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Landscape Heterogeneity of Differently Aged Soil Organic Matter Constituents at the Forest–Alpine Tundra Ecotone, Niwot Ridge, Colorado, U.S.A.

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Abstract

One of the major remaining obstacles to understanding how ecosystems process carbon (C) and nitrogen (N) within soil organic matter (SOM) is landscape heterogeneity. While many studies have investigated landscape heterogeneity in total SOM C and N, less information exists on landscape patterns for differently aged constituents within SOM. These differently aged constituents can show distinct landscape-level patterns and levels of heterogeneity that contribute to our understanding of the production and decomposition processes that create SOM. Using field measurements from an alpine-subalpine ecosystem and geostatistical analyses, I show here that C and N in the older more recalcitrant SOM of mineral soil have more defined spatial patterns and are less heterogeneous than C and N in the newer more labile SOM of mineral soil at the forest-alpine tundra ecotone (SOM C: CV = 45% in older, 59% in newer; partial sill [sill minus nugget, i.e., percent of variation explained by spatial autocorrelation] = 38% in older, 11% in newer; SOM N: CV = 50% in older, 48% in newer; partial sill = 6% in older, 44% in newer). I also demonstrate that C:N ratios show better spatial patterns and reduced landscape heterogeneity when compared with their constituent C and N concentrations (CV of total SOM C = 41%, total SOM N = 31%, total SOM C:N = 20%; partial sill of total SOM C = 15%, total SOM N = 18%, total SOM C:N = 64%). The reduced heterogeneity and strong relationships between C and N in older SOM suggest that landscape variation in the chemical composition of the SOM in mineral soils converges over time, possibly as a result of greater chemical variation in plant inputs relative to the products of decomposition reactions.

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Introduction

Soil organic matter (SOM) is a complex mixture of chemical constituents that vary widely in their properties. SOM contains both fresh labile material that enters the ecosystem via primary production and more recalcitrant material formed during microbial decomposition, which can have residence times of decades or centuries (Gaudinski et al., 2000). While many studies have examined the chemistry, decomposition rates, and relative abundances of these differently aged constituents (e.g., Baisden et al., 2002; Neff et al., 2002; Sollins et al., 2006), we have little information on landscape-level geostatistical patterns for these constituents within the SOM of mineral soils. Studies of landscape-level geostatistical patterns in *total* SOM carbon and nitrogen have shown both that SOM C and N can be spatially correlated over distances of 100–1000 m and that substantial variation can be present even over short distances in flat terrain (e.g., Robertson et al., 1993; Cambardella et al., 1994; Gallardo, 2003; Rodionov et al., 2007). Understanding these patterns geostatistically for both total SOM and constituents within SOM is important for understanding how variation in biotic and abiotic conditions across a landscape affects total SOM levels and rates of SOM processing (Hugelius and Kuhry, 2009). For instance, variation in SOM chemistry across a landscape may help determine how SOM levels in different landscape patches respond to climate change.

Ecosystems with complex terrain such as mountains are valuable for studying landscape heterogeneity because they contain considerable variation in climatic, geomorphic, and biotic factors within a small physical space. The importance of landscape heterogeneity in alpine-subalpine biogeochemistry is described in a conceptual model called the Landscape Continuum Model, which hypothesizes that higher-elevation alpine meadows subsidize lower-elevation forests and waterways with water and nutrients through transport (Seastedt et al., 2004). Niwot Ridge, which is part of the Long Term Ecological Research (LTER) network, is an alpine-subalpine ecosystem in the Front Range of the Rocky Mountains (Colorado, U.S.A.) and a model system for studying complex terrain (Bowman and Seastedt, 2001; Seastedt et al., 2004). The complex terrain and landscape continuum on Niwot Ridge provide a good opportunity to examine soil carbon and nitrogen chemistry in organic-rich soils across a range of biotic and abiotic conditions (Hansen-Bristow, 1981). The Niwot Ridge landscape includes both an elevation gradient from alpine tundra to subalpine forest and a topographic/snow gradient of snow depth and snow cover duration that varies with landscape slope and aspect in relation to the prevailing westerly winds. Previous work on Niwot Ridge has shown high levels of variation and moderately well defined spatial patterns in soil carbon across the topographic/snow gradient in the alpine (Litaor et al., 2002). However, no spatially explicit work has examined either soil carbon along the elevation gradient, or nitrogen along either

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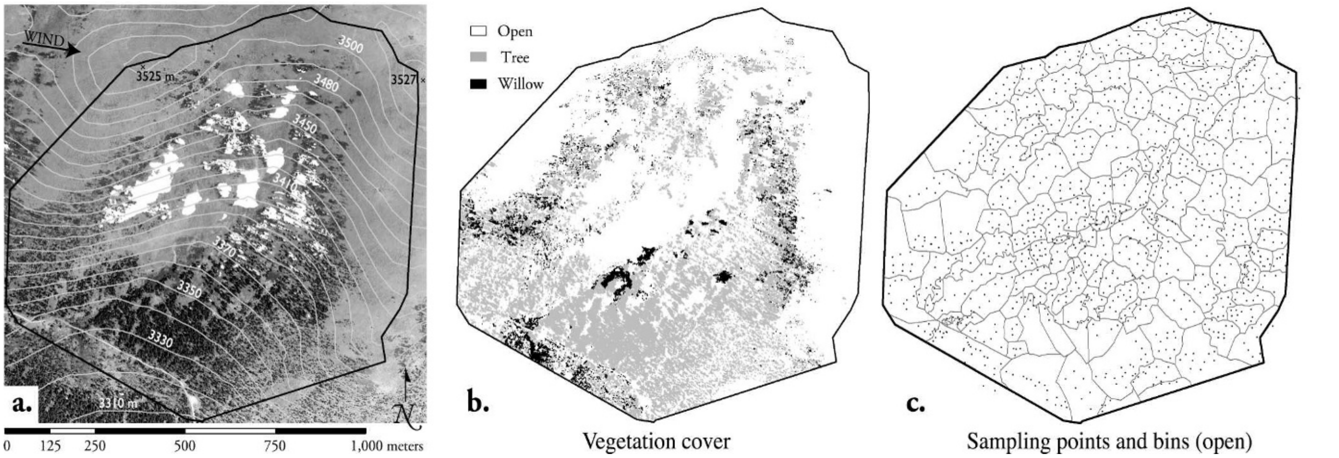


