) (SAMAB 1996).

§ Soil series: B-C, Buladean-Chestnut complex, both series formed in residuum; P-U, Porters-Unaka complex, both series formed in residuum; T-T, Toecane-Tusquitee complex, both series formed in colluvium.

|| Sites where nitrogen mineralization and nitrification were measured.

¶ Sites where cyclic sampling design was used.

Ridge Province described by Braun (1950), with canopies dominated by tulip tree (*Liriodendron tulipifera*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), oak (*Quercus* spp.), basswood (*Tilia americana*), hickory (*Carya* spp.), and sweet birch (*Betula lenta*). While hemlock (*Tsuga canadensis*) and rhododendron (*Rhododendron maximum*) were encountered, we avoided extensive stands of either species.

Historical land use in these watersheds includes disturbance from agriculture or logging, and was determined from landowner interviews, rigorous examination of historical records, physical evidence (e.g., stand-age distribution, fences, stumps, roadbeds) and a chronosequence of aerial photographs (Table 1; Pearson et al. 1998, Wear and Bolstad 1998). Farming practices consisted of grazing animals on moderately steep, cleared lands where stumps were removed and pasture grasses were seeded (cultivation was mainly reserved for bottomlands, which were not sampled). There is no indication that amendments were added to the soil or that row crops were planted on these lands, and records suggest that they were best suited to pasture because of stoniness (Goldston et al. 1954). Logged stands, often located on steeper grades, were high-graded or clear-cut (USFS Continuous Inventory of Stand Conditions [CISC] data as in SAMAB 1996, Davis 2000); we did not recover charcoal from any of the logged sites, and thus assume that these areas were not burned. Land abandonment during the first half of the 20th century allowed most land to revert to forest, creating a landscape composed of stands of different ages with an underlying mosaic of land-use histories. Stands that showed no evidence of human disturbance and contained plant species that are typical of old-growth forest (e.g., *Dryopteris goldiana*) were employed as reference sites when they occurred near historically pastured or logged stands.

Site selection and sampling strategy

We selected 13 sites located on north-facing slopes on private and public (U.S. Forest Service) land from the three watersheds (Fig. 1). All sites within an historical land-use category were positioned at the same slope, although different landforms were sampled (e.g., foot and toe slopes). Sites that differed by past land use also differed in slope because of constraints imposed by the availability of potential study sites (i.e., pastured sites always occurred on moderate slopes, whereas reference sites always occurred on steeper slopes). Pilot work conducted in 2001 indicated that slope position did not affect the mean distribution of soil properties within a site, and Mowbray and Oosting (1968) reached a similar conclusion in their study of soil characteristics in a southern Blue Ridge gorge. These findings collectively suggest that differences in slope did not introduce biases into the data. Moreover, an analysis of soil texture indicated that soils in each

site were derived from similar parent material and had undergone little erosion.

Because not all of the historical land uses studied were practiced in each watershed, we chose adjacent sites within each watershed that were similar in elevation and soil series but varied by past land use. This resulted in the designation of four watershed/elevation groups that encompassed broad-scale differences among the sites (Table 1). Matching sites in this manner precluded direct comparisons between pastured and reference sites, because they never occurred at the same elevation. However, since logged sites were present at a range of elevations, we paired them with the other land uses to provide a means for comparison. The sites differed in size and environmental variability (i.e., topography, moisture); consequently the number of plots needed to capture the range of conditions encountered varied by site. We therefore established between one and four 20 × 20 m plots at least 150 m apart in each site ($N = 43$ plots total; Table 1). Although this approach contributed to an unbalanced sampling design, it also enhanced the accuracy of estimates and increased our inference space.

Samples were collected in each plot from the upper 15 cm of mineral soil during June 2001 or June 2002 with a 5.2 cm diameter cylindrical polyvinyl chloride corer spaced regularly throughout the plots to estimate nutrient concentration, pool sizes, and their variability. We collected 13 cores per plot ($N = 18$) in nine sites the first year to describe nutrient variability across multiple scales (Table 1). We increased the spatial extent of the study and determined N turnover rates in the second year, collecting 5 soil cores per plot ($N = 16$) in eight sites (Table 1). Although we sampled different numbers of cores per plot in different years, comparable numbers of cores were collected in each watershed for the historical land uses represented.

Forty cores were collected from nine additional plots using a cyclic sampling design to characterize explicit spatial patterns and estimate distributions of nutrient pools at fine scales. Plots in pastured and logged sites were sampled in 2001, and plots in reference sites were sampled in 2002 (Table 2). This cyclic design is derived from time series analysis and enables the detection of autocorrelation at several multiples of the smallest lag distance with a minimum number of sampling points (Clinger and Van Ness 1976). We chose a repeating series that samples 3 of every 7 points in the east–west direction, and 4 of every 12 points in the north–south direction, with 4 additional points placed at greater lag distances within the plot (Fig. 2). The smallest lag distance was 1 m and the largest lag was 27.6 m.

Laboratory analyses

Samples were returned to the laboratory and sieved to <4 mm to remove coarse roots and rocks and to homogenize the soil prior to subsampling. Particles that did not pass through the sieve were weighed and their

TABLE 2. Mineral soil (0–15 cm depth) properties (mean, with 1 SE in parentheses) by prior land use for forests in the southern Appalachian Mountains of western North Carolina, USA.

Soil property	Past land use		
	Pasture	Logging	Reference
Mass (Mg/ha)	80 ^a (9)	53 ^{ab} (6)	41 ^b (4)
Bulk density (g/cm ³)	0.84 ^a (0.10)	0.55 ^{ab} (0.06)	0.42 ^b (0.04)
Coarse fraction (%)	5.3 (0.4)	5.5 (0.9)	4.1 (0.1)
pH	5.6	5.3	5.4
C (g/kg)	47.8 (6.7)	81.1 (9.6)	97.5 (6.7)
N (g/kg)	2.29 (0.26)	3.20 (0.44)	4.15 (0.24)
P (mg/kg)	46.7 (13.0)	39.4 (6.1)	48.0 (7.3)
K (mg/kg)	11.9 (1.6)	10.0 (0.8)	10.1 (0.2)
Ca (mg/kg)	8.46 (0.94)	7.86 (1.93)	12.0 (1.21)
Mg (mg/kg)	1.38 (0.33)	1.36 (0.20)	1.33 (0.27)
C:N	21.2 (1.5)	26.1 (1.5)	24.7 (0.8)
C:P	1.21 (0.34)	2.41 (0.47)	2.18 (0.33)
Potential net N mineralization [†]	9.68 (1.99)	43.3 (6.98)	87.8 (11.9)
Potential net nitrification [‡]	10.1 (2.12)	35.9 (6.55)	89.2 (12.4)

Notes: Bulk density was calculated using the volume of the sample used for elemental analysis and was corrected for coarse fraction. Superscript letters signify Tukey's honestly significant differences between land-use types (within a row) ($P < 0.05$).

[†] Units are mg NH₄ + NO₃-N·kg dry soil⁻¹·28 d⁻¹.

[‡] Units are mg NO₃-N·kg dry soil⁻¹·28 d⁻¹.

average volume estimated by water displacement. The mass and volume of these particles were used to correct soil bulk density, which was calculated for each sample. Although the field technique we employed can be degraded by compaction in the core relative to a bulk density sampler, the same method was used on all samples to avoid biasing the data.

Samples collected in 2002 from the Dillingham Creek watershed ($N = 16$ plots and $N = 80$ cores) were used to determine potential net N mineralization (Table 1). Subsamples of fresh soil (10 g) were extracted in

100 mL of 1 mol/L KCl immediately and after a 28-d incubation at 25°C, during which water was added to keep soil at constant moisture (Robertson 1999). Extracts were frozen until analysis for ammonium and nitrite plus nitrate by Lachat QC8000 flow injection analyzer (LACHAT Instruments, Milwaukee, Wisconsin, USA, methods 12-107-06-2-A and 12-107-04-1-B). Potential net mineralization was calculated as the net change in ammonium and nitrate between fresh and incubated samples. Potential net nitrification was calculated as the net change in nitrate. We determined gravimetric soil moisture for each sample by drying 20-g subsamples at 105°C for 24 h. Remaining soil was air dried prior to further analysis.

Total C was determined by dry combustion with a Tekmar-Dohrmann 183 TOC Boat Sampler DC-190 (Tekmar-Dohrmann, Mason, Ohio, USA) using triplicate 0.5-g finely ground subsamples, and total N was estimated with a micro-Kjeldahl procedure (Jackson 1958). Acid-extractable P was measured colorimetrically using the Truog method (Schulte et al. 1987) and a 0.001 mol/L H₂SO₄ digestion. Extractable K, Ca, and Mg were determined by atomic absorption after extraction with H₂SO₄ (Schulte et al. 1987). Soil pH in water was measured using a 1:1 mass:volume ratio. Nutrient pools and turnover rates were calculated on both a per-dry-soil-mass basis and on an areal basis using bulk density and coarse fraction estimates to correct for differences in soil compaction among management types.

