

# Variation in Aboveground Cover Influences Soil Nitrogen Availability at Fine Spatial Scales Following Severe Fire in Subalpine Conifer Forests

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## ABSTRACT

Following fire, fine-scale variation in early successional vegetation and soil nutrients may influence development of ecosystem structure and function. We studied conifer forests burned by stand-replacing wildfire in Greater Yellowstone (Wyoming, USA) to address two questions: (1) How do the variability and spatial structure of aboveground cover and soil nitrogen availability change during the first 4 years following stand-replacing fire? (2) At fine scales (2–20 m), are postfire soil inorganic N pools and fluxes related to aboveground cover? Aboveground cover, soil N pools, and annual net N transformations were measured from 2001 to 2004 using a spatially explicit sampling design in four 0.25-ha plots that burned during summer 2000. Within-stand variability

(coefficient of variation) in postfire live vegetative cover declined with time since fire, whereas variability in bare mineral soil, charred litter and fresh litter was greatest 2–3 years postfire. The soil nitrate pool was more variable than the soil ammonium pool, but annual net nitrification was less variable than annual net N mineralization. Spatial structure (quantified by semivariograms) was observed in some aboveground cover variables (for example, graminoids and fresh litter), but there was little spatial structure in soil N variables and no obvious congruence in spatial scales of autocorrelation for soil N and aboveground cover. Significant Spearman correlations (at the sample point) indicated that aboveground cover and soil N were coupled following severe fire, and the dominant influence was from aboveground cover to soil N, rather than from soil N to vegetation. Initial patterns of fire severity and re-vegetation contributed to fine-scale heterogeneity in soil N availability for at least 4 years after severe fire.

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## INTRODUCTION

Natural disturbances are important sources of heterogeneity in ecological systems, and the effects of disturbances on ecosystem dynamics (for example, Vitousek and Reiners 1975; Vitousek and Melillo 1979; Chapin and others 2002) and landscape patterns have been widely studied (for example, Foster and others 1998; Turner 2010). Recent studies suggest that disturbance also affects the magnitude and spatial structure of variability in ecosystems at finer scales (Fraterrigo and others 2005; Kashian and others 2005; Gallardo and others 2006; Gundale and others 2006). However, relatively few studies have examined the structure of variability within disturbed patches and how it changes through time (for example, Gross and others 1995; Lane and BassiriRad 2005). Understanding such variability could provide new insights about the interactions between pattern and process (Fraterrigo and Rusak 2008), and the dynamic patchiness of post-disturbance vegetation offers an opportunity to elucidate the role of spatial heterogeneity in ecosystem function (Turner and Chapin 2005). Understanding heterogeneity—and when it matters—can determine the nature of coupling between vegetation and soil processes (that is, whether vegetation patterns develop in response to spatial patterns of soil nutrients, or the vegetation patches shape the soil nutrient patterns), thereby enhancing understanding of fundamental ecosystem processes.

Soil nutrient pools and transformations are notoriously heterogeneous in terrestrial ecosystems, and the scale(s) of variability in such patterns are not well known. At broad spatial scales, variation in nutrient cycling is associated with differences in community structure, topography, soils, and successional stage (for example, Zak and others 1989; Fan and others 1998; Pastor and others 1998). However, within a site, nutrient pools and transformations can vary tremendously over small distances (for example, Robertson and others 1988; Schimel and Bennett 2004), and the spatial variability can change through time (Gross and others 1995; Cain and others 1999). Such fine-scale heterogeneity in soil nutrients can have important implications for plants at the individual, population, and community level (Hutchings and others 2003; Lane and BassiriRad 2005; Gallardo and others 2006; Gundale and others 2006). However, plants also influence soil nutrient pools and transformations through nutrient uptake, litter inputs, root exudates, and modification of microclimate (for example, Hobbie 1992; Prescott 2002; Ayres

and others 2009). Characterizing fine-scale variation in vegetation and soil nutrients after disturbance could enhance understanding of how ecosystem structure and function develop during early succession and help elucidate the nature of the vegetation–soil interaction. In this study, we quantified spatial variation in aboveground cover and soil nitrogen following stand-replacing wildfire to determine whether and how vegetation and nitrogen cycling were coupled during early postfire succession.

Stand-replacing fire is a key component of the natural disturbance regime in conifer forests of western North America (Turner and Romme 1994; Schoennagel and others 2004). The frequency of large fires has increased in recent decades in association with climate warming (Westerling and others 2006), and understanding patterns of postfire vegetation and nutrient availability is a research priority for ecosystem scientists and forest managers (Smithwick and others 2005a; Gundale and others 2006). Of particular interest is how fire affects the availability and spatial distribution of nitrogen (N) because N often limits production of western conifer forests (Fahey and others 1985), and N dynamics following natural stand-replacing fire are not well known (Smithwick and others 2005a; Koyama and others 2010). Soil inorganic N concentrations typically increase postfire following pyrolysis of organic matter and ash deposition (Wan and others 2001; Smithwick and others 2005a). Ammonium is a direct product of both combustion and the mineralization of organic matter, and ammonium can be held by the soil because it is adsorbed onto negatively charged surfaces of minerals and organic compounds (Certini 2005). Ammonium may subsequently be nitrified, and a pulse of ammonium that lasts up to a year may be followed by increased soil nitrate (Wan and others 2001; Smithwick and others 2005a). Studies of post-fire N mineralization rates have yielded conflicting results, with both increases and decreases reported (Wan and others 2001). Fire also alters the soil microbial community (for example, through selective heat-induced mortality), and such changes may be associated with local variation in N transformation rates (for example, Bååth and others 1995; Prieto-Fernandez and others 1998; Hart and others 2005). However, few studies have examined fine-scale spatial variation in nutrient transformations following severe fire (but see Smithwick and others 2005b).

Prior studies suggest that spatial patterns of postfire vegetation in Greater Yellowstone may initially be decoupled from the spatial patterns of soil nutrients at some scales. Following the 1988 fires in Yellowstone National Park, the rapid recovery of understory vegetation was driven by the pre-fire plant community and by local fire severity. The 1988 fires generally did not burn deeply into the soil, and many roots and rhizomes survived (Turner and others 1999). Thus, many perennials present before the fires resprouted and produced propagules that colonized areas in the burned forest within a few years (Turner and others 1997, 1999); this recovering vegetation was spatially patchy. Similarly, the large variation in postfire density of lodgepole pine (*Pinus contorta* var. *latifolia*) resulted from differences in the prevalence of pre-fire trees bearing serotinous cones and local fire severity (for example, Turner and others 1997, 2003), and neither pine seedling density nor productivity appeared related to variation in soils (Turner and others 2004). Plot-level studies of net N mineralization and plant productivity (Turner and others 2007) and a fertilization experiment (Romme and others 2009) in recently burned forests also suggested that lodgepole pine may not be N-limited during the first several years following the fire. Nitrogen limitation was not evident even 15 years after the 1988 fires, except in stands where postfire tree density was greater than 100,000 stems ha<sup>-1</sup> (Turner and others 2009). Plant demand for N may not exceed supply until tree biomass and associated nutrient demand increase substantially, and Harden and others (2003) suggested that this “fire fertilization effect” may last up to 25 years. MacKenzie and DeLuca (2006) posited that disturbance-driven N availability dominates soon after fire, but vegetation-driven N availability dominates later in succession. Thus, postfire vegetation may initially be decoupled from soil nutrients at fine scales (that is, no significant relationship and/or spatial patterns not congruent), or the dominant direction of the relationship may be from aboveground cover (for example, vegetation and litter) to soil N availability, rather than vice versa. In this study, we quantified changes in the magnitude and spatial structure of variation in vegetation and soil N for 4 years after severe forest fires to address two questions:

(1) *How do the variability and spatial structure of aboveground cover and soil nitrogen availability change during the first 4 years following stand-replacing fire?* We expected variability in biotic cover to decline and the scale of spatial structure to increase with time since fire as plants grew and established in the

stand. We expected the variability of soil N pools and transformations to be high initially because of fine-scale variation in ash deposition, depth of soil heating, organic residue, and so on. Variability in soil N was then expected to decline in response to a variety of processes, including gradual increases in vegetation cover and biomass, selective root foraging in high N patches, and an increase in C-rich substrates that lead to increased N immobilization (Gundale and others 2006). We also expected little initial spatial structure in N variables because fire effects were likely to be spatially random, but we expected that spatial structure would develop with vegetation recovery during early postfire succession.

