

Spatial heterogeneity and soil nitrogen dynamics in a burned black spruce forest stand: distinct controls at different scales

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Abstract. We evaluated spatial patterns of soil N and C mineralization, microbial community composition (phospholipid fatty acids), and local site characteristics (plant/forest floor cover, soil pH, soil %C and %N) in a 0.25-ha burned black spruce forest stand in interior Alaska. Results indicated that factors governing soil N and C mineralization varied at two different scales. *In situ* net N mineralization was autocorrelated with microbial community composition at relatively broad scales (~8 m) and with local site characteristics ('site' axis 1 of non-metric scaling ordination) at relatively fine scales (2–4 m). At the scale of the individual core, soil moisture was the best predictor of *in situ* net N mineralization and laboratory C mineralization, explaining between 47 and 67% of the variation ($p < 0.001$). Ordination of microbial lipid data showed that bacteria were more common in severely burned microsites, whereas fungi were more common in low fire severity microsites. We conclude that C and N mineralization rates in this burned black spruce stand were related to different variables depending on the scale of analysis, suggesting the importance of considering multiple scales of variability among key drivers of C and N transformations.

Introduction

Forest soil carbon (C) and nitrogen (N) transformations reflect variation among multiple interacting controls including substrate quantity and quality, microclimate, and microbial community composition and activity, each of which may vary at a different spatial scale. In particular, microbial community dynamics, which are closely linked to soil C and N transformations (Waldrop et al. 2000; Balsler et al. 2002; Waldrop and Firestone 2004; Balsler and Firestone 2005), may vary in response to changes in the dominant vegetation (Myers et al. 2001), substrate quantity (Baath et al. 1995), or both (Saetre and Baath 2000). Despite the importance of these interacting controls and their

potential heterogeneity across space, few studies have examined these relationships spatially.

Heterogeneity is frequently considered an experimental problem that generates large sample-to-sample variation and non-significant or inconclusive results (Van Cleve and Oliver 1982; Dyrness et al. 1989). However, explicitly recognizing and understanding spatial variation can lead to new insights on the controls of ecosystem processes (Beneditti-Cecchi 2003; Kashian et al. 2005). For instance, the survival and establishment of individual plant species and ultimately the biodiversity of plant communities may be a response to spatial heterogeneity in soil resources (Chen and Stark 2000). Denitrification rates vary in response to changes in interstitial soil water content (Christensen et al. 1990), and nutrient levels may reflect the spacing of individual plants (Schlesinger et al. 1990; Jackson and Caldwell 1993) or the distribution of vegetation types across landscapes (Fan et al. 1998; Ludwig et al. 2000; Beedlow et al. 2004). After disturbance, patterns of forest productivity and soil nutrient availability may vary spatially at fine and coarse scales (Tinker et al. 1994; Turner et al. 1997; Fraterrigo et al. in press).

Studies of fine-scale variation in postfire soil N dynamics provide an opportunity to use local environmental variation to explore the controls over post-fire N cycling without confounding effects of broad-scale variations in climate, topography, and biotic history. Study of fine-scale variation in factors controlling soil N dynamics may help explain fire effects on N cycling at multiple spatial scales.

Our goal in this paper is to characterize post-fire spatial heterogeneity of soil C and N mineralization rates within a burned black spruce (*Picea mariana*) forest stand in central Alaska. Stand-replacing fires characterize the natural disturbance regimes of many boreal forests. In Alaska, for example, 73% of the area burned between 1950 and 1999 occurred during extensive fire years (Kasischke et al. 2002). In 2004, 2.7 million hectares (6.7 million acres) burned in interior Alaska, the largest recorded burned area (Alaska Fire Service, BLM). By evaluating spatial heterogeneity in a burned stand, we provide information on an important landscape component of boreal black spruce forests. We asked three questions. (1) How variable are within-stand C and N mineralization rates (*in situ* and laboratory N mineralization, and laboratory C mineralization) after fire? (2) What is the spatial structure of C and N mineralization rates? (3) What factors govern within-stand variation in C and N mineralization rates?

Factors that may strongly affect spatial patterns of soil N transformations after stand-replacing fire include patterns in abiotic conditions caused by the removal of the canopy and subsequent reduction in plant transpiration (affecting soil moisture), patterns in fire severity (affecting duff consumption, ash deposition, soil heat penetration, plant survival), patterns in soil organic layer depth and composition, and patterns in aboveground vegetation and forest floor cover (Smithwick et al. 2005). Variation in substrates and microclimatic conditions after fire is likely to affect microbial community

composition and activity, affecting soil N transformations. Given the extensive occurrence of stand-replacing fires and N limitation in many boreal forests (Yarie and Van Cleve in press), identifying the factors governing soil N transformations and their spatial variability after fire may be important for understanding long-term ecosystem productivity.

Methods

Site description

Stand-replacing fires dominate the disturbance regime of black spruce forest stands in central Alaska, with an average fire return interval of 26 to 113 years (Yarie 1981). In 2001, a stand-replacing fire (the Survey Line fire) burned a section of the Tanana Flats south of the Bonanza Creek Experimental Forest (BCEF), located 20 km west of Fairbanks. We established a study plot in this burn in 2002, in what had been an open black spruce/feathermoss (*P. mariana*/*Pleurozium schreberi*) forest (64.654° N, –148.278° W; elevation = 131 m a.s.l.).

The climate at nearby BCEF is strongly continental and is characterized by temperature extremes which can range from –50 °C to +35 °C. The mean annual temperature is –2.9 °C (ranging from 16.9 °C in July to –23.4 °C in January). The average annual precipitation at Fairbanks is 287 mm, with approximately 35% falling as snow from mid-October to April, which remains as a permanent cover for 6–7 months each year. (Hinzman et al. in press).

Field methods

We established a 0.25-ha study plot with an intensive grid of 5-cm diameter PVC cores to evaluate spatial variability of soil N transformations (Figure 1). On May 31st, 2002, cores ($n = 81$) were placed in the organic layer to a depth of 15 cm. The average (± 1 standard deviation) depth of the post-fire organic layer was 12.1 ± 6 cm and ranged from 3 to 30 cm; thus 15 cm captured most of dynamics of the organic layer. One ion-exchange resin bag was placed at the bottom of each soil core. Cores were spaced 2, 4 m, or 8 m apart along one of nine rows, each separated by 2 m. Each row had nine cores, for a total of 81 soil cores. The sampling design was reversed in the middle three rows to account for anisotropy. This sampling design facilitated the study of spatial patterning by creating comparable power at different lag distances and maximizing sampling efficiency (Clayton and Hudelson 1995). The minimum detectable autocorrelation distance is 2 m.

We used local site characteristics (plant/forest floor cover, soil %N, soil %C, and soil pH) present 1 yr after fire to represent variation in fire severity. We assumed that sites with higher % cover of aboveground vegetation and unburned litter and moss represented areas of lower fire severity. In contrast,

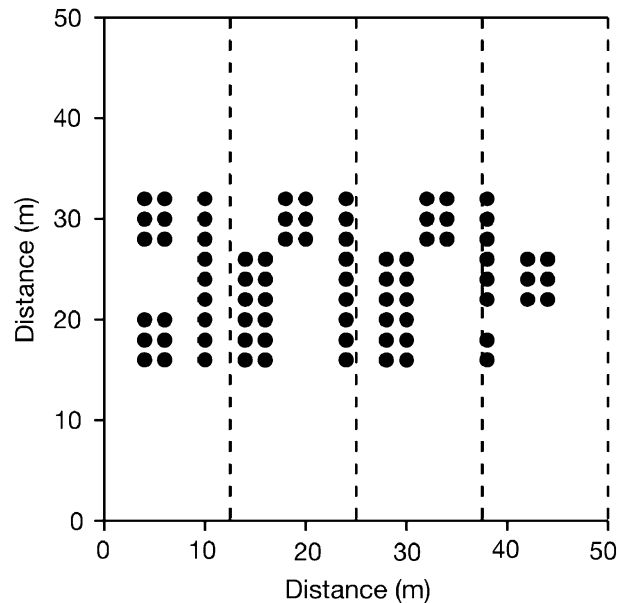


Figure 1. Cyclic sampling design used to measure soil C and N transformations, microbial community composition, and local site characteristics at the Survey Line fire site. Points represent location of soil cores.

sites with higher % of exposed mineral soil, burned forest floor material and/or ash were likely to have experienced higher fire severity. Specifically, we measured the percent (%) cover of plant, moss, coarse woody debris (CWD, ≥ 7.5 cm diameter, touching or elevated), ash, and litter, in a 0.25 m^2 circular sampling frame centered around each core in 2002. Cover values were frequently $>100\%$ due to overlapping vegetation. Because mosses are known to affect C and N cycling in boreal systems (Turetsky 2003), we also recorded the dominant moss species present within the sampling frame.

