

# Treeline shifts in the Ural mountains affect soil organic matter dynamics

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## Abstract

Historical photographs document that during the last century, forests have expanded upwards by 60–80 m into former tundra of the pristine Ural mountains. We assessed how the shift of the high-altitude treeline ecotone might affect soil organic matter (SOM) dynamics. On the gentle slopes of Mali Iremel in the Southern Urals, we (1) determined the differences in SOM stocks and properties from the tundra at 1360 m above sea level (a.s.l.) to the subalpine forest at 1260 m a.s.l., and (2) measured carbon (C) and nitrogen (N) mineralization from tundra and forest soils at 7 and 20 °C in a 6-month incubation experiment. C stocks of organic layers were  $3.6 \pm 0.3 \text{ kg C m}^{-2}$  in the tundra and  $1.9 \pm 0.2 \text{ kg C m}^{-2}$  in the forest. Mineral soils down to the bedrock stored significantly more C in the forest, and thus, total soil C stocks were slightly but insignificantly greater in the forest ( $+3 \text{ kg C m}^{-2}$ ). Assuming a space for time approach based on tree ages suggests that the soil C sink due to the forest expansion during the last century was at most  $30 \text{ g C m}^{-2} \text{ yr}^{-1}$ . Diffuse reflective infrared spectroscopy and scanning calorimetry revealed that SOM under forest was less humified in both organic and mineral horizons and, therefore, contained more available substrate. Consistent with this result, C mineralization rates of organic layers and A horizons of the forest were two to four times greater than those of tundra soils. This difference was similar in magnitude to the effect of increasing the incubation temperature from 7 to 20 °C. Hence, indirect climate change effects through an upward expansion of forests can be much larger than direct warming effects ( $\Delta 0.3 \text{ K}$  across the treeline). Net N mineralization was 2.5 to six times greater in forest than in tundra soils, suggesting that an advancing treeline likely increases N availability. This may provide a nutritional basis for the fivefold increase in plant biomass and a tripling in productivity from the tundra to the forest. In summary, our results suggest that an upward expansion of forest has small net effects on C storage in soils but leads to changes in SOM quality, accelerates C cycling and increases net N mineralization, which in turn might stimulate plant growth and thus C sequestration in tree biomass.

*Keywords:* carbon sequestration, climate change, decomposition, microclimate, nitrogen mineralization, Siberia, soil incubation, temperature dependency, tundra

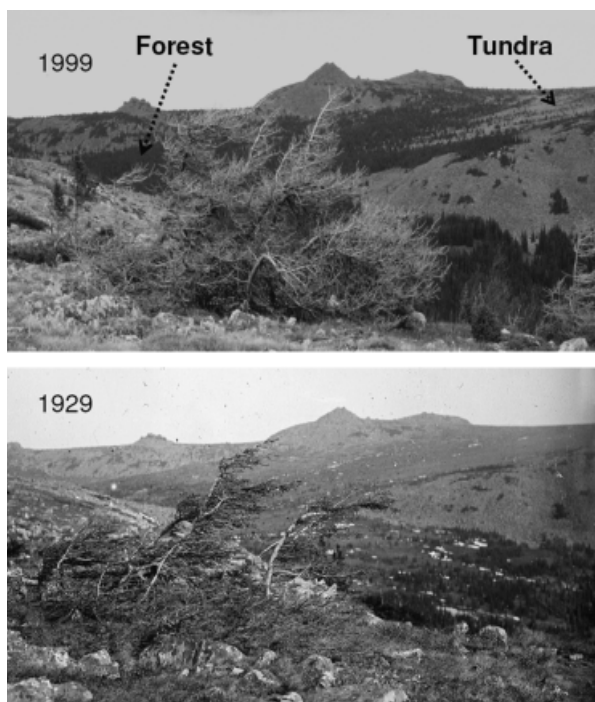
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## Introduction

Treelines are natural boundary ecosystems where dominant plant species, life forms, and plant productivity

change drastically within a small altitudinal gradient and a short distance (Körner & Paulsen, 2004; Holtmeier & Broll, 2005). In the Ural mountains, historical fixed-point landscape photographs document that positions of high-altitude treeline have advanced by 60–80 m in altitude and that the forest of the treeline ecotone has become denser during the last century (Moiseev &

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**Fig. 1** The altitudinal gradient across the treeline ecotone at Mali Iremel in 1929 and 1999. The tundra site at 1360 m a.s.l. is on the uppermost part of the slope at the right. The forest site at 1260 m a.s.l. is at the lower part of the slope just behind the hill with the bush in the foreground.

Shiyatov, 2003; Devi *et al.*, 2008; Fig. 1). These changes of the forest–tundra ecotone likely result from a changing climate because high-altitude treeline positions are thought to be limited by vegetation period temperature (Körner, 1998) in locations, such as the highest mountains of the Urals, which have never been impacted by human land-use (Moiseev *et al.*, 2004). Similar upward and northward shifts of treeline ecotones have been reported from North America, Scandinavia, and Siberia (Kullman, 2002; Moiseev & Shiyatov, 2003; Esper & Schweingruber, 2004; Lloyd, 2005), showing that these climate-induced advances occur in large areas of the Northern Hemisphere.

The advancing forest will alter carbon (C) cycling and sequestration by increasing C storage in forest biomass. Effects on soil C, however, are less certain because the upward-shifting treeline ecotone will not only change the quantity and quality of C inputs into soils, but will also lead to a more favourable microclimate with more snow accumulating and hence warmer soils in winter (Holtmeier & Broll, 1992; Sjögersten & Wookey, 2002), which may stimulate respiration losses from soils. By measuring soil organic C stocks under trees of different ages in a Canadian arctic forest–tundra landscape, Steltzer (2004) estimated that C pools under trees increased by  $18.5 \text{ g C m}^{-2} \text{ yr}^{-1}$ . In contrast, Seastedt & Adams (2001) observed that soil C stocks decreased

with the passage of ‘migrating’ tree islands in alpine tundras of the Rocky mountains. Similarly, Wilmking *et al.* (2006) reported that soils on river terraces under forest in Northwestern Alaska contained less soil organic C than adjacent tundra soils. Furthermore, Sjögersten *et al.* (2003) observed that tundra soils of the Fennoscandian mountain range had more labile C than soils of a birch forest. This suggests that a northward and upward expansion of forests will lead to C losses from ecosystems. It has been argued that increased decomposition mobilizes nitrogen (N) and other soil nutrients and thereby enhances plant growth and C sequestration in plants rather than in soils (Shaver *et al.*, 1992; Schmidt *et al.*, 2002; Weintraub & Schimel, 2003). For instance, Melillo *et al.* (2002) reported that increased plant C uptake after 10 years of experimental warming, as a result of stimulated N mineralization, could exceed C losses via respiration. For Interior Alaska, Sturm *et al.* (2005) proposed that an increase in shrub abundance leads to deeper snow, which promotes higher winter soil temperatures, greater microbial activity and more plant-available N. Similar feedbacks between vegetation, snow, and N might exist in treeline ecotones. They could lead to strong changes in plant productivity and species composition from treeless tundra to forests across a small gradient in air temperature.

In our study, we aimed to estimate how the ongoing upward shift of the treeline ecotone might affect soil C and N dynamics. We determined soil organic matter (SOM) quantity and quality along an altitudinal gradient in the Southern Ural, assuming that ecosystems at different altitudes reflect different stages of the upward-shifting subalpine forest. The Southern Ural mountains are ideal for this ‘space for time’ approach: the slopes are gentle and evenly inclined, soils are almost stone free and developed on homogeneous ‘old’ parent material, and the mountain areas are not influenced by humans (Moiseev *et al.*, 2004). We quantified SOM pools across the treeline ecotone of Mali Iremel in the Southern Ural. The quality of SOM was assessed by Diffuse Reflectance Infrared Fourier Transform (DRIFT) spectroscopy and differential scanning calorimetry (DSC). In addition, we incubated soils for 6 months in the laboratory to measure C and N mineralization as well as dissolved organic carbon (DOC) production at different temperatures. Our objectives were to study (1) how SOM quantity and quality are linked to the strong gradients in plant productivity and species composition across the treeline ecotone, (2) how the climatic-driven upward expansion of forests potentially affects C mineralization either directly through increasing temperatures or indirectly through changes in vegetation, (3) if the upward shift of the subalpine forest stimulates or suppresses net N mineralization, and (4) if the

changes in SOM cycling might lead to positive or negative feedbacks under climate warming.