(2) *At fine scales, are postfire soil inorganic N pools and fluxes related to aboveground cover?* We considered several alternative relationships that could indicate fine-scale coupling or decoupling of vegetation and soils (Figure 1). If vegetation and soils were decoupled (that is, no measurable effect of one on the other), there would be *no significant correlation* between measures of aboveground cover and soil nitrogen availability (Figure 1A) and no congruence in their scales of spatial autocorrelation. If vegetation and soils were coupled, we assumed that a significant correlation would be detected but the direction could vary. If postfire vegetation influenced soil N, we would expect cover of live vegetation and new unburned litter to be *negatively correlated* with soil N (Figure 1B). This would occur

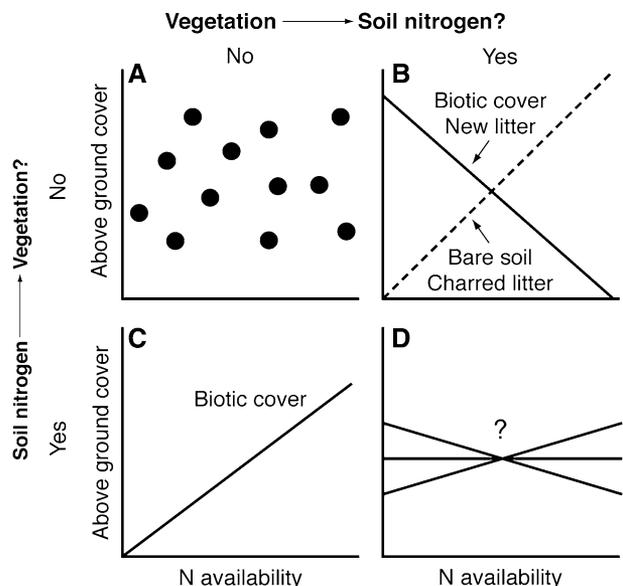


Figure 1. Summary of hypothesized relationships between aboveground cover and soil N availability in early postfire successional subalpine forest stands.

if the vegetation reduced soil N by uptake and by litter production that led to N immobilization as N was translocated from soil to litter during the immobilization phase of decomposition (for example, Yavitt and Fahey 1986; Laiho and Prescott 1999; Remsburg and Turner 2006). If the soil N supply remained adequate for plant growth, the reduction in soil N would not influence the vegetation (Tateno and Chapin 1997). We also expected local nitrate availability could be positively correlated with cover of charred litter (DeLuca and others 2006) and bare mineral soil (Metzger and others 2008) (Figure 1B). If N was limiting postfire vegetation, we would expect live vegetative cover to be *positively correlated* with soil N variables because plant growth would increase with nutrient supply (Figure 1C). Finally, if vegetation and soil nitrogen were coupled and influences were reciprocal, correlations would vary with the relative strength of the relationships, or we might observe no correlation if relationships countered each other (Figure 1D).

## METHODS

Our study sites were located in coniferous forests within Grand Teton National Park and the adjacent Rockefeller Parkway (northwestern Wyoming, USA) that were burned by the Glade and Moran Fires during summer 2000. The 1,280-ha Glade Fire was located just south of Yellowstone National Park in 150 and 120-year old lodgepole pine (*P. contorta* var. *latifolia*) forests that developed following stand-replacing fires in 1856 and 1879, respectively. The parent material consisted of Quaternary rhyolite bedrock and rhyolite-dominated glacial deposits; soils were loamy-skeletal, mixed superactive Lithic Haplocrypts (Hechtman soil series). The 840-ha Moran Fire on the western shore of Jackson Lake burned in mixed forests of lodgepole pine, Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) that had not burned previously for at least 200 years. The parent material consisted of glacial moraine deposits, containing material from Precambrian crystalline igneous and metamorphic rocks as well as Paleozoic sedimentary rocks; soils were loamy-skeletal, mixed, superactive Ustic Haplocrypts and Haplocryolls (Taglake-Sebud association). Both sites were at approximately 2150 m elevation on gently rolling topography. Although one flank of the Glade Fire was actively suppressed to protect park developments, most of the area (including our study sites) burned without active suppression. Because fire retardant typically contains inorganic N, we were careful to select a

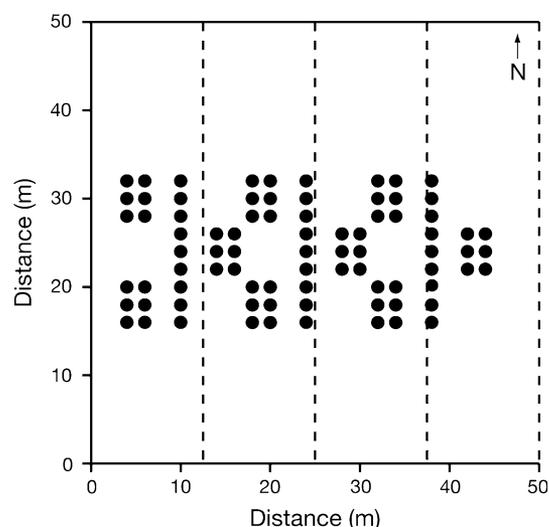
study area where no fire retardant was applied. The Moran Fire burned entirely without interference and with no retardant application. The nearest weather station is at Moran, WY, approximately 25 km away in the same mountain valley as the two study sites and at similar elevation. This station has recorded average air temperatures of  $-9.6^{\circ}\text{C}$  in December and  $16^{\circ}\text{C}$  in July, and average annual precipitation of 575 mm. During the years of our study, annual precipitation was 568, 484, 580, and 745 mm for water years 2001, 2002, 2003, and 2004, respectively. Relative to monthly 30-year averages (1971 to 2000), the summer of 2001 was extremely dry, receiving only one-third of average precipitation from June through August. The summer of 2003 was similarly dry in June-July, but above average in August; and summer precipitation for 2002 and 2004 was near or above average.

We established four  $50 \times 50$ -m plots in July 2001, with two plots each in the two sites (the Glade and Moran Fires); these four plots were a subset of 10 plots that comprised a broader study (Turner and others 2007). All plots were in stand-replacing burns in which all trees were killed and the litter layer was consumed; however, one plot at each site was in an area burned by crown fire and one was in an area of severe-surface fire (Table 1). Pre-fire stand basal area, density, and tree species composition were quantified during summer 2001 by sampling within three parallel  $50 \times 2$  m belt transects in each plot. The abundance of pre-fire coarse wood was also quantified during summer 2001 using the planar intercept method (Brown 1974). Fire-severity classes followed Turner and others (1997, 1999). In brief, in areas of crown fire, the needles of canopy trees were completely consumed by fire, the soil organic layer was almost entirely consumed, and soil was bare with no litter. In areas of severe-surface burn, the canopy trees were also killed by fire but the needles were not all consumed; the soil organic layer was almost entirely consumed, but there were dead needles that fell from the canopy to the soil surface after the fire. Postfire soils had no O horizon. Except for these differences in fire severity, the two plots at each site were similar with respect to topography and pre-fire vegetation structure. Plots were oriented toward true north, separated by at least 200 m, and initially positioned by extending a central 50-m transect due north from a random starting point.

In each plot, we established a spatially explicit sampling grid ( $n = 81$ ) with a minimum separation distance of 2 m between sampling points and a cyclic (that is, repeated) sequence of points (Figure 2). The grid covered an  $18 \times 40$  m area

**Table 1.** General Characteristics of Four 0.25-ha Study Plots in Greater Yellowstone that Experienced Stand-replacing Fire during Summer 2000

Variable	Glade Fire		Moran Fire	
Fire severity (all were stand replacing)	Crown	Severe-surface	Crown	Severe-surface
Pre-fire stand density (trees ha <sup>-1</sup> )	700	500	733	1133
Relative density (%) lodgepole pine	90	93	0	43
Relative density (%) Engelman spruce	10	7	73	0
Relative density (%) subalpine fir	0	0	27	57
Pre-fire basal area (m <sup>2</sup> ha <sup>-1</sup> )	10.4	9.4	31.8	21.2
Relative basal area (%) lodgepole pine	94	98	0	44
Relative basal area (%) Engelman spruce	6	2	84	0
Relative basal area (%) subalpine fir	0	0	16	56
Pre-fire downed coarse wood (kg m <sup>-2</sup> )	8.8	6.2	3.1	6.1
General soil characteristics				
pH	5.6	5.6	5.9	5.5
Soil organic matter (g kg <sup>-1</sup> )	32	37	30	53
P (g kg <sup>-1</sup> )	0.010	0.015	0.075	0.045
Exchangeable K (g kg <sup>-1</sup> )	0.36	0.43	0.38	0.45
Exchangeable Ca (g kg <sup>-1</sup> )	1.12	0.99	2.41	1.98
Exchangeable Mg (g kg <sup>-1</sup> )	0.15	0.13	0.22	0.24
Total N (g kg <sup>-1</sup> )	1.0	1.1	<0.1	0.8