Adjacent to each sampling frame, soil samples were taken with another 5-cm diameter PVC core to a depth of 15 cm for estimation of initial inorganic N availability, microbial community composition, and general soil characteristics. A subset of these samples ($n = 27$) was used in laboratory incubations to determine laboratory N mineralization and nitrification as well as laboratory C mineralization (see below). Soil samples were placed in a plastic bag and kept cool for transport to the laboratory. Intact resin bags and soil in the core were retrieved approximately 1 yr later on June 6th, 2003.

Laboratory

Soil samples were homogenized and roots (>4 mm), twigs, and green vegetation were discarded using forceps. From each soil sample ($n = 81$),

sub-samples were used to measure initial and final inorganic N (NH_4^+ -N and NO_3^- -N), soil moisture, pH, microbial community composition, and general soil characteristics. Sub-samples for general soil characteristics were air dried and sent to the Soils and Plant Analysis Lab at the University of Wisconsin, Madison. A micro-Kjeldahl procedure was used for total N determination (Jackson 1958). Acid extractable phosphorus (P) was analyzed colorimetrically using the Truog method (Schulte et al. 1987) and potassium (K), calcium (Ca), and Magnesium (Mg) were measured by atomic absorption after extraction with H_2SO_4 (Schulte et al. 1987). Percent organic matter was determined by dry combustion using the Tekmar-Dohrman 183 TOC Boat Sampler DC-190 (Tekmar-Dohrman, Mason OH). Soil pH was measured in the lab in Alaska with a 5-g sub-sample suspended in 10 ml of a CaCl_2 solution (0.01 M). Gravimetric soil moisture was determined from dry and wet soil weights after oven-drying (70 °C) for 48 h.

Inorganic N was extracted by adding 75 ml of 2 M KCl to 20 ± 0.02 g of soil in a plastic urinalysis cup, modified after Binkley and Matson (1983). Samples were shaken for 1 h, on a mechanized shaker table. After shaking, samples rested for 24 h and were then filtered using syringe filters (in 2002) or a vacuum filter (in 2003) and KCl-rinsed Whatman No. 2 filter paper. Extracts were frozen (-18 °C) for future analysis. Concentrations of NH_4^+ -N and NO_3^- -N were determined for all samples on a Lachat QuikChem autoanalyzer (Lachat Instruments, Milwaukee, Wisconsin, USA). Extractable organic C was estimated by extracting 20 g of soil in 0.5 M K_2SO_4 following the same protocol as the 2 M KCl soil extractions (Balser and Firestone 2005). Extracts were frozen pending analysis. Samples were processed on a carbon analyzer (I.O. Corp, College Station, TX) at the University of Wisconsin (Madison, WI).

We used a standard aerobic laboratory incubation of soil from the initial cores to examine potential C and N mineralization and nitrification on a subset of the cores ($n = 27$) (Hart et al. 1997). We chose soils from the last three rows of the cyclic sampling design (Figure 1) to include in the subset. The lower overall sample size reduces the chances of determining a significant semi-variogram model; however, all lag separations were equally represented. From each soil core, a 10-g subsample (oven dry equivalent) was brought up to field capacity with deionized water, placed in a 230 ml, wide-mouth Mason jar with an opening diameter of 7.6 cm, and covered with polyethylene film. Jars were incubated in the dark at room temperature (approximately 20 °C) for 12 d. Rates of CO_2 production were assayed after 5, 101, 182, and 278 h of incubation. At each time point, the polyethylene films were removed, jars were allowed to equilibrate with the atmosphere, and then jars were capped with Mason jar lids fitted with Hungate septa. Initial and final (12 h) samples of the jar headspace were removed and immediately analyzed for CO_2 concentration with a LI-COR 6252 (Lincoln, NE). We calculated the respiration rate from the change in CO_2 concentration over time. We report laboratory C mineralization as cumulative CO_2 mineralized over the incubation, which was

determined by multiplying the CO₂ production rate at each time point by the duration of the sampling interval, and summing all intervals. After 12 days, inorganic N was extracted from soil with KCl as described above. Net N mineralization and nitrification were calculated as the difference between initial and final NH₄⁺ + NO₃⁻ concentration, or initial and final NO₃⁻ concentration, respectively.

We used microbial lipid analysis (extraction of signature lipid biomarkers from the cell membrane and wall of microorganisms (White and Ringelberg 1998)) to assess the microbial community composition at each sampling location ($n = 81$). Immediately after returning from the field, we shipped refrigerated samples overnight to the University of Wisconsin (Madison, WI) where they were homogenized and frozen before analysis. All glassware was baked at 475 °C for 4 h to remove any organic contaminants. We extracted, purified and identified PLFAs from microbial cell membranes in 1-g samples of lyophilized soil using a hybrid lipid extraction based on a modified Bligh and Dyer (1959) technique, combined with fatty acid methyl ester analysis (FAME) as described by Microbial ID Inc. (Hayward, CA). Briefly, lipids were extracted from 4 g of freeze-dried soil using a chloroform-methanol extraction with a phosphate buffer (potassium phosphate (3.6 ml), methanol (8 ml), and CHCl₃ (4 ml)) in 25-ml glass tubes, shaken for 1 h and centrifuged. Supernatant was then decanted to 30-ml tubes and potassium phosphate buffer and chloroform were re-added and the tubes were vortexed for 30 s. The phases were allowed to separate overnight at room temperature. The top layer was aspirated off, saving the chloroform phase, and the volume was reduced in a RapidVap. We then follow the procedure for FAME as given by Microbial ID Inc.; sodium hydroxide was added for saponification and the solution was heated in a water bath for 30 min, followed by mild alkaline methanolysis.

Fatty acids were analyzed using a Hewlett-Packard 6890 Gas Chromatograph equipped with a flame ionization detector and split/splitless inlet and a 25 m × 0.2 mm inside diameter × 0.33 μm film thickness Ultra 2 (5%-phenyl, 95% methyl) capillary column (Agilent) using hydrogen as the carrier gas, N as the make-up gas, and air to support the flame. Gas chromatograph conditions are set by the MIDI Sherlock program (MIDI, Inc. Newark, DE). Peaks were identified with using bacterial fatty acid standards and Sherlock peak identification software (MIDI, Inc. Newark, DE). Fatty acids were quantified by comparisons of peak areas from the sample compared with peak areas of two internal standards, 9:0 (nonanoic methyl ester) and 19:0 (nonadecanoic methyl ester), of known concentration. In all subsequent analyses we used only fatty acids that were identifiable and present at >0.5 mol percent.