## Materials and methods

### Study site

The study site was on the gentle ( $\sim 5^\circ$ ), southwest facing slope of Mali Iremel [1449 m above sea level (a.s.l.); Fig. 1] in the central part of the Southern Ural ( $54^\circ 32'N$ ,  $58^\circ 51'E$ ). Here, the treeline ecotone is located between 1200 and 1400 m a.s.l. and it is composed of a patchwork of Siberian spruce (*Picea obovata* Ledeb.) forest and open land without trees. Across the altitudinal gradient reaching from the subalpine forest to the uppermost trees (1260–1360 m a.s.l.), there is a strong decrease in forest cover from 62% to 7.5% and in total biomass from 150 to 30 t ha<sup>-1</sup> (P. Moiseev, unpublished results). At the upper end, some isolated 50–60-year-old tree islands (average height 1.7 m) are spread across the tundra. The tundra is dominated by dwarf shrubs (*Vaccinium uliginosum*, *Vaccinium vitis-idaea*) and grasses (*Carex vaginata*, *Festuca igoschiniae*). Below 1330 m a.s.l. *P. obovata* forms an open forest, in which tree groups alternate with open areas where productive herbs (*Polygonum bistorta*, *Polygonum alpinum*) grow to a height of 1.5 m (for details on forest structure see Moiseev *et al.*, 2004). The climate is continental with an annual precipitation of about 800 mm yr<sup>-1</sup>. Mean air temperature is approximately  $-14^\circ\text{C}$  in winter (December until March) and approximately  $11^\circ\text{C}$  in summer (June until August). Soils across the treeline ecotone had very thin Cv horizons, with the B horizons almost directly above the quartzite bedrock. Firsova (1977) classified the soils as mountain Cambisols (buraya gorno-lesnaya pochva), without any signs of podzolization. In the FAO classification system (IUSS Working Group WRB, 2006) the soils represented Haplic Cambisols.

### Sampling

**Sampling design.** On the gentle slopes of Mali Iremel, we established an altitudinal transect across the treeline ecotone with four macroplots (radius = 8 m) at each of the following three altitudinal levels: (i) the current treeline, the species line at 1360 m a.s.l. dominated by tundra with some tree islands, called 'tundra', (ii) the so-called 'open-forest' at 1310 m a.s.l., and (iii) the subalpine forest at 1260 m a.s.l., called 'forest'. The horizontal distance between the 'tundra' and subalpine forest was 1500 m. The macroplots at each altitudinal level spanned a horizontal distance of 200 m. Each macroplot consisted of tree groups and 'open land', which included dwarf shrub-dominated tundra at the higher site and 1.5 m high herbs in the forest.

**Soil sampling – C-pools.** In August 2004, we sampled soils under tree canopies and in open land in each of the four macroplots at all three altitudinal levels. Based on previous dendrochronological measurements (Moiseev *et al.*, 2004), we chose trees representing the typical age class of the altitudinal level: 100–110 years at 1260 m a.s.l., 70 years at 1310 m a.s.l., and 40–50 years at 1360 m a.s.l. At each tree, we dug two profiles under the canopy and in the surrounding open land (distance to trunk 2.5–6 m). In total, we dug 16 profiles per altitudinal level, eight under trees and eight in the 'open land'. Volume-based soil samples were taken from the Oi, Oe, and Oa horizons, from the mineral soils at depths of 0–7 cm (approximately corresponding to the A horizon), and where possible from 7 to 25 cm depth and from 25 cm to the bedrock. Organic layers were collected with a frame of 20 cm  $\times$  20 cm, while mineral soils were sampled with soil cores (50 cm<sup>2</sup> at 0–7 cm and 20 cm<sup>2</sup> for depths below 7 cm). Soil material was sieved to 4 mm in the field to remove stones and roots. After weighing the total mass of soils, sub samples of all soil material were taken to the laboratory, where aliquots were dried at  $60^\circ\text{C}$  for chemical analysis and sieved to 2 mm. Additional aliquots were dried at  $105^\circ\text{C}$  to determine water content and to calculate fine earth bulk density.

**Soil sampling – incubation study.** For the C and N mineralization experiment, soil material was collected separately at the end of field work in mid August 2004 to maximize freshness of the samples. We only sampled soils from the tundra (1360 m a.s.l.) and the subalpine forest site (1260 m a.s.l.), and we only took total organic layers and mineral soils (0–7 cm depth) from under the tree canopy and from the open land at each altitudinal level. In addition to C pools, a fifth tree at each level was sampled. Soils were stored in a cooling box after the sampling, refrigerated the next day and stored at  $-20^\circ\text{C}$  for 3 months until the experiment started. Finally, the soil material was sieved to 4 mm and homogenized, and roots as well as stones were removed. Aliquots were dried at  $60^\circ\text{C}$  for chemical analysis.

### Microclimatic measurements

In August 2004, we buried temperature loggers (Maxim iButton, DS1921G, Sunnyvale, CA, USA) 10 cm below the Oi and Oe horizons to monitor soil temperatures continuously during 1 year. At the species line and in the subalpine forest, we placed four loggers under the trees and in the 'open land', directly beside our soil pits. In addition, we buried four loggers in the 'open-forest' at 1310 m a.s.l. and in the tundra at 1430 m a.s.l., but only in the 'open land'. Snow depth was measured with a ski pole in two campaigns in March 2004 and 2006. The

depths were recorded in the 'open land' of all our 15 macroplots and of 75 additional macroplots, which had been established for forest structure research between 1200 and 1440 m.a.s.l. (described in Moiseev *et al.*, 2004).

#### *Incubation experiment*

To investigate SOM decomposability, we incubated organic layers and mineral soils (0–7 cm depth) in microlysimeters at 7 and 20 °C for 6-month in the dark, measuring soil respiration, DOC mobilization and net N mineralization. The lower temperature corresponded to soil temperatures at 10 cm depth during the vegetation period at high-altitude treelines (Körner & Paulsen, 2004), while the higher temperature was chosen to gain insight into the temperature dependency of the different processes. The microlysimeters were 250 mL filtration systems with 0.45 µm durapore membrane filters (Stericup, Millipore, Bedford, MA, USA) protected with 3 g acid-washed glass wool, which enabled the simultaneous measurement of CO<sub>2</sub> production, DOC leaching, and net N mineralization (Nadelhoffer & Fry, 1988; Hagedorn *et al.*, 2004). We put 20 g of fresh organic layer material and 40 g of mineral soils into the microlysimeters and covered them with glass wool. The different sample weights were chosen to obtain approximately the same respiration rates and to have similar sample volumes. After preparation, samples were stored at 4 °C for 1 week to adjust microbial activity. In total, we incubated 80 samples (two altitudes, two vegetation types, two horizons, two temperatures, five replicates). At each measurement cycle (0, 1, 2, 4, 6, 10, 14, 20, and 26 weeks after the incubation started), we leached the samples and then measured CO<sub>2</sub> production on the following day. For the leaching, 100 mL of an artificial rain solution was added to the microlysimeters and slowly leached 30 min later by applying a suction of 50 hPa with a vacuum pump. The artificial rain was composed of 2.5 µM H<sub>3</sub>BO<sub>3</sub>, 400 µM CaCl<sub>2</sub>, 100 µM KH<sub>2</sub>PO<sub>4</sub>, 50 µM K<sub>2</sub>SO<sub>4</sub>, 0.2 µM MnSO<sub>4</sub>, 5 µM CuSO<sub>4</sub>, 50 µM MgSO<sub>4</sub>, and 0.2 µM ZnCl. Soil respiration was quantified by putting the samples into 2.4 L airtight containers, flushing the containers with CO<sub>2</sub>-free air, and measuring the increase in CO<sub>2</sub> concentration for 12 h. CO<sub>2</sub> concentrations were determined by passing air from the container through an infrared gas analyser (LI 6252, LI-COR, Lincoln, NE, USA) in a closed cycle for 1 min.

