

LETTER

A tipping point in carbon storage when forest expands into tundra is related to mycorrhizal recycling of nitrogen

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Abstract

Tundra ecosystems are global belowground sinks for atmospheric CO₂. Ongoing warming-induced encroachment by shrubs and trees risks turning this sink into a CO₂ source, resulting in a positive feedback on climate warming. To advance mechanistic understanding of how shifts in mycorrhizal types affect long-term carbon (C) and nitrogen (N) stocks, we studied small-scale soil depth profiles of fungal communities and C–N dynamics across a subarctic-alpine forest-heath vegetation gradient. Belowground organic stocks decreased abruptly at the transition from heath to forest, linked to the presence of certain tree-associated ectomycorrhizal fungi that contribute to decomposition when mining N from organic matter. In contrast, ericoid mycorrhizal plants and fungi were associated with organic matter accumulation and slow decomposition. If climatic controls on arctic-alpine forest lines are relaxed, increased decomposition will likely outbalance increased plant productivity, decreasing the overall C sink capacity of displaced tundra.

Keywords

Arctic warming, carbon sequestration, decomposition, functional genes, meta-barcoding, mycorrhizal type, nitrogen cycling, soil fungal communities, stable isotopes, treeline ecotone.

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INTRODUCTION

Arctic and alpine tundra experience shifts in plant community composition with increasing dominance of deciduous shrubs in response to recent warming (Elmendorf *et al.* 2012; Myers-Smith *et al.* 2015; Scharnagl *et al.* 2019). At the same time, previous low stature tundra vegetation is displaced by tall shrub or forest species, as their distribution advances along latitudinal and altitudinal gradients (Mayor *et al.* 2017; Brodie *et al.* 2019; Myers-Smith *et al.* 2019). Despite low primary production, many tundra ecosystems have accumulated large belowground stocks of organic matter (Post *et al.* 1982; Smith & Shugart 1993). Climate warming puts these C stocks at risk through permafrost thaw and accelerated decomposition that may amplify climate change (IPCC 2014). Responses to warming are complex, because increasing plant growth and litter production coincide with changes in litter quality and belowground microclimate that may either hamper or accelerate decomposition (Chapin III *et al.* 2005; Cornelissen *et al.* 2007). Furthermore, the most responsive deciduous shrubs and trees form ectomycorrhizal symbioses, in contrast to the ericoid mycorrhizal dwarf shrubs that dominate tundra heaths and the non-mycorrhizal sedges that characterize wetter tundra types. The mycorrhizal type of vegetation has been highlighted as an important predictor of belowground nutrient cycling and C storage (Phillips *et al.* 2013; Averill *et al.* 2014; Clemmensen *et al.* 2015; Steidinger *et al.* 2019). However, the boreal-arctic transition has received little attention in this context, although mycorrhiza-mediated plant–soil feedbacks potentially control the

magnitude and direction of tundra ecosystem feedbacks to the global climate.

Altitudinal ecosystem gradients are long-term manifestations of how global and local climatic conditions control vegetation characteristics and belowground organic matter dynamics (Post *et al.* 1982; Smith & Shugart 1993; Körner 1998; Mayor *et al.* 2017). Across the forest line in Fennoscandian mountain ranges, belowground organic matter stocks approximately double from birch forest to alpine tundra heaths without permafrost (Sjögersten *et al.* 2003; Hartley *et al.* 2012; Parker *et al.* 2015). The lower stocks in the forest coincide with higher soil respiration and greater production of ectomycorrhizal mycelium (Hartley *et al.* 2012; Parker *et al.* 2015). However, the alpine heath soil has a higher proportion of labile C compounds (Sjögersten *et al.* 2003), making it susceptible to increased decomposition caused by warming and related vegetation shifts. In order to predict potential transitional effects and feedbacks based on vegetation characteristics (IPCC 2014), mechanisms of plant–soil interactions and how they change across the forest-tundra transition require further investigation.

Plant growth in arctic and boreal ecosystems is generally constrained by low N availability (Tamm 1991), and warming-induced increases in decomposition and N mineralization have been considered prerequisites for climate warming to increase plant growth (IPCC 2014). However, advancement of shrubs and trees has been proposed to slow down decomposition because of their woody litter and increased shading and surface cooling, potentially leading to a negative plant–soil feedback that retards further plant advancement (Chapin