Lipids were assigned to microbial guilds based on the literature (Vestal and White 1989; Baath et al. 1995; Frostegard and Baath 1996; Wilkinson et al. 2002). Terminology to describe lipid biomarkers is described by 'A:Bω C' where 'A' indicates the total number of C atoms, 'B' the number of double bonds (unsaturations), and 'ω' indicates the position of the double bond from the methyl end of the molecule (Arao 1999; Bååth and Anderson 2003;

Steenwerth et al. 2003. Lipid biomarkers were therefore stratified into guilds based on their chemical structure that may loosely correlate to known ecosystem functions (Vestal and White 1989). The guilds included two general fungi guilds: saprotrophic fungi (18:1 ω 9, 18:2 ω 6,9) and arbuscular mycorrhizal fungi (AMF, 16:1 ω 5) (Frostegard and Baath 1996; Baath and Anderson 2003). Protozoa were identified using lipid biomarker 18:3 ω 6. Bacteria could be separated into Gram-positive (Gm+) or Gram-negative (Gm-) bacteria. Gm+ were identified as branched lipids (denoted with the prefixes 'i' and 'a' that refer to iso and anti-iso methyl branching) (Zelles et al. 1992; Wilkinson et al. 2002). Gm- bacteria were identified as hydroxy biomarkers (denoted by 'OH'), cyclopropyl biomarkers (denoted by 'cy'), or monounsaturated biomarkers (Wilkinson 1998). Saturated (denoted by lack of double bonds) and alcohol guilds were also included. We included several "summed" fatty acids that could not be uniquely resolved by the GC software due to their high relative abundance; we refer to these markers as 'unknown.'

Calculations and statistics

To quantify the variation in rates of soil N dynamics (Question 1), we calculated means, standard errors, and coefficients of variation (standard deviation/mean *100) for all variables.

To integrate information from the multivariate data sets generated by the PLFA, we used ordination axes derived from non-metric multidimensional scaling (NMS) (PC-ORD (McCune and Mefford 1999)) as summary variables describing (1) the microbial community and (2) local site characteristics (aboveground vegetation and forest floor cover and general soils information in each sampling frame). We ordinated soil cores by their PLFA composition based on the relative mole fraction of individual lipids. We chose NMS because it avoids the assumption of linear relationships among variables and it uses rank distances, minimizing error produced by the "zero-truncation" problem common to community data (McCune and Grace 2002). All mole percent data were arcsine square-root transformed (McCune and Grace 2002). NMS was run using the "slow and thorough" autopilot option, with 40 runs with real data and 50 random runs.

We used geostatistics (Isaaks and Srivastava 1989; Rossi et al. 1992) to evaluate spatial dependence of all variables (Question 2). We used semi-variograms (Rossi et al. 1992; Schlesinger et al. 1996) to calculate the average variance among samples taken at increasing distances, i.e., the *lag* interval. If the semi-variogram does not change with increasing distance, the data are randomly distributed in space. If, however, the data are spatially patterned, the semi-variogram will exhibit autocorrelation at smaller lag distances and then reach an asymptote where semi-variance is relatively constant. The scale over which patterning is present is quantified by the semi-variogram *range*. We compared semi-variogram ranges determined for ecosystem rates with those

determined for plant/forest floor cover, soil characteristics, and microbial community composition.

In addition to comparing the spatial patterning of variables, we also assessed how correlations between net N mineralization and the independent variables differed with increasing spatial scale. We calculated average values ($n = 9$) of contiguous samples at increasing spatial scales (2×2 m, 2×4 m, and 4×6 m) and compared Pearson correlation coefficients with net N mineralization at each scale.

To determine the potential causes of variation in soil N dynamics (Question 3), we used stepwise multiple linear regression using backward selection. Models were run with soil, cover, and microbial characteristics as independent variables and N and C mineralization rates as response variables. Prior to running the stepwise procedure, Pearson correlation coefficients among all variables were calculated to assess multicollinearity. The variables selected by a stepwise procedure as the best predictors of N and C mineralization rates were combined in a linear model. The residuals were examined and indicated no obvious violation of the model assumptions.

Results

How variable are within-stand soil mineralization rates after fire?

Carbon and N mineralization rates were extremely variable among sampling locations (Table 1). The range of measured *in situ* and laboratory net N mineralization rates was large (-5 to $305 \text{ mg-N kg}^{-1} \text{ yr}^{-1}$, and -243 to $400 \text{ mg-N kg}^{-1} \text{ yr}^{-1}$, respectively). Coefficients of variation (CV) were lowest for C mineralization, intermediate for *in situ* N mineralization (ranging from 102 to 171%), and highest for laboratory nitrification and N mineralization (Table 1).

CV for local site characteristics ranged from 15% (pH) to 780% (% forbs) (Table 1). Most local soil characteristics (e.g., pH, % soil moisture, %N, and %C) had CVs $< 100\%$. CV were generally $> 100\%$ for aboveground vegetation and forest floor cover. Coefficients of variation for microbial guilds ranged from 42% for branched lipids to 148% for cyclopropyl lipids (Table 1). In general, the most common lipids were least variable.

The NMS ordination of microbial community composition resulted in 2 axes (confirmed by examination of the scree plots), explaining 94% of the variance (Figure 2a). Most of the variance was explained by 'microbial' axis 1 (81%); 'microbial' axis 2 explained 13%. 'Microbial' axis 1 was defined by a strong negative correlation with saprotrophic fungal biomarkers (18:2 ω 6, 18:1 ω 9) and the protozoa biomarker (18:3 ω 6). 'Microbial' axis 2 was defined by a strong negative correlation with the AMF biomarker (16:1 ω 5). Both axes were positively correlated with cyclopropyl and monounsaturated bacterial

Table 1. Variation (mean, standard error (SE), and coefficient of variation (CV)) of nitrogen and carbon mineralization rates, local site characteristics, and microbial guilds ($n = 81$).

| | Mean | ± 1 SE | CV (%) |
|---|------|------------|--------|
| <i>N and C mineralization rates</i> | | | |
| Net N mineralization (mg-N kg ⁻¹ yr ⁻¹) | 62 | 7 | 102 |
| Net ammonification | 39 | 5 | 104 |
| Net nitrification | 23 | 4 | 171 |
| Laboratory N mineralization | 2 | 27 | >6000% |
| Laboratory nitrification | 55 | 41 | 369 |
| Laboratory C mineralization (mg g ⁻¹ d ⁻¹) | 0.02 | 0.003 | 79 |
| <i>Local site characteristics</i> | | | |
| Organic matter (%) | 18.5 | – | – |
| Extractable organic C (mg l ⁻¹) | 18.3 | 0.8 | – |
| Ca (kg ha ⁻¹) | 5671 | – | – |
| Mg (kg ha ⁻¹) | 628 | – | – |
| P (kg ha ⁻¹) | 102 | – | – |
| Total N (%) | 0.8 | 0.1 | 63 |
| Total C (%) | 23.5 | 1.8 | 66 |
| pH | 5.1 | 0.1 | 15 |
| Gravimetric soil moisture (%) | 206 | 0.2 | 74 |
| Total understory cover (%) ^a | 9.7 | 1.4 | 134 |
| Forb cover (%) | 0.7 | 0.6 | 780 |
| Graminoid cover (%) | 4.8 | 0.7 | 142 |
| Shrub cover (%) | 4.1 | 1.0 | 210 |
| Moss + litter cover (%) | 73.6 | 2.5 | 30 |
| Rock cover (%) | 0 | – | – |
| CWD cover (%) | 6.8 | 1.1 | 146 |
| Mineral soil cover (%) | 4.8 | 1.6 | 299 |
| Ash cover (%) | 1.8 | 0.9 | 450 |
| Depth of organic layer (cm) | 12.1 | 0.7 | 52 |
| <i>Microbial guild, relative mole %</i> | | | |
| Saturated | 23.5 | 1.3 | 49 |
| Alcohol | 0.8 | 0.1 | 111 |
| Branched (Gm+ bacteria) | 11.0 | 0.5 | 43 |
| Hydroxy (Gm– bacteria) | 5.1 | 0.4 | 70 |
| Cyclopropyl (Gm– bacteria) | 3.3 | 0.5 | 148 |
| Monounsaturated (Gm– bacteria) | 29.2 | 1.4 | 45 |
| Saprotrophic fungi | 16.7 | 1.1 | 59 |
| AMF | 1.4 | 0.2 | 144 |
| Unknown | 9.1 | 1.2 | 117 |

Guilds were: Gm+ bacteria (branched), Gm– bacteria (hydroxy, cyclopropyl, monounsaturated), saturated, alcohol, saprotrophic fungi, AMF, or unknown.