Statistical analyses

Mineral soil properties were averaged for each site across both years to evaluate differences in mean nutrient concentration and content; nitrogen turnover rates were averaged for each plot. Given the large num-

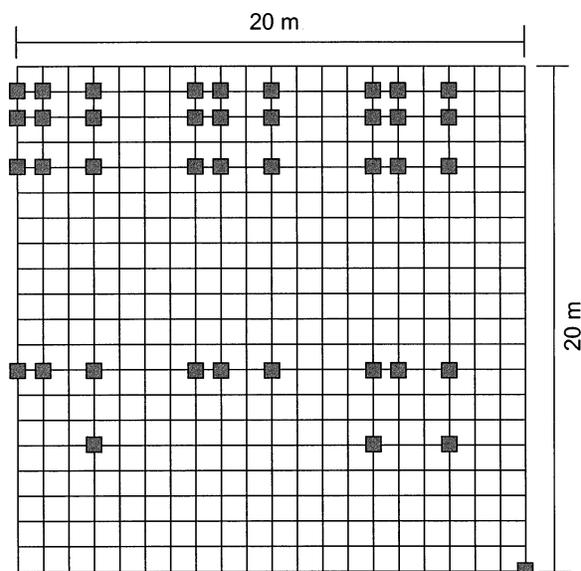


FIG. 2. Illustration of the cyclic sampling design used to construct spatial relationships among soil properties and to determine the spatial structure of their variability. Gray squares signify points where soil cores were collected.

ber of response variables, we initially used two-way multivariate analysis of variance with land use and watershed/elevation as main effects to determine whether it was appropriate to proceed with multiple univariate tests. Because collinearity among variables can mask treatment effects, we excluded bulk density and pH and analyzed C, N and P, and cations separately. Pillai's trace statistic, which is best suited for data with a diffuse noncentrality structure (i.e., multiple variables driving differences; Zar 1999), was used to evaluate the tests. If the analysis of either nutrient concentration or content was marginally significant ($P < 0.10$) we proceeded with univariate analysis of variance (ANOVA) for all response variables using land use as a fixed effect and watershed/elevation category as a random effect. In addition to accounting for topographical variation, this modeling approach also accounted for differences in the duration and cessation of land-use practices that existed among the sites (Table 1). Pairwise differences among land-use types were evaluated with Tukey's honestly significant difference procedure.

We investigated how past land use affected the variability of soil properties and how that variability was dispersed across spatial scales (Question 1) by estimating variance components for nutrient concentrations and pools, and for soil mass, which influenced the variability of nutrient pools. Variance components were estimated by land use for data collected in a single year (2001), which prevented annual differences from influencing variability estimates. Sites that shared the same past land use were located at a similar elevation (Table 1). We used fully nested models with site and plot as random effects, which provided estimates for between-site (minimum 1 km apart) and within-site (minimum 150 m apart) scales and allowed for inferences about variance to be extended beyond the specific sites and plots sampled. Because we sampled N turnover in only two pastured and reference sites, we estimated within-site and within-plot variance but not between-site variance for N mineralization and nitrification. Maximum likelihood was chosen as the method of estimation to force positive estimates of variance (Scheiner and Gurevitch 2001). Laboratory replicates of soil analyses were not available, so variance attributed to the within-plot (i.e., among-sample; <28 m apart) scale could not be directly estimated and was instead inferred from the error term. Throughout, we relate variance attributed to between-site measurements with coarse-scale variability, and variance attributed to within-plot measurements with fine-scale variability. Variance attributed to within-site measurements is associated with coarse-scale variability, since plots within a site were separated by at least 150 m.

We examined the spatial structure of soil nutrients at fine scales (Question 2) using semivariance analysis. Nutrient concentration data from cyclically sampled plots ($N = 9$; Table 1) were first detrended to remove variance contributed by the slope of the plot using gen-

eralized additive modeling. Specifically, a local regression model, in which predicted values at each point are weighted most heavily by neighboring observations, was fit to each set of nutrient data with the plot coordinates corresponding to the slope as the predictor variable (Rossi et al. 1992, Kaluzny 1998). We constructed semivariograms from the residuals for each element from each plot to a maximum distance of 20 m using 10 lags, which resulted in an average of 76 pairs per lag interval (min. = 23; max. = 117). We standardized each semivariogram by dividing it by the sample variance for each plot (Rossi et al. 1992), which bounded the semivariance by 0 and 1, and then fit the spherical model using nonlinear least-squares regression weighted by the number of pairs used to estimate the semivariance at each lag (Webster 1985, Cressie 1993). We used the spherical model because it has proven effective in the analysis of two-dimensional data and we wanted a consistent means for comparing parameters among land uses (Webster 1985, Schlesinger et al. 1996). Moreover, we chose to use a post hoc modeling procedure instead of other methods that model spatial covariance simultaneously (i.e., mixed models), because it allows graphical interpretation of a model's fit and employs only user-specified lags in the algorithm. If the model did not fit the semivariogram generated for a particular element in a particular plot (i.e., $P > 0.05$), we removed it from future analyses.

In addition to describing the spatial structure of elemental distributions in each plot, we compared spatial patterns among sites that shared similar land-use histories. The range (A), or the distance beyond which autocorrelation between pairs of points is effectively 0, and the sill (C), the value of semivariance at the range, were estimated for each element from each plot. The variability of A and C within a particular land-use history was then evaluated for each element using Levene's test for equality of variance. This test is typically performed to check whether data meet assumptions of variance homogeneity for ANOVA procedures using means, but it is also useful for evaluating whether variance across groups is significantly different (Schultz 1985). In this instance, a traditional F test from an ANOVA was calculated using the absolute deviation of each observation (A or C) from the group mean as the response. The group mean was calculated from the three estimates for A or C that we had for each element from plots with the same land-use history. Levene's test is robust to violations in assumptions of normality and independence and has more power than other tests for equality of variance (Schultz 1985).

RESULTS

Mean soil properties and N turnover

Multivariate analysis using Pillai's trace statistic indicated that past land use significantly affected soil nutrient content (C, N, P, $F_{6,6} = 2.53$, $P = 0.09$; cations,