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III *et al.* 2005; Cornelissen *et al.* 2007; Wookey *et al.* 2009). On the other hand, shrubs and trees with ericoid or ectomycorrhizal symbioses may be independent of N mineralization, as their fungal partners have direct access to N in soil organic matter (Read 1991). By competing for organically bound nutrients, mycorrhizal associations may boost nutrient recycling to host plants (Northup *et al.* 1995; Lindahl & Tunlid 2015), thereby creating a positive plant–soil feedback that promotes further proliferation of shrubs. Ericoid mycorrhizal fungi have previously been hypothesized to be superior to ectomycorrhizal fungi in accessing organically bound N (Read & Perez-Moreno 2003), but more recent evidence suggests that some Agaricomycetes (Basidiomycota) involved in ectomycorrhizal symbiosis have particularly high capacity for decomposition of recalcitrant soil organic matter to access nutrients (Bödeker *et al.* 2014; Lindahl & Tunlid 2015; Deslippe *et al.* 2016; Shah *et al.* 2016). Thus, functional properties may diverge among ectomycorrhizal fungal lineages (Lindahl & Tunlid 2015; Lindahl *et al.* 2021), supposedly in conjunction with their contrasting mycelial morphologies and foraging strategies to acquire soil resources (Agerer 2006). Furthermore, Ascomycota associated with roots of ericaceous shrubs have been proposed to contribute to belowground organic matter accumulation through production of recalcitrant necromass, progressively locking up nutrients (Clemmensen *et al.* 2015; Fernandez & Kennedy 2018). Self-reinforcing, feedbacks between certain plants, mycorrhizal fungi and biogeochemical processes (Bennett *et al.* 2017) should result in abrupt and coordinated shifts in vegetation, microbial communities and soil organic matter dynamics across the landscape.

We used an altitudinal gradient from alpine heath tundra into subalpine birch forest in northern Sweden to test the hypothesis that an abrupt decrease in belowground organic matter stocks at the heath to forest transition is coupled to a shift in the dominant type of mycorrhizal association, from ericoid mycorrhiza in the heath tundra to ectomycorrhiza in the forest. We sampled four sites along the shift from heath tundra to established forest, constituting a space-for-time substitution series to illustrate a future warming scenario of current alpine heath tundra. Soils of arctic and boreal ecosystems typically consist of an organic topsoil resting on mineral soil or bedrock. Due to climatic and edaphic constraints on soil fauna, the organic layer builds up with negligible vertical mixing, and small-scale depth profiles also represent age gradients, in which organic matter age and degree of decomposition increase with depth (Clemmensen *et al.* 2013; Hartley *et al.* 2013; Kyaschenko *et al.* 2018). We used fine-scaled vertical profiling of organic matter characteristics and microbial communities to infer differences in long-term C and N dynamics across the treeline ecotone. There was little evidence to suggest that the decreased C stocks in the forest were driven by a general transition from ericoid to ectomycorrhizal dominance. Instead, our results suggested that certain ectomycorrhizal fungal species drove faster organic matter decomposition, outbalancing the larger plant production, in the forest. Experimental exclusion of tree roots confirmed their stimulatory effect on organic matter decomposition in the forest.

MATERIAL AND METHODS

Vegetation gradient

The study was conducted 5 km south-east of Abisko in Northern Sweden (Fig. S1). The forest-heath gradient consisted of four sites situated 50–300 m apart on the same mountain slope, representing characteristic vegetation types of the area: arctic downy birch (*Betula pubescens* ssp. *czerepanovii* ((N.I Orlova) Hämet-Ahti)) forest (68°19'49.6" N 18°50'53.1" E; 500 m above sea level), forest edge (68°19'41.0" N 18°50'56.4" E; 510 m), shrub-dominated heath (68°19'35.4" N 18°51'12.9" E; 530 m) and dwarf shrub heath (68°19'33.8" N 18°51'16.1" E; 540 m). The four sites were placed in areas of homogeneous vegetation without abrupt elevational shifts in the immediate surroundings. At all sites, the organic soil layer rests on well-drained mineral soil with glacial till, without permafrost, while only forest soil was distinctly podzolized (Fig. S1). The climate is subarctic, with mean summer and winter temperatures of 10 °C and –9 °C, respectively, an annual precipitation of ~300 mm and a snow-free season from late May to early October (Abisko Scientific Research Station). Temperature was logged in the litter layer and 5 cm down in the organic soil layer with TinyTag data loggers every half hour between 14 June and 20 August 2009 ($n = 3$ per site; Table S1).

Within each site, six 1 m × 1 m sampling plots ($n = 6$) were established 10 m apart on transects. For each plot, species composition and aboveground C stocks of field vegetation (i.e. species coverage excluding birch trees) were estimated. Birch tree densities and C stocks were assessed within a 5 m radius of each plot. Mycelial production in the soil was estimated based on incubation of sand-filled 45- μ m mesh bags at multiple depths in each sampling plot.