^a%Forbs + %Gram + %Shrub + %Black spruce + %Aspen + %Peltigera.

biomarkers and several unresolved lipids. The axes appeared to define gradients of fungi to bacteria.

The NMS ordination of local site characteristics explained 97% of the variance (Figure 2b). Most of the variance was explained by ‘site’ axis 1 (65%); ‘site’ axis 2 explained 32%. The axes were defined by a strong positive correlation with variables representing low fire severity (e.g., depth of the

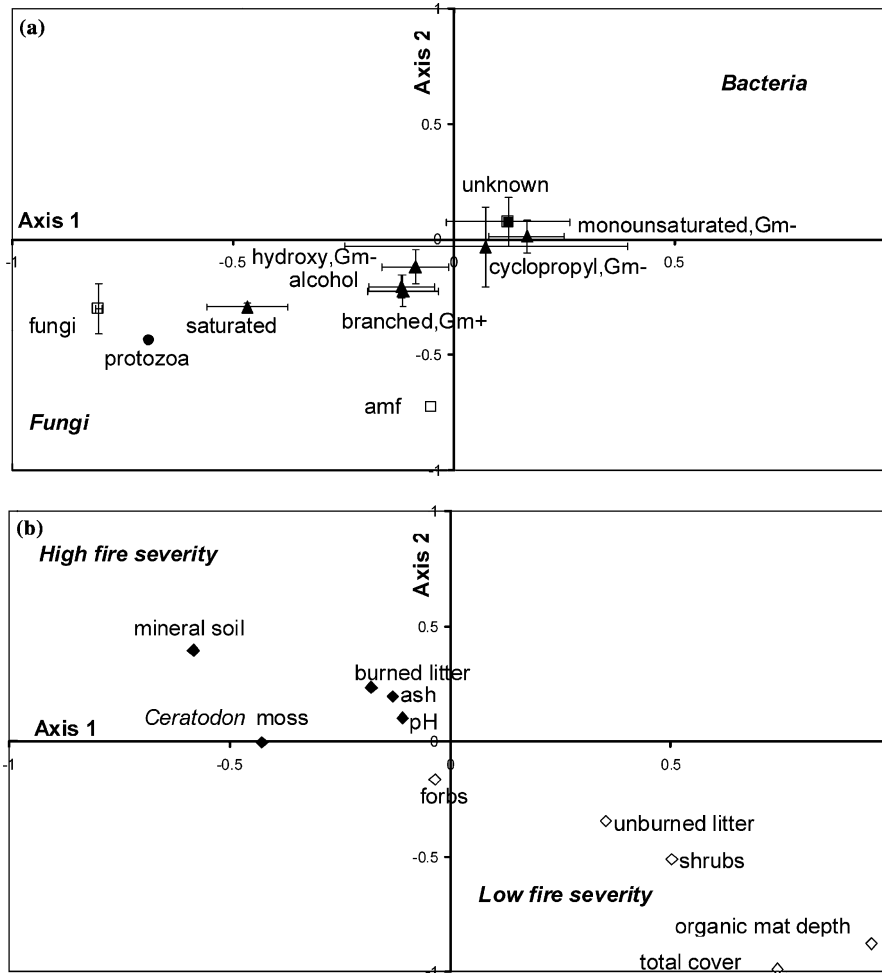


Figure 2. (a) Correlation of microbial functional guilds to NMS ordination axes of microbial lipid composition. Points represent mean correlation (± 1 standard error) of lipids within that guild. Guild names are in Table 1. (b) Correlation of variables indicating high (filled diamonds) or low (open diamonds) fire severity to NMS ordination axes of local site characteristics (i.e., aboveground cover and general soils characteristics).

organic layer, total cover, % shrubs) and a negative correlation with variables representing high fire severity (e.g., % mineral soil, % ash, % burned litter). Thus, they can be considered as integrated variables representing fire severity. Nitrogen and C mineralization rates were not correlated with the axes from either of the two ordinations, suggesting that microbial community

composition and fire severity were not the primary controls over N and C mineralization at the level of the individual core.

What is the spatial structure of C and N mineralization rates?

The spatial structure of *in situ* net N mineralization was similar to that of several microbial guilds and total microbial lipid abundance (Figure 3). Based on similar spatial ranges, it appeared that mineralization rates were closely linked to microbial community composition (Figure 4). Specifically, semi-variogram ranges were 5.1 m for NH_4^+ mineralization, 6.3 m for NO_3^- mineralization, and 8.3 m for total N mineralization, while microbial guilds ranged from 3.4 to 7.2 m. Similarly, N pool size (soil %N) and 'microbial' axis 2 had similar spatial ranges (12 m vs. 10 m, respectively). The semi-variogram of C mineralization rates was not significant suggesting no spatial structure in C mineralization rates at the scale of our observed measurements. However, C pool sizes (extractable organic C and %C) and local site characteristics had similar spatial ranges. These ranges did not overlap with distances observed for N mineralization rates and microbial variables (with the exception of branched lipids) and were observed at larger (16.0 m) and smaller (2.7 m) scales than the community and mineralization variables (Figure 4).

When contiguous samples were aggregated into groups of differing spatial extent (2×2 m, 2×4 m, or 4×6 m), the variables showing the strongest

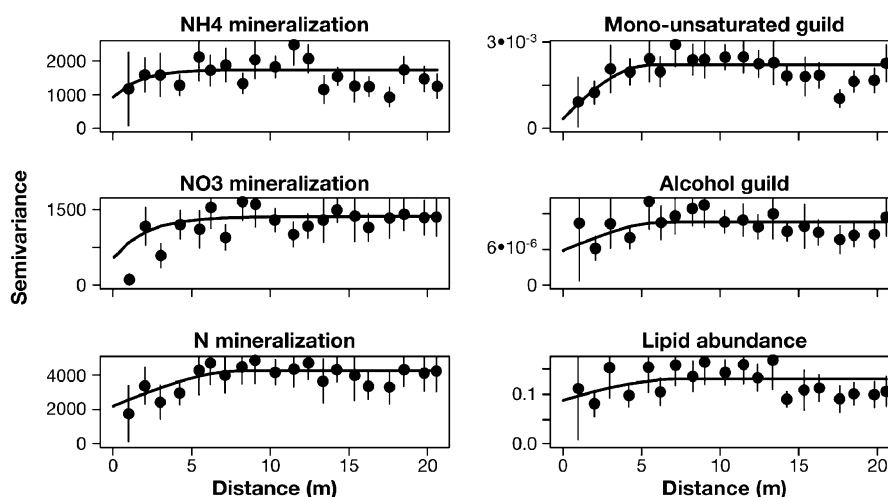


Figure 3. Semi-variograms of nitrogen mineralization rates and microbial variables fit to exponential or spherical models (best model selected). Error bars = 95% CI.