#### *Chemical analysis*

Soil C and N concentrations were determined using a CN-analyser (NC 2500, Carlo Erba Instruments, Milano, Italy). In addition, we characterized incubation samples chemically by DRIFT, providing information on the contribution of major functional groups to SOM. Special attention was paid to the degree of aromaticity as

derived from the ratio of aliphatic to aromatic moieties. We first ground samples to <63 µm, mixed them with KBr to obtain a 3% (by weight) sample concentration, and measured the spectra with a Perkin Elmer (Wellesley, MA, USA) Spectrum One B spectrometer with DRIFT equipment. Aliphatic C was quantified according to Leifeld (2006), and semiquantitative structural information was derived from the ratio of peak heights at 2960 (aliphatic) to 780 (aromatic) cm<sup>-1</sup> for baseline-corrected spectra. Thermal stabilities of all samples were measured by DSC (type Q100, Waters Inc., New Castle, DE, USA). The thermal stability of an organic sample is a function of its chemical composition and its degree of polymerization (Leifeld, 2008). Briefly, 0.5 mg C equivalents were weighed into open Al-pans and heated under oxidative conditions to 600 °C. Peak temperatures and 50% burnoff values (i.e. the temperature at which 50% of the total heat evolved) served as thermal stability indicators. For details about the measurements, see Leifeld *et al.* (2006).

In the leachates of the microlysimeters, we measured DOC concentrations using a Shimadzu (Tokyo, Japan) TOC-V analyser. NH<sub>4</sub><sup>+</sup> concentration was determined colorimetrically by automated flow injection analysis (PE FIAS-300, Perkin-Elmer, Norwalk, CT, USA) and NO<sub>3</sub><sup>-</sup> concentration was determined by ion chromatography (DX-120, Dionex, Sunnyvale, CA, USA).

#### *Calculations and statistical analysis*

*Cumulative CO<sub>2</sub> production* was estimated by linearly interpolating between measurements. *Net N mineralization* was calculated from the amount of inorganic N leached from the microlysimeters after the given time without the initial leaching (Nadelhoffer & Fry, 1988). The amount of inorganic N (NH<sub>4</sub><sup>+</sup> + NO<sub>3</sub><sup>-</sup>) was the sum of inorganic N leached during all leaching cycles after the initial leaching (eight cycles for the whole incubation). The *labile C and N pools* in the tundra and forest soils were estimated by multiplying the C and N pools in the organic layers and mineral soils (0–7 cm depth) by the fraction of C and N mineralized at 7 °C during 6 months. Because the tree cover increased from the tundra to the forest and the vegetation type (tree vs. open land) significantly affected pools and mineralization rates, we used tree cover – mapped in all macroplots at all altitudinal levels – to calculate C and N pools for the tundra and subalpine forest.

All statistical analyses were made on untransformed data with R 2.4.1 software. We used a split-split unit design for the analysis of variance with altitude as main units, macroplots as first subunits and vegetation, temperature (for the incubation experiment) and soil horizon (for DRIFT data and thermal stabilities) as second sub-

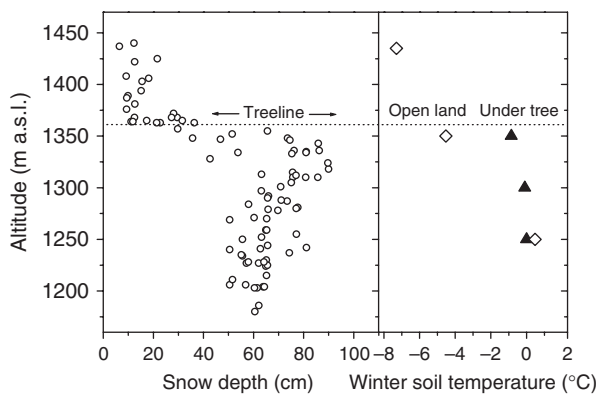
units. The macroplot factor was incorporated to improve our model, but is not shown in the statistical tables.

Where interactions were significant, we used a *post hoc* means separation test (Tukey's HSD). We also used contrasts to test for differences between the two forest sites (1260 and 1310 m a.s.l.) and the tundra site (1360 m a.s.l.). In addition, we used general linear models to analyse correlations between decomposability and various soil parameters.

## Results

### Microclimate across the treeline ecotone

Snow depths of the treeline ecotone at Mali Iremel were strongly influenced by trees (Fig. 2). Between an altitude of 1330–1370 m a.s.l. across the species line, snow depth abruptly increased from 20 cm in the tundra to 75–90 cm in the open and subalpine forest. At the species line (1360 m a.s.l.), predominant west winds caused snow to drift and accumulate under the tree



**Fig. 2** Snow depths and mean soil temperatures at 10 cm depth during winter across the treeline ecotone of Mali Iremel. Snow depths are from a measuring campaign in March 2006, and soil temperatures from January to March 2005 ( $n = 4$ ).

canopy and on the leeward side of tree islands, while the snow in the surrounding tundra remained shallow. The strong increase in snow depths from the tundra to the forest was also reflected in winter soil temperatures. While mean air temperatures in winter 2005 differed by  $<1^{\circ}\text{C}$  across the treeline ecotone, soil temperatures at 10 cm depth were around  $0^{\circ}\text{C}$  in the subalpine forest,  $-0.9^{\circ}\text{C}$  in the uppermost tree islands, but  $-4.6^{\circ}\text{C}$  in the surrounding 'open land' (Fig. 2). In summer, soil temperatures reached up to  $+10^{\circ}\text{C}$  at both altitudinal levels and they were  $1^{\circ}\text{C}$  lower under trees (data not shown).

### Soil morphology and SOM pools

Soil characteristics were similar in all 48 profiles along the altitudinal gradient across the treeline ecotone. All soils were developed on blocky quartzite had thin Cv horizons of  $<5$  cm depth and stone content below 10%. Particle size distributions spanned a narrow range with clay fractions of 20%, 18%, and 21% in the A horizons at altitudes of 1260, 1310, and 1360 m a.s.l., respectively. Soil pH in A horizons ranged between 3.4 and 3.8 at all altitudes (Table 1). Exchangeable calcium and magnesium did not differ in the organic layer or in the A horizon among the three altitudes (Table 1).

In contrast to the inorganic characteristics of mineral soils, organic layers differed significantly across the treeline ecotone. The organic layers were thicker at the treeline (10 cm under trees, 7 cm in the tundra) than in the forest (8 cm under trees, 2.5 cm in the open land). In addition, Oa horizons dominated the organic layers at the treeline (6 cm), but they were completely lacking in the forest at 1260 m a.s.l., where the organic layers consisted only of a Oi and a Oe horizon.