From each plot, eight 4-cm diameter cores were collected to the full depth of the organic layer (10–25 cm) in August 2008 and divided into three litter layers (L1, L2a and L2b), and three humus layers (H1, H2 and H3) based on visual inspection (Fig. S1, Table S2). Mineral soil was inconsistently present and not considered. Material from different cores but the same layer was mixed per plot to give a composite, homogenized sample for each layer. Living roots and rhizomes with a diameter of 1–5 mm were collected and dried for dry mass determination, while finer roots were kept in the sample and stems with larger diameter were discarded. In total, this sample set consisted of 140 composite, organic layer samples (24 plots × 6 layers, except litter 2b that was lacking in three forest plots and one forest edge plot). Samples were analysed for pH, organic matter content, total and dissolved C and N pools, stable isotope ratios, fungal biomass (ergosterol, $n = 3$ per site) and microbial communities.

Decomposition experiment

Decomposition bags constructed of 45 μ m nylon mesh (Sintab, Sweden) were filled with organic substrates: intact litters collected at the soil surface (corresponding to L1 layer) in the forest or the heath, forest humus (mixed H1-3), upper heath humus (mixed H1-2) or lower heath humus (H3). After

removal of roots > 1 mm diameter, substrates were dried at 40 °C until attaining constant weight and bags were filled with 2 g litter or 4 g humus. To test the effect of living tree roots on decomposition, bags were incubated at 2–10 cm depth in the six forest plots, both in 60 cm diameter sub-plots where tree root ingrowth was severed by permanent barriers (trenching), and in paired sub-plots with intact tree roots. Root exclusion plots were constructed by cutting out a turf with a spade well into the mineral soil, removing the intact turf and insulating the circumference of the hole with a double, sealed plastic sheet before replacing the turf (Fig. S1). This plastic liner allowed drainage through the bottom and the understory vegetation remained undamaged throughout the experiment. Two sets of substrates were incubated from July 2009 until either August 2010 or August 2012. Upon recovery in 2010, bags were directly frozen at –20 °C and later freeze-dried and weighed to assess mass loss. In 2012, bags were carefully transported to the laboratory and respiration measured, block-wise, within 10 h. The intact bags were placed in a closed chamber (173 cm³) connected to an infrared gas analyzer (EGM-4 Environmental Gas Monitor; PP Systems, Amesbury, MA, USA) and linear increase in CO₂ concentration was monitored over 4 min at 18 ± 1 °C and field moisture conditions. The bags were then frozen at –20 °C and later freeze-dried, weighed and milled to a fine powder for analyses of ergosterol and fungal community composition. This sample set consisted of 57 samples from the first harvest (three lost during incubation) and 60 samples from the second harvest.

Analyses of microbial communities

DNA extracts were obtained from all soil profile samples and from the second harvest of the decomposition experiment. Gene copy numbers of the bacterial 16S and the fungal ITS2 regions were quantified by real-time PCR to reflect total bacterial and fungal abundances (gradient samples, Table S3). Ammonia-oxidizing (potential NO₃⁻ production) and denitrifying (potential N₂ release) microbial communities were quantified by targeting key enzyme-coding genes specific for these pathways. Fungal ITS2 amplicons for sequencing were generated from DNA extracts using a PCR protocol optimized for quantitative amplification (Castaño *et al.* 2020) and subjected to 454 sequencing (LGC Genomics GmbH, Berlin, Germany) on a GS-FLX Titanium system (Roche, Basel, Switzerland).

Sequences were quality filtered and clustered using the bioinformatics pipeline SCATA (<http://scata.mykopat.slu.se>) as specified by Clemmensen *et al.* (2015). In short, sequences passing quality control were clustered into species-level clusters (hereafter referred to as species) by single-linkage clustering with a 98.5% sequence similarity criterion for assignment to a cluster. Fungal reference sequences in the UNITE database (Abarenkov *et al.* 2010) were included in the clustering process to verify that clustering approximated species delimitation and to enable direct identification. The most abundant 657 and 232 fungal species for the gradient and decomposition studies, respectively, represented 93% of the fungal sequences and were further assessed for taxonomical identity and functional guild (Table S4). Ectomycorrhizal species were further

categorized into exploration types (Agerer 2006), with the contact, short, medium-distance-smooth types designated as 'short-distance types' and the medium-distance-fringe and long exploration types designated as 'long-distance types'.

Statistical analysis

Univariate data were analysed by linear models using SAS 9.4 (Statistical Analysis System Institute, Cary, NC, USA) and multivariate fungal community data were analysed by correspondence analyses with CANOCO 5 (Microcomputer Power, Ithaca, NY, USA). Detailed methodological information is available in Material and Methods S1.