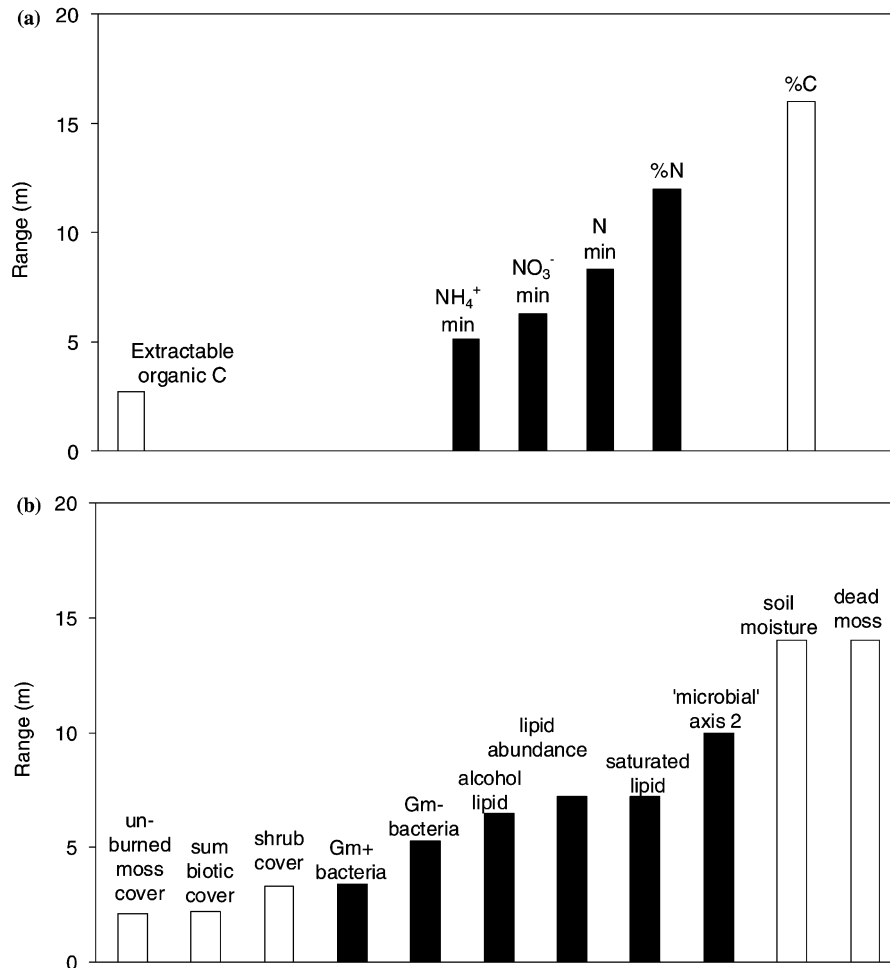


Figure 4. Semi-variogram ranges for (a) soil C and N rates or pools and (b) microbial variables or local site characteristics. Only significant semi-variogram models are shown. Gram positive (Gm+) bacteria were branched lipids and Gram negative (Gm-) bacteria were monounsaturated lipids.

correlation to *in situ* N mineralization differed (Table 2). In general, ammonification and *in situ* N mineralization were related to microbial variables at the larger spatial extent (4×6 m), consistent with the ranges determined from the semi-variograms models. *In situ* N mineralization was also related to soil moisture and soil %C at the 4×6 m extent, similar to the calculated semi-variogram ranges of soil moisture and soil %C (>10 m). At smaller scales (2×2 m), *in situ* N mineralization was related to % mineral soil, % CWD, and 'site' axis 1 (positive correlation with low fire severity). This is also consistent with semi-variogram ranges showing that mineralization was related to local

Table 2. Significant ($*p < 0.10$, $**p < 0.05$) Pearson correlation coefficients (r) between net NH_4^+ mineralization and independent variables ($n = 9$) at multiple spatial extents (only significant variables shown). 'Site' axis 1 and 2 are the ordination scores from the non-metric scaling ordination of local site characteristics (see Figure 2b).

| | Spatial extent | | |
|--------------------------------------|------------------|------------------|------------------|
| | 2 m \times 2 m | 2 m \times 4 m | 4 m \times 6 m |
| Mineral soil | -0.57* | | |
| CWD | -0.57* | | |
| 'Site' axis 1 | +0.65* | | |
| Soil moisture | | -0.58* | -0.62* |
| pH | | -0.69* | -0.68* |
| %C | | | +0.58* |
| % Forbs | | | -0.71** |
| % Equisitum | | | +0.81** |
| Sum total cover | | | +0.69* |
| 'Site' axis 2 | | | -0.64* |
| AMF guild | | | +0.62* |
| Cyclopropyl guild (Gm- bacteria) | | | +0.70** |
| Monounsaturated guild (Gm- bacteria) | | | +0.58* |

site characteristics (Figure 4). Thus, *in situ* net N mineralization rates appeared to be governed by different factors at different spatial extents.

What factors govern local, within-stand variation in C and N mineralization rates?

The axis scores from the NMS ordinations, as well as the individual variables, were used to predict N and C mineralization rates using stepwise multiple linear regression at the level of the individual core ($n = 81$ for field data, $n = 27$ for laboratory data). However, despite the inclusion of microbial and local site data, soil moisture (% gravimetric) was the variable that best explained *in situ* N mineralization (Table 3). Cores with higher soil moisture had high rates of nitrification (partial $r^2 = 14\%$), ammonification (partial $r^2 = 38\%$), and total N mineralization (partial $r^2 = 46\%$). Soil moisture also explained 68% of the variance in laboratory C mineralization, even though all samples were incubated at the same soil moisture (field capacity). However, soil moisture did not significantly explain variation in laboratory nitrification or N mineralization. Laboratory nitrification was positively correlated with variables representing higher fire severity (% cover of mineral soil), and negatively correlated with variables representing lower fire severity (forbs, unburned moss, unburned litter). Interestingly, moss type was included in the final model for both laboratory and *in situ* nitrification.

Because soil moisture co-varied with local site characteristics, it is difficult to determine whether N and C mineralization rates reflect soil moisture directly,

Table 3. Results from stepwise multiple regression to predict *in situ* and laboratory mineralization rates.

| | DF | r^2 , adj r^2 | F | p |
|--|----|-------------------|-------|--------|
| <i>In situ nitrification</i> | | | | |
| Soil moisture | 1 | 0.14 | 15.4 | <0.001 |
| Moss type | 5 | 0.11 | 2.5 | <0.05 |
| CWD position | 3 | 0.08 | 2.8 | <0.05 |
| Saturated guild | 1 | 0.04 | 5.0 | <0.05 |
| Final model | 70 | 0.37,0.28 | 4.1 | <0.001 |
| <i>In situ ammonification</i> | | | | |
| Soil moisture | 1 | 0.38 | 56.5 | <0.001 |
| pH | 1 | 0.10 | 15.38 | <0.001 |
| Final model | 78 | 0.48,0.47 | 36.0 | <0.001 |
| <i>In situ N ($NO_3^- + NH_4^+$) mineralization</i> | | | | |
| Soil moisture | 1 | 0.46 | 67.2 | <0.001 |
| Final model | 79 | 0.46,0.45 | 67.2 | <0.001 |
| <i>Laboratory nitrification</i> | | | | |
| Unburned litter | 1 | 0.06 | 5.2 | <0.05 |
| Mineral soil | 1 | 0.23 | 21.6 | <0.001 |
| Dead, unburned moss | 1 | 0.18 | 16.7 | <0.01 |
| Forbs | 1 | 0.08 | 7.2 | <0.05 |
| Moss type | 4 | 0.31 | 7.3 | <0.01 |
| Final model | 14 | 0.85,0.77 | 10.0 | <0.001 |
| <i>Laboratory C mineralization</i> | | | | |
| Soil moisture | 1 | 0.68 | 50.0 | <0.001 |
| Final model | 23 | 0.68,0.67 | 50.0 | <0.001 |
| <i>Laboratory N mineralization – no significant model</i> | | | | |

Adjusted r^2 are only presented for the final model.

or are indirectly related to post-fire vegetation and soil conditions. For example, *in situ* net N mineralization and laboratory C mineralization were positively correlated with vegetation and forest floor cover variables that reflect low fire severity and negatively correlated with cover variables that reflect high fire severity (Table 4). In addition, the %C and %N of the soil organic matter, an index of substrate availability to microbes, was positively correlated with mineralization rates. However, after normalizing by pool size (soil %C), specific laboratory C mineralization was positively correlated with measures of high fire severity (Table 4). Although we do not have more quantitative measures of substrate quality (e.g., C:N or lignin:N ratios), this relationship suggests that substrate quality (more than pool size) may be an important factor for predicting C mineralization in individual soil cores.