Total C pools in soils decreased slightly but insignificantly from the subalpine forest to the tundra (Fig. 3; Table 2). The greatest soil C stocks occurred under trees in the subalpine forest ( $13.3\text{ kg m}^{-2}$ ) and the lowest

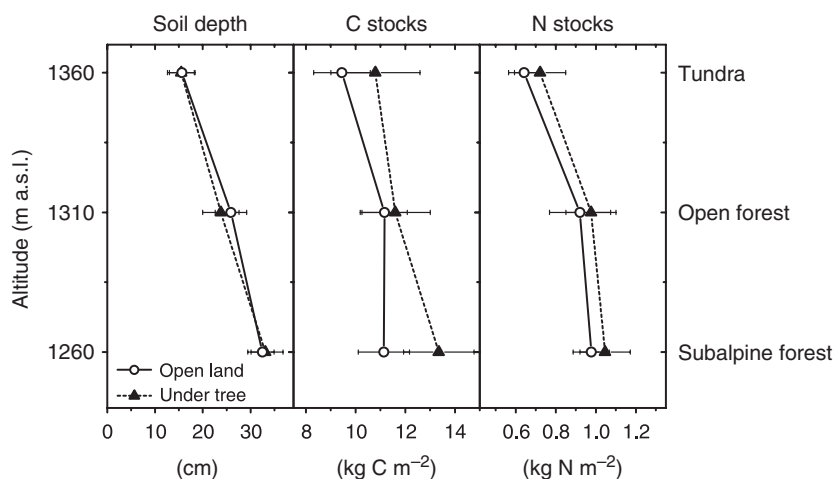
**Table 1** Properties of organic layers and mineral topsoils used for the incubation experiment

			pH*	$\Sigma(\text{CaMg})^{\dagger}$ ( $\text{mmol}_C \text{ kg}^{-1}$ )	Fine earth bulk density ( $\text{g cm}^{-3}$ )	$C_{\text{org}}$ (%)	$N_t$ (%)	C/N
Tundra	Open land	O	3.4 (0.1)	13.2 (1.4)	0.26 (0.03)	22.2 (1.6)	1.67 (0.1)	13.3 (0.3)
		0–7 cm	3.5 (0.1)	29.6 (2.1)	0.55 (0.01)	8.2 (1.0)	0.58 (0.1)	14.1 (0.2)
1360 m a.s.l.	Tree	O	3.6 (0.1)	21.8 (2.3)	0.15 (0.01)	29.2 (1.8)	1.82 (0.1)	16.0 (0.5)
		0–7 cm	3.4 (0.1)	39.0 (3.3)	0.48 (0.10)	12.4 (3.0)	0.88 (0.2)	13.9 (0.5)
Forest	Open land	O	4.5 (0.1)	12.8 (1.1)	0.09 (0.01)	33.1 (1.7)	2.21 (0.1)	15.0 (0.5)
		0–7 cm	3.7 (0.2)	34.3 (8.0)	0.46 (0.03)	9.1 (0.3)	0.84 (0.1)	10.8 (0.2)
1260 m a.s.l.	Tree	O	4.0 (0.1)	18.7 (5.2)	0.11 (0.02)	35.7 (3.0)	1.76 (0.1)	20.2 (0.8)
		0–7 cm	3.4 (0.1)	42.0 (7.2)	0.55 (0.04)	8.1 (0.6)	0.67 (0.1)	12.0 (0.1)

Means and standard errors of five plots.

\*Measured in  $0.01 \text{ mol L}^{-1} \text{ CaCl}_2$ .

†Exchangeable with  $1 \text{ mol L}^{-1} \text{ KCl}$ .



**Fig. 3** Soil depths and soil organic carbon (C) and nitrogen (N) stocks along the altitudinal gradient of the Mali Iremel in the Southern Ural. Means and standard errors of four plots each sampled with two soil profiles per vegetation type.

**Table 2** ANOVA results for SOC stocks

	Total SOC		Organic layer SOC		Mineral soil SOC	
	F value	P (>F)	F value	P (>F)	F value	P (>F)
Altitude (1260, 1310, and 1360 m a.s.l.)	1.67	0.21	52.8	<0.001***	8.99	<0.01**
Vegetation (tree and open land)	1.94	0.18	3.30	<0.001***	0.05	0.82
Altitude × vegetation	0.29	0.75	4.33	<0.01**	0.14	0.87

Levels of each factor are shown in parenthesis ( $n = 8$ ).

\* $P < 0.1$ ;

\*\* $P < 0.01$ ;

\*\*\* $P < 0.001$ .

SOC, soil organic carbon.

occurred in the open land at the treeline ( $9.4 \text{ kg m}^{-2}$ ). At all three altitudes, soils stored more C under trees than in the open land (Fig. 3), but this effect of vegetation cover was not significant (Table 2). Taking tree cover (62% in the forest and 7.5% in the tundra) into account, forest soils stored  $3 \text{ kg C m}^{-2}$  more SOC than tundra soils.

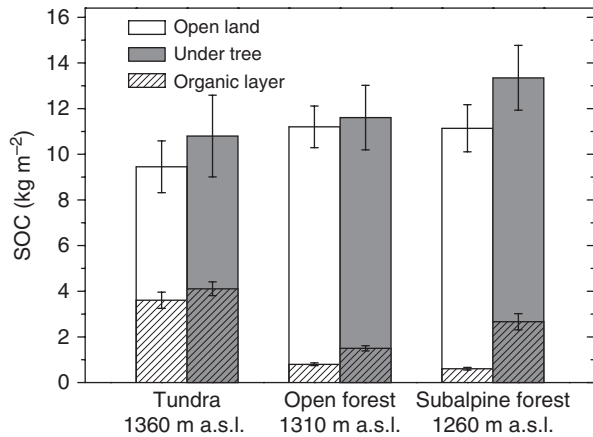
In contrast to total C stocks, the distribution of C pools within the soil profile changed strongly across the treeline ecotone. The greater thicknesses of organic layers in the tundra than in the forest were also reflected in significantly greater C stocks in the tundra (Fig. 4;  $P < 0.001$ ). Organic layers of the tundra stored  $3.7 \text{ kg C m}^{-2}$ , while those of the forest contained only  $2.0 \text{ kg C m}^{-2}$  (accounting for tree cover). As opposed to organic layers, mineral soils of the forest had considerably greater C stocks than those of the tundra (contrast of mineral SOC stocks in the tundra vs. those in the forest at 1310 and 1260 m a.s.l.,  $P < 0.001$ ) (Fig. 3). Concentrations of mineral soil C, however, were similar at all altitudes (Table 1), but the deeper forest soils contained more C.

The influence of trees on organic layer C significantly depended on the altitudinal level (Fig. 4;  $P_{\text{altitude} \times \text{vegetation}} < 0.01$ ). In the tundra, organic layers of tree islands ( $\sim 50$  years old, height 1.5–3 m) contained amounts of C similar to those of the dwarf shrub-dominated open land. In the forest, however, the organic layers under trees (100–110 years old, height 15 m) stored significantly more C than those of the open land ( $P < 0.001$ ), which consisted of only a thin layer of herb litter. Tree cover did not affect C storage in the mineral soil.

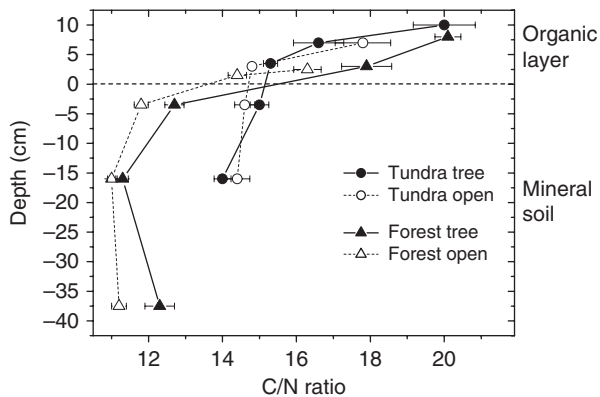
Total N stocks showed the same pattern as C stocks (Fig. 3), but in contrast to C the altitude effect was significant ( $P < 0.01$ ) with 60% greater N stocks in the forest at 1260 m a.s.l. than in the tundra at 1360 m a.s.l. The greater increase in N than in C stocks with decreasing altitude resulted from smaller C/N-ratios in the mineral soils of the forest (Fig. 5).