RESULTS

Tree biomass and soil C stocks are inversely related across the forest line

The multi-stemmed *Betula pubescens* ssp. *czerepanovii* (arctic downy birch) trees had a density of about 12 trees per 100 m² in the forest, corresponding to 1.2 kg C m⁻² (Fig. 1). In the forest, *B. pubescens* was the only ectomycorrhizal species, but several ectomycorrhizal plants contributed to the vegetation at the forest edge and above the tree line. The highest coverage of ectomycorrhizal species in the field vegetation, that is, excluding trees, across all sites, was found in the shrub tundra, where *Betula nana* (dwarf birch) was abundant (Fig. 1a; Table S5). However, the field vegetation was dominated by ericoid mycorrhizal dwarf shrubs at all sites, and their total coverage was higher in the forest than in the heath. The total C pool in the vegetation doubled from just under 1 kg C m⁻² in the heath to around 2 kg C m⁻² in the forest (Fig. 1b). The total C pool in the organic soil layer, however, decreased from more than 6 kg m⁻² in the heath to about 2 kg m⁻² in the forest. The litter layer amounted to 283 ± 17 g C m⁻² across all sites, and the humus layer accounted for 88% (forest) and 95% (other sites) of the organic soil C stocks (Fig. 1b).

The average C-to-N ratio of the entire organic horizon was higher in the forest (27.5 ± 0.8) than in the other sites (18.9–20.1; $F = 14.0$; $P < 0.001$; Fig. S2) and correlated negatively with C stocks (Fig. S3). Higher birch tree densities were related both to smaller soil C stocks and higher C-to-N ratios in the organic layer across all plots ($r^2 = 0.74$ and $r^2 = 0.66$, respectively; $P < 0.01$) and among forest plots only ($r^2 = 0.54$ and $r^2 = 0.61$, respectively; $P < 0.01$; Fig. S2). However, coverage of ectomycorrhizal plants in the field vegetation correlated positively with soil C stocks across all plots ($P < 0.01$; Fig. S3) or showed no relationship with C stocks when excluding the forest site ($r^2 = 0.11$, $P > 0.05$).

Carbon–nitrogen dynamics

Fresh litter inputs (uppermost L1 layer) had highest C-to-N ratios in the heath and shrub, and C-to-N ratios decreased with depth from the fresh litter (L1) to the fragmented litter layer (L2, second layer) and the upper humus layer (H1, third layer) at all sites (Fig. 2a; Table S6). The C-to-N ratios kept decreasing with humus depth (H1–H3) in the heath, shrub

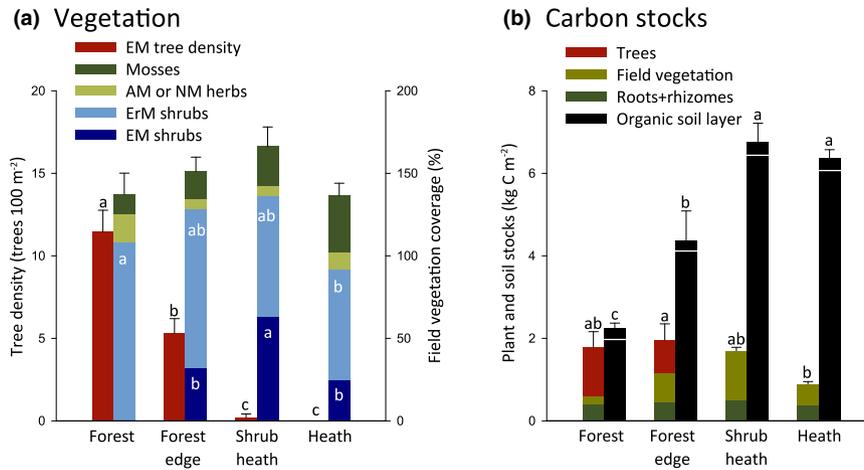


Figure 1 Vegetation composition and ecosystem carbon (C) stocks at four sites along a subarctic-alpine forest-heath vegetation gradient in northern Sweden. (a) Density of arctic downy birch trees (left axis) and field layer vegetation coverage (% of ground surface; right axis). Lichens covered less than 2%. (b) Total C stocks in birch trees, field vegetation, roots and rhizomes and in the organic soil layer to the full (10–25 cm) depth. Field vegetation C stocks (vascular and non-vascular) are based on published data from the same or similar sites. For soil C stocks, the horizontal white line delimits stocks in the litter (above) and in the humus (below). Error bars represent standard errors of the means of total vegetation characteristic or C stock. Means with the same letter, or without letters, are not significantly different, $\alpha = 0.05$, $n = 6$. Letters above bars represent the entire bar, whereas letters within bars represent the specified fraction. EM: ectomycorrhizal; AM: arbuscular mycorrhizal; NM: non-mycorrhizal; ErM: ericoid mycorrhizal.

and forest edge. In the forest, in contrast, C-to-N ratio reached a minimum in the uppermost humus (H1) and then rose again in deeper humus layers (H2–H3). While $\delta^{13}\text{C}$ patterns were similar for all sites (Fig. 2c), $\delta^{15}\text{N}$ showed a steeper increase with depth in the forest and forest edge than in the shrub and heath (Fig. 2b).