**Figure 2.** Spatially explicit (cyclic) sampling design with 81 sampling points positioned within a 0.25-ha plot used for sampling aboveground cover, soil nitrogen, and nitrogen transformations within four 0.25-ha stands burned during summer 2000. Minimum distance between sampling points was 2 m. All plots were oriented toward true north.

positioned in the center of the plot and included nine parallel rows, each separated by 2 m. Each row included three 14-m cycles in which three of seven grid points (at 0, 2, and 6 m) were sampled; the middle three rows were offset by 6 m to account for potential anisotropy. A cyclic design is efficient when geostatistics are planned, as it gives

similar statistical power over a range of lag distances (Burrows and others 2002). The 2-m spatial resolution was based on the observed patchiness of aboveground vegetation given our focus on the relationship between vegetation and soil nutrients. Vegetation and soils (see below) were sampled from 2001 to 2004 at each sampling point (4 plots  $\times$  81 sampling points per plot,  $n = 324$  sampling points per year).

### Aboveground Cover

Within each plot, we measured percent cover within a 0.25-m<sup>2</sup> circular frame at each sampling point in July 2001, 2002, 2003, and 2004. Abiotic cover categories included all non-living classes, such as bare mineral soil, rock, coarse wood, unburned litter (which was deposited after the fires, for example, newly fallen pine needles) and charred litter. Biotic cover categories included living vegetation; cover was recorded by species for two potential nitrogen fixers, *Lupinus argenteus* and *Ceanothus velutinus*, and by functional group (forb, graminoid, shrub, and tree seedling) for all other live vegetation. Cover summed to 100% in each frame.

### N Pools and In Situ N Mineralization

The resin core incubation method (Binkley and Hart 1989) was used to estimate initial pools of NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup> and annual rates of net N mineralization at each sampling point ( $n = 81$ ) in each

plot from July 2001 to 2004 (that is, three 1-year incubations). Incubations used open PVC tubes, 5 cm in diameter and 15 cm deep, buried such that the top of the tube was level with the soil surface, with a resin bag at the bottom (DiStefano and Gholz 1986). At each core location, cores were placed in a consistent relative position each year (facing north, east and south in 2001, 2002, and 2003, respectively) and were within 0.25 m of each other.

Resin bags contained 20 g wet mass of mixed bed exchange resin (#4631, J. T. Baker Laboratory Chemicals, Phillipsburg, New Jersey, USA) in commercial nylon stocking material. Initial soil samples were collected to the same depth (15 cm) adjacent to each resin core using a clean PVC tube and processed within 24 h. To determine the initial ammonium and nitrate pools at the onset of incubation, the soil was homogenized, and a 20 g sub-sample was extracted in 75 ml of 2 M KCl by shaking the sample for 1 h. Extracts were filtered after a brief settling time (between 1 and 3 h) with 0.7-micron sample-rinsed filter paper, and frozen for subsequent analysis. At the end of the 1-year incubation, the resin bags and the soil within the PVC tube above the bag were collected and returned to the lab and a new set of cores was installed. The soil from the tube was homogenized, weighed and a 20 g sub-sample was extracted in 75 ml 2 M KCl. Resin bags were extracted in 50 ml of 2 M KCl. Extracts were frozen and subsequently analyzed colorimetrically for nitrate and ammonium using a flow-injected autoanalyzer (Lachat Instruments, Milwaukee, WI). Soil moisture content was determined for the pre- and post-incubation soils by oven-drying at 105°C for 24 h. Net N mineralization was calculated as the post-incubation ammonium plus nitrate in the soil and resin bag minus the quantity in the pre-incubation soil and expressed as  $\text{mg N kg}_{\text{soil}}^{-1} \text{y}^{-1}$ .

### General Soil Characteristics

To characterize soil properties in each stand, we collected 20 samples of the upper 15 cm of mineral soil at random locations in each plot in 2002 (Metzger and others 2006). Samples were homogenized and composited by plot, air dried and analyzed at the Soil and Plant Analysis Lab at the University of Wisconsin, Madison (<http://uwlab-soils.wisc.edu/madison/>). Total C was determined by dry combustion using a Tekmar-Dohrman 183 TOC Boat Sampler DC-190 (Tekmar-Dohrman, Mason OH). A micro-Kjeldahl procedure was used for total N determination. Acid extractable P was

analyzed colorimetrically using the Truog method, and potassium (K), calcium (Ca), and magnesium (Mg) were extracted from the soil using 1 N  $\text{NH}_4\text{OAc}$  at pH 7.0 then analyzed by atomic absorption.

### Statistical Analyses

As a precursor to the analyses of variability and spatial structure, repeated measures ANOVA was used to determine how aboveground cover, soil N pools and net N mineralization rates varied through time, between sites, and with fire severity. Variance components analysis was performed by year to identify the level at which variation in the sample population was most pronounced (for example, between sites (2 levels); between burn severity classes (2 plots per site); or among sample points ( $n = 81$  cores) within a plot). To examine within-stand variability and spatial structure (question 1), the coefficient of variation (CV) was used to describe the magnitude of within-stand variation in aboveground cover and N variables in each plot for each year. The CV is a relative measure of variability that is straightforward to interpret and useful for comparing variability among different biological properties (Fraterrigo and Rusak 2008).

Semivariogram analysis (Cressie 1993) was then used to evaluate spatial dependence in aboveground cover and N variables in each plot for each year. Semivariances and their 95% confidence intervals were computed for lag distances to 25 m, and two models for each variable were fitted using maximum likelihood: (1) a linear model with independent errors (that is, no spatial structure), and (2) a linear model with spatially autocorrelated errors fit to an exponential variogram with nugget variance (Pinheiro and Bates 2000, Chapter 5). A likelihood ratio test was used for model comparison, and a  $P$  value  $< 0.05$  provided evidence for spatial dependence. For those that showed significant spatial structure, we estimated standard parameters for each variogram: (1) the nugget ( $C_0$ ), the intercept of the model variogram representing variance at scales less than the minimum lag distance or which arises from measurement error and cannot be resolved, (2) the sill ( $C_0 + C$ ), or maximum semivariance; and (3) the range ( $r$ ), which represents the limit of spatial dependence or the distance over which measurements are autocorrelated. We report the proportion of structural variance [ $C/(C_0 + C)$ ] and the range as estimates of the magnitude and scale, respectively, of spatial dependence in the data. All data were tested for

normality and transformed if needed before analysis.

To determine whether within-stand measures of soil inorganic N pools and N transformations were related to aboveground cover (question 2), we computed Spearman rank-order correlations between soil N variables and aboveground cover by sampling point ( $n = 324$ ) for each year. All geo-statistical analyses were performed in *R*, and all other statistical analyses were conducted using SAS (SAS Institute 2003).