FIGURE 1. (a) Aerial photo of the study site, which is on Niwot Ridge in the Front Range of the Rocky Mountains, Colorado, U.S.A. The predominant wind direction is shown by the arrow in the upper left. The contour interval is 10 m. (b) Vegetative physiognomy in the study site. (c) Sampling design. Each point represents a soil core. These soil cores were composited in the field into bins shown by the gray polygons. This figure shows only the soil cores from open areas; an equivalent representation could be shown for tree- or willow-covered areas.

gradient. Nitrogen is a key nutrient influencing NPP and species composition and important from a management perspective due to the documented effects of anthropogenic N deposition (Bowman et al., 1993, 2006; Williams and Tonnessen, 2000).

One way to divide the SOM of mineral soils into meaningful fractions is to separate it by density. Separating SOM by density creates fractions that vary substantially in average susceptibility to decomposition, and thus, average residence time (Christensen, 1992; Sollins et al., 2006). Less dense fractions contain most of the fresh plant material while more dense fractions contain more heavily processed byproducts of decomposition (Sollins et al., 2006). Recent studies of SOM decomposition have suggested that, regardless of plant input chemistry, a relatively homogeneous set of microbially derived products build up as recalcitrant SOM (Grandy and Neff, 2008). Due to this evidence, we can hypothesize that landscape heterogeneity is lower in the more dense fraction that contains older, more recalcitrant material.

In this study, I use spatially explicit soil core composite samples of the top 10 cm of mineral soil and the density separation technique to test the hypothesis that older, more recalcitrant carbon and nitrogen are less heterogeneous across the landscape than younger more labile material in an alpine-subalpine ecosystem on Niwot Ridge. I also test the same hypothesis for C:N ratios to examine how the relationship between C and N pool sizes varies with SOM age. To quantify landscape heterogeneity, I evaluated three different aspects of heterogeneity—overall variation, the magnitude of spatial autocorrelation, and the scale of spatial autocorrelation using three corresponding metrics: the coefficient of variation (CV) is used as a metric of overall variation, the relative magnitude of the modeled variogram nugget and sill is used as a metric of the magnitude of spatial autocorrelation, and the variogram range is used as a metric of the scale of spatial autocorrelation (Robertson et al., 1988; Cambardella et al., 1994; Schlesinger et al., 1996). To further explore the relationship between C and N pool sizes, I also examine correlations between C and N in each SOM age fraction as well as between C:N ratios in the different SOM age fractions.

Methods

STUDY SITE

The study site is a 0.89 km^2 alpine-subalpine ecosystem on Niwot Ridge (40°2′58.47″N 105°34′18.27″W; Fig. 1A). This site was chosen because the forest-alpine tundra ecotone provides considerable landscape heterogeneity for its size (Hansen-Bristow, 1981). The study site begins at the crest of Niwot Ridge (3510 m a.s.l.) and continues into the subalpine forest (3290 m a.s.l.). The site contains several gradients such as the snow gradient from deep snowfields to dry windblown meadows created by topography and tree islands (Holtmeier and Broll, 1992; Seastedt and Adams, 2001; Walker et al., 2001); the windward and leeward slopes that range from 0 to 22°; and the ridgetop-sideslope-toeslope topography. The site also contains small seasonal wetlands and is drained by several intermittent streams that typically run May through July. Many different soil types have been identified within the study site. The open areas primarily contain Inceptisols such as Cryumbrepts and Cryochrepts, while the tree-covered areas contain Alfisols such as Cryoboralfs (Burns, 1980). The forested areas have organic horizons of variable thickness (~1–50 cm) consisting primarily of conifer needles. The open areas have some bare soil and some organic horizons that are much thinner (~1–3 cm) than those of the forest and consist of the previous year's litter.

Using a digital orthophoto with 0.3 m × 0.3 m pixels (USGS, 2004), the locations of trees and willows in the study site were digitized using ArcGIS 9.2 (ESRI). This digitized representation of vegetative physiognomy shows that the study site is 4% willow and other shrubs, 24% trees, and 72% open areas dominated by low-growing herbs (Fig. 1B). Most of the trees in the study area are either *Picea engelmannii* or *Abies lasiocarpa*. There are also some patches of *Pinus flexilis*. Common willow species include *Salix planifolia* and *Salix glauca*.