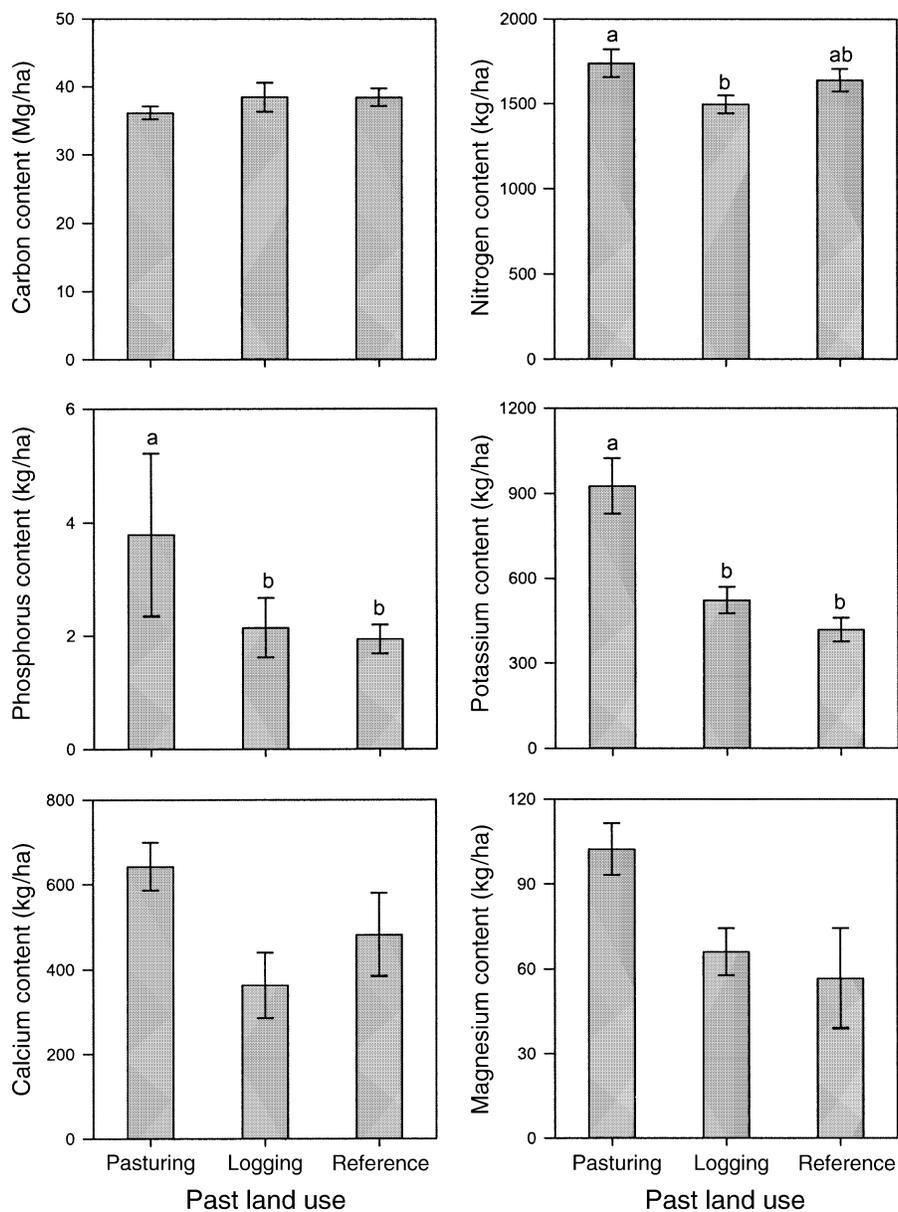


FIG. 3. Nutrient stocks (mean \pm 1 SE) in the 0–15 cm mineral soil by land-use history. Samples were converted using corrected bulk density (without the coarse fraction). Bars with different letters are significantly different ($P < 0.05$).

$F_{6,6} = 3.12$, $P = 0.05$), so univariate tests were used to interpret results for individual physical and chemical properties. Mineral soil mass and bulk density increased significantly with past land use (mass, $F_{2,10} = 5.22$, $P = 0.04$; bulk density, $F_{2,10} = 4.85$, $P = 0.03$; Table 2). Yet for most nutrients, no detectable effect of former land use on mean values was observed. There was no relationship between past land use and mean soil C, N, P, Ca, K, or Mg concentrations (C, $F_{2,10} = 3.75$, $P = 0.08$; N, $F_{2,10} = 3.88$, $P = 0.07$; P, $F_{2,10} = 0.66$, $P = 0.54$; Ca, $F_{2,10} = 1.78$, $P = 0.24$; K, $F_{2,10} = 2.42$, $P = 0.16$; Mg, $F_{2,10} = 0.01$, $P = 0.99$; Table 2). Nor was there a relationship between former land use

and mean soil C, Ca, or Mg content (C, $F_{2,10} = 0.36$, $P = 0.71$; Ca, $F_{2,10} = 2.83$, $P = 0.13$; Mg, $F_{2,10} = 3.06$, $P = 0.11$; Fig. 3). Differences in N were amplified by changes in soil bulk density, however, which resulted in a significant decrease in N content in logged sites ($F_{2,10} = 5.18$, $P = 0.04$; Fig. 3). Soil compaction differences also accounted for significantly higher extractable soil P and K content in former pastures than in logged and reference sites (P: $F_{2,10} = 4.95$, $P = 0.05$, K: $F_{2,10} = 16.9$, $P < 0.01$; Fig. 3). Prior land use marginally influenced C:N ratio ($F_{2,10} = 3.89$, $P = 0.07$) but did not affect C:P ratio ($F_{2,10} = 2.42$, $P = 0.16$) or soil pH ($F_{2,10} = 0.67$, $P = 0.54$).

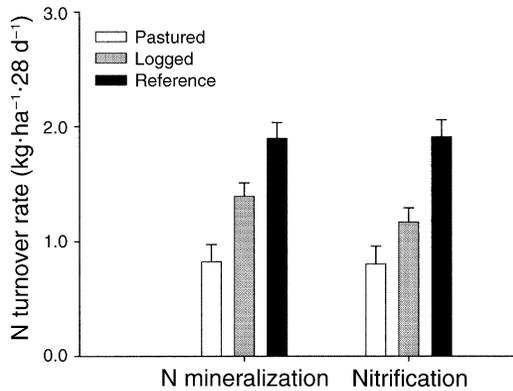


FIG. 4. Mean potential net N mineralization and nitrification per hectare in 0–15 cm mineral soil collected during June 2002. Error bars indicate +1 SE. Samples were converted using corrected bulk density (without the coarse fraction).

Previous pastures and logged sites had lower N cycling rates than reference sites (Table 2; Fig. 4). However, neither mass-based rates nor area-based rates differed significantly with respect to past land use (mass-based: net N mineralization $F_{2,14} = 2.04$, $P = 0.17$, nitrification: $F_{2,14} = 3.13$, $P = 0.08$; area-based net N mineralization: $F_{2,14} = 1.33$, $P = 0.30$, nitrification: $F_{2,14} = 1.65$, $P = 0.23$).

Variability and spatial scale

Despite few differences in mean nutrient properties, former land use appears to have substantially altered nutrient heterogeneity across several scales of interest. Overall, two general and opposing patterns in nutrient variability were detected: (1) concentrations of C, N, and Ca and pools of C and N varied the least in former pastures and the most in reference stands (Figs. 5 and 6), and (2) concentrations and contents of P, K, and Mg varied the most in former pastures and the least in reference stands (Figs. 5 and 6). However, pools of Ca were least variable in logged stands (Fig. 6).

Differences in nutrient heterogeneity with past land use were most conspicuous and consistent at a local scale. Within plots, variance of soil C, N, and Ca concentration and C and N content was highest in reference stands compared with formerly logged and pastured sites, whereas the variance of K and Mg concentration and content and P stocks was highest in previous pastures and lowest in reference sites (Figs. 5 and 6). However, variance of soil Ca content was high in both pastured and reference sites at this scale, and no differences were observed in soil P concentration variance. There were also only minor differences in the variance of soil mass among former land uses at this scale (pastured = 223 Mg/ha, logged = 216 Mg/ha, reference = 148 Mg/ha).

At the within-site scale, differences in nutrient heterogeneity were less consistent. Variance of soil C, N, and Ca concentration behaved as it did at the within-

plot scale, but C and N content did not differ with former land use at the within-site scale, and Ca content variance was high only in reference sites. The variance of K concentration and content was slightly elevated within both logged and pastured sites, but we observed no substantial differences in the variance of P concentration or Mg pools with past land use at this scale. There was also little variability in within-site soil Mg concentration except in reference stands, where variance increased markedly (Fig. 5). These inconsistencies appeared related to within-site variability in soil mass, which was high in reference sites (60 Mg/ha) compared with pastured and logged sites (21 Mg/ha and 18 Mg/ha, respectively).

With little exception, nutrient concentrations in reference sites varied little at the between-site scale, and patterns of variability for former pastures and cut-overs were similar to but less prominent than those exhibited at the within-plot scale. Among the exceptions were P concentration and content variance (Figs. 5 and 6), which increased sharply in former pastures, and Mg concentration variance, which was noticeably elevated in both former pastures and logged sites (Fig. 5). Soil Ca concentration variance was high only in logged sites at this scale. Between-site differences in soil mass variance with past land use likely influenced these patterns, as soil mass variance was low in reference sites (27 Mg/ha) compared with pastured and logged sites (136 Mg/ha and 184 Mg/ha, respectively).

Variance of N cycling rates differed markedly with past land use, especially at the within-plot scale. At this scale, we observed approximately equal amounts of variance for mass- and area-based mineralization and nitrification rates in logged and reference stands, and no or less variance for pastured stands (Fig. 7a, b). Within-site patterns were similar to those at the within-plot scale for N mineralization and nitrification rates determined on a mass basis, but we observed no variance in the area-based rates of reference sites and equivalent levels of variance for area-based measurements within pastured and logged sites (Fig. 7a, b).