#### SOM characteristics

Soil C/N ratios, DRIFT spectroscopy and DSC showed that SOM characteristics changed substantially with



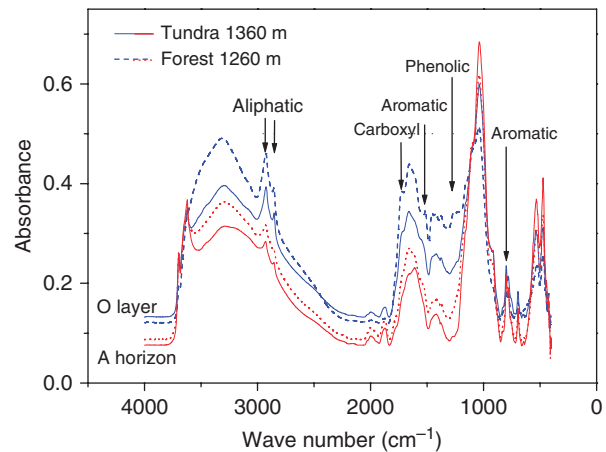
**Fig. 4** Total soil organic carbon (SOC) stocks and SOC stocks in the organic layer along the altitudinal gradient of the Mali Iremel. Means and standard errors of four plots each sampled with two soil profiles per vegetation type.



**Fig. 5** Soil C/N mass ratios in soil profiles in the tundra at 1360 m a.s.l. and in the forest at 1260 m a.s.l. at Mali Iremel. Means and standard errors of four plots each sampled with two soil profiles per vegetation type.

altitude. For instance, C/N ratios strongly declined with depth in the forest soils, but remained almost constant between the Oa layer and the mineral soil in the tundra (Fig. 5). Also, mineral soils of the forest at 1260 m a.s.l. had smaller C/N ratios than those of the tundra at 1360 m a.s.l. (Fig. 5). Litter layer C/N ratios were greater under trees than in the open land, but they were the same at the two altitudes under trees. In the open land, however, C/N ratios of the litter layer were smaller in the herb-dominated open land of the forest than in the dwarf shrub-dominated tundra, suggesting a better litter quality at the lower altitude.

Infrared spectra (DRIFT) from forest soils indicated a higher share of aromatic C = C ( $1610, 780 \text{ cm}^{-1}$ ) and phenolic C ( $1270 \text{ cm}^{-1}$ , assignment according to Niemeyer *et al.*, 1992) compared with tundra soils



**Fig. 6** Diffuse Reflectance Infrared Fourier Transform (DRIFT) spectroscopy of forest and tundra soils in the Southern Urals ( $n = 5$ ). Means of four plots each sampled with two soil profiles under trees.

(Fig. 6). Aliphatic C ( $3020\text{--}2800 \text{ cm}^{-1}$ ) was more abundant in the tundra. In the forest, aliphatic C accounted for  $22.8 (\pm 0.5)\%$  and  $15.7 (\pm 0.5)\%$  of soil C in the A and O horizon, respectively, whereas corresponding values were  $25.8 (\pm 1.0)\%$  and  $17.8 (\pm 1.2)\%$  in the tundra. The ratio between aliphatic and aromatic C revealed a higher aromaticity in the organic layers of the forest ( $P < 0.01$ ). For the A horizon, however, this difference was not significant ( $P = 0.55$ ).

The thermal stability of SOM, serving as a proxy for the chemical stability of SOM, was significantly greater in the organic layers than in the A horizons ( $P < 0.001$ ), indicating that it decreases during humification (Fig. 7). Forest SOM had a greater thermal stability than tundra SOM ( $P < 0.01$ ), while differences between open land and tree were not significant within groups of the same horizon or altitude for any of the thermal parameters.

Overall, there was a decline in soil C/N ratio, aliphatic C assessed by DRIFT, and the thermal stability from the organic layer to the mineral soil, reflecting changes in SOM properties during humification. In the organic layers, these properties were all smaller in the tundra at 1360 m a.s.l. than in the forest at 1260 m a.s.l. ( $P < 0.01$ ), implying that the thicker organic layers in the tundra contained more humified organic matter than those of the subalpine forest.

#### C mineralization and DOC production

During the 180-day incubation period organic layers lost between 3% and 26% and mineral soils lost between 2% and 7% of their initial C content. The largest fraction of C was respired as  $\text{CO}_2$ , while DOC leaching contributed only 3–9% of total C loss (Table 3). Respiration



**Table 3** Cumulative C and N mineralization and DOC production during 182 days

			CO <sub>2</sub> -C (mg g SOC <sup>-1</sup> )		DOC (mg g SOC <sup>-1</sup> )		N (NH <sub>4</sub> <sup>+</sup> + NO <sub>3</sub> <sup>-</sup> ) (mg g N <sup>-1</sup> )	
			7 °C	20 °C	7 °C	20 °C	7 °C	20 °C
Tundra	Open land	O	31.1 (1.9)	63.1 (5.7)	1.6 (0.3)	2.2 (0.5)	9.2 (1.3)	30.5 (5.6)
		0–7 cm	16.9 (0.8)	33.8 (1.9)	1.2 (0.2)	3.1 (0.6)	5.8 (0.9)	17.4 (1.8)
1360 m.a.s.l.	Tree	O	43.2 (2.5)	116.6 (9.1)	2.3 (0.5)	3.6 (0.5)	11.3 (3.6)	52.5 (4.7)
		0–7 cm	17.9 (2.2)	33.3 (2.7)	1.1 (0.1)	3.3 (0.8)	6.0 (0.5)	18.8 (0.8)
Forest	Open land	O	97.1 (4.6)	254.2 (12.6)	4.0 (0.8)	7.2 (0.9)	50.3 (13.9)	175.9 (3.7)
		0–7 cm	25.4 (2.0)	56.2 (5.9)	1.0 (0.1)	1.5 (0.1)	19.0 (1.3)	42.3 (4.4)
1260 m.a.s.l.	Tree	O	86.8 (3.5)	205.6 (8.1)	6.2 (0.6)	8.2 (0.9)	47.1 (3.6)	138.0 (6.7)
		0–7 cm	26.0 (1.1)	66.0 (5.9)	2.1 (0.1)	4.1 (0.7)	9.6 (1.9)	42.2 (6.4)

Means and standard errors of five plots.

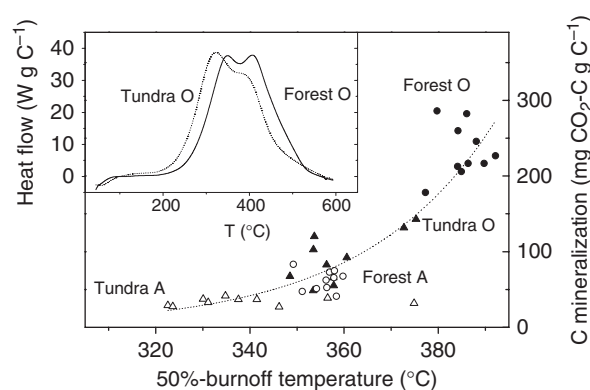
DOC, dissolved organic carbon; C, carbon; N, nitrogen.

rates declined substantially over time (Fig. 8). Final respiration rates were 40–70% lower than initial rates.

The incubation experiment clearly showed that SOM quality differed between the altitudinal levels. In the forest at 1260 m.a.s.l., C mineralization and DOC production from organic layers and mineral soils was much greater than in the tundra 100 m higher. Organic layers in the forest lost two to four times more C than those of the tundra (Fig. 8). Tree cover affected C mineralization, but this effect depended on the altitudinal level ( $P_{\text{altitude} \times \text{vegetation}} < 0.01$ ). In the tundra, C mineralization from organic layers under trees was significantly greater than from the dwarf shrub-dominated open land (+70%;  $P < 0.001$ ). In contrast, in the forest (1260 m.a.s.l.), the organic layer lost 20% more C under herbs than under trees ( $P < 0.01$ ). C mineralization from mineral soils showed the same trends as those from the organic layers, with 1.5 to two times greater rates in the forest than in the tundra. However, in contrast to the organic layers, tree cover did not affect C mineralization rates from mineral soils ( $P = 0.25$ ).