SAMPLE COLLECTION

In July–October 2006, I collected 1850 georeferenced soil cores (3 cm diameter, 10 cm depth) throughout the study site. Organic horizons were excluded, and the top 10 cm of mineral soil were used. Despite their importance to SOM C in many ecosystems (Rinke et al., 2008), organic horizons were excluded for three reasons: (1) it was not possible to measure both horizons due to sample size limitations; (2) at least 10 cm of mineral soil were present at all sample sites unlike the variable organic horizon; and (3) mineral soils may provide more general information since not all soils have organic horizons. To achieve a manageable sample size for laboratory analysis, the soil cores were pooled into 240 samples (Fig. 1C: points are cores and gray polygons are composites). Soil cores were pooled in the field by mixing in a bucket. Composites were made only among samples taken in areas of similar physiognomy: open, trees, or shrubs. Composites consisted of 3–10 cores. Their locations were chosen by subsampling within areas that were internally homogeneous relative to their surroundings based on visible landscape features such as vegetation and land cover. Fewer cores were collected in smaller patches and individual core locations were chosen haphazardly within the patches. The number of cores was varied among composites in order to keep an even distance among cores whether the patches were large or small; thus, smaller composite sizes show smaller areas on the map. Composites were collected instead of single-core measurements in order to reduce the large amounts of heterogeneity that can be created by core-to-core variation. Thus, the composites are better suited to showing larger-scale landscape patterns than point measurements. The average distance between the soil core composite centroids was 61 m and the average area represented by a composite was 3700 m^2. Locations for the soil cores were collected using a Trimble TDC1 datalogger with sub-meter accuracy.

LABORATORY ANALYSIS

The 240 soil core composites were each sieved through a 2 mm sieve, then wetted to field capacity with 50 mL deionized water. The soil samples were then frozen and freeze dried in order to break up aggregates. Soil composites were then separated into two fractions using sodium polytungstate at a separation density of 1.8 g cm^{-3}. The density separation procedure is described in Christensen (1992) and Six et al. (1999). The less dense fraction will hereafter be referred to as the light fraction and the more dense fraction as the heavy fraction. Neff et al. (2002) reported that on Niwot Ridge, organic matter less dense than 1.6 g cm^{-3} showed a ^{14}C signature indicative of a turnover time of about a decade while the more dense fraction was shown to be, on average, older than atmospheric testing of nuclear weapons in the middle of the 20th century, indicating a turnover time of decades to centuries. Because I used a higher density cutoff (1.8 g cm^{-3} vs. 1.6 g cm^{-3}) in this study, that difference in residence times is likely larger. To eliminate large quartz crystals in samples of the heavy fraction, the samples were sieved through a 250 μm sieve and only the smaller particles were analyzed. Elemental analyses (Shimadzu) showed that the smaller particles contained >90% of the SOM in the heavy fraction. Samples of the sieved heavy fraction and light fraction were then ground with a mortar and pestle, weighed to the nearest microgram, packaged in tins and analyzed for C and N concentrations using a continuous flow PDZ Europa Scientific 20/20 Mass Spectrometer with an attached ANCA/SL elemental analyzer at the Center for Stable Isotope Biogeochemistry, University of California, Berkeley.

DATA ANALYSIS

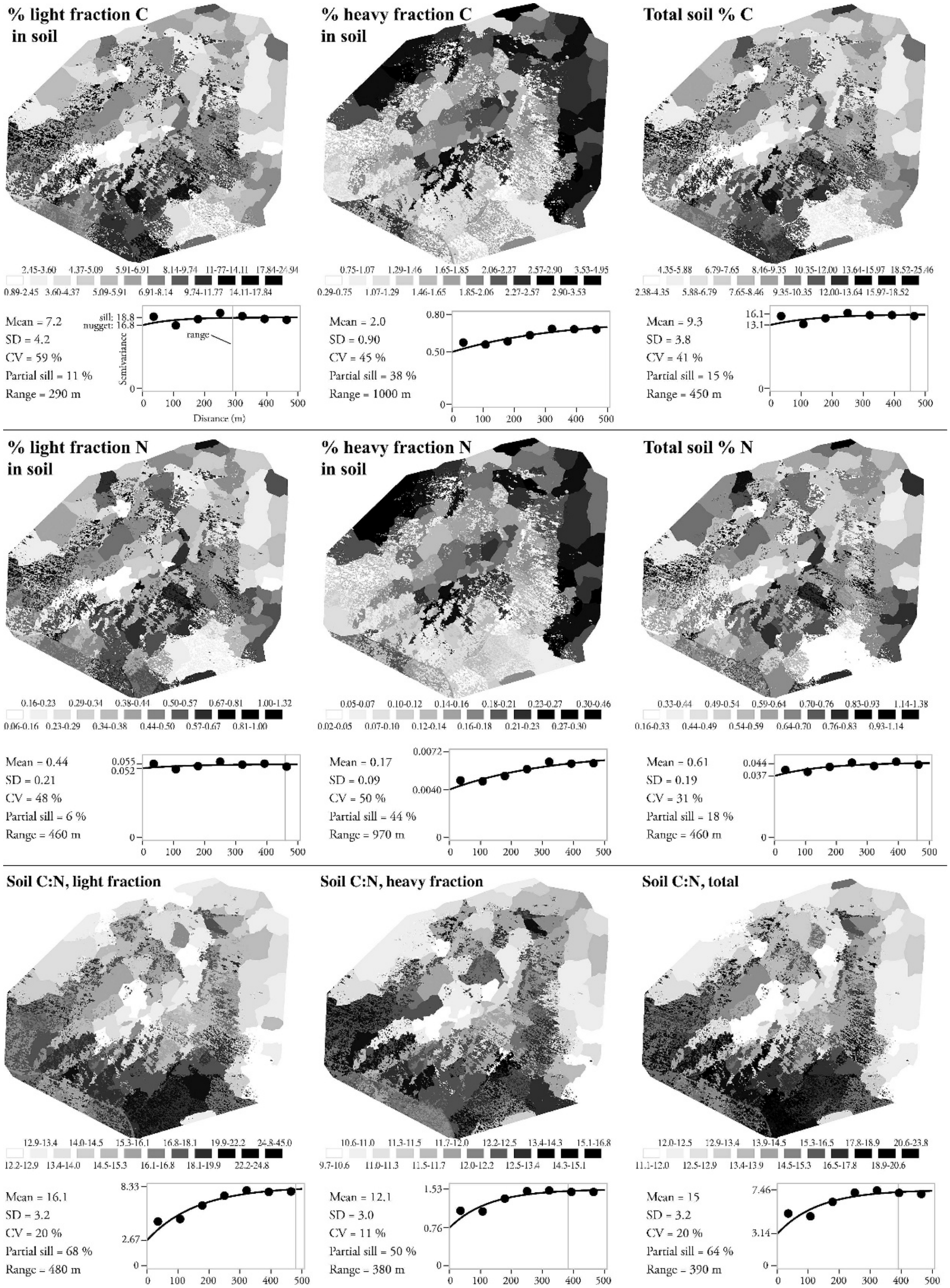
Heavy and light C and N values were multiplied by their relative fraction abundance so that the reported values are the amount of heavy and light material at the different collection points instead of the percentages within the density fractions (i.e., % light fraction C or N in *total* soil instead of % C or N within *light fraction* soil). I chose to report the % of light fraction C and N in total soil because I wanted to explore heterogeneity in the amount of these SOM constituents across the landscape instead of the heterogeneity in the concentration of these constituents within fractions.. Values for the total soil C and N percentages were calculated as the sum of the light and heavy fraction components.