Fungal biomass (as inferred from ergosterol concentration) generally declined with depth. Fungal biomass in the upper three layers (L1, L2 and H1) was about half in the heath compared to the other sites (Fig. 2d; Table S6). Mycelial growth was about 10 times higher in the forest than in the heath (Fig. 2i), while mycelial C-to-N ratios (ranging from 17.3 to 19.2), $\delta^{13}\text{C}$ (–26.3 to –27.5) and $\delta^{15}\text{N}$ (0.2–2.2) were similar across sites ($n = 1$ –6) and matched levels previously measured in ectomycorrhizal fungi (Clemmensen *et al.* 2006).

Dissolved organic C and N concentrations were highest in forest, and the ratio between these pools was lowest in the heath (Fig. 2e,f,g). Inorganic N concentrations were highest in the heath (Fig. 2h), and heath and shrub had higher abundances of bacteria and archaea involved in inorganic N transformations (Fig. 2k,l). Total bacterial-to-fungal ratios also seemed higher in the heath as indicated by the 16S-to-ITS copy ratio (Fig. 2j).

Fungal communities

Fungal community composition varied along three independent gradients. At all sites, communities shifted with soil depth, with saprotrophic fungi dominating in litter layers and mycorrhizal and other root-associated fungi dominating in humus layers (along the second CA axis explaining 8.3% of variation; Fig. 3a,b). Fungal communities also shifted along the vegetation gradient from heath to forest, both in the humus (along the first CA axis; 9.8%; Fig. 3a,b) and litter layers (along the third CA axis; 4.8%; Fig. S4). CCA analysis

confirmed the significance of differences in communities among sites and depths (Table S7).

The relative abundance of root-associated Ascomycota (including ericoid mycorrhizal fungi) was highest in the forest, whereas the relative abundance of ectomycorrhizal fungi was highest in the heath and shrub habitats (Fig. 3b,c; Table S6). The share of ectomycorrhizal fungi with less differentiated mycelia (short-distance exploration types) was higher in the heath and shrub heath, while the share of ectomycorrhizal species with mycelia differentiated for long-distance transport increased towards the forest (Fig. 3c; Table S6). Long-distance ectomycorrhizal species belonging to the genus *Cortinarius* were particularly abundant in the forest and forest edge humus, but *Leccinum* and *Piloderma* species were also common, while short-distance ectomycorrhizal species, particularly *Inocybe* and *Tomentella* species, dominated communities in the heath and shrub humus (Fig. 4). Communities of other root-associated fungi in humus also shifted gradually along the vegetation gradient, but whereas the relative abundance of root-associated Basidiomycota (Sebacinales) was higher in heath and shrub, there were no clear shifts among Ascomycota classes (Fig. S5). The most well-characterized ericoid mycorrhizal fungus *Pezoloma ericae* (earlier named *Hymenoscyphus ericae*) was most abundant in forest.

Within the saprotrophic communities in the litter layers, moulds increased towards the heath and shrub, whereas some Basidiomycota genera were only found among the dominant fungi in the forested sites (*Sistotrema*, *Trechispora* and *Luelia*), while *Mycena* species were found along the entire vegetation gradient (Fig. S5).

Tree root exclusion decreases decomposition

After 3 years of field incubation, both forest and heath litter substrates were dominated by free-living saprotrophic