## RESULTS

### General Trends

#### Aboveground Cover

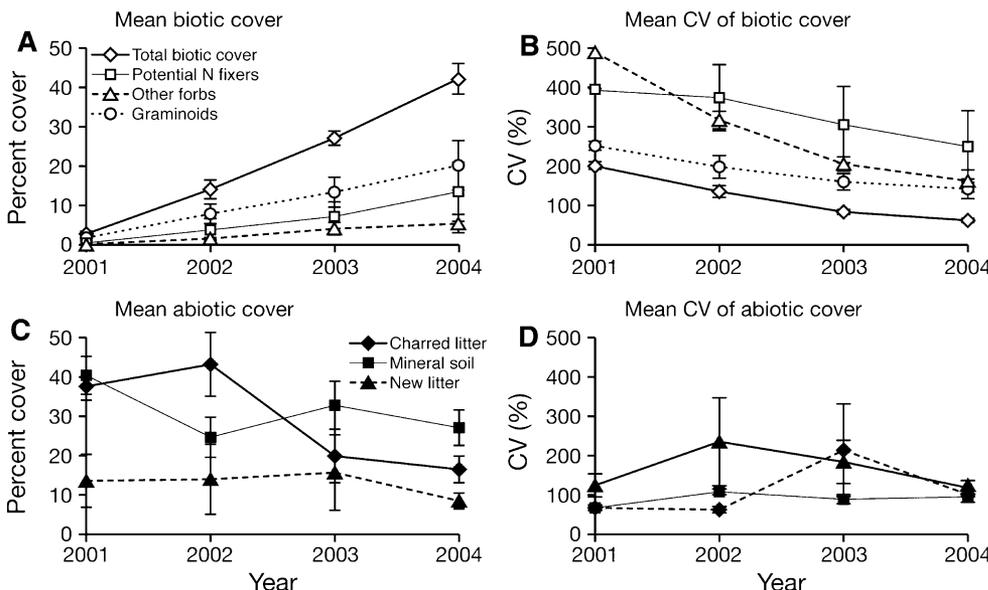
From 2001 to 2004, total biotic cover increased from 2.8 to 42.4% (Figure 3A). Biotic cover differed between sites (Glade > Moran;  $F = 13.18$ ,  $P < 0.0001$ ) but did not differ between crown and severe-surface fire (see Appendix 1 in Supplementary Material). Graminoids were the most abundant functional group, averaging 20% cover by 2004 (Figure 3A). Cover of potential N fixing species (*Lupinus argenteus* and *Ceanothus velutina*) was relatively high, averaging 15% cover by 2004 (Figure 3A). Shrub cover (largely *Vaccinium scoparium*) was negligible. Cover of bare mineral soil declined from 40% in 2001 to 27% in 2004 (Figure 3C). Cover of charred litter peaked in 2002 with sloughing of burned bark (personal observation), then declined (Figure 3C); much of the charred material remained present but was increasingly obscured by the recovering vegetation.

Cover of new unburned litter (primarily pine needles fallen after the fire) averaged about 15% through 2003 then declined (Figure 3C), and unburned litter was greater in severe-surface than in crown fire.

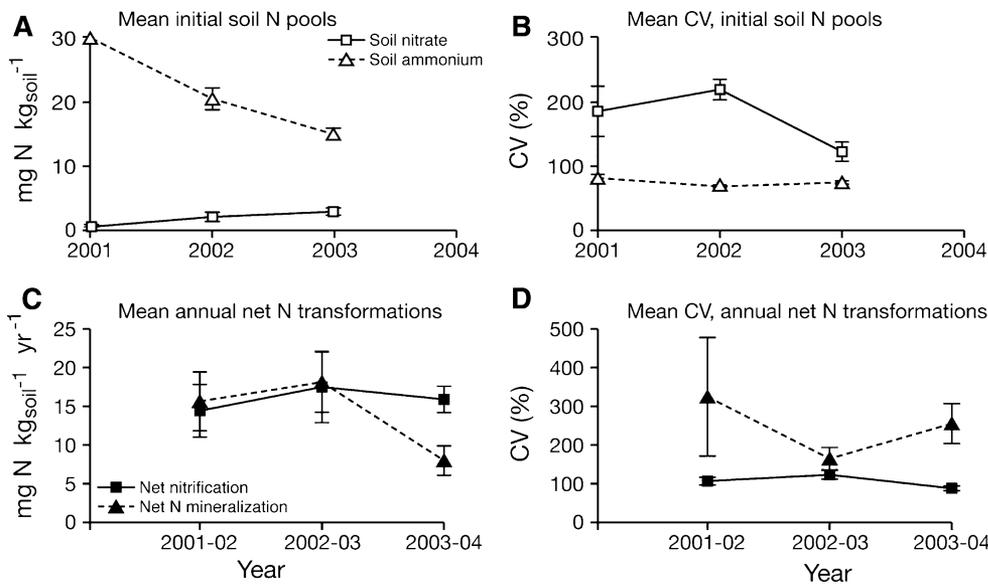
For aboveground total biotic cover in 2001, variance components indicated no variation between sites, only 4% between plots differing in burn severity, and 96% of the variation among the sample points. By 2004, 11% of the variation occurred between sites and 89% among sample points. For unburned litter, variance in 2001 was evenly split between plots (51%), consistent with plot-level differences in fire severity within each site, and among sample points (49%). By 2004, variability in litter between plots declined (12%), and variation among sample points increased (88%).

#### Soil N Pools and Transformations

Soil ammonium concentrations decreased by about half from 2001 to 2003 (Figure 4A). Soil nitrate concentrations were much lower than soil ammonium concentrations, but nitrate pools increased four- to five-fold from 2001 to 2003 (Figure 4A). Soil nitrate concentrations differed with burn severity (crown > surface fire;  $F = 33.03$ ,  $P < 0.0001$ ) and between sites (Moran > Glade;  $F = 19.06$ ,  $P < 0.0001$ ) (see Appendix 2 in Supplementary Material). Soil ammonium pools also varied with burn severity and between sites, but the overall explained variance was lower than for soil nitrate (see Appendix 2 in Supplementary Material). Most variation (80–89%) in soil nitrate pools was among sample points (cores) in a plot, with some (15–20%) variance reflecting fire



**Figure 3.** Mean and coefficient of variation for aboveground biotic cover (A, B) and abiotic cover (C, D) in four forest stands that burned during summer 2000. Each plot-level mean and CV was computed from 81 sampling points; error bars are  $\pm 1$  SE ( $n = 4$  plots).



**Figure 4.** Mean cover and coefficient of variation for soil N pools (**A**, **B**) and net annual N transformations (**C**, **D**) in four forest stands that burned during summer 2000. Each plot-level mean and CV was computed from 81 sampling points; error bars are  $\pm 1$  SE ( $n = 4$  plots).

severity, but essentially no variance attributed to site. Most variation in soil ammonium pools was also among cores in a plot, and this component increased from 90% in 2001 to 99% in 2003; there was a small amount of variance in ammonium pools due to fire severity in 2001 (10%) and 2002 (5%), and essentially no variance due to site.

Nitrification accounted for most of the observed net N mineralization each year (Figure 4C). However, by the 2003–2004 incubation, net nitrification was substantially higher than net N mineralization in all four plots, indicating that consumption of ammonium exceeded gross production, and soil ammonium pools were being depleted (Figure 4C). Annual net nitrification rates did not differ among years but varied between sites (Moran > Glade;  $F = 22.72$ ,  $P < 0.0001$ ) and with burn severity (crown > severe-surface fire;  $F = 9.10$ ,  $P < 0.0001$ ), but these factors explained only 11% of the variance in the data (see Appendix 2 in Supplementary Material). Annual net N mineralization rates varied by year (see Appendix 2 in Supplementary Material), with the third year (2003–2004) rates significantly lower than the prior 2 years (Figure 4C). There was a small but significant difference in annual net N mineralization between sites (Moran > Glade;  $F = 5.11$ ,  $P = 0.0017$ ), but no difference with burn severity ( $F = 2.54$ ,  $P = 0.0553$ ). As observed for soil N pools, variance in annual net N transformation rates was most pronounced among soil cores. For 2001–2002 annual net nitrification rates, variance components analysis revealed that most variance (85%) was among cores with 14% of the variance between burn severity classes. By 2003–2004, 95% of the

variance in net nitrification was observed among cores. For net N mineralization rates over all years, nearly all variance (94 to 97%) was observed among cores, with at most 4% occurring between sites and 3% between burn severities.

## Within-Plot Variability

### Aboveground Cover

Variability in biotic cover, as measured by the CV ( $n = 81$  per plot), declined with time since fire for all plant functional groups (Figure 3B). Abiotic cover classes were relatively less variable than biotic cover classes and changed less over time (Figure 3D). Variability in charred litter and new unburned litter peaked in 2002 and 2003, respectively.

### Soil N Pools and Transformations

Within-plot variability was greater for soil nitrate pools (CVs > 100%) than for soil ammonium pools (CVs < 100%) (Figure 4B). The CVs for soil nitrate pools declined in 2003, whereas the CVs for soil ammonium pools changed little over time. Within-plot variability was greater for net N mineralization than for net nitrification, but variability did not change consistently over time (Figure 4D).

## Spatial Structure of Within-Plot Variability

### Aboveground Cover

Spatial structure was detected in some aboveground cover measurements during the first four

postfire years, but there were no consistent trends through time (Table 2). Graminoid cover, which comprised about half of total vegetative cover, was notably patchy in the Glade plots, with estimated ranges generally between 2 and 7 m (Table 2). New unburned litter was spatially structured in the severe-surface burns with estimated ranges generally between 12 and 23 m (Table 2), reflecting extensive patches of needles shed from fire-killed trees. Charred litter and bare mineral soil showed evidence of spatial structure only at Glade (Table 2), with estimated ranges greater in the severe-surface burn than in crown fire during the first 2 years postfire.