Our rough estimate of changes in the labile C pool across the treeline by combining C stocks, C mineralization and tree cover indicated that the labile C pool was 50% greater in the forest than in the tundra soils (Fig. 9;  $P < 0.01$ ).

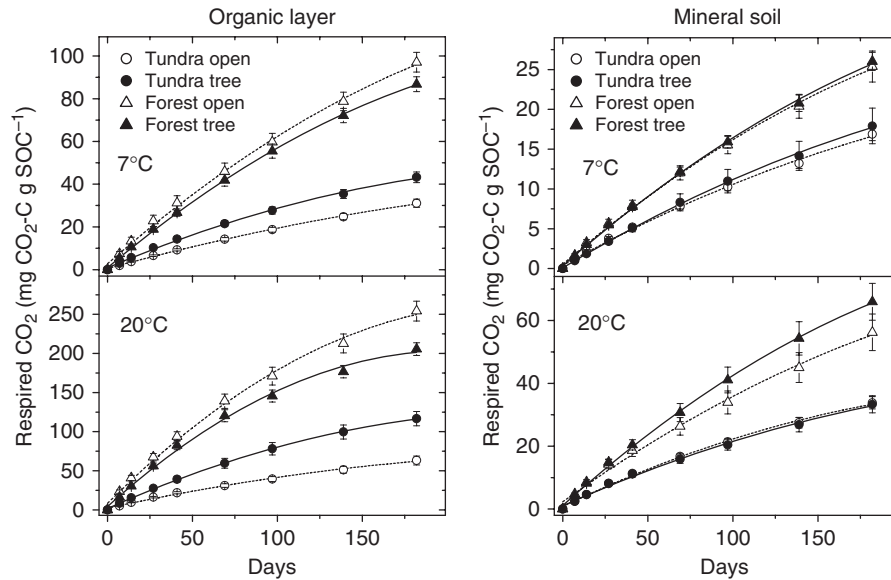
Changes in DOC production from soils across the treeline ecotone and vegetation types were similar to changes in C mineralization. Total DOC leaching correlated significantly with total C mineralization from the organic layers ( $r = 0.95$ ,  $n = 40$ ,  $P < 0.001$ ), but not with that from the mineral soils. Production of DOC was greater from the organic layers of the forest than from those of the tundra (Table 3;  $P < 0.001$ ). Vegetation had a significant effect on total DOC leaching from organic layers ( $P < 0.01$ ), with 35% more C leached from under trees than from the open land.



**Fig. 7** Differential scanning calorimetry (inset, top-left) for organic layers in the tundra and in the forest (under trees). The relationship between 50% burnoff temperature and carbon mineralization for organic layers (filled symbols) and A horizons (empty symbols) in the forest (circle) and at the treeline (triangle) ( $n = 5$ ).

The thermal stability of SOM showed the closest correlation with C mineralization of all soil chemical parameters (Fig. 7). At 20 °C, correlation coefficients between C mineralization and peak 1 temperature, peak 2 temperature, and 50% burnoff temperature were 0.82, 0.71, and 0.87 [all  $P < 0.001$  for  $\ln(C_{\text{mineralized}})$ ]. For organic layers only, total C mineralization was closely related to initial C content ( $r = 0.85$  at 20 °C,  $P < 0.001$ ), but this correlation was lacking for the mineral soils. C/N ratios of organic layers correlated positively with C mineralization ( $r = 0.98$ ,  $n = 15$ ), but only when the organic layers of the open land in the forest, which showed the highest C mineralization rates despite low C/N ratios, were removed from the analysis. This result indicates that the organic layer under the tall herbs, which consisted of only a litter layer, differed in quality and structure from the more 'decomposed' organic





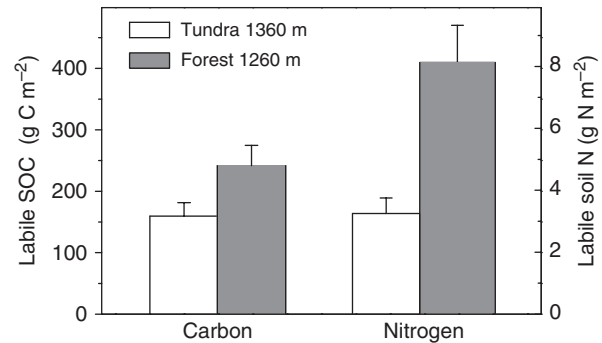
**Fig. 8** Cumulative carbon (C) mineralization of soils at 1260 m a.s.l. (forest) and at 1360 m a.s.l. (tundra). Means and standard errors of five plots. The lines are fitted with a second-order exponential function. Note the different scales of the *y*-axis between 7 and 20 °C (factor of 3) and between organic layers and mineral soils.

layers of the other sites. Apparently, this litter layer contained more favourable organic substrate for micro-organisms than any of the other organic layers.

#### *N* mineralization

During the 6-month incubation period, considerable amounts of N, up to 18% of the total N content, were mineralized (Table 3). From the microlysimeters, N was mainly leached as nitrate, indicating that net nitrification occurred. Net N mineralization per unit soil N was 1.5–6.5 times lower than losses of soil C via soil respiration and DOC leaching per unit soil C (Table 3; Fig. 10), which shows a relative N enrichment of soils during decomposition. The temporal patterns of C and N mineralization also differed. While C mineralization rates declined exponentially with time, net N mineralization remained almost constant. This resulted in a nonlinear relationship between C and N mineralization, indicating that some of the initially mineralized N was immobilized (Fig. 10).

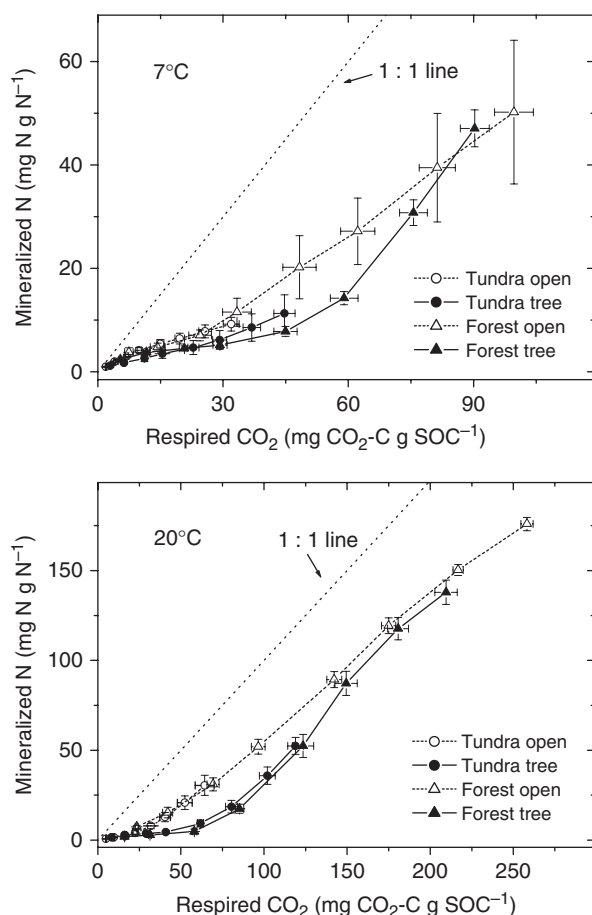
The differences in net mineralization of N between the two altitudinal levels were more pronounced than those in C mineralization (Table 3; Fig. 9). In the organic layers, net N mineralization was 2.6–5.8 times greater in forest than in tundra soils. The loss of C relative to N was significantly greater in organic layers from tundra than in those from the forest (Fig. 10;  $P < 0.01$ ), which means that N was immobilized for a longer period in tundra than in forest soils.