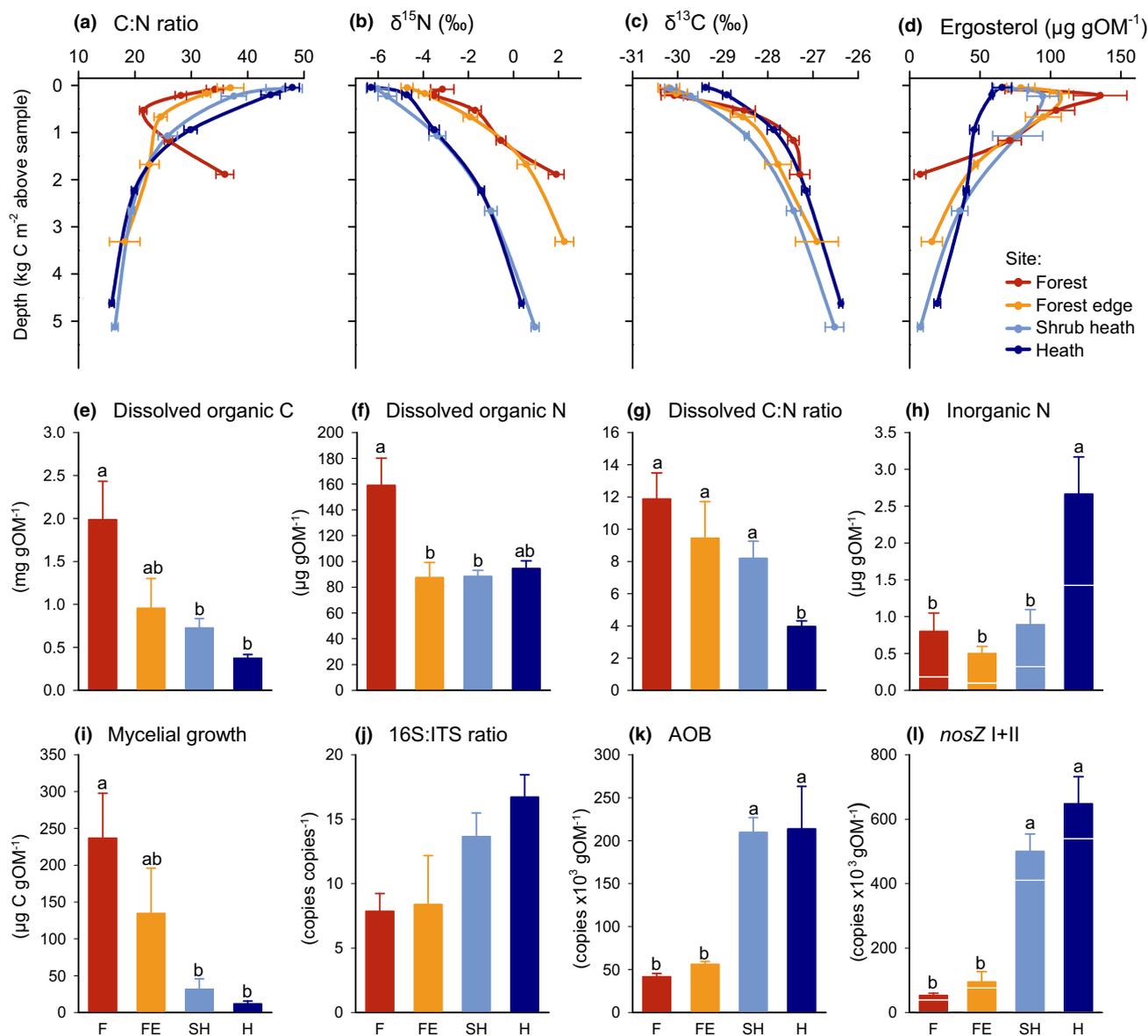


Figure 2 Indicators of mode of N cycling in four ecosystem types along a subarctic-alpine forest-heath vegetation gradient in northern Sweden. (a–d): Depth profiles of C:N, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ and ergosterol concentration of organic matter (OM; dried mass). Values for five depth layers (litter: L1, L2; humus: H1–H3) are plotted against depth-wise cumulative C stocks; values for L2 are mass-weighted averages of L2a and L2b samples, which represented the same depth. (e–l): Humus layer concentrations of dissolved C and N pools, fungal and bacterial abundances and functional markers. Bars show mass-weighted averages of values of three humus layers. In (h), ammonium amount is shown below and nitrate amount above the horizontal line. In (l), *nosZI* copy numbers are shown below and *nosZII* above the horizontal line. AOB: ammonia-oxidizing bacteria, based on bacterial *amoA* gene coding for ammonia monooxygenase (genetic potential for ammonium to nitrate transformation); *nosZI* and *II*: gene variants coding for nitrous oxide reductase (genetic potential for N_2 release). F: forest; FE: forest edge; SH: shrub heath; H: heath. Error bars indicate ± 1 standard error of the mean, $n = 6$, except for (d) where $n = 3$.

fungi, whereas humus substrates were dominated by root-associated fungal communities, although forest humus also had a large proportion of moulds and yeasts (Fig. 5a). Mass loss, respiration and fungal biomass were overall higher in litter than in humus. First year mass loss was faster for forest litter than for heath litter but, slower for forest humus than for heath humus (Fig. 5b,c,d; Tables S8 and S9). Exclusion of living birch roots decreased fungal biomass slightly and almost eliminated ectomycorrhizal

fungal colonization of the decomposition bags, while other root-associated fungi, including ericoid mycorrhizal ones, remained unaffected (Fig. 5a,c; Table S8). Presence of living roots overall increased mass loss of both litter and humus substrates after 3 years (Fig. 5b; Table S9). While litter substrates continued to decrease in mass throughout the incubation, the mass of humus samples increased between years 1 and 3, particularly in plots without living birch roots (Fig. 5b; Table S9).