#### *Soil N Pools and Transformations*

There was some spatial structure in the soil N pools but no obvious trends through time or distinctions among plots (Table 3). For soil nitrate pools, estimated ranges varied between 2 and 3 m when spatial structure was present. Estimated ranges for soil ammonium pools were larger (ca. 3 to 11 m) when spatial structure was detected. The proportion of structural variance in ammonium pools was less than observed in soil nitrate pools (Table 3). There was very little spatial dependence in net N mineralization rates at the scales we measured (Table 3). For annual net nitrification, only 2 of 12 potential plot–year combinations showed significant spatial structure, and only 1 of 12 for annual net N mineralization (Table 3).

#### Relationships Between Soil N and Aboveground Cover

Soil N variables and aboveground cover were correlated at the level of the individual soil core, and the direction of these relationships remained consistent through time (Table 4). Soil ammonium and nitrate pools were negatively correlated with aboveground measurements related to plant nutrient demand and/or inputs of organic matter and to abundance of potential N fixers. For soil ammonium, the negative relationship with total biotic cover was stronger than the relationship for unburned litter cover, and soil ammonium was positively correlated with cover of bare mineral soil (Table 4). For soil nitrate, there were no significant correlations with aboveground cover 1 year following fire, a time period when soil nitrate concentrations were also very low. Correlations between soil nitrate and aboveground cover increased in 2002 and 2003, with a strong relationship observed with unburned litter (negative) and with bare mineral soil (positive) (Table 4). For annual net N mineralization, there were very few

significant relationships detected with aboveground cover (Table 4). Net N mineralization was positively correlated with percent cover of charred litter in 2002–2003 and 2003–2004. Annual net nitrification decreased with increasing cover of unburned litter and increased with both cover of charred litter and bare mineral soil (Table 4).

#### DISCUSSION

The variability of aboveground vegetation and soil N was dynamic during the first 4 years after stand-replacing fire, and variance in both cover and soil N was most pronounced at fine scales (that is, within plot) rather than between plots differing in fire severity or between the Glade and Moran sites. Spatial structure was observed in some aboveground cover variables (for example, graminoids and fresh litter), but there was little spatial structure in soil N variables and no obvious congruence in spatial scales of autocorrelation for soil N and aboveground cover. These results indicate a lack of spatial coupling at scales related to the patchiness of early postfire successional vegetation. Nevertheless, significant correlations between aboveground cover and soil N at the core level indicate coupling at a finer spatial scale, and the nature of these relationships is consistent with a dominant influence from aboveground cover to the soil N and an adequate N supply for the vegetation (Figure 1B).

It was surprising that little of the variation in soil N availability was at the site level, despite differences in pre-fire forest composition, stand age, and basal area between Glade and Moran (Table 1). These results suggest that severe, stand-replacing fire affected N availability in these subalpine forests in similar ways. Opening of the canopy by fire increases average daily temperature and the range between daily minima and maxima; temperature changes should be comparable between the two sites and can strongly influence N transformations (for example, Yermakov and Rothstein 2006; Koyama and others 2010; Griffin and others 2011). Herbaceous vegetation in the early postfire stands was similar, although tree regeneration should ultimately lead to differences in forest composition (for example, pine vs. spruce) and feedbacks to the soil (Prescott 2002). Similarity in postfire environments may minimize N variability between sites.

#### Within-Plot Variability

Our predictions about changes in within-stand variability of aboveground cover during the first 4 years postfire were largely supported. Relative

**Table 2.** Summary of Spatial Dependence in Aboveground Cover

Site	Fire severity	2001			2002			2003			2004		
		Range	C/(C + C <sub>0</sub> )	P	Range	C/(C + C <sub>0</sub> )	P	Range	C/(C + C <sub>0</sub> )	P	Range	C/(C + C <sub>0</sub> )	P
Total biotic cover													
Glade	Crown	1.8	1.00	0.0065	2.0	1.00	0.0004	1.6	1.00	0.0096	1.8	0.95	0.0121
	Sev-surf	-	-	-	-	-	-	-	-	-	-	-	-
Moran	Crown	-	-	-	-	-	-	-	-	-	-	-	-
	Sev-surf	5.9	0.30	0.0384	4.8	0.37	0.0273	-	-	-	-	-	-
Graminoids													
Glade	Crown	1.9	1.00	0.0038	2.1	1.00	0.0004	1.9	0.96	0.0001	2.0	0.84	0.0098
	Sev-surf	3.2	0.81	0.0083	2.9	0.61	0.0201	-	-	-	7.4	0.34	0.0278
Moran	Crown	-	-	-	-	-	-	-	-	-	-	-	-
	Sev-surf	5.8	0.33	0.03262	5.3	0.49	0.0009	-	-	-	-	-	-
Litter													
Glade	Crown	-	-	-	-	-	-	-	-	-	-	-	-
	Sev-surf	11.8	0.77	<0.0001	17.3	0.44	<0.0001	-	-	-	21.2	0.36	0.0001
Moran	Crown	-	-	-	-	-	-	-	-	-	-	-	-
	Sev-surf	15.6	0.79	<0.0001	22.9	0.80	<0.0001	4.5	0.47	0.0070	-	-	-
Charred litter													
Glade	Crown	-	-	-	2.8	0.51	0.0165	-	-	-	-	-	-
	Sev-surf	15.5	0.53	<0.0001	17.9	0.33	0.0010	-	-	-	-	-	-
Moran	Crown	-	-	-	-	-	-	-	-	-	-	-	-
	Sev-surf	-	-	-	-	-	-	-	-	-	-	-	-
Bare mineral soil													
Glade	Crown	-	-	-	2.3	0.54	0.0493	-	-	-	3.0	0.48	0.0235
	Sev-surf	7.5	0.54	0.0004	5.4	0.54	0.0008	-	-	-	1.8	1.00	0.0048
Moran	Crown	-	-	-	-	-	-	-	-	-	-	-	-
	Sev-surf	-	-	-	-	-	-	-	-	-	-	-	-
Potential N fixers													
Glade	Crown	-	-	-	-	-	-	-	-	-	-	-	-
	Sev-surf	-	-	-	-	-	-	-	-	-	9.9	0.30	0.0046
Moran	Crown	-	-	-	17.5	0.34	0.0394	-	-	-	-	-	-
	Sev-surf	-	-	-	-	-	-	-	-	-	-	-	-

At each site, the stand-replacing fire was either crown fire (plot A) or severe-surface fire (plot B). All variograms were fitted using exponential models and compared to a model of random variation. When spatial dependence was significant ( $P < 0.05$ ), we report the scale of spatial dependence (range), and magnitude of spatial dependence (the proportion of structural variance,  $C/(C + C_0)$ ), where C is the variance explained by autocorrelation,  $C_0$  is the nugget, and  $C + C_0$  is the sill), and the P value for the LRT. The '-' indicates no significant spatial autocorrelation at the scales measured in this study.

**Table 3.** Summary of Spatial Dependence in Soil N Pools and Transformations

Site	Fire severity	2001–2002			2002–2003			2003–2004		
		Range (m)	C/(C + C <sub>0</sub> )	P	Range (m)	C/(C + C <sub>0</sub> )	P	Range (m)	C/(C + C <sub>0</sub> )	P
Initial soil NO <sub>3</sub> <sup>-</sup> pool (log transformed)										
Glade	Crown	1.80	1.00	0.0052	–	–	–	2.26	1.00	0.0002
	Sev-surf	–	–	–	–	–	–	–	–	–
Moran	Crown	2.74	0.93	0.0006	–	–	–	–	–	–
	Sev-surf	–	–	–	2.34	0.80	–	1.69	1.00	0.0026
Initial soil NH <sub>4</sub> <sup>+</sup> pool (log transformed)										
Glade	Crown	2.68	0.61	0.0206	–	–	–	–	–	–
	Sev-surf	–	–	–	11.17	0.56	<0.0001	7.22	0.51	0.0001
Moran	Crown	–	–	–	–	–	–	–	–	–
	Sev-surf	–	–	–	7.83	0.28	–	–	–	–
Annual net nitrification rate										
Glade	Crown	1.85	1.00	0.0068	–	–	–	–	–	–
	Sev-surf	–	–	–	–	–	–	22.78	0.27	0.0189
Moran	Crown	–	–	–	–	–	–	–	–	–
	Sev-surf	–	–	–	–	–	–	–	–	–
Annual net N mineralization rate										
Glade	Crown	2.81	0.83	0.0002	–	–	–	–	–	–
	Sev-surf	–	–	–	–	–	–	–	–	–
Moran	Crown	–	–	–	–	–	–	–	–	–
	Sev-surf	--	–	–	–	–	–	–	–	–

At each site, the stand-replacing fire was either crown fire (plot A) or severe-surface fire (plot B). All variograms were fitted using exponential models and compared to a model of random variation. When spatial dependence was significant ( $P < 0.05$ ), we report the scale of spatial dependence (range), and magnitude of spatial dependence (the proportion of structural variance,  $C/(C + C_0)$ ), where  $C$  is the variance explained by autocorrelation,  $C_0$  is the nugget, and  $C + C_0$  is the sill), and the  $P$  value for the LRT. The “–” indicates “no significant” spatial autocorrelation at the scales measured in this study.