Differences in spatial structure

Former land use appears to have altered the spatial structure of several elements (Table 3). The range of autocorrelation for soil C and K varied little among former pastures compared with logged and reference stands, indicating that these elements were similarly distributed within formerly grazed areas (C, $F_{2,7} = 12.9$, $P = 0.007$; K, $F_{2,6} = 143.7$, $P < 0.001$). However, sill estimates did not differ (C, $F_{2,7} = 0.72$, $P = 0.52$; K, $F_{2,6} = 9.42$, $P = 0.02$). The range of autocorrelation of soil P varied significantly among past land uses as well, with the greatest deviation in reference stands ($F_{2,7} = 10.1$, $P = 0.01$). However, these differences were highly influenced by a single observation at the Walker Cove site (Table 3). When this value was removed, variability in the range of autocorrelation was significantly greater

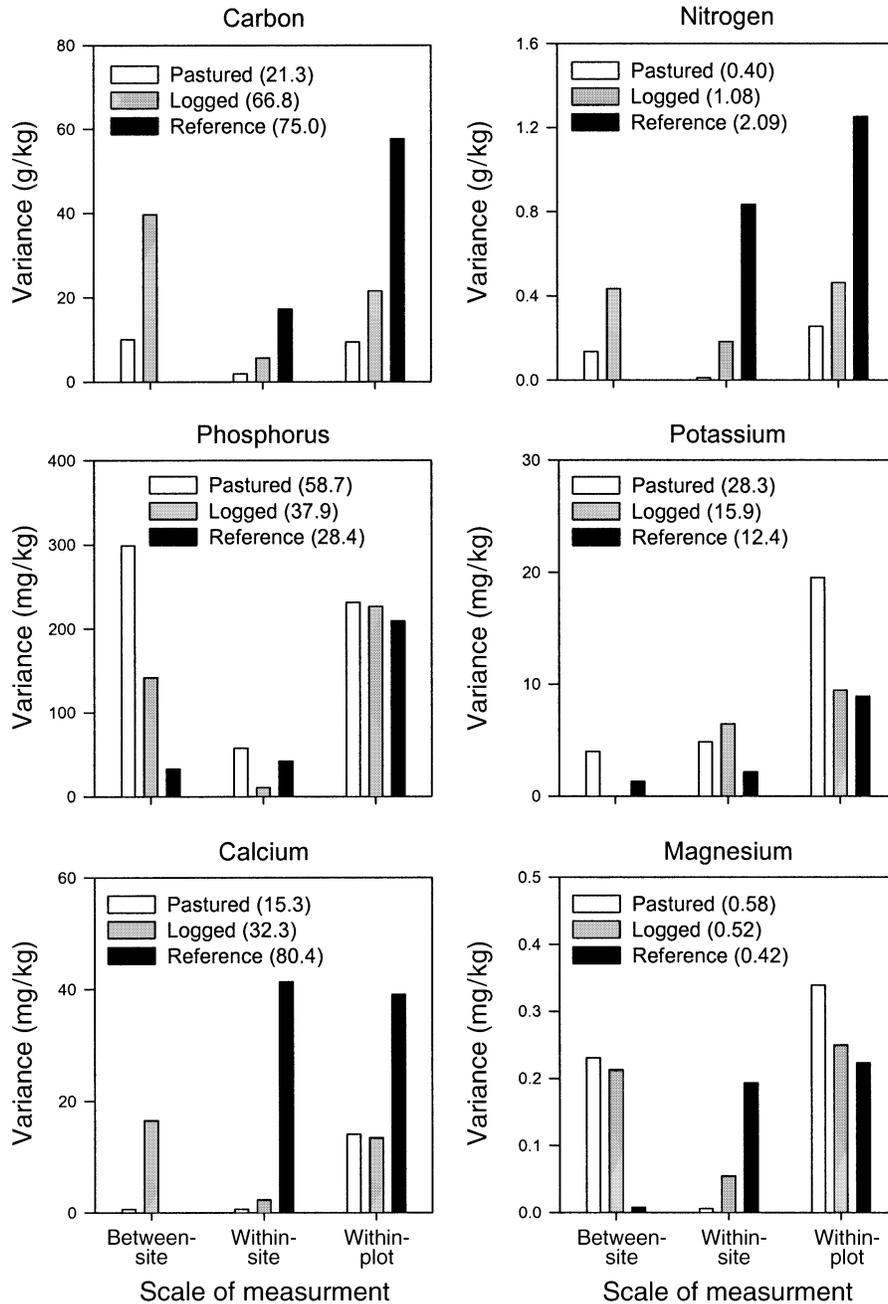


FIG. 5. Estimated variance of soil nutrient concentrations accounted for by different scales of measurement, for data collected during June 2001. Total variance is reported in parentheses in the units plotted on the graph.

among old pastures ($F_{2,6} = 8.30, P = 0.03$). Variability in the sill did not differ substantially in either case ($F_{2,7} = 0.43, P = 0.67, F_{2,6} = 1.72, P = 0.27$). Variability in the spatial distribution of Ca also changed appreciably with past land use (Table 3). Deviation in the range of autocorrelation for Ca was significantly greater in logged stands than in former pastures and reference stands ($F_{2,7} = 5.68, P = 0.04$). In addition, large differences in the sill among logged stands resulted in a significant difference in structural variance among land-use histories

($F_{2,7} = 5.18, P = 0.05$). There was no relationship between the spatial patterning of soil Mg or N (Mg range, $F_{2,6} = 4.09, P = 0.09$; Mg sill, $F_{2,6} = 2.91, P = 0.15$; N range, $F_{2,7} = 0.47, P = 0.65$; N sill, $F_{2,7} = 0.10, P = 0.90$).

DISCUSSION

Past human activities corresponded with dramatic changes in the heterogeneity of soil nutrients and N cycling rates that were not always detected when values

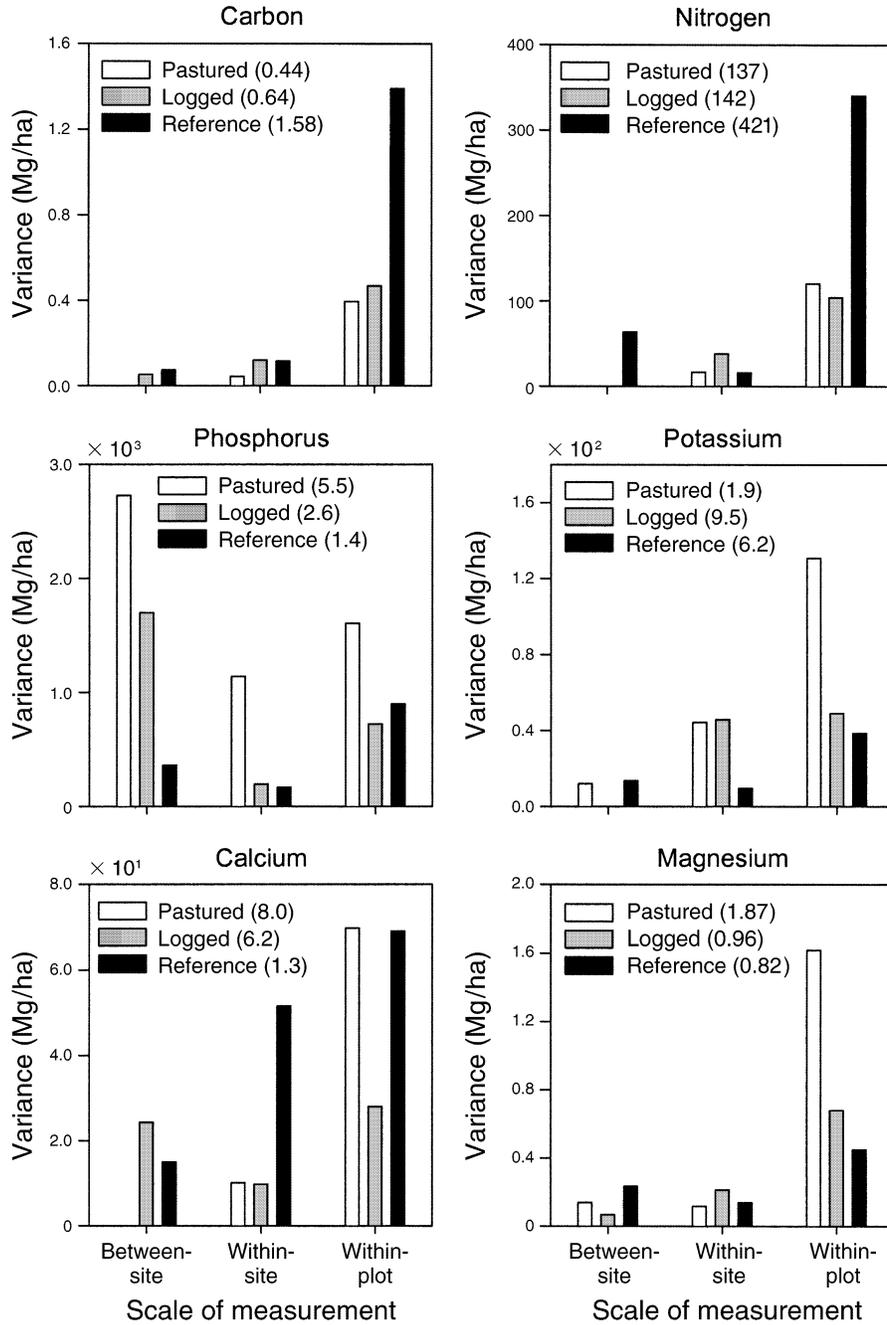


FIG. 6. Estimated variance of soil nutrient pools accounted for by different scales of measurement, for data collected during June 2001. Total variance is reported in parentheses in the units plotted on the graph. Note that y-axis scale numbers and total variance must be multiplied by the power of 10 shown above each panel to obtain actual values.

were averaged across sites. One reason that patterns of variance might have differed from those based on means may be that nutrient distributions and turnover rates were influenced by other drivers, whose effects could not be isolated from those of past land use. It is well documented that interactions between parent material, climate, and topography cause fundamental differences in soil resource patterns, even at local scales

(Jenny 1941, Stone 1975). Over time, there is greater likelihood that biotic processes will affect nutrient dynamics too (Hobbie 1992). Successional changes in plant species composition and nutrient accumulation and retention capabilities, for example, can have a substantial impact on soil resource patterns (Bormann and Likens 1967, Odum 1969, Vitousek and Reiners 1975, Likens et al. 1978, Pastor and Post 1986, Aber et al.