In addition to the division of the landscape by vegetative physiognomy (trees, shrubs, open), the study site was also divided into polygons representing the extent of each soil core composite; three such divisions were made: one for open herbaceous areas, one for tree-covered areas, and one for willow-covered areas (the open division is shown in Fig. 1C). These polygons were created by modifying a Voronoi tessellation of the sets of points in each composite so that the polygon edges more closely matched landscape features visible in the aerial photograph. Using the maps of cover, the bin polygons, and the field data, best estimates for light, total, and heavy carbon and nitrogen, as well as C:N ratio were made for the entire study site. Estimates for open areas were made from soil core composites collected in open areas; estimates for tree- and willow-covered areas were likewise made from composites collected in those physiognomic types.

For each of the nine variables considered in this study (%C, %N, and C:N ratio for each of the three SOM density fractions: light, heavy, and total), descriptive statistics (mean, SD, and coefficient of variation) were calculated using mean and variance values that were weighted by the ground area represented by each soil core composite. Using these weighted numbers gives a more valid estimate for the study site as a whole without introducing bias due to differences in spatial sampling intensity. Correlations among variables were evaluated using ordinary least squares linear regressions, also weighted by ground area. Coefficients of variation are used as metrics for overall variation, the first of three metrics used in this study to represent landscape heterogeneity.

To evaluate the magnitude and the scale of spatial autocorrelation for the nine variables, empirical and modeled variograms[1] using the locations of the soil composite centroids were constructed using the package geoR in R 2.6.0 (Diggle and Ribeiro, 2007). Variogram bins were chosen to divide half of the maximum distance between points (ca. 500 m) into 70 m sections, which was chosen to be close in size to the average distance between soil composite centroids (61 m). Exponential functions were used to model the variograms, and from these, the nugget variance (τ^2), sill variance ($\tau^2 + \sigma^2$), and practical range ($3f$) were estimated (Diggle and Ribeiro, 2007). Since variogram lag distances are usually calculated using point measurements instead of composite centroids, the variogram parameters calculated here are not directly comparable to parameters from other studies that are estimated from point measurements. However, the variogram

[1] The variogram is a standard geostatistical technique used to explore the level of spatial correlation among samples at different distances. Residual variation at points with no distance between them is referred to as the *nugget* variance. The distance at which points are no longer spatially correlated is referred to as the *range*, and the variance at the range is the *sill* variance. See Cressie (1993) for classical treatment; Diggle and Ribeiro (2007) for use in modern statistical software; and Schlesinger et al. (1996) for an application in ecology.



parameters calculated here are well suited to test this study's hypothesis, which focuses on comparing different constituents (older and newer SOM) within the same soil. The use of composites is advantageous for these comparisons due to the reduction in core-to-core variation that might otherwise mask landscape-level patterns. The partial sill, which is the sill variance minus the nugget variance, expressed as a percentage of the total sill variance ($1 - \tau^2/\sigma^2$) is used to represent the magnitude of spatial autocorrelation, the second of three metrics used to represent heterogeneity. The final metric of heterogeneity is the practical range, which is used to measure the scale of spatial autocorrelation.

Results

LANDSCAPE HETEROGENEITY IN HEAVY AND LIGHT FRACTION SOM

The three metrics of landscape heterogeneity supported the hypothesis that there is reduced heterogeneity in the older SOM C and N pools of mineral soils within the study site (Fig. 2). SOM C concentrations in the heavy fraction showed lower coefficients of variation than the SOM C in the light fraction (45% vs. 59%) as well as higher levels of spatial autocorrelation (partial sill = 38% vs. 11%) over longer distances (range = 1000 m vs. 290 m). SOM N concentrations in the heavy fraction also showed higher levels of spatial autocorrelation than SOM N in the light fraction (partial sill = 44% vs. 6%) that extend over longer distances (range = 970 m vs. 460 m). However, coefficients of variation in SOM N were similar in the light and heavy fractions (48% vs. 50%).