**Table 4.** Spearman Correlation Coefficients (with  $P$  values) for Soil N Variables and Aboveground Cover Measurements in Plots that Burned with Stand-replacing Fire during Summer 2000

Aboveground cover at beginning of incubation	Initial soil N pools					
	Soil ammonium			Soil nitrate		
	2001 ( $n = 307$ )	2002 ( $n = 313$ )	2003 ( $n = 320$ )	2001 ( $n = 307$ )	2002 ( $n = 313$ )	2003 ( $n = 320$ )
Total biotic cover	<b>-0.19</b> (0.0007)	<b>-0.21</b> (0.0001)	<b>-0.14</b> (0.0099)	ns	<b>-0.18</b> (0.0016)	<b>-0.25</b> (<0.0001)
Potential N fixers	<b>-0.13</b> (0.0228)	-0.10 (0.0691)	<b>-0.18</b> (0.0015)	ns	<b>-0.24</b> (<0.0001)	ns
Unburned litter	<b>-0.17</b> (0.0029)	-0.11 (0.0565)	-0.11 (0.0518)	ns	<b>-0.38</b> (<0.0001)	<b>-0.38</b> (<0.0001)
Bare mineral soil	<b>0.23</b> (<0.0001)	<b>0.24</b> (<0.0001)	<b>0.16</b> (0.0043)	ns	<b>0.24</b> (<0.0001)	<b>0.39</b> (<0.0001)
Charred litter	ns	ns	ns	ns	ns	<b>0.17</b> (0.0017)
Aboveground cover at beginning of incubation	Soil N transformations					
	Annual net nitrification			Annual net N mineralization		
	2001–2002 ( $n = 305$ )	2002–2003 ( $n = 312$ )	2003–2004 ( $n = 309$ )	2001–2002 ( $n = 305$ )	2002–2003 ( $n = 312$ )	2003–2004 ( $n = 309$ )
Total biotic cover	ns	<b>-0.18</b> (0.0018)	ns	ns	ns	ns
Potential N fixers	ns	<b>-0.17</b> (0.0031)	<b>-0.14</b> (0.0133)	ns	ns	<b>-0.15</b> (0.0093)
Unburned litter	<b>-0.23</b> (<0.0001)	<b>-0.27</b> (<0.0001)	<b>-0.19</b> (<0.0009)	ns	ns	ns
Bare mineral soil	ns	<b>0.12</b> (0.0319)	<b>0.13</b> (0.0238)	ns	ns	ns
Charred litter	<b>0.12</b> (0.0430)	<b>0.18</b> (0.0018)	<b>0.12</b> (0.0322)	ns	<b>0.12</b> (0.0310)	<b>0.11</b> (0.0490)

Bold value indicates  $P \leq 0.05$ .

variability in biotic cover declined with time since fire and was consistently greater than observed for soil and litter cover. These trends are consistent with autogenic successional processes in which biotic cover initially is very sparse and dominated by re-sprouting herbaceous vegetation. Biotic cover increased as surviving plants increased in size, flowered, and produced seed, leading to infilling of unvegetated space and less variability in total cover. During this early postfire time period, tree regeneration contributed little to cover (and biomass) because the tree seedlings were small (Turner and others 1997).

The magnitude of variation in soil N concentrations was similar to that reported in other studies (for example, Cain and others 1999; Rodríguez and others 2009), but our expectations for within-plot variability were only partially supported. We expected variability in soil N to decline with time since fire and observed such declines for soil nitrate concentrations and annual net nitrification rate. However, variability in soil ammonium concentration was low and remained low during this study; variability in annual net N mineralization rate fluctuated but showed no obvious trend. The greater variability in soil nitrate concentration likely reflects the greater sensitivity of nitrifiers to soil heating and the greater environmental constraints (for example, pH, temperature, water potential, and nutrient status) on nitrification (Killham 1990; Ste-Marie and Paré 1999). The decline in the CV for soil nitrate could reflect postfire recovery of the soil microbial community and/or more consistent constraints, especially C availability, on nitrate availability (Koyama and others 2010). Elevated concentrations of soil ammonium repress microbial uptake of alternative N sources, including nitrate (Bradley 2001; Geisseler and others 2010). The factors that influence the relative importance of different pathways of nitrogen utilization by soil microorganisms likely vary in space and time during the first several years postfire.

### Spatial Structure of Within-Plot Variability

Spatial structure was observed in some response variables, but our predictions were only partially supported. For biotic cover, we expected the scale of autocorrelation to increase over time, but the scale of autocorrelation remained similar during the first 4 years postfire. Thus, the initial spatial pattern of postfire vegetation established early and persisted for at least 4 years. The larger range estimate for new unburned litter in severe-surface

burns was consistent with our field observations of contiguous areas covered by needles shed from the fire-killed trees.

For soil N availability, we predicted that spatial structure would be minimal initially then increase with time since fire as plant cover increased. Although there was some spatial structure in soil ammonium and nitrate pools, there were no consistent temporal patterns in their spatial structure. Furthermore, there was a surprising absence of spatial structure in soil N transformations at the scales we sampled. Within-stand spatial structure in N availability—if present—is apparently at finer scales (<2 m) unrelated to the larger patches of aboveground cover. Another study also observed no clear temporal trends in the magnitude and scale of spatial variability in soil nutrients following experimental disturbance in a pine forest (Guo and others 2004). Other research has demonstrated variation in soil N rates at fine scales related to the spatial arrangement of soil particles and microbes (for example, Ritz and others 2004; Schimel and Bennett 2004), and substantial microscale variability in soil N-cycling processes may limit detection of larger patterns (Walley and others 1996).

### Relationship Between Soil N and Aboveground Cover

We did not observe consistent patterns in the estimated ranges of aboveground cover and soil N; this lack of congruence indicates that the spatial patterns of these variables were not coupled at scales between 2 and 25 m during the initial 4 years postfire. Other authors also have reported a lack of congruence in spatial autocorrelation between soils and vegetation at comparable scales (for example, Frelich and others 2003; Guo and others 2004). Heterogeneity perceived by above- and below-ground organisms differs greatly, and the effects of disturbance on soil biodiversity are more variable at fine scales than for aboveground organisms (Hutchings and others 2003; De Deyn and Van der Putten 2005). The spatial coupling of soil resources and vegetation will likely strengthen as succession proceeds, particularly if plant nutrient demand exceeds N supply as the trees approach peak growth rates and sequester nutrients (Kaye and Hart 1997). Tree spacing may become increasingly important (Bruckner and others 1999; Ettema and Wardle 2002). This study provides a baseline from which changes in vegetation and soils can be tracked through successional time—especially as tree biomass increases, a forest floor litter layer develops, and the influence of vegetation on soil processes strengthens (Binkley and others 1995;

Giardina and others 2001; Hart and others 2005; Bengtson and others 2007; Laughlin and others 2010).

Nonetheless, the significant relationships detected between soil N and aboveground cover at the core level indicated local coupling, and the directions of these correlations were consistent with a dominant influence of aboveground cover on soil N (Figure 1B). Live vegetation likely reduced soil N availability through plant uptake and by producing litter that will initially immobilize soil N. Several common postfire herbaceous species (for example, *Calamagrostis rubescens*, *C. canadensis*) increase N uptake when inorganic N is augmented via fire or fertilization (Hangs and others 2003; Goodman and Hungate 2006; Romme and others 2009). Because charcoal in soils can stimulate nitrification for decades following fire (DeLuca and others 2006; DeLuca and Aplet 2008), the fine-scale variation of postfire charred litter could leave a long-term legacy for heterogeneity in nitrification rates. For net N mineralization, the absence of relationships with aboveground cover could indicate either de-coupling (Figure 1A) or processes that cancel each other (Figure 1D), but our data cannot distinguish between these alternatives. Additional research that examines component processes (for example, gross N transformations) and variability in C and N substrates could aid in elucidating these relationships (for example, Bengtson and others 2006; Geisseler and others 2010).