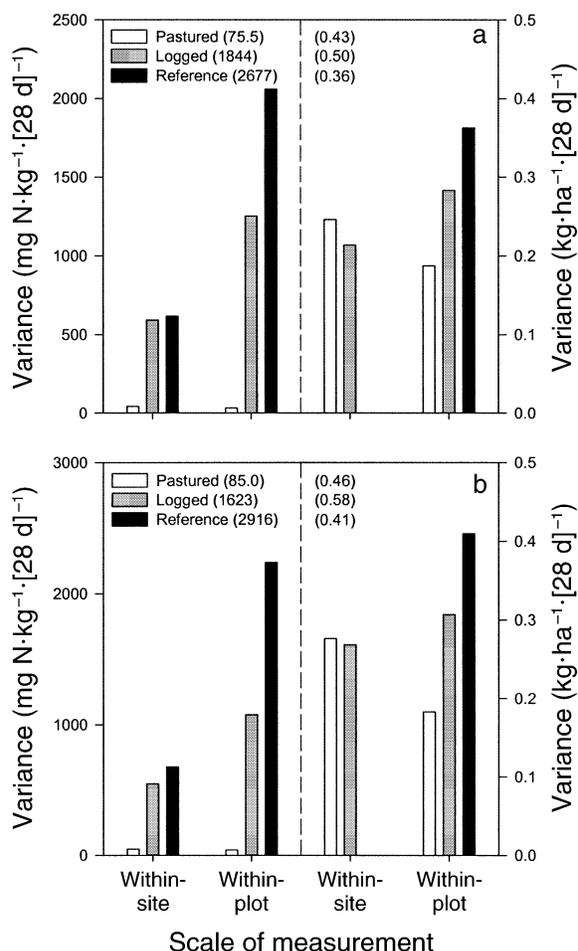


FIG. 7. Estimated variance of (a) N mineralization and (b) nitrification rates on the basis of mass (left panel) and area (right panel) across multiple spatial scales and by past land use. Data were collected during June 2002 in western North Carolina. Total variance is reported in parentheses in the units plotted on the graph.

1998). Because measures of variability reflect the range of responses produced by the influence of temporally changing drivers, they may be better at revealing the often muted legacies of land use.

In our study, it is likely that some observed differences in nutrient heterogeneity were produced not only by historical changes in land use, but also by the biotic processes these activities initiated. From the outset, forest clearance may have reduced nutrient variability in both pastures and cut-overs by redistributing and removing organic matter. Although we are not aware of studies that document this directly, Johnson et al. (1991) reported abundant mixing of soil horizons by harvesting practices, and others have observed persistent, appreciable C, N, and Ca losses when plant inputs were experimentally reduced or eliminated (Bormann and Likens 1979, Kelly et al. 1996, Likens et al. 1998), which together could decrease local differences in nu-

trient levels. In pastures, uniform organic matter inputs from forage grasses may have maintained reduced C and N variability. Relative to the litter produced by native plants, grasses would have provided a consistent quantity and quality of organic matter (Lavado et al. 1996). There is evidence for the long-term damping of fine-scale variability by plant monocultures in cultivated systems (Robertson et al. 1993) and by different plant growth forms and in successional forests (Gross et al. 1995). Guggenberger et al. (1995) showed that forage grasses also increase contents of undegraded, plant-derived soil organic matter in tropical mineral soils, indicating a highly resistant chemical signature. Removal of tree stumps may have further homogenized the post-pasture sites. Hooker and Compton (2003) demonstrated that bole wood is the primary reservoir for C and N during the first century after agricultural abandonment in re-establishing forests. Because trees were excluded from former pastures for several decades, there would have been no major pathways for enhancing C and N heterogeneity during this period. In contrast, tree resprouting and rapid woody recolonization of logged areas would have enabled C and N to begin accumulating and spatially differentiating sooner. In contrast, tree stump removal would have prevented resprouting by most of the species that previously occurred in pastures (Hicks and Pearson 2003), and the duration of land use would have severely compromised the viability of the seed bank (Wijdeven and Kuzee 2000, Bossuyt and Hermy 2001), effectively constraining the tree community to disturbance-adapted species (e.g., those with wind-dispersed, robust seeds). Not surprisingly, previous pastures are dominated by even-aged stands of tulip poplar; the average relative importance of this species is 0.61 in former pastures, compared with 0.36 in logged sites and 0.06 in reference sites (J. M. Fraterrigo, *unpublished data*). If litter inputs correspond linearly to tree abundance, then plant tissue from tulip poplar alone would comprise a majority of the organic matter in the forest floor of previous pastures. This may contribute not only to the low variability in C and N concentrations at fine scales, but also to the local reduction in mineral soil Ca variability, because tulip poplar concentrates Ca in its leaves (Coile 1937, Kalisz 1986), and trees that pump Ca from the deep soil can sustain high amounts of available Ca in the surface soil (Dijkstra and Smits 2002).

Patterns of C, N, and Ca heterogeneity at the within-site scale generally mirrored those at the within-plot scale, which suggests that similar processes were driving nutrient dynamics at spatial extents up to ~ 150 m (the distance between plots). At the between-site scale, however, patterns diverged, with nutrient variability in logged stands and former pastures increasing. Given that harvesting spanned several decades, it is possible that this landscape-scale heterogeneity among cut-overs is due to changes in logging technology and the

TABLE 3. Spherical model parameters for standardized semivariograms (C , structural variance; A , range) generated from soil nutrient concentration data.

Historical land use	Soil constituent					
	C		N		P	
	C	A	C	A	C	A
Pasture						
Bruce Farm	0.80	26	0.57	20	0.23	9
Picnic Area	0.30	15	0.09	12	0.34	94
Staire Branch	0.55	15	0.31	46	0	<1
Difference from mean	0.17	5.0	0.17	13.2	0.13	39.7
Logged						
Bruce Farm	0	<1	0.00	<1	0.21	9
Ivy Knob	0.23	305	0.32	10	0	<1
Little Andy	0.69	34	0.62	30	0.44	24
Difference from mean	0.26	128	0.21	10.1	0.15	8.8
Reference						
Cane River Gap	0.32	26	0.51	23	0	<1
Ivy Knob	0.03	6	0.05	8	0	<1
Walker Cove	0	<1	0	<1	0.45	291
Difference from mean	0.13	10.1	0.21	8.3	0.20	129

Notes: Semivariograms are derived from cyclically sampled plots ($N = 9$). Ellipses indicate that the spherical model was not significant (i.e., $P > 0.05$). The “difference from mean” value is the mean absolute difference of observations from the mean for the group of values that share a particular land-use history. The structural variance in the spherical model (C) is bounded by 0 and 1 to reflect the standardized semivariogram: if $h < A$, then $\gamma(h) = (1 - C) + C[(3h/2A) - (1/2)(h/A)^3]$, else $\gamma(h) = 1$, where h is the lag interval, A is the range, and C is the structural variance.

intensity of biomass removal (Yanai et al. 2003). It is also possible that land management varied enough among landowners to cause differences in nutrient dynamics, as Davis (2000) showed that practices contrasted widely among ethnic groups that settled the southern Appalachians. There is some evidence for this from the tropics, where Neill et al. (1997) found that small changes in historic grazing practices resulted in long-term differences in C and N accumulation patterns in re-establishing forests. Nutrient patterns at this scale may have been influenced by re-establishing vegetation as well. In contrast to local tree community patterns, landscape-scale composition was diverse in stands that had histories of logging or grazing, while reference stands were less so. The species pool included 14 tree species in reference stands, compared with 22 and 28 in former pastures and cut-overs, respectively (J. M. Fraterrigo, *unpublished data*). Interestingly, these differences are consistent with the large peak in between-site variability of C, N, and Ca observed in the logged stands and the smaller peak in old pastures.