In comparison to *in situ* N mineralization, laboratory N mineralization showed the opposite relationship to cover variables (Table 4). Laboratory N mineralization was positively correlated with cover variables that reflect high fire severity and negatively correlated with cover variables that reflect low fire severity. The direction of these correlations did not change when laboratory N mineralization was normalized by pool size.

Table 4. Within-stand correlation of soil moisture, 'microbial' axis 1 ordination scores (see Figure 2a for correlation with individual guilds) and C or N mineralization rates with local site characteristics ($n = 81$).

| Local site characteristics | Soil moisture | 'Microbial' axis 1 | Mineralization rates | | | | |
|----------------------------|---------------|--------------------|----------------------|----------|------------------|----------|------------------|
| | | | Net N | Lab N | Lab N (Specific) | Lab C | Lab C (Specific) |
| <i>High fire severity</i> | | | | | | | |
| pH | -0.67*** | -0.21 | -0.56*** | +0.40** | +0.58*** | -0.78*** | +0.90*** |
| <i>Ceratodon</i> moss | -0.51*** | -0.08 | -0.49*** | +0.65*** | +0.91*** | -0.58*** | +0.56*** |
| % burned litter | -0.59*** | +0.51*** | -0.61*** | +0.48** | +0.34 | -0.57*** | +0.33 |
| % mineral soil | -0.48*** | -0.14 | -0.43*** | +0.65*** | +0.93*** | -0.53*** | +0.63*** |
| <i>Low fire severity</i> | | | | | | | |
| Unburned litter | +0.59*** | -0.69*** | +0.58*** | -0.32 | -0.14 | +0.52*** | -0.40* |
| Organic matter depth | +0.43** | -0.04 | +0.43*** | -0.48*** | -0.58*** | +0.54*** | -0.34* |
| % forbs | +0.60*** | -0.92*** | +0.58*** | -0.39** | -0.12 | +0.52*** | -0.31 |
| % soil N | +0.98*** | -0.35 | +0.94*** | -0.20 | -0.31 | +0.98*** | -0.78*** |
| % soil C | +0.95*** | -0.22 | +0.90*** | -0.25 | -0.37* | +0.99*** | -0.84*** |

* $p < 0.01$, ** $p < 0.001$, *** $p < 0.0001$.

Discussion

Ecosystem ecologists generally recognize that different spatial patterns emerge at different scales of investigation (Wiens 1989) yet rarely are studies implemented that specifically define the scale of the patterns controlling ecological processes (e.g., ecological neighborhoods, sensu Addicott et al. (1987)). In this paper, we show that spatial variation of soil N transformations within a 0.25-ha plot results from controlling factors that operate at several different spatial scales. At relatively broad scales (> 8 m), net N mineralization was related to microbial community composition and abundance. At finer spatial scales (2–4 m), local, post-fire site characteristics appeared to govern patterns of net N mineralization. At the level of individual cores, net N mineralization was related primarily to variation in soil moisture.

Variation in microbial community composition at broad scales (8 m) may reflect the topographical variation of our site. Subtle topographical variation is a common feature of floodplain black spruce forests, affecting drainage patterns and soil moisture. Soil water content has a direct impact on soil organisms by changing water film thickness and modifying predation rates by protozoa. Topographical variation may also affect total vegetation composition and abundance (positive correlation with total cover, Table 2), which may affect litter quality and quantity. Others have shown that variation in substrates affects microbial community composition (e.g., Bending and Turner 1999; Grayston et al. 2001) and microbially mediated soil transformations in boreal forests (Van Cleve et al. 1993; Hobbie 2000; Hobbie et al. 2000). Another factor that is likely to vary topographically through our site is temperature of the organic mat and mineral soil, which can modify mineralization

rates (Van Cleve et al. 1993; Viereck et al. 1993), although we did not measure variation in soil or surface temperature. Thus, microbial community composition and activity is likely vary in response to subtle changes in topography at this relatively broad scale.

Specific microbial functional groups may be more or less sensitive to broad-scale variation in plant/forest floor cover and soil characteristics (%moisture, pH,%C,%N). Due to their presence in surface litter, fungal hyphae are sensitive to high surface temperatures and are expected to fare worse in severe fires relative to bacteria (Dahlberg 2002). Among individual cores, we found that fungi were more abundant where cover variables indicated less severe fire. However, it is difficult to determine whether the relative dominance of fungi in low severity areas was caused by their loss during the fire or whether they were responding to more favorable cover and soil conditions in the low severity areas. The fact that saprotrophic and arbuscular mycorrhizal fungi were located on different ordination axes is not surprising since fungal communities can be expected to respond differently to the same fire event. For example, ectomycorrhizal fungi have been shown to be negatively affected by fire for 15 years in Alaska, whereas AMF were briefly affected (Treseder et al. 2004), perhaps due to associations with grasses and herbs that recover quickly after fire (Merila et al. 2002).

At the 2–4 m scale, mineralization rates reflected spatial variation in local site characteristics rather than microbial community composition or soil moisture. While broad scale variation in topography may modify total plant cover, local variation in cover and soil C may result from patchiness in fire severity and/or changes to post-fire vegetation composition (positive correlation with ‘site’ axis 1, Table 2). The lack of a strong microbial signal at the 2–4 m scale may be due to homogeneity of microbial substrates around plant or tree rhizospheres, which have been correlated with microbial communities (Pennanen et al. 1999). Liski (1995) found that soil organic C was greater within 1–3 m from trees in a boreal forest stand, which agrees well with the semi-variogram ranges we detected for soil extractable organic C and plant cover variables. In addition, burn severity tends to be greater close to tree trunks, so patterns in mineralization at this scale may reflect legacy effects of prefire soil organic matter and tree locations.

At the level of the individual core, soil moisture was the best predictor of *in situ* net N mineralization rates and laboratory C mineralization. Soil moisture was also highly correlated with soil C and N pool sizes, so mineralization rates may simply reflect C and N availability to microorganisms. To test this idea, we normalized rates by pool size, and showed that laboratory C mineralization was positively correlated with local site characteristics reflecting high fire severity. An increase in C mineralization in burned areas is surprising since fire is generally known to increase the resistance of C compounds (e.g., charcoal, waxes). Instead this result suggests that C quality is somehow increased after fire. One possible explanation for an increase in C quality in burned areas may simply be an artifact of our sampling. Fire results in a reduction of the organic

matter profile and we may have sampled deeper in the profile where C bio-availability may have been greater. Changes in the vertical distribution of nutrients and soil biota after fire has been shown previously to impact C cycling (Harden et al. 2004). On the other hand, fire results in ash deposition and changes in the quality of organic matter (Raison 1979), which may have stimulated C and N mineralization rates. Higher laboratory N mineralization in high fire severity areas (Table 4) would occur if substrate quality was higher, despite lower total C substrates. Interestingly, severely burned areas were dominated by Gm⁻ bacteria, which utilize labile C sources and may have shorter turnover times compared to fungi and Gm⁺ bacteria (Marumoto et al. 1982), suggesting that the microbial community composition may be important.