Differences in landscape heterogeneity between SOM C:N ratios in the light fraction and heavy fraction were less clear. While coefficients of variation show the hypothesized pattern, with lower levels of variation in the heavy fraction than the light fraction (CV 10% vs. 20%), the magnitude and scale of spatial autocorrelation show trends in the opposite direction: a larger partial sill was observed in the light fraction SOM C:N ratios when compared with the heavy fraction (68% vs. 50%); and a larger range of spatial autocorrelation was observed in the light fraction (480 m vs. 380 m). Thus, for C and N concentrations, the hypothesis of reduced heterogeneity was supported, while for C:N ratios, the hypothesis was supported for overall variation (as measured by CV%) but not for range and magnitude of spatial autocorrelation.

Averaged across the study site, SOM carbon comprises 9.3 ± 3.8% (mean ± SD, range = 2–25%) of the rock-free soil mass in the top 10 cm of mineral soil. Nitrogen comprises 0.61 ± 0.19% (range = 0.13–1.38%; Fig. 2). The light fraction contained most of the SOM C and N (77% of C and 72% of N). Soils below tree canopies have higher percentages of C and N (mean ± SD C = 13.3 ± 3.7%, N = 0.70 ± 0.20%) than the open areas (C = 7.7 ± 2.4%, N = 0.58 ± 0.18%), a difference of 5.6 ± 0.9 (mean ± 95% CI) for C and 0.12 ± 0.06 for N (Fig. 2). Aside from the difference between trees and open areas, there are no other obvious spatial patterns in the light fraction SOM C or N. However, there are several patches within the study site that are more internally homogenous: for example, the low levels of light fraction SOM C in the southeastern corner of the study site coincide with a relatively dry area that burned in the late 19th century. The patterns in *total* SOM C and N are similar to those in the light fraction because the light fraction makes up more of the total fraction and there is less variation in the heavy fraction. Stronger landscape-level patterns are present in the heavy fraction, with a greater buildup of heavy fraction SOM C and N in the top 10 cm of mineral soil in the alpine dry meadows above the krummholz and in the wet subalpine meadows that are interspersed with the dense stands of tall trees on the toeslope (Fig. 2).

While overall the light fraction material made up 42 ± 21% (mean ± SD) of the total collected soil mass (top 10 cm of mineral soil), tree-covered areas had 58 ± 21%, and open areas had 32 ± 14% light fraction material (Fig. 3). The heavy fraction that was smaller than 250 μm—on which the analyses were done—made up 34 ± 12% of the soil mass, and the larger heavy fraction made up 24 ± 11% (Fig. 3). Corresponding to the higher amounts of light fraction material, the mineral soils under trees also had lower amounts of total heavy fraction material (24 ± 11% under trees, 38 ± 8% in open areas) as well as heavy fraction C and N (1.1 ± 0.4% C under trees, 2.4 ± 0.8% C in open areas; 0.07 ± 0.03% N under trees vs. 0.21 ± 0.07% N in open areas). The mass of C and N in the light fraction at any given area is strongly correlated with the mass of soil material within that fraction (r^2 = 0.83 for C, 0.87 for N). This indicates that a reasonable estimate of the amount of light fraction SOM C or N can be made by measuring the light fraction mass. The correlation is, however, weaker for the heavy fraction (r^2 = 0.45 for C, 0.43 for N). There is also a very poor correlation between percent light material and percent C or N within the light fraction (r^2 = 0.01 for C, 0.03 for N). Finally, within the light fraction, the percentage of C and N are relatively consistent (18.8 ± 3.9% for C and 1.15 ± 0.18 for N).

RELATIONSHIPS BETWEEN C AND N

Carbon and nitrogen concentrations are moderately correlated in the light fraction SOM (r^2 = 0.24), but strongly correlated in the heavy fraction SOM (r^2 = 0.95) (Figs. 4A, 4B). The mean C:N ratio for the study site is 15 ± 3.0 (mean ± SD), with the light fraction being 16.1 ± 3.2 and the heavy fraction being 12.1 ± 1.3. The C:N ratios in SOM were higher under trees than in open areas: 19.3 ± 1.9 under trees vs. 13.5 ± 1.7 in open areas (mean ± SD), a difference of 5.9 ± 0.5 (mean ± 95% CI). C:N ratios were also substantially less variable than their constituent C and N pools (CV% of total SOM C = 41%, total SOM N = 31%, total SOM C:N = 20%) and showed higher levels of spatial autocorrelation (partial sill of total SOM C = 15%, total SOM N = 18%, total SOM C:N = 64%). The range of spatial autocorrelation was slightly lower for total SOM C:N ratios (390 m vs. 450 m for SOM C and 460 m for SOM N). Unlike the constituent C and N pools, which show poor correlations between the light and heavy fraction (r^2 = 0.07 and 0.13, Figs. 4D, 4E), C:N ratios in the light and heavy SOM fractions were well correlated (r^2 = 0.60, Figs. 2, 4F). C:N ratios in both the light and heavy fraction were generally lowest in the dry alpine meadows above the krummholz trees and the steep, relatively unvegetated sideslope in the center of the watershed (Fig. 2). In the heavy fraction SOM, low levels of variation (CV = 10%) were observed around the median of 11.9 (Fig. 4C).