**Fig. 9** Labile carbon (C) and nitrogen (N) pools in tundra and forest soils at Mali Iremel. The labile pools were estimated by multiplying the cumulative C and N mineralization of organic layers and mineral soils (0–7 cm depth) at 7 °C with the corresponding C and N pools and accounting for the tree cover. Means and standard errors of four plots per altitudinal level.

#### Temperature response

As expected, C mineralization was strongly related to temperature, with two to 2.7 times greater rates at 20 °C than at 7 °C (Fig. 8). The corresponding  $Q_{10}$  values of the cumulative C mineralization were between 1.7 and 2.2, with significantly lower temperature sensitivity in the mineral soils than in the organic layers ( $P < 0.05$ ) and a greater sensitivity in forest than in tundra soils ( $P < 0.05$ ). A temperature effect on DOC mobilization was only observed after the initial flushing: between day 40 and 182 of the incubation, DOC production from



**Fig. 10** Relation between cumulative carbon (C) and nitrogen (N) mineralization from organic layers. The 1:1 line visualizes the same mineralization rates of N per unit soil N as of C per unit soil C. Smaller rates of net N than of C mineralization are indicative for N immobilization. Means and standard errors of five plots.

the organic layers was approximately 2.3 times greater at 20 °C than at 7 °C ( $Q_{10} = 1.9 \pm 0.2$ ).

Net N mineralization was more sensitive to temperature than C mineralization, as indicated by significantly smaller ratios of C to N mineralization at 20 °C. Figure 10 shows that the ratio of C to N mineralization was closer to the 1:1 line at 20 °C than at 7 °C. The  $Q_{10}$  values of the cumulative net N mineralization were  $2.9 \pm 0.3$ .

## Discussion

### *Soil C turnover but not C stocks change across the treeline ecotone*

Our results show that across the treeline ecotone at Mali Iremel, SOM quality and degradability changed significantly, but total soil C stocks increased only slightly

with increasing forest cover (Figs 3 and 8). On the same altitudinal gradient, historical photographs and dendrochronological assessments document that the high-altitude treeline has shifted upwards by 60–80 m and the formerly forest–tundra ecotone has become a closed forest during the last century (Moiseev *et al.*, 2004; Fig. 1). Therefore, the current subalpine forest was at the species line about 100 years ago and thus, by applying a ‘space for time’ approach, altitudinal changes in SOM along the homogenous slope reflect the impacts of treeline shifts and forest expansion on SOM.

Across the treeline ecotone at Mali Iremel, which spans only 100 m in altitude, biomass increased from 30 to 150 t ha<sup>-1</sup> and understory vegetation changed from dwarf shrubs to 1.5 m tall herbs (Moiseev *et al.*, 2004), which imply that the upward-shifting forest zone has fundamentally altered the quantity and quality of C inputs to soils. Our study indicates that these ecosystem changes have primarily affected SOM properties and cycling rates (Fig. 8). For instance, the distribution of C between organic layers and mineral soils shifted across the treeline ecotone: thickness and SOM stocks of the organic layer decreased from the tundra to the subalpine forest, whereas mineral soil C stocks increased (Fig. 4). Organic layers comprised 38% of total SOC in the tundra soils (1360 m a.s.l.), while they contributed only 15% in the forest soils (1260 m a.s.l.). The increasing thickness of organic layers with altitude agrees with a treeline study in the Taganai Mountains, 100 km north-east of our study site (Van der Meer *et al.*, 2004), and with observations of Sveinbjörnsson *et al.* (1995) in the Chugach Mountains of South-Central Alaska. At first glance, the greater accumulation in the organic layer seems to support the view that harsher conditions lead to an accumulation of labile SOM, as reported from high latitude soils (Neff & Hooper, 2002; Sjögersten *et al.*, 2003). However, the results of our mineralization experiment indicate that both organic layers and A horizons of the tundra were less decomposable, meaning that less labile C accumulated in the tundra even when pool size was taken into account (Figs 8 and 9). Consistently, DOC mobilization from tundra soils was <40% of that from forest soils. This implies that SOM quality was lower in the tundra, which is supported by the characteristics of the organic layers: Oa horizons dominated the organic layers in the tundra but they were completely lacking in the forest. Because the Oa horizons contained small fractions of minerals, part of the lower decomposability can be attributed to stabilization of SOM by mineral surfaces (Six *et al.*, 2002). In the A horizons, soils of the two altitudes had the same SOM content but mineralization rates in the forest soils were still twice as high as those in the tundra soils (Fig. 8), indicating that SOM quality

of the A horizon was indeed better in the forest. Measurements of SOM characteristics support this conclusion: (1) DRIFT spectra from forest were characterized by a higher contribution of lignin moieties, indicative of intact lignocelluloses, in SOM (Fig. 6). In addition, spectra not only showed that the mineral soil was richer in aliphatic C than the organic layer and thus more transformed, but also that SOM in the tundra was more aliphatic than in the forest. (2) The thermal stability of organic matter was greater in forest than in tundra SOM (Fig. 7). Because the thermal stability generally decreases during polymer breakdown and increases with increasing lignocellulosic content (Leifeld, 2008), a thermally more stable SOM in the forest than in the tundra indicates more 'fresh' substrate. (3) Soil C/N ratios declined much more rapidly from organic to mineral soils in the forest (Fig. 5), which implies a more rapid SOM transformation in the forest than in the tundra.

Despite the large differences in the quality and decomposability of SOM, total C stocks were only slightly greater in the forest than in the tundra ( $+3 \text{ kg C m}^{-2}$ ; Figs 3 and 4). When we assume that the soil C stocks have increased from the tundra to the subalpine forest at same rate as the forest has been established – 100 years based on maximal tree ages and historic photographs – the C accumulation rate would only be  $30 \text{ g C m}^{-2} \text{ yr}^{-1}$ . This corresponds closely to the study of Steltzer (2004) in a Canadian arctic forest–tundra landscape, where soil C storage increased with increasing tree age by  $18.5 \text{ g C m}^{-2} \text{ yr}^{-1}$ . These values are, however, not greater than estimates of the C sinks in European Forest soils due to increased litter production ranging between 20 and  $110 \text{ g C m}^{-2} \text{ yr}^{-1}$  (Liski *et al.*, 2002; Janssens *et al.*, 2003). In the Ural mountains, we think that the actual rates of soil C accumulation due to the advancing forest were even smaller, because soil C stocks increased only in the mineral soils, which were

deeper and further developed in the forest (Fig. 3). Therefore, it is likely that the increasing C stock from the tundra to the forest rather reflects a more progressed pedogenesis during the last millennia than a C sink during the last century.

Our estimates of the labile SOM pools by combining C mineralization rates with soil C pools showed that forest soils were not only more decomposable but also contained 50% more labile C than tundra soils (Fig. 9). Field studies by Davis *et al.* (1991) and Sjögersten & Wookey (2002) in Northern Fennoscandia support our laboratory results. They showed that  $\text{CO}_2$  fluxes during the vegetation period were 30–75% greater from forest than from treeline soils. Given that soil temperatures during winter dropped to  $-7^\circ\text{C}$  above the treeline but remained unfrozen in the forested zone at lower altitudes (Fig. 2) indicate that the differences in C mineralization will even be greater when winter is included and thus, on an annual basis. We interpreted the faster and greater C mineralization from forest than from tundra soils as an indication that the conserving effects of the harsher winter conditions in the tundra were less important than C inputs and thus, substrate availability. Annual aboveground plant productivity was three times greater in the forest than in the tundra ( $60$  vs.  $180 \text{ g C m}^{-2}$ ; M. Trubina, unpublished results). This strongly suggests that the relatively small difference in soil C storage across the altitudinal gradient resulted from a balancing of C gains and C losses: the increased C input into soils through higher plant productivity is compensated by accelerated decomposition, resulting in relative small net changes.