The final regression model for laboratory nitrification reflected the potential importance of local site characteristics. The moss species that we recorded were *Ceratodon* spp., *Pleurozium shreberi*, *Politrichum* spp., *Alocomnium*, and *Dicranum* spp. Both *Ceratodon* and *Politrichum* establish on mineral soil and thus represent high fire severity areas, while the other three moss types likely represent low fire severity areas because they generally require decades to establish following fire. Although we did not directly test for this, it is possible that specific moss species influence soil N transformations (Turetsky 2003). Moreover, the selection of moss type in the final regression model likely represents variation in site characteristics reflecting fire severity.

Correctly understanding the factors that control soil N transformations also requires that soil N transformations be studied at appropriate temporal scales. For example, the factors governing N mineralization at our site operate on dissimilar timescales. Within-stand fire patchiness may result from weather conditions at the time of fire, whereas broad-scale patterns in plant community composition or topography may result from decadal or longer (i.e., geomorphic) timescales. Moreover, the timescales over which microbial communities respond to fire is unknown. Thus, predicting soil N transformations would err if a single controlling factor was assumed to be important across different spatial and temporal scales.

In this paper, we combined geostatistics (Rossi et al. 1992; Bell et al. 1993) with information on N mineralization and microbial community composition. By informing future sampling designs and statistical analyses, these methods could produce new insights into the complex mechanisms underpinning spatial heterogeneity of soil processes and patterns (Bell et al. 1993; Bolstad et al. 1998; Legendre et al. 2002).

We conclude that C and N mineralization rates in this burned black spruce stand were related to different variables depending on the scale of analysis, suggesting the importance of attending to multiple scales of variation among key drivers of C and N transformations. Based on the results from this study, soil moisture could be used to predict field rates of mineralization at the core level, but post-fire plant/forest floor cover, soil C and N, and/or microbial community composition were better predictors at broader scales. Although soil moisture may have a mediating effect on substrate availability and microbial

community composition (through modification of plant cover and via differences in drainage patterns), cover characteristics and microbial community composition were more proximate factors explaining net N mineralization at scales >2 m. Thus, assuming a single factor controls N mineralization rates might generate misleading projections if patterns and processes operating at different scales are ignored. Quantification of within-stand spatial heterogeneity may elucidate ecological mechanisms that might otherwise be obscured, leading to insights about the complex relationships between soil microbial communities and ecosystem processes.

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References

- Addicot J.F., Aho J.M., Antolin M.F., Padilla D.K., Richardson J.S. and Soluk D.A. 1987. Ecological neighborhoods: scaling environmental problems. *Oikos* 49: 340–346.
- Arao T. 1999. In situ detection of changes in soil bacterial and fungal activities by measuring ^{13}C incorporation into soil phospholipid fatty acids from ^{13}C acetate. *Soil Biol. Biochem.* 31: 1015–1020.
- Baath E. and Anderson T.-H. 2003. Comparison of soil fungal/bacterial ratios in a pH gradient using physiological and PLFA-based techniques. *Soil Biol. Biochem.* 35: 955–963.
- Baath E., Frostegard A., Pennanen T. and Fritze H. 1995. Microbial community structure and pH response in relation to soil organic matter quality in wood-ash fertilized, clear-cut or burned coniferous forest soils. *Soil Biol. Biochem.* 27: 229–240.
- Balser T., Kinzig A. and Firestone M.K. 2002. Linking soil microbial communities and ecosystem functioning. In: Kinzig A., Pacala S. and Tilman D. (eds), *The Functional Consequences of Biodiversity: Empirical Progress and Theoretical Extensions*. Princeton University Press, pp. 265–356.
- Balser T.C. and Firestone M.K. 2005. Linking microbial community composition and soil processes in a California annual grassland and mixed-conifer forest. *Biogeochemistry* 73: 395–415.
- Beedlow P.A., Tingley D.T., Phillips D.L., Hogsett W.E. and Olszyk D.M. 2004. Rising atmospheric CO_2 and carbon sequestration in forests. *Front. Ecol. Environ.* 2: 315–322.
- Bell G., Lechowicz M.J., Appenzeller A., Chandler M., DeBlois E., Jackson L.E., Mackenzie B., Preziosi R., Schallenberg M. and Tinker N. 1993. The spatial structure of the physical environment. *Oecologia* 96: 114–121.
- Bending G.D. and Turner M.K. 1999. Interaction of biochemical quality and particle size of crop residues and its effects on the microbial biomass and nitrogen dynamics following incorporation into soil. *Biol. Fert Soils* 29: 319–327.
- Beneditti-Cecchi L. 2003. The importance of the variance around the mean effect size of ecological processes. *Ecology* 84: 2335–2346.

- Binkley D. and Matson P.A. 1983. Ion exchange resin bag method for assessing forest soil nitrogen availability. *Soil Sci. Soc. Am. J.* 47: 1050–1052.
- Bolstad P., Swank W.T. and Vose J. 1998. Predicting southern Appalachian overstory vegetation with digital terrain data. *Lands Ecol.* 13: 271–283.
- Chen J. and Stark J. 2000. Plant species effects and carbon and nitrogen cycling in a sagebrush-crested wheatgrass soil. *Soil Biol. Biochem.* 32: 47–57.
- Christensen S., Simkins S. and Tiedje J.M. 1990. Spatial variation in denitrification: Dependency of activity centers on the soil environment. *Soil Sci. Soc. Am. J.* 54: 1608–1613.
- Clayton M.K. and Hudelson B.D. 1995. Confidence intervals for autocorrelations based on cyclic samples. *J. Am. Stat. Assoc.* 90: 753–757.
- Dahlberg A. 2002. Effects of fire on ectomycorrhizal fungi in Fennoscandian Boreal forests. *Silva Fennica* 36: 69–80.
- Dyrness C.T., Van Cleve K. and Levison J.D. 1989. The effect of wildfire on soil chemistry in four forest types in interior Alaska. *Can. J. For. Res.* 19: 1389–1396.
- Fan W., Randolph J.C. and Ehman J.L. 1998. Regional estimation of nitrogen mineralization in forest ecosystems using geographic information systems. *Ecol. Appl.* 8: 734–747.
- Fraterrigo J.M., Turner M.G., Pearson S.M. and Dixon P. 2005. Effects of past land use on spatial heterogeneity of soil nutrients in southern Appalachian forests. *Ecol. Monogr.* 75: 215–230.
- Frostegard A. and Baath E. 1996. The use of phospholipid fatty acid analysis to estimate bacterial and fungal biomass in soil. *Biol. Fert Soils* 22: 59–65.
- Grayston S.J., Griffith G.S., Mawdsley J.L., Campell C.D. and Bardgett R.D. 2001. Accounting for variability in soil microbial communities of temperate upland grassland ecosystems. *Soil Biol. Biochem.* 33: 533–551.
- Harden J.W., Neff J.C., Sandberg D.V., Turetsky M.R., Ottmar R., Gleixner G., Fries T.L. and Manies K.L. 2004. Chemistry of burning the forest floor during the FROSTFIRE experimental burn, interior Alaska, 1999. *Global Biogeochem. Cycles* 18: GB3014, doi:3010.1029/2003GB002194.
- Hart S.C., Binkley D. and Perry D.A. 1997. Influence of red alder on soil nitrogen transformations in two conifer forests of contrasting productivity. *Soil Biol. Biochem.* 29: 1111–1123.
- Hinzman L.D., Viereck L.A., Adams P.C., Romanovsky V.E. and Yoshikawa K. (in press). Climatic and permafrost dynamics of the Alaskan boreal forest. In: Chapin F.S. III, Oswood M., Van Cleve K., Viereck L.A. and Verbyla D.L. (eds), *Alaska's Changing Boreal Forest*. Oxford University Press, Oxford. (in press).
- Hobbie S.E. 2000. Interactions between litter lignin and soil nitrogen availability during leaf litter decomposition in a Hawaiian montane forest. *Ecosystems* 3: 484–494.
- Hobbie S.E., Schimel J.P., Trumbore S.E. and Randerson J.R. 2000. Controls over carbon storage and turnover in high-latitude soils. *Global Change Biol.* 6: 196–210.
- Isaaks E.H. and Srivastava R.M. 1989. *An Introduction to Applied Geostatistics*. Oxford University Press, New York, NY.
- Jackson M.L. 1958. *Soil Chemical Analysis*. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.
- Jackson R.B. and Caldwell M.M. 1993. Geostatistical patterns of soil heterogeneity around individual perennial plants. *J. Ecol.* 81: 683–692.
- Kashian D.M., Turner M.G., Romme W.H. and Lorimer C.G. 2005. Variability and convergence in stand structure with forest development on a fire-dominated landscape. *Ecology* 86: 643–654.
- Kasischke E.S., Williams D. and Barry D. 2002. Analysis of the patterns of large fires in the boreal forest region of Alaska. *Int. J. Wildland Fire* 11: 1331–1144.
- Legendre P., Dale M.R.T., Fortin M.-J., Gurevitch J., Hohn M. and Myers D. 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography* 25: 601–615.
- Liski J. 1995. Variation in soil organic carbon and thickness of soil horizons within a boreal forest stand – effects of trees and implications for sampling. *Silva Fennica* 29: 255–266.