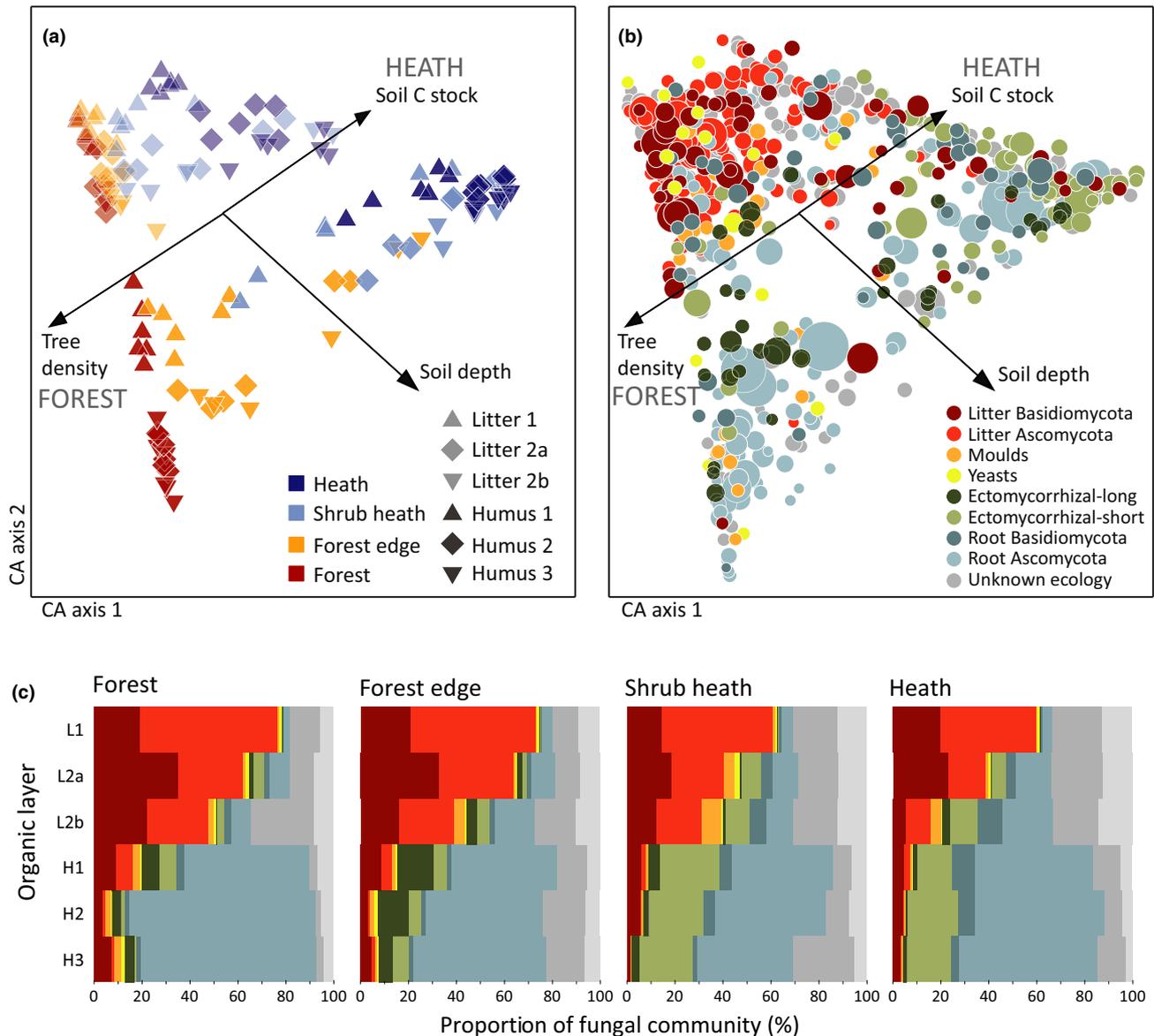


Figure 3 Fungal community composition in organic soil profiles of four ecosystems along a subarctic-alpine forest-heath vegetation gradient in northern Sweden. Sample (a) and species (b) plot of a correspondence analysis (CA) of the fungal communities across 139 samples, including the most abundant 654 fungal species assessed for ecological guild. CA axes 1, 2 and 3 accounted for 9.8, 8.3 and 4.8%, respectively, of the total variation of 6.92, when accounting for sequencing depth of each sample. The sample and species plots are at the same scale. The vectors indicate direction and degree of correlation between the CA axes and sampling depth (i.e. from litter to humus), tree density and soil C stock, the latter two representing multiple factors shifting along the vegetation gradient from heath to forest (Figure S3). (c) Average relative abundance of fungal guilds in depth-wise organic layers at each of the four sites ($n = 6$). Symbols/bars are coded according to ecosystem and organic layer (a) or fungal guild (b and c; unclassified fungi included in light grey in c) and with symbol area indicating relative amplicon abundance (b). L: litter; H: humus.