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FIGURE 2. Maps and semivariograms of SOM C, SOM N, and SOM C:N ratio in the study site. For map scale, see Figure 1. These maps combine the field-measured soil data with the remotely sensed physiognomy data. Areas with open physiognomy only show values from soil cores taken in open areas while areas with tree- or willow-cover physiognomy only show values from soil cores taken under the canopies of trees or willows. See Figure 1B for the distribution of trees and willows. On the variograms, the points show an empirical variogram for half of the maximum study site distance (ca. 500 m) divided into 7 bins (70 m each, similar to the average distance between soil core composite centroids). The black curves show exponential functions (Diggle and Ribeiro, 2007) that have been fitted to the empirical variograms. For all variograms, the vertical axis is the semivariance. The vertical axis is labeled at 0, the nugget, and the sill (see top left panel). The horizontal axis is distance (m). The variogram range is marked on the variograms as a vertical gray line. To the left of the variograms, summary statistics are shown—mean and standard deviation—as well as the three metrics of landscape heterogeneity used in this study: coefficients of variation (CV%), the partial sill of the variogram, and the variogram range. Estimates of mean, SD, and coefficients of variation (CV%) were weighted by the area represented by each sample, thus providing landscape-relevant estimates.

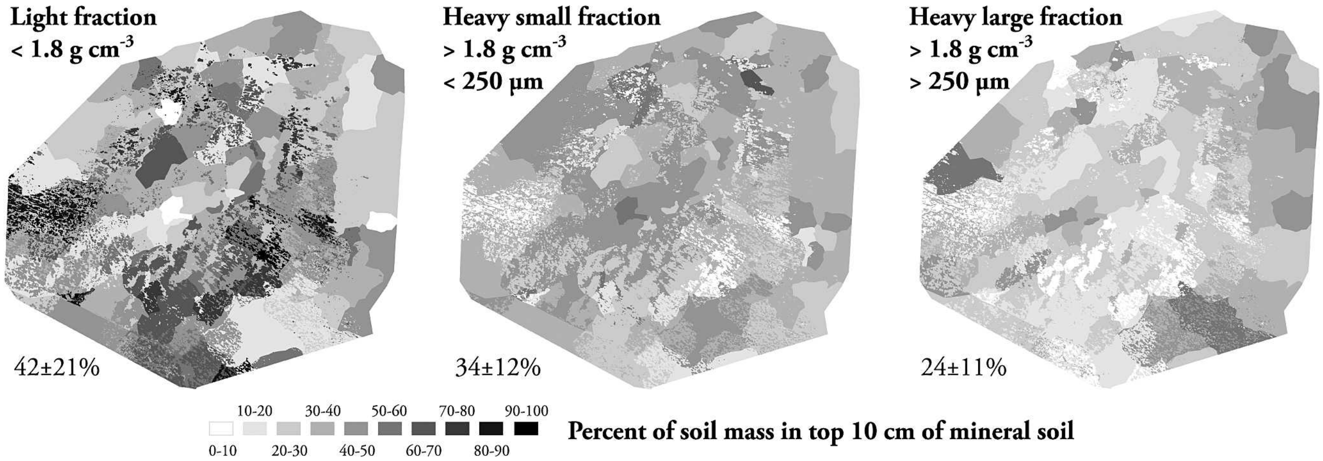

FIGURE 3. Percentages of soil by mass in the density and size fractions used in this study. All samples were taken from the top 10 cm of mineral soil, excluding organic layers. The light fraction consisted of material less dense than 1.8 g cm^{-3}. The heavy fraction material was more dense than 1.8 g cm^{-3} and was divided by size into two further fractions with particle sizes larger or smaller than 250 μm. Measurements were made on the SOM in the light fraction and the smaller heavy fraction. The larger heavy fraction was separated for ease of analysis and contained little SOM. The overall percentages of soil in each fraction are shown at the lower left of each map (mean ± SD).

Discussion

LANDSCAPE HETEROGENEITY IN OLDER AND NEWER SOM

Overall, the hypothesis that older SOM C and N concentrations in the top 10 cm of mineral soil are less heterogeneous across the study site than younger SOM C and N concentrations is supported. The results of this study are consistent with a model of decomposition in which microbial processing leads to SOM that is more chemically homogeneous than its plant-derived inputs (Grandy and Neff, 2008). Although many factors can influence landscape heterogeneity in SOM, a good explanation for the difference between the density fractions observed in this study is that there are different scales of variation for factors controlling production and decomposition rates. The heterogeneity in the light fraction SOM C and N may reflect the scale at which plant