Whereas past land use and the biotic changes it initiated may have mutually affected the heterogeneity of some nutrients, historical human activities are likely to be the primary cause of changes in P, K, and Mg distributions. Increased variance of P, K, and Mg in former pastures, particularly at fine scales, is consistent with the patchy deposition of animal excreta, which has previously been shown to influence nutrient heterogeneity (Augustine and Frank 2001). High P, K, and Mg availability from manure would also promote efficient plant uptake of these nutrients (Eghball et al. 2002, Hao and Chang 2002) and their subsequent cycling in surface

horizons (Reiners et al. 1994, Garcia-Montiel et al. 2000). This suggests one possible mechanism for the persistence of the irregular pattern of distribution. Although N is also a primary constituent of manure, it may be less easily converted to plant-available forms (Eghball et al. 2002) and predisposed to short residence times, which may make detecting historical patterns more difficult. High P and Mg variability across the landscape may be related to differences in farming practices. The type of animals stocked and the intensity of their grazing may have varied considerably among farms (Davis 2000). Unfortunately, the description of these items in the agricultural record is too coarse to resolve the patterns further. Differences in land-use duration and cessation may have also influenced P and Mg variability in former pastures and logged stands.

In some instances, we found differences between patterns of variance based on nutrient concentrations and contents that appeared related to changes in soil bulk density. Soil texture analysis indicated that soils sampled experienced only minor erosion, thus suggesting that consolidation of the A horizon in previous pastures and logged areas compacted the upper 15 cm of the profile with some of the underlying, more mineral-dominated layers. Others have reported similar findings (Burke et al. 1995, Motzkin et al. 1996, McGrath et al. 2001, Markewitz et al. 2002, Murty et al. 2002), which suggests that land use has a consistently large effect on soil bulk density. Because nutrient concentration and content were both evaluated in our study, we were able to identify the influence of soil bulk density differences on the observed distribution patterns and adjust our interpretation accordingly. Yet these patterns

TABLE 3. Extended.

Soil constituent						
K		Ca		Mg		
C	A	C	A	C	A	
0.52	12	0.49	12	0.71	12	
0.80	17	0.41	15	0.48	12	
0.46	23	0.51	17	0.51	16	
0.14	3.7	0.04	1.7	0.10	2.0	
0.50	10	1.03	12	0.82	11	
0.73	10	0	2	0.23	11	
0.47	32	0.64	30	0.74	21	
0.11	9.5	0.37	10.1	0.24	4.6	
0	<1	0.27	9	0.40	10	
...	...	0.24	10	0	<1	
0.61	102	0.33	9	
0.31	51.1	0.03	0.3	0.20	5.1	

clearly reinforce the importance of correcting soil volume for differences in bulk density and coarse fraction, because nutrient pool size depends partly on the extent of soil compaction (Markewitz et al. 2002). The patterns may also explain discrepancies in N cycling variance patterns, because high bulk density variance could translate to increased heterogeneity in per area rates, as seen in former pastures, and low variance in soil compaction could minimize variance in per area rates, as seen in reference stands.

Overall, changes in the heterogeneity of N turnover rates may be associated with the same processes that reduced organic matter variability. Biomass removal during forest clearance may have evened out the otherwise patchy distribution of decomposable material, resulting in locally homogenous N cycling rates. Newly established tree communities, particularly if dominated by a single species, may have further entrenched these fine-scale patterns. While more information on organic matter constituents under various land-use practices is necessary to attribute these patterns to differences in plant composition, there is sufficient evidence to suggest that tree community characteristics, through their effects on substrate quality, markedly influence N cycling variability (Knoepp and Swank 1998, Lovett et al. 2004). Other possible explanations for reduced variability of N turnover rates include decreased soil porosity and mixing, which may have negatively affected microbial activity (Doran 1980, Reiners et al. 1994). In addition, increased availability of grass-derived, labile C may have stimulated heterotrophic microbial growth, and in turn lowered mineralization and nitrification rates. However, the close relationship between microbial abundance and present vegetation may limit the duration of these effects.

In the case where disturbance legacies are being considered, measures of variability may facilitate the de-

tection of changes in soil resources. Initial site conditions are often not known, and researchers must assume that study areas with different histories are comparable (Motzkin et al. 1996, Compton and Boone 2000). If key parameters vary substantially across sites for reasons unrelated to past land use, an effect will be indistinguishable. In terms of classical ANOVA techniques, a high level of within-group variation around the mean relative to between-group variation will swamp a treatment effect, even after satisfying homogeneity of variance assumptions (Zar 1999). Had analysis been limited to mean responses in our study, long-term consequences of land use practices would be identified for only three soil constituents (N, P, and K stocks). By comparison, we observed substantial variation with past land use in the spatial distribution of all six of the elements investigated and N turnover rates; this variation alone might have impeded the detection of a signal from past land use in the averaged soil properties. Relying solely on mean values to evaluate disturbance effects may therefore be misleading when there are concomitant changes in the variance of the response (Benedetti-Cecchi 2003), and heterogeneity may yield a more comprehensive depiction of nutrient distribution patterns.

Evaluating differences in spatial structure may likewise provide insights about the effects of past land use. Our analysis revealed how previous human activities altered the spatial relationship between nutrient concentrations at both fine and coarse scales. Frequently, our findings corresponded with the results of the non-spatially explicit variance analysis, as they did for soil C, P, and Ca. This may indicate a particularly strong response on the part of these nutrients to land-use change. In other instances, however, there was no agreement between results. The spatial structure of soil N, for example, exhibited approximately the same mag-

nitude of deviation in each land use type, whereas that of K and Mg showed the most deviation in reference stands. This may indicate that there is a higher degree of scale dependency in the patterns than was captured by the sampling techniques. It may also suggest that past land use is not the only determinant of nutrient spatial structure.

*Implications of nutrient heterogeneity
for ecosystem recovery*

In post-abandonment forests, the spatial configuration of nutrients may be an important factor underpinning ecosystem recovery from disturbance. The successful colonization and persistence of vegetation relies to some extent on the availability of soil resources as well as life-history strategy and other abiotic factors (Meier et al. 1995). Indeed, despite the well-developed secondary forests in the southern Appalachians, several herbaceous species are absent or reduced in abundance in forests previously logged or farmed (Duffy and Meier 1992, Pearson et al. 1998, Mitchell et al. 2002). Because nutrient-enriched patches can support higher rates of productivity (Day et al. 2003a) and can sometimes enhance species diversity (Cornwell and Grubb 2003), it is possible that patterns of nutrient heterogeneity initiated by land-use practices will persist for well over a century. These differences may in turn affect long-term nutrient accumulation and retention (Mou et al. 1993) and influence other systems down-slope of recovering forests (e.g., aquatic ecosystems; Harding et al. 1998, Goodale et al. 2000). Site history and land-use induced changes in nutrient heterogeneity clearly warrant more attention if progress is to be made toward understanding forest ecosystem processes in dynamic landscapes.