### Caveats and Conclusions

Several caveats should be noted when interpreting the results of this study. We included only four plots because of cost and logistic constraints, reflecting the trade-off between the required fine-scale sampling and the need for replication (Oksanen 2001). Sample size at the plot level was limited, but this is one of few studies to replicate an intensive sampling design ( $n = 324$  sample points per year) through multiple years. We did not consider other pathways (for example, organic N uptake; Lindahl and others 2002) or belowground variables (for example, soil organic matter, microbial biomass) that could reveal different relationships with aboveground cover. Finally, although we observed statistically significant relationships, much variance remains unexplained—as has been reported in other studies at comparable scales (for example, Frelich and others 2003; Smithwick and others 2005b). Explaining the spatial variability in soil processes remains challenging.

In conclusion, we observed substantial variability in aboveground cover and soil N pools and trans-

formations during the first 4 years after severe, stand-replacing wildfire. Most of the variation in soil N availability was fine-scale (that is, within-stand), and although spatial structure was observed in some response variables, the patches of vegetation observed in the field were not related to the spatial scale of soil N availability. However, significant correlations at the level of individual soil cores indicated that aboveground cover influenced soil N, at least for the first four postfire years when plant biomass and nutrient requirements were low. Thus, the initial patterns of fire severity and re-vegetation within burned stands contributed to fine-scale heterogeneity in soil N availability. The nature of the vegetation–soil relationship will change through time as succession proceeds and plant demand for available N increases (Hart and others 2005), and long-term studies at multiple scales could help elucidate the evolving spatial dynamics of vegetation–soil relationships.

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### REFERENCES

- Ayres E, Steltzer H, Berg S, Wallenstein MD, Simmons BL, Wall DH. 2009. Tree species traits influence soil physical, chemical and biological properties in high elevation forests. *PLoS ONE* 4(6):e5964. doi:10.1371/journal.pone.0005964.
- Bååth E, Forstegård A, Pennanen T, 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* 27:229–40.
- Bengtson P, Falkengren-Grerup U, Bengtsson G. 2006. Spatial distributions of plants and gross N transformation rates in a forest soil. *J Ecol* 94:754–64.

- Bengtson P, Basiliko N, Prescott CE, Grayston SJ. 2007. Spatial dependency of soil nutrient availability and microbial properties in a mixed forest of *Tsuga heterophylla* and *Pseudotsuga menziesii* in coastal British Columbia, Canada. *Soil Biol Biochem* 39:2429–35.
- Binkley D, Hart S. 1989. The components of nitrogen availability assessments in forest soils. *Adv Soil Sci* 10:57–112.
- Binkley DB, Smith FW, Son Y. 1995. Nutrient supply and declines in leaf area and production in lodgepole pine. *Can J For Res* 25:621–8.
- Bradley RL. 2001. An alternative explanation for the post-disturbance  $\text{NO}_3^-$  flush in some forest ecosystems. *Ecol Lett* 4:412–16.
- Brown JK. 1974. Handbook for inventorying downed woody material. Gen Tech Rep INT-16, USDA For Serv, Interm For Rang Exp Stn Ogden, UT.
- Bruckner A, Kandeler E, Kampichler C. 1999. Plot-scale spatial patterns of soil water content, pH, substrate-induced respiration and N mineralization in a temperate coniferous forest. *Geoderma* 93:207–23.
- Burrows SN, Gower ST, Clayton MK, Mackay DS, Ahl DE, Norman JM, Diak G. 2002. Application of geostatistics to characterize leaf area index (LAI) from flux tower to landscape scales using a cyclic sampling design. *Ecosystems* 5:667–79.
- Cain ML, Subler S, Evans JP, Fortin M-J. 1999. Sampling spatial and temporal variation in soil nitrogen availability. *Oecologia* 118:397–404.
- Certini G. 2005. Effects of fire on properties of forest soils: a review. *Oecologia* 143:1–10.
- Chapin FS, Matson PA, Mooney HA. 2002. Principles of terrestrial ecosystem ecology. New York: Springer.
- Cressie NAC. 1993. Statistics for spatial data, revised edition. New York: Wiley.
- De Deyn GB, Van der Putten WH. 2005. Linking aboveground and belowground diversity. *Trends Ecol Evol* 20:625–33.
- DeLuca TH, Aplet GH. 2008. Charcoal and carbon storage in forest soils of the Rocky Mountain West. *Front Ecol Environ* 6:18–24.
- DeLuca TH, MacKenzie MD, Gundale MJ, Holben WE. 2006. Wildfire-produced charcoal directly influences nitrogen cycling in forest ecosystems. *Soil Sci Soc Am J* 70:448–53.
- DiStefano JF, Gholz HL. 1986. A proposed use of ion-exchange resins to measure nitrogen mineralization and nitrification in intact soil cores. *Commun Soil Sci Plant Anal* 17:989–98.
- Ettema C, Wardle D. 2002. Spatial soil ecology. *Trends Ecol Evol* 17:177.
- Fahey TJ, Yavitt JB, Pearson JA, Knight DH. 1985. The nitrogen cycle in lodgepole pine forests, southeastern Wyoming. *Biogeochemistry* 1:257–75.
- Fan WH, Randolph JC, Ehman JL. 1998. Regional estimation of nitrogen mineralization in forest ecosystems using geographic information systems. *Ecol Appl* 8:734–47.
- Foster DR, Knight DH, Franklin JF. 1998. Landscape patterns and legacies resulting from large infrequent forest disturbances. *Ecosystems* 1:497–510.
- Fraterrigo JM, Rusak JA. 2008. Disturbance-driven changes in the variability of ecological patterns and processes. *Ecol Lett* 11:756–70.
- Fraterrigo JM, Turner MG, Pearson SM, Dixon P. 2005. Effects of past land use on spatial heterogeneity of soil nutrients in Southern Appalachian forests. *Ecol Monogr* 75:215–30.
- Frelich LE, Machado J-L, Reich PB. 2003. Fine-scale environmental variation and structure of understorey plant communities in two old-growth pine forests. *J Ecol* 91:283–93.
- Gallardo A, Parra R, Covelo F. 2006. Differences between soil ammonium and nitrate spatial pattern in six plant communities. Simulated effect on plant populations. *Plant Soil* 279:333–46.
- Geisseler D, Horwath WR, Joergensen RG, Ludwig B. 2010. Pathways of nitrogen utilization by soil microorganisms: a review. *Soil Biol Biochem* 42:2058–67.
- Giardina CP, Ryan MG, Hubbard RM, Binkley D. 2001. Tree species and soil textural controls on carbon and nitrogen mineralization rates. *Soil Sci Soc Am J* 65:1272–9.
- Goodman LF, Hungate BA. 2006. Managing forests infested by spruce beetles in south-central Alaska: effects on nitrogen availability, understory biomass, and spruce regeneration. *For Ecol Manag* 227:267–74.
- Griffin JM, Turner MG, Simard M. 2011. Nitrogen cycling following mountain pine beetle disturbance in lodgepole pine forests of Greater Yellowstone. *For Ecol Manag* 261:1077–89.
- Gross KL, Pregitzer KS, Burton AJ. 1995. Spatial variation in nitrogen availability in three successional plant communities. *J Ecol* 83:357–67.
- Gundale MJ, Metlen KL, Fiedler CE, DeLuca TL. 2006. Nitrogen spatial heterogeneity influences diversity following restoration in a ponderosa pine forest, Montana. *Ecol Appl* 16:479–89.
- Guo D, Mou P, Jones RH, Mitchell RJ. 2004. Spatio-temporal patterns of soil available nutrients following experimental disturbance in a pine forest. *Oecologia* 138:613–21.
- Hangs RD, Knight JD, Van Rees KCJ. 2003. Nitrogen uptake characteristics for roots of conifer seedlings and common boreal forest competitor species. *Can J For Res* 33:156–63.
- Harden JW, Mack M, Veldhuis H, Gower ST. 2003. Fire dynamics and implications for nitrogen cycling in boreal forests. *J Geophys Res* 108(D3):8223. doi:10.1029/2001JD000494.
- Hart SC, DeLuca TH, Newman GS, MacKenzie MD, Boyle SI. 2005. Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. *For Ecol Manag* 220:166–84.
- Hobbie SE. 1992. Effects of plant-species on nutrient cycling. *Trends Ecol Evol* 7:336–9.
- Hutchings MJ, John EA, Wijesinghe DK. 2003. Toward understanding the consequences of soil heterogeneity for plant populations and communities. *Ecology* 84:2322–34.
- Kashian DM, Turner MG, Romme WH. 2005. Changes in leaf area and stemwood increment with stand development in Yellowstone National Park: Relationships between forest stand structure and function. *Ecosystems* 8:48–61.
- Kaye JP, Hart SC. 1997. Competition for nitrogen between plants and soil microorganisms. *Trends Ecol Evol* 12:139–43.
- Killham K. 1990. Nitrification in coniferous forest soils. *Plant Soil* 128:31–44.
- Koyama A, Kavanagh KL, Stephan K. 2010. Wildfire effects on soil gross nitrogen transformation rates in coniferous forests of central Idaho, USA. *Ecosystems* 13:1112–26.
- Laiho R, Prescott CE. 1999. The contribution of coarse woody debris to carbon, nitrogen and phosphorus cycles in three Rocky Mountain coniferous forests. *Can J For Res* 29:1592–603.
- Lane DR, Bassirrad H. 2005. Diminishing spatial heterogeneity in soil organic matter across a prairie restoration chronosequence. *Restor Ecol* 13:403–12.