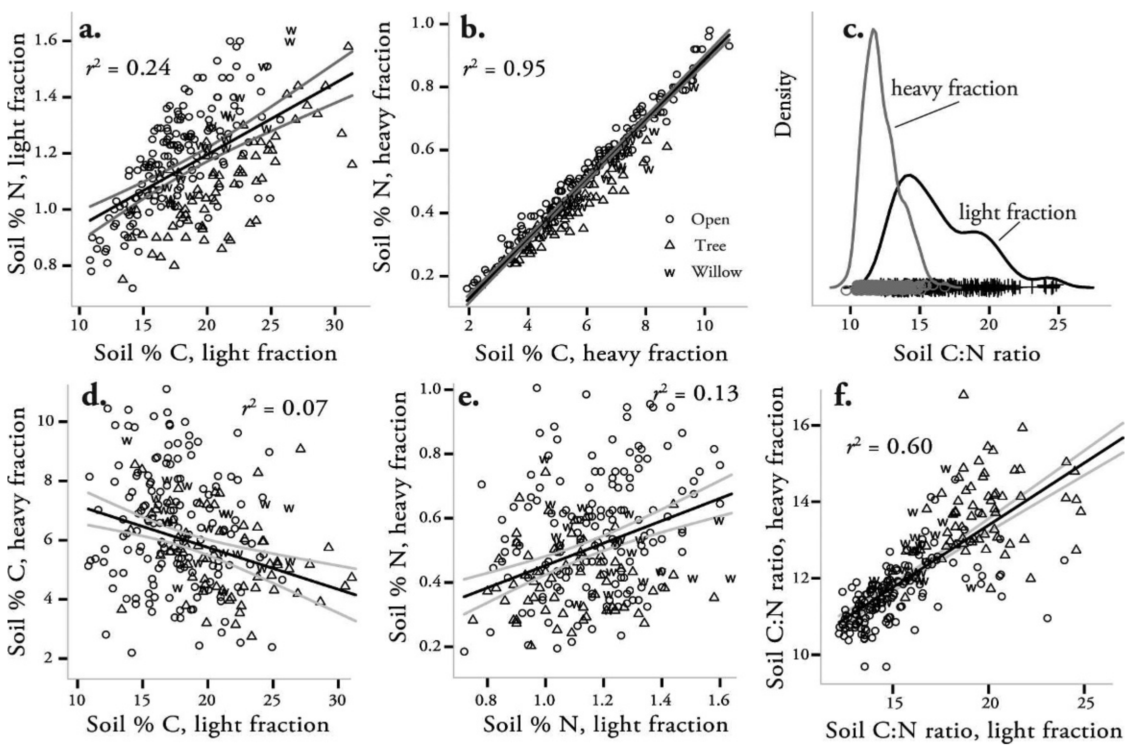

FIGURE 4. Correlations between carbon and nitrogen in (a) the light soil density fraction and (b) the heavy soil density fractions. Black lines indicate linear regressions weighted by soil composite polygon area. Ninety-five percent confidence intervals for these regressions are shown as gray curves. Correlation coefficients (r^2) values are weighted by soil composite polygon area. (c) Density plots of the C:N ratio in light and heavy soil organic matter (Sarkar, 2007). (Density plots are a non-binned generalization of the histogram that use kernel density estimates. Instead of grouping data into arbitrarily sized histogram bins, a moving window [kernel] is evaluated at each data point to estimate the underlying probability density function.) Values for individual soil core composites are shown as "+" for the heavy fraction and "O" for the light fraction. (d–f) Correlations between light and heavy fractions of SOM for C:N ratio, C, and N.

production and chemistry vary in the study site, leading to the observed high variability and low spatial correlation in light fraction SOM. In other ecosystems, individual plants have been shown to have a strong influence on SOM concentrations (Jackson and Caldwell, 1993). Likewise, larger-scale patterns in the heavy fraction SOM C and N may reflect larger scales of variability associated with the climatic and geomorphic controls over decomposition and SOM transformation. Plants can still influence decomposition by affecting microbial habitat and activity, but the snowpack-generated differences in temperature and moisture are thought to be the most important controls on decomposition in alpine environments (Seastedt et al., 2001; Saha et al., 2006).

Heavy fraction SOM comprises a greater proportion of the SOM in the top 10 cm of mineral soils in the dry alpine meadows above the krummholz trees, indicating either high inputs or low outputs of recalcitrant organic compounds in those areas. Heavy fraction SOM is also low in the soils sampled below tree canopies. There are many possible explanations for these differences among landscape patches. Differential inputs of resistant materials from the labile fraction into the recalcitrant fraction may play a role: graminoids (most commonly *Carex rupestris*) are dominant in the dry meadows (Komarkova and Webber, 1978; Walker et al., 2001) and may have compounds in their litter that are more likely to contribute to the heavy fraction. However, this is counter to what we might expect since conifer litter often decomposes more slowly than graminoid litter (Preston and Trofymow, 2000; Silver and Miya, 2001). There may also be differential incorporation of heavy fraction SOM into deeper soils. The heavier compounds in tree-covered areas may be found in soil horizons below the top 10 cm of mineral soil while in the dry meadows they are closer to the surface.

These patterns may also reflect the relatively low rates of decomposition in the dry alpine meadows, which are drier and colder than the tree-covered areas and the lower-elevation meadows. The dry meadows in this study site have little snow cover throughout the year (Darrouzet-Nardi, unpublished data), which can lead to soil temperatures well below 0 °C and lower summer soil moisture, thus leading to reduced microbial activity (Brooks and Williams, 1999; Sjögersten and Wookey, 2002; Schmidt et al., 2007). Due to the low snow cover, the dry meadows also experience more freezing and thawing, which could affect decomposition rates and hence the concentration of SOM constituents. Additionally, the organic layer in the forest may insulate forest soils (Mazhitova et al., 2004). Finally, leaching of dissolved organic matter from SOM by snow meltwater is known to be an important export pathway for SOM in high elevation ecosystems, and the low snow cover in the dry meadows may reduce leaching rates (Williams et al., 2007).

The relatively high variation in landscape-level SOM C and N in the top 10 cm of mineral soil (ranging from 2 to 25%) is mostly due to variation in the light fraction SOM, which is also strongly correlated with the amount of heavy and light soil material. However, the poor correlation between percent light material and percent C or N *within* the light fraction suggests that the light fraction does not get larger due to larger proportions of organic material. One explanation for this correlation is that as plants contribute more organic matter, those materials become enmeshed with a certain ratio of mineral soil (~4:1 mineral:organic), thus creating the light fraction.