- Ludwig J.A., Wiens J.A. and Tongway D.J. 2000. A scaling rule for landscape patches and how it applies to conserving soil resources in savannas. *Ecosystems* 3: 84–97.
- Marumoto T., Anderson J.P.E. and Domsch K.H. 1982. Decomposition of ¹⁴C- and ¹⁵N-labelled microbial cells in soil. *Soil Biol. Biochem.* 14: 461–467.
- McCune B. and Grace J.B. 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach Oregon, USA.
- McCune B. and Mefford M.J. 1999. *PC-ORD Multivariate Analysis of Ecological Data*. Version 4.0. MjM Software Design, Gleneden Beach Oregon, USA.
- Merila P., Strommer R. and Fritze H. 2002. Soil microbial activity and community structure along a primary succession transect on the land-uplift coast in western Finland. *Soil Biol. Biochem.* 34: 1647–1654.
- Myers R.T., Zak D.R., White D.C. and Peacock A.D. 2001. Landscape-level patterns of microbial community composition and substrate use in upland forest ecosystems. *Soil Sci. Soc. Am. J.* 65: 359–367.
- Pennanen T., Liski J., Kitunen V., Uotila J., Westman C.J. and Fritze H. 1999. Structure of the microbial communities in coniferous forest soils in relation to site fertility and stand development stage. *Microb. Ecol.* 38: 168–179.
- Raison R.J. 1979. Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations: a review. *Plant Soil* 51: 73–108.
- Rossi R.E., Mulla D.J., Journel A.G. and Franz E.H. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. *Ecol. Monogr.* 62: 277–314.
- Saetre P. and Baath E. 2000. Spatial variation and patterns of soil microbial community structure in a mixed spruce-birch stand. *Soil Biol. Biochem.* 32: 909–917.
- Schlesinger W.H., Raikes J.A., Hartley A.E. and Cross A.F. 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77: 364–374.
- Schlesinger W.H., Reynolds J.F., Cunningham G.L., Huenneke L.F., Jarrell W.M., Virginia R.A. and Whitford W.G. 1990. Biological feedbacks in global desertification. *Science* 247: 1043–1048.
- Schulte E.E., Peters J.B. and Hodgson P.R. 1987. *Wisconsin Procedures for Soil Testing, Plant Analysis and Feed and Forage Analysis*. Department of Soil Science, University of Wisconsin, Madison, WI.
- Smithwick E.A.H., Turner M.G., Mack M.C. and Chapin F.S. III 2005. Post-fire soil N cycling in northern conifer forests affected by severe, stand-replacing wildfires. *Ecosystems* 8: 163–181.
- Steenwerth K.L., Jackson L.E., Calderon F.J., Stromberg M.R. and Scow K.M. 2003. Soil microbial community composition and land use history in cultivated and grassland ecosystems of coastal California. *Soil Biol. Biochem.* 35: 489–500.
- Tinker D.B., Romme W.H., Hargrove W.W., Gardner R.H. and Turner M.G. 1994. Landscape-scale heterogeneity in lodgepole pine serotiny. *Can. J. For. Res.* 24: 897–903.
- Treseder K., Mack M.C. and Cross A. 2004. Relationships among fires, fungi, and soil dynamics in Alaskan boreal forests. *Ecol. Appl.* 14: 1826–1838.
- Turetsky M.R. 2003. The role of bryophytes in carbon and nitrogen cycling. *Bryologist* 106: 395–409.
- Turner M.G., Romme W.H., Gardner R.H. and Hargrove W.H. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecol. Monogr.* 67: 411–433.
- Van Cleve K. and Oliver L.K. 1982. Growth response of postfire quaking aspen (*Populus tremuloides* Michx.) to N, P, and K fertilization. *Can. J. For. Res.* 13: 160–165.
- Van Cleve K., Yarie J., Erickson R. and Dyrness C.T. 1993. Nitrogen mineralization and nitrification in successional ecosystems on the Tanana River floodplain, interior Alaska. *Can. J. For. Res.* 23: 970–978.
- Vestal J.R. and White D.C. 1989. Lipid analysis in microbial ecology. *Bioscience* 39: 535–541.
- Viereck L.A., Van Cleve K., Adams P.C. and Schlentner R.E. 1993. Climate of the Tanana River floodplain near Fairbanks, Alaska. *Can. J. For. Res.* 23: 899–913.
- Waldrop M.P., Balsler T.C. and Firestone M.K. 2000. Linking microbial community composition to function in a tropical soil. *Soil Biol. Biochem.* 32: 1837–1846.

- Waldrop M.P. and Firestone M.K. 2004. Altered utilization patterns of young and old soil C by microorganisms caused by temperature shifts and N additions. *Biogeochemistry* 67: 235–248.
- White D.C. and Ringelberg D.B. 1998. Signature lipid biomarker analysis. In: Burlage R.S., Atlas R., Stahl D., Geesey G. and Saylor G. (eds), in *Techniques in Microbial Ecology*. Oxford University Press, New York, pp. 255–272.
- Wiens J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3: 385–397.
- Wilkinson S.C., Anderson J.M., Scardelis S.P., Tisiafouli M., Taylor A. and Wolters V. 2002. PLFA profiles of microbial communities in decomposing conifer litters subject to moisture stress. *Soil Biol. Biochem.* 34: 189–200.
- Wilkinson S.G. 1998. Gram negative bacteria. In: Ratledge C. and Wilkinson S.G. (eds), *Microbial Lipids*. Academic Press, London, pp. 299–488.
- Yarie J. 1981. Forest fire cycles and life tables: a case study from interior Alaska. *Can. J. For. Res.* 11: 554–562.
- Yarie J. and Van Cleve K. (in press). Controls on taiga forest production in interior Alaska. In: Chapin F.S. III, Oswald M., Van Cleve K., Viereck L. and Verbyla D. (eds), *Alaska's Changing Boreal Forest*. Oxford University Press, Oxford.
- Zelles L., Bai Q.Y., Beck T. and Beese F. 1992. Signature fatty acids in phospholipids and lipopolysaccharides as indicators of microbial biomass and community structure in agricultural soils. *Soil Biol. Biochem.* 24: 317–323.