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LITERATURE CITED

- Aber, J., W. McDowell, K. Nadelhoffer, A. Magill, G. Berntson, M. Kamakea, S. McNulty, W. Currie, L. Rustad, and I. Fernandez. 1998. Nitrogen saturation in temperate forest ecosystems—hypotheses revisited. *BioScience* **48**:921–934.
- Afzal, M., and W. A. Adams. 1992. Heterogeneity of soil mineral nitrogen in pasture grazed by cattle. *Soil Science Society of America Journal* **56**:1160–1166.
- Augustine, D. J. 2003. Long-term, livestock-mediated redistribution of nitrogen and phosphorus in an East African savanna. *Journal of Applied Ecology* **40**:137–149.
- Augustine, D. J., and D. A. Frank. 2001. Effects of migratory grazers on spatial heterogeneity of soil nitrogen properties in a grassland ecosystem. *Ecology* **82**:3149–3162.
- Bakker, C., J. M. Blair, and A. K. Knapp. 2003. Does resource availability, resource heterogeneity or species turnover mediate changes in plant species richness in grazed grasslands? *Oecologia* **137**:385–391.
- Beckage, B., and J. S. Clark. 2003. Seedling survival and growth of three forest tree species: the role of spatial heterogeneity. *Ecology* **84**:1849–1861.
- Benedetti-Cecchi, L. 2003. The importance of the variance around the mean effect size of ecological processes. *Ecology* **84**:2335–2346.
- Bergelson, J., J. A. Newman, and E. M. Floresroux. 1993. Rate of weed spread in spatially heterogeneous environments. *Ecology* **74**:999–1011.
- Blomqvist, M. M., H. Olff, M. B. Blaauw, T. Bongers, and W. H. van der Putten. 2000. Interactions between above- and belowground biota: importance for small-scale vegetation mosaics in a grassland ecosystem. *Oikos* **90**:582–598.
- Bormann, F. H., and G. E. Likens. 1967. Nutrient cycling. *Science* **155**:424–429.
- Bormann, F. H., and G. E. Likens. 1979. Pattern and process in a forested ecosystem: disturbance, development and the steady state based on the Hubbard Brook Ecosystem Study. Springer-Verlag, New York, New York, USA.
- Bossuyt, B., and M. Hermy. 2001. Influence of land use history on seed banks in European temperate forest ecosystems: a review. *Ecography* **24**:225–238.
- Braun, L. E. 1950. Deciduous forests of Eastern North America. Blakiston, Philadelphia, Pennsylvania, USA.
- Buckley, D. H., and T. M. Schmidt. 2001. The structure of microbial communities in soil and the lasting impact of cultivation. *Microbial Ecology* **42**:11–21.
- Burke, I. C., W. K. Lauenroth, and D. P. Coffin. 1995. Soil organic matter recovery in semiarid grasslands: implications for the conservation reserve program. *Ecological Applications* **5**:793–801.
- Clinger, W., and J. W. Van Ness. 1976. On unequally spaced time points in time series. *Annals of Statistics* **4**:736–745.
- Coile, T. S. 1937. Composition of the leaf litter of forest trees. *Soil Science* **43**:349–355.
- Compton, J. E., and R. D. Boone. 2000. Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. *Ecology* **81**:2314–2330.
- Cornwell, W. K., and P. J. Grubb. 2003. Regional and local patterns in plant species richness with respect to resource availability. *Oikos* **100**:417–428.
- Covington, W. W. 1981. Changes in forest floor organic matter and nutrient content following clear cutting in northern hardwoods. *Ecology* **62**:41–48.
- Cressie, N. 1993. *Statistics for spatial data*. Wiley, New York, New York, USA.
- Davidson, E. A., and I. L. Ackerman. 1993. Changes in soil carbon inventories following cultivation of previously untilled soils. *Biogeochemistry* **20**:161–193.
- Davis, D. E. 2000. *Where there are mountains: an environmental history of the Southern Appalachians*. University of Georgia Press, Athens, Georgia, USA.
- Day, K. J., M. J. Hutchings, and E. A. John. 2003a. The effects of spatial pattern of nutrient supply on the early stages of growth in plant populations. *Journal of Ecology* **91**:305–315.
- Day, K. J., M. J. Hutchings, and E. A. John. 2003b. The effects of spatial pattern of nutrient supply on yield, structure and mortality in plant populations. *Journal of Ecology* **91**:541–553.
- Dijkstra, F. A., and M. M. Smits. 2002. Tree species effects on calcium cycling: the role of calcium uptake in deep soils. *Ecosystems* **5**:385–398.

- Doran, J. W. 1980. Soil microbial and biochemical changes associated with reduced tillage. *Soil Science Society of America Journal* **44**:765–771.
- Duffy, D. C., and A. J. Meier. 1992. Do Appalachian herbaceous understories ever recover from clearcutting? *Conservation Biology* **6**:196–201.
- Dupouey, J. L., E. Dambrine, J. D. Laffite, and C. Moares. 2002. Irreversible impact of past land use on forest soils and biodiversity. *Ecology* **83**:2978–2984.
- Eghball, B., B. J. Wienhold, J. E. Gilley, and R. A. Eigenberg. 2002. Mineralization of manure nutrients. *Journal of Soil and Water Conservation* **57**:470–473.
- Fearnside, P. M., and R. I. Barbosa. 1998. Soil carbon changes from conversion of forest to pasture in Brazilian Amazonia. *Forest Ecology and Management* **108**:147–166.
- Federer, C. A. 1984. Organic matter and nitrogen content of the forest floor in even-aged northern hardwoods. *Canadian Journal of Forest Research* **14**:763–767.
- Foster, D. R. 1992. Land-use history (1730–1990) and vegetation dynamics in Central New-England, USA. *Journal of Ecology* **80**:753–772.
- Foster, D. R., G. Motzkin, and B. Slater. 1998. Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. *Ecosystems* **1**:96–119.
- García-Montiel, D. C., C. Neill, J. Melillo, S. Thomas, P. A. Steudler, and C. C. Cerri. 2000. Soil phosphorus transformations following forest clearing for pasture in the Brazilian Amazon. *Soil Science Society of America Journal* **64**:1792–1804.
- Goldston, E. F., C. W. Croom, W. A. Davis, and W. Gettys. 1954. Soil survey of Buncombe County, North Carolina. USDA, Washington, D.C., USA.
- Goodale, C. L., and J. D. Aber. 2001. The long-term effects of land-use history on nitrogen cycling in northern hardwood forests. *Ecological Applications* **11**:253–267.
- Goodale, C. L., J. D. Aber, and W. H. McDowell. 2000. The long-term effects of disturbance on organic and inorganic nitrogen export in the White Mountains, New Hampshire. *Ecosystems* **3**:433–450.
- Gross, K. L., K. S. Pregitzer, and A. J. Burton. 1995. Spatial variation in nitrogen availability in three successional plant communities. *Journal of Ecology* **83**:357–367.
- Guggenberger, G., W. Zech, and R. J. Thomas. 1995. Lignin and carbohydrate alteration in particle-size separates of an oxisol under tropical pastures following native savanna. *Soil Biology and Biochemistry* **27**:1629–1638.
- Guo, L. B., and R. M. Gifford. 2002. Soil carbon stocks and land use change: a meta analysis. *Global Change Biology* **8**:345–360.
- Haile, M. W. 1979. *Dillinghams of Big Ivy, Buncombe County, NC and related families*. Gateway Press, Baltimore, Maryland, USA.
- Hao, X. Y., and C. Chang. 2002. Effect of 25 annual cattle manure applications on soluble and exchangeable cations in soil. *Soil Science* **167**:126–134.
- Harding, J. S., E. F. Benfield, P. V. Bolstad, G. S. Helfman, and E. B. D. Jones. 1998. Stream biodiversity: the ghost of land use past. *Proceedings of the National Academy of Sciences (USA)* **95**:14843–14847.
- Hicks, N. G., and S. M. Pearson. 2003. Salamander diversity and abundance in forests with alternative land use histories in the southern Blue Ridge Mountains. *Forest Ecology and Management* **177**:117–130.
- Hobbie, S. E. 1992. Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution* **7**:336–339.
- Hooker, T. D., and J. E. Compton. 2003. Forest ecosystem carbon and nitrogen accumulation during the first century after agricultural abandonment. *Ecological Applications* **13**:299–313.
- Huntington, T. G., and D. F. Ryan. 1990. Whole-tree-harvesting effects on soil-nitrogen and carbon. *Forest Ecology and Management* **31**:193–204.
- Hutchings, M. J., E. A. John, and D. K. Wijesinghe. 2003. Toward understanding the consequences of soil heterogeneity for plant populations and communities. *Ecology* **84**:2322–2334.
- Jackson, M. L. 1958. *Soil chemical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey, USA.
- Jenny, H. 1941. *Factors of soil formation*. McGraw-Hill, New York, New York, USA.
- Johnson, C. E., A. H. Johnson, T. G. Huntington, and T. G. Siccama. 1991. Whole-Tree clear-cutting effects on soil horizons and organic-matter pools. *Soil Science Society of America Journal* **55**:497–502.
- Johnson, D. W., and P. S. Curtis. 2001. Effects of forest management on soil C and N storage: meta analysis. *Forest Ecology and Management* **140**:227–238.
- Jurena, P. N., and S. Archer. 2003. Woody plant establishment and spatial heterogeneity in grasslands. *Ecology* **84**:907–919.
- Jussy, J. H., W. Koerner, E. Dambrine, J. L. Dupouey, and M. Benoit. 2002. Influence of former agricultural land use on net nitrate production in forest soils. *European Journal of Soil Science* **53**:367–374.
- Kalish, P. J. 1986. Soil properties of steep Appalachian old fields. *Ecology* **67**:1011–1023.
- Kaluzny, S. P. 1998. *S+SpatialStats: user's manual for Windows and UNIX*. Springer, New York, New York, USA.
- Kelly, R. H., I. C. Burke, and W. K. Lauenroth. 1996. Soil organic matter and nutrient availability responses to reduced plant inputs in shortgrass steppe. *Ecology* **77**:2516–2527.
- Knoepp, J. D., and W. T. Swank. 1998. Rates of nitrogen mineralization across an elevation and vegetation gradient in the southern Appalachians. *Plant and Soil* **204**:235–241.
- Knops, J. M. H., and D. Tilman. 2000. Dynamics of soil nitrogen and carbon accumulation for 61 years after agricultural abandonment. *Ecology* **81**:88–98.
- Koerner, W., E. Dambrine, J. L. Dupouey, and M. Benoit. 1999. $\delta^{15}\text{N}$ of forest soil and understorey vegetation reflect the former agricultural land use. *Oecologia* **121**:421–425.
- Lavado, R. S., J. O. Sierra, and P. N. Hashimoto. 1996. Impact of grazing on soil nutrients in a Pampean grassland. *Journal of Range Management* **49**:452–457.
- Likens, G. E., F. H. Bormann, R. S. Pierce, and W. A. Reiners. 1978. Recovery of a deforested ecosystem. *Science* **199**:492–496.
- Likens, G. E., C. T. Driscoll, D. C. Buso, T. G. Siccama, C. E. Johnson, G. M. Lovett, T. J. Fahey, W. A. Reiners, D. F. Ryan, C. W. Martin, and S. W. Bailey. 1998. The biogeochemistry of calcium at Hubbard Brook. *Biogeochemistry* **41**:89–173.
- Lovett, G. M., K. C. Weathers, M. A. Arthur, and J. C. Schultz. 2004. Nitrogen cycling in a northern hardwood forest: Do species matter? *Biogeochemistry* **67**:289–308.
- Lovett, G. M., K. C. Weathers, and W. V. Sobczak. 2000. Nitrogen saturation and retention in forested watersheds of the Catskill Mountains, New York. *Ecological Applications* **10**:73–84.
- Maestre, F. T., J. Cortina, S. Bautista, J. Bellot, and R. Vallejo. 2003. Small-scale environmental heterogeneity and spatiotemporal dynamics of seedling establishment in a semi-arid degraded ecosystem. *Ecosystems* **6**:630–643.
- Markewitz, D., F. Sartori, and C. Craft. 2002. Soil change and carbon storage in longleaf pine stands planted on marginal agricultural lands. *Ecological Applications* **12**:1276–1285.
- McGrath, D. A., C. K. Smith, H. L. Gholz, and F. D. Oliveira. 2001. Effects of land-use change on soil nutrient dynamics in Amazonia. *Ecosystems* **4**:625–645.