RELATIONSHIPS BETWEEN C AND N

In contrast to the high levels of heterogeneity in light and total SOM C and N in the top 10 cm of mineral soil across the study site, patterns of C:N ratios showed substantially lower heterogeneity in both the light and heavy fractions, with smaller coefficients of variation and larger partial sills. The stronger landscape-level patterns in C:N ratios in the top 10 cm of mineral soil suggests that, at the sampling scale used in this study, broad-scale landscape factors have more influence on SOM stoichiometry of surface mineral soils than on rates of SOM input from plants and decomposition. One factor that may contribute to the stronger patterns in soil C:N ratios is variation in plant input chemistry across the study site. For example, coniferous tree tissues and litter had higher C:N ratios than herbaceous plants and contribute more to SOM at the lower elevations in the study site where the trees are larger and cover more area. Another factor that could be contributing to the strong pattern in C:N ratios is differences in abiotic conditions that affect loss and gain of C and N. Areas where low C:N ratios were observed, such as the alpine dry meadows that have low snow cover, may have conditions that favor C loss or N retention.

The strong correlation between C:N ratios in the light fraction with C:N ratios in the heavy fraction (Fig. 4F) is discordant with the lack of correlation in the underlying C and N pools. Thus, this correlation suggests a stoichiometric connection between the two density fractions that might not be expected based on the known differences in chemical composition between the fractions (Sollins et al., 2006). The correlation suggests that the stoichiometry of the products of decomposition of the light fraction materials directly influences the stoichiometry of decomposition inputs to the heavy fraction SOM. The nature of this influence is uncertain, but could be related to the identity and physiology of the saprotrophs (e.g., fungal vs. bacterial) or the particular decomposition enzymes and reactions that are activated depending on litter stoichiometry (Sinsabaugh et al., 2008).

The particularly low levels of variation in C:N ratios in the heavy soil fraction across the study site (CV = 10%) further indicate that there may be common chemical constituents in recalcitrant SOM regardless of plant inputs (Grandy and Neff, 2008). These low levels of variation in heavy fraction SOM C:N ratios have also been reported for soils of widely divergent origins, which also showed a similar ratio of around 12:1 (Sollins et al., 2006). These constituents could be remnants of undecomposed plant matter and/or recalcitrant microbially synthesized compounds. The cause of the recalcitrance could be either biochemical resistance to degradation or physical or chemical occlusion in the soil (Six et al., 2002). The convergence of C:N ratios on 12:1 in recalcitrant SOM in both this study and in Sollins et al. (2006) suggests that this may be a general phenomenon.

IMPLICATIONS FOR MANAGEMENT OF SOIL CARBON STORAGE AND ANTHROPOGENIC N DEPOSITION

Due to their low rates of decomposition, soils in cold ecosystems have relatively high levels of terrestrial carbon storage compared to warmer ecosystems. A complete accounting of carbon storage at this study site would need to include soil depth, bulk density and the >2 mm rock fraction (Rodionov et al., 2007). A more comprehensive treatment of soil horizonation, including the organic layer would also be necessary since different trends are likely for these different soil horizons. Nonetheless, the substantial coefficients of variation (~50%) in both light and heavy fraction C and N within the top 10 cm of mineral soil suggest that landscape heterogeneity is an important factor in understanding both long-term and short-term carbon storage at the forest-alpine tundra ecotone. Furthermore, the small partial sills (<40%) for these

SOM constituents suggest that simple environmental correlates such as snow depth will not be sufficient to predict landscape-level carbon stocks. Such predictions might be easier for the heavy fraction C and N with their higher partial sills, but these constituents make up less of the total SOM.

The variation in SOM N concentrations across the study site suggest that inputs and/or outputs to the SOM N pool in mineral soil vary substantially across the study site. Because of variation in N reaction and/or transport rates, we might also expect that the effects of anthropogenic N deposition will vary across the landscape. For example, areas with larger SOM N pools, especially in the recalcitrant heavy fraction, may indicate areas where nitrogen builds up due to low rates of mineralization. With low natural rates of N supply through mineralization, these areas may be particularly susceptible to increases in N supply. A spatially explicit N addition experiment (e.g., paired fertilized and control plots in a stratified random grid across the study site) would be necessary to demonstrate whether these dry meadow areas are in fact more susceptible to anthropogenic N deposition.

In the dry alpine meadows on Niwot Ridge, the heavy fraction SOM C has been shown to stabilize while the light fraction SOM C decomposes more quickly when N is added experimentally (Neff et al., 2002). A study in the Swiss Alps corroborates this finding by showing that N additions slowed decomposition of older SOM (Hagedorn et al., 2003). We can now consider these results in a landscape context. The heavy fraction makes up a large portion of the carbon in dry meadow areas where the N addition experiment took place. In contrast, other parts of the study site have a much larger quantity of light fraction material. This could mean that the effects of N deposition will result in greater carbon losses in these other soils. However, differences in litter chemistry and lower levels of actual N deposition would have to be taken into account. A spatially explicit N addition experiment as described above would also be a useful next step in understanding the effects of N deposition on soil carbon storage.

CONCLUSION

The results of this study suggest that the high levels of heterogeneity that are often observed in SOM are influenced more by the younger, more labile constituents in the SOM, which in turn may be controlled by landscape heterogeneity in plant inputs. The results of this study also show strong relationships between the carbon and nitrogen cycles in all parts of the landscape, especially in the older, more recalcitrant SOM constituents of mineral soils. The high levels of heterogeneity in these SOM pools suggests that a landscape-level perspective is necessary to understand total ecosystem function at the forest-alpine tundra ecotone.

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