- Laughlin DC, Hart SC, Kaye JP, Moore MM. 2010. Evidence for indirect effects of plant diversity and composition on net nitrification. *Plant Soil* 330:435–45.
- Lindahl BO, Taylor AFS, Finlay RD. 2002. Defining nutritional constraints on carbon cycling in boreal forests—towards a less ‘phytcentric’ perspective. *Plant Soil* 242:123–35.
- MacKenzie MD, DeLuca TH. 2006. Charcoal and shrubs modify soil processes in ponderosa pine forest of western Montana. *Plant Soil* 287:257–66.
- Metzger KL, Romme WH, Turner MG. 2006. Foliar nitrogen in early postfire vegetation in the Greater Yellowstone Ecosystem (Wyoming, USA). For *Ecol Manag* 227:22–30.
- Metzger KL, Smithwick EAH, Tinker DB, Romme WH, Balsler TC, Turner MG. 2008. Influence of pine saplings and coarse wood on nitrogen mineralization and microbial communities in young post-fire *Pinus contorta*. For *Ecol Manag* 256:59–67.
- Oksanen L. 2001. Logic of experiments in ecology: is pseudoreplication a pseudoissue? *Oikos* 94:27–38.
- Pastor J, Dewey B, Moen R, Mladenoff DJ, White M, Cohen Y. 1998. Spatial patterns in the moose-forest-soil ecosystem of Isle Royale, Michigan, USA. *Ecol Appl* 8:411–24.
- Pinheiro J, Bates D. 2000. Mixed-effects models in S and S-Plus. New York: Springer.
- Prescott CE. 2002. The influence of the forest canopy on nutrient cycling. *Tree Physiol* 22:1193–200.
- Prieto-Fernandez A, Acea MJ, Carballas T. 1998. Soil microbial and extractable C and N after wildfire. *Biol Fertil Soils* 27:132–42.
- Rensburg AJ, Turner MG. 2006. Amount, position, and age of coarse wood influence litter decomposition in postfire *Pinus contorta* stands. *Can J For Res* 36:2112–23.
- Ritz K, McNicol JW, Nunan N, Grayston S, Millard P, Atkinson D, Gollette A, Habeshaw D, Boag B, Clegg CD, Griffiths BS, Wheatley RE, Glover LA, McCaig AE, Prosser JI. 2004. Spatial structure in soil chemical and microbiological properties in an upland grassland. *FEMS Microbiol Ecol* 49:191–205.
- Robertson GP, Huston MA, Evans FC, Tiedje JM. 1988. Spatial variability in a successional plant community: patterns of nitrogen availability. *Ecology* 69:1517–24.
- Rodríguez A, Duran J, Fernandez-Palcios JM, Gallardo A. 2009. Short-term wildfire effects on the spatial pattern and scale of labile organic-N and inorganic-N and P pools. For *Ecol Manag* 257:739–46.
- Romme WH, Tinker DB, Stakes GH, Turner MG. 2009. Does inorganic nitrogen availability limit plant growth 3–5 years after fire in a Wyoming lodgepole pine forest? For *Ecol Manag* 257:829–35.
- SAS Institute. 2003. SAS Version 9.1.3. Cary, NC: SAS Institute Inc.
- Schimel JP, Bennett J. 2004. Nitrogen mineralization: challenges of a changing paradigm. *Ecology* 85:591–602.
- Schoennagel T, Veblen TT, Romme WH. 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. *BioScience* 54:661–76.
- Smithwick EAH, Turner MG, Mack MC, Chapin FSIII. 2005a. Post-fire soil N cycling in northern conifer forests affected by severe, stand-replacing wildfires. *Ecosystems* 8:163–81.
- Smithwick EAH, Mack MC, Turner MG, Chapin FSIII, Zhu J, Balsler TC. 2005b. Spatial heterogeneity and soil nitrogen dynamics in a burned black spruce forest stand: distinct controls at different scales. *Biogeochemistry* 76:517–37.
- Ste-Marie C, Paré D. 1999. Soil, pH and N availability effects on net nitrification in the forest floors of a range of boreal forest stands. *Soil Biol Biochem* 31:1579–89.
- Tateno M, Chapin FSIII. 1997. The logic of carbon and nitrogen interactions in terrestrial ecosystems. *Am Nat* 149:734–44.
- Turner MG. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91:2833–49.
- Turner MG, Chapin FSIII. 2005. Causes and consequences of spatial heterogeneity in ecosystem function. In: Lovett GM, Jones CG, Turner MG, Weathers KC, Eds. *Ecosystem function in heterogeneous landscapes*. New York: Springer. p 9–30.
- Turner MG, Romme WH. 1994. Landscape dynamics in crown fire ecosystems. *Landsc Ecol* 9:59–77.
- Turner MG, Romme WH, Gardner RH, Hargrove WW. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecol Monogr* 67:411–33.
- Turner MG, Romme WH, Gardner RH. 1999. Prefire heterogeneity, fire severity and plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. *Int J Wildland Fire* 9:21–36.
- Turner MG, Romme WH, Tinker DB. 2003. Surprises and lessons from the 1988 Yellowstone fires. *Front Ecol Environ* 1:351–8.
- Turner MG, Tinker DB, Romme WH, Kashian DM, Litton CM. 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). *Ecosystems* 7:751–75.
- Turner MG, Smithwick EAH, Metzger KL, Tinker DB, Romme WH. 2007. Inorganic nitrogen availability following severe stand-replacing fire in the Greater Yellowstone Ecosystem. *Proc Natl Acad Sci USA* 104:4782–9.
- Turner MG, Smithwick EAH, Tinker DB, Romme WH. 2009. Variation in foliar nitrogen and aboveground net primary production in young postfire lodgepole pine. *Can J For Res* 39:1024–35.
- Vitousek PM, Melillo JM. 1979. Nitrate losses from disturbed forests—patterns and mechanisms. For *Sci* 25:605–19.
- Vitousek PM, Reiners WA. 1975. Ecosystem succession and nutrient retention: a hypothesis. *BioScience* 25:376–81.
- Walley FL, Van Kessel C, Pennock DJ. 1996. Landscape-scale variability of N mineralization in forest soils. *Soil Biol Biochem* 28:383–91.
- Wan S, Hui D, Luo Y. 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. *Ecol Appl* 11:1349–65.
- Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science* 313:940–3.
- Yavitt JB, Fahey TJ. 1986. Litter decay and leaching from the forest floor in *Pinus contorta* (lodgepole pine) ecosystems. *J Ecol* 74:525–45.
- Yermakov Z, Rothstein DE. 2006. Changes in soil carbon and nitrogen cycling along a 72-year wildfire chronosequence in Michigan jack pine forests. *Oecologia* 149:690–700.
- Zak DR, Host GE, Pregitzer KS. 1989. Regional variability in nitrogen mineralization, nitrification and overstory biomass in northern lower Michigan. *Can J For Res* 19:1521–6.