In summary, the large increase in biomass and plant productivity from the tundra to the forest across the treeline ecotone was associated with strong changes in SOM properties and quality but only insignificant increases in soil C stocks. Mineralization rates were much greater in forest than in tundra, which suggests that the

**Table 4** ANOVA table for cumulative carbon (c) mineralization

	Organic layer		Mineral soil (0–7 cm)	
	F value	P (>F)	F value	P (>F)
Altitude (1260 and 1360 m a.s.l.)	140.9	<0.001***	64.8	<0.001***
Vegetation (tree and open land)	0.04	0.84	1.49	0.25
Temperature (7 and 20 °C)	135.0	<0.001***	134.2	<0.001***
Altitude × vegetation	14.4	<0.01**	1.23	0.30
Altitude × temperature	26.9	<0.001***	18.7	<0.01**
Vegetation × temperature	0.01	0.93	0.73	0.42

Levels of each factor are shown in parenthesis ( $n = 8$ ). Organic layers and mineral soils were analysed separately.

\* $P < 0.1$ ;

\*\* $P < 0.01$ ;

\*\*\* $P < 0.001$ .

greater C inputs into forest soils were counterbalanced by accelerated decomposition. This implies that (1) an upward shift in treeline has relatively small net effects on SOM stocks and (2) C turnover rates increase from the tundra to the subalpine forest within a very small gradient in altitude and thus in temperature.

#### *Direct and indirect vegetation effects*

The effects of the vegetation cover (trees vs. open land) at each altitudinal level on SOC stocks were small and only detectable in the organic layer (Fig. 4). In the subalpine forest, organic layers stored significantly more C under the up to 150-year-old and 15 m high trees than under the herb-dominated open land (+ 2.3 kg C m<sup>-2</sup>). In contrast, the 50-year-old <3 m high tree islands in the tundra had no significant effects on organic layer C stocks, probably because the tree presence was too short to induce any substantial changes in the 7–10 cm thick organic layers.

We mainly attributed the greater differences in SOM quality between altitudes than between vegetation types to the distinct change in winter climate caused by forest establishment and thus, to an indirect vegetation effect. Although air temperatures differed between forest and tundra by <1 K throughout the year, soils remained unfrozen in the forest during winter but froze to -4.6 °C at 10 cm depth under the open land of the tundra (Fig. 2). The clear difference in winter soil temperature stems from the loss of an insulating snow cover due to wind above the 'closed' forest. For instance, in March 2004 and 2006, snow depth was only 20 cm in the tundra but between 50 and 90 cm in the forest. As a consequence, forest soils are 'active' throughout the year, which likely leads to accelerated decomposition and more intense incorporation of organic layer material into the mineral soil. Our conclusion is supported by experimental snow enrichment experiments in the Alaskan tundra and monitoring studies of winter CO<sub>2</sub> effluxes in the Rocky mountains, which indicate that snow depth plays a crucial role in winter microbial activity and in the overall soil C balance (Schimel *et al.*, 2003; Monson *et al.*, 2006). In summary, we think that the drastic change in SOM quality across the treeline ecotone can be ascribed to both direct effects of greater litter input and indirect effects of a more favourable winter climate, which contributes to countering the tripled productivity with enhanced SOM turnover.

#### *Direct and indirect temperature effects*

In line with other incubation studies (e.g. Kätterer *et al.*, 1998; Reichstein *et al.*, 2000; Neff & Hooper, 2002),

mineralization rates strongly depended upon temperature (Fig. 8). Nevertheless, we conclude that indirect effects through vegetation change will be greater than direct temperature effects in treeline ecosystems of the Southern Ural because: (1) the difference in mineralization rates between the two altitudinal levels, covering a gradient in mean annual temperature of 0.3 K, was of the same magnitude as that of a temperature rise from 7 to 20 °C (Table 4, Fig. 8). (2) The upward expansion of forests will continue under the ongoing and predicted climatic warming, while soil respiration will 'acclimatize' to increasing temperature either by physiological adaptations of the microbial community or by declining resource availability (Luo *et al.*, 2001; Melillo *et al.*, 2002; Kirschbaum, 2004).

We suggest that indirect temperature effects on SOM dynamics through a change in vegetation will be particularly large in boundary ecosystems such as treeline ecotones because species composition and annual productivity increase sharply within a small gradient. Currently, forests are expanding upward and northward into former tundra in large areas of the Northern Hemisphere (Kullman, 2002; Moiseev & Shiyatov, 2003; Esper & Schweingruber, 2004; Lloyd, 2005; Devi *et al.*, 2008). We therefore conclude that these indirect temperature effects on SOM dynamics play an important role in the feedbacks between climate change and SOM cycling.

#### *Net N mineralization increases from tundra to forest*

Overall, net N mineralization per unit soil N was much smaller than that of C mineralized per unit soil C, indicating that C was preferentially lost during decomposition and that soil C/N ratios decreased during humification (Fig. 10). The ratio of C to N mineralization was particularly high during the initial phase, while towards the end of the experiment N and C were mineralized at almost the same rate. Weintraub & Schimel (2003) observed a similar lag in net N mineralization compared with C mineralization during the incubation of Arctic tundra soils. They interpreted the lag in net N mineralization as an indication for N limitation of soil microorganisms, while the subsequent parallel increase of mineralized N and C reflects a saturation of microbial N demand. In our experiment, the lag in net N mineralization was greater in organic layers under trees, which had wide C/N ratios, than in organic layers of the open land (Fig. 10), suggesting that soil microorganisms were more limited in N under trees. Also, soils incubated at 20 °C had a much shorter initial N immobilization phase than at 7 °C, which likely reflected an earlier saturation of microbial N demand. As a result, net N mineralization had a greater temperature dependency than C mineralization.

A higher release of N induced either by increased temperature or by a change in vegetation may induce a positive feedback loop: warmer soils, particularly in winter, lead to greater net N mineralization, thereby providing more N for plant growth. In turn, plants grow better and become richer in N, and their litter becomes more decomposable and releases more N into soils. In the Southern Ural the occurrence of such a positive feedback is supported by the drastic change from the N-poor dwarf shrub-dominated tundra to the *P. alpinum*-dominated open patches of the forest within 50 m of altitude. A similar positive feedback loop between soils and plants was proposed by Sturm *et al.* (2005) for Northern Alaskan tundra where increasing shrub abundance leads to deeper snow and hence, to higher winter temperatures; in turn, this promotes greater microbial activity and therefore more plant-available N. Such an acceleration of N cycling could potentially increase C storage in ecosystems when a large fraction of the mineralized N is taken up by plants. A greater transfer of N from soils to plants would increase net primary production and thus, plant C stocks across this treeline ecotone of the Southern Ural.

## Conclusion

Most studies investigating the impact of climate change on soil C focus on direct warming effects. Our study in the pristine treeline ecotones of the Ural mountains indicates that indirect climate change effects on SOM dynamics through altered vegetation cover – influencing both litter inputs and microclimatic conditions – can be more important than direct warming effects. Across the treeline ecotone covering a gradient in mean annual air temperature of only 0.3 K, SOM quality changed substantially, with tundra soils storing significantly more C in organic layers but less C in mineral soils than forest soils. Further, SOM of the subalpine forest was more mineralizable than that of the tundra. Because differences in total soil C stocks were small, it seems likely that both mineralization and litter inputs increased significantly from the tundra to the forest but the two processes remained roughly balanced. This suggests that a climate change-driven rise in treeline will accelerate C turnover but will have only small effects on soil C pools. Faster SOM cycling under forest expansion is associated with an increase in net N mineralization, which in turn might provide a nutritional basis for the drastic increases in plant biomass and productivity from the tundra to the forest.

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