- Meier, A. J., S. P. Bratton, and D. C. Duffy. 1995. Possible ecological mechanisms for loss of vernal-herb diversity in logged eastern deciduous forests. *Ecological Applications* **5**:935–946.
- Melillo, J. M., J. D. Aber, and J. F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* **63**:621–626.
- Mitchell, C. E., M. G. Turner, and S. M. Pearson. 2002. Effects of historical land use and forest patch size on myrmecochores and ant communities. *Ecological Applications* **12**:1364–1377.
- Motzkin, G., D. Foster, A. Allen, J. Harrod, and R. Boone. 1996. Controlling site to evaluate history: vegetation patterns of a New England sand plain. *Ecological Monographs* **66**:345–365.
- Mou, P., T. J. Fahey, and J. W. Hughes. 1993. Effects of soil disturbance on vegetation recovery and nutrient accumulation following whole-tree harvest of a northern hardwood ecosystem. *Journal of Applied Ecology* **30**:661–675.
- Mowbray, T. B., and H. J. Oosting. 1968. Vegetation gradients in relation to environment and phenology in a southern Blue Ridge gorge. *Ecological Monographs* **38**:309–344.
- Murty, D., M. U. F. Kirschbaum, R. E. McMurtrie, and H. McGilvray. 2002. Does conversion of forest to agricultural land change soil carbon and nitrogen? A review of the literature. *Global Change Biology* **8**:105–123.
- Neill, C., J. M. Melillo, P. A. Steudler, C. C. Cerri, J. F. L. De Moraes, M. C. Piccolo, and M. Brito. 1997. Soil carbon and nitrogen stocks following forest clearing for pasture in the southwestern Brazilian Amazon. *Ecological Applications* **7**:1216–1225.
- Odum, E. P. 1969. The strategy of ecosystem development. *Science* **164**:262–270.
- Ollinger, S. V., M. L. Smith, M. E. Martin, R. A. Hallett, C. L. Goodale, and J. D. Aber. 2002. Regional variation in foliar chemistry and N cycling among forests of diverse history and composition. *Ecology* **83**:339–355.
- Pastor, J., and W. M. Post. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. *Biogeochemistry* **2**:3–27.
- Paz-Gonzalez, A., and M. T. Taboada. 2000. Nutrient variability from point sampling on 2 meter grid in cultivated and adjacent forest land. *Communications in Soil Science and Plant Analysis* **31**:2135–2146.
- Paz-Gonzalez, A., S. R. Vieira, and M. T. T. Castro. 2000. The effect of cultivation on the spatial variability of selected properties of an umbric horizon. *Geoderma* **97**:273–292.
- Pearson, S. M., A. B. Smith, and M. G. Turner. 1998. Forest patch size, land use, and mesic forest herbs in the French Broad River Basin, North Carolina. *Castanea* **63**:382–395.
- Reiners, W. A., A. F. Bouwman, W. F. J. Parsons, and M. Keller. 1994. Tropical rain forest conversion to pasture: changes in vegetation and soil properties. *Ecological Applications* **4**:363–377.
- Ribas, C. R., J. H. Schoereder, M. Pic, and S. M. Soares. 2003. Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. *Austral Ecology* **28**:305–314.
- Richter, D. D., D. Markewitz, P. R. Heine, V. Jin, J. Raikes, K. Tian, and C. G. Wells. 2000. Legacies of agriculture and forest regrowth in the nitrogen of old-field soils. *Forest Ecology and Management* **138**:233–248.
- Richter, D. D., D. Markewitz, S. E. Trumbore, and C. G. Wells. 1999. Rapid accumulation and turnover of soil carbon in a re-establishing forest. *Nature* **400**:56–58.
- Robertson, G. P. 1999. *Standard soil methods for long-term ecological research*. Oxford University Press, New York, New York, USA.
- Robertson, G. P., J. R. Crum, and B. G. Ellis. 1993. The spatial variability of soil resources following long-term disturbance. *Oecologia* **96**:451–456.
- Robertson, G. P., M. A. Huston, F. C. Evans, and J. M. Tiedje. 1988. Spatial variability in a successional plant community: patterns of nitrogen availability. *Ecology* **69**:1517–1524.
- Rossi, R. E., D. J. Mulla, A. G. Journel, and E. H. Franz. 1996. Geostatistical tools for modeling and interpreting ecological spatial dependence. *Ecological Monographs* **62**:277–314.
- SAMAB (Southern Appalachian Man and the Biosphere). 1996. *The Southern Appalachian Assessment: Terrestrial Resources Technical Report 5*. USDA Forest Service, Southern Region, Atlanta, Georgia, USA.
- Scheiner, S. M., and J. Gurevitch, editors. 2001. *Design and analysis of ecological experiments*. Second edition. Oxford University Press, Oxford, UK.
- Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. E. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* **77**:364–374.
- Schulte, E. E., J. B. Peters, and P. R. Hodgson. 1987. Wisconsin procedures for soil testing, plant analysis and feed and forage analysis. Department of Soil Science, University of Wisconsin, Madison, Wisconsin, USA.
- Schultz, B. B. 1985. Levene's test for relative variation. *Systematic Zoology* **34**:449–456.
- Stone, E. L. 1975. Effects of species on nutrient cycles and soil change. *Philosophical Transactions of the Royal Society of London B* **271**:149–162.
- Verheyen, K., G. R. Guntenspergen, B. Biesbrouck, and M. Hermy. 2003. An integrated analysis of the effects of past land use on forest herb colonization at the landscape scale. *Journal of Ecology* **91**:731–742.
- Vitousek, P. M., and W. A. Reiners. 1975. Ecosystem succession and nutrient retention: a hypothesis. *BioScience* **25**:376–381.
- Wear, D. N., and P. Bolstad. 1998. Land-use changes in Southern Appalachian landscapes: spatial analysis and forecast evaluation. *Ecosystems* **1**:575–594.
- Webster, R. 1985. Quantitative spatial analysis of soil in the field. *Advances in Soil Science* **3**:1–70.
- Wijdeven, S. M. J., and M. E. Kuzee. 2000. Seed availability as a limiting factor in forest recovery processes in Costa Rica. *Restoration Ecology* **8**:414–424.
- Yanai, R. D., W. S. Currie, and C. L. Goodale. 2003. Soil carbon dynamics after forest harvest: an ecosystem paradigm reconsidered. *Ecosystems* **6**:197–212.
- Yarnell, S. L. 1998. *The Southern Appalachians: a history of the landscape*. General Technical Report SRS-18, USDA Forest Service Southern Research Station, Asheville, North Carolina, USA.
- Zar, J. H. 1999. *Biostatistical analysis*. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.