DISCUSSION

Soil C stocks are linked to ectomycorrhizal fungal traits rather than mycorrhizal type

Tree biomass and soil C stocks were inversely related across the forest line. Along the heath-forest gradient, the increase in woody biomass was outbalanced by a decrease in soil C stocks, suggesting a potentially decreased ecosystem sink if previous tundra heath transitions into birch forest in this region (Dahlberg *et al.* 2004; Hartley *et al.* 2012; Parker *et al.*

2015). In all vegetation types, fungal communities were vertically stratified, with free-living saprotrophs dominating more recently deposited litter layers and mycorrhizal and other root-associated fungi dominating deeper, more decomposed humus layers, similar to previous observations in various forest types (Lindahl *et al.* 2007; McGuire *et al.* 2013; Clemmensen *et al.* 2015). Fungal communities shifted from heath to forest, both in the humus and litter layers, but considering that the humus comprised a major part of the soil C stocks, root-associated fungal communities are more likely than litter-associated communities to influence variation in overall stocks

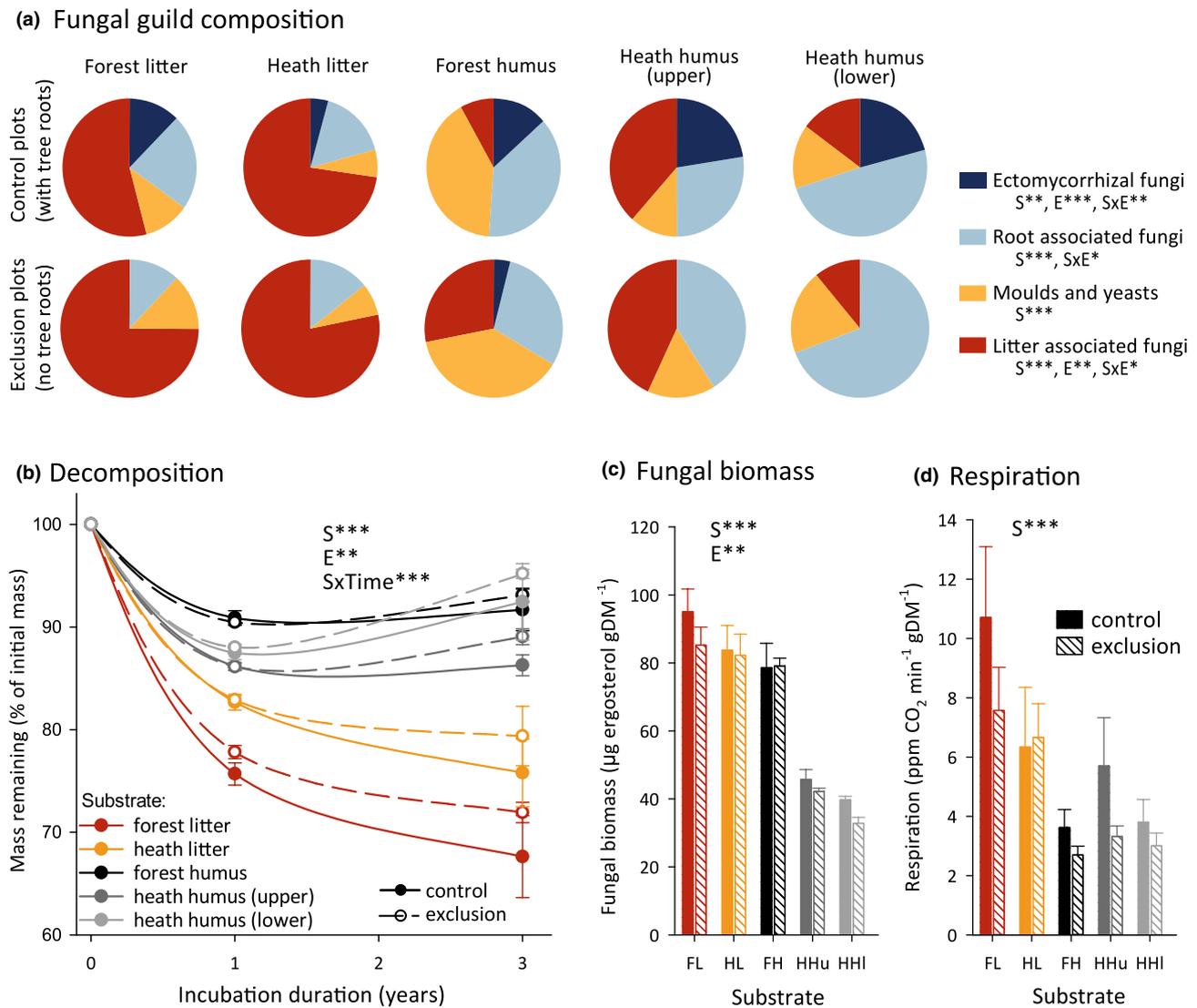


Figure 5 Decomposition of five organic substrates in the presence or absence of tree roots and ectomycorrhizal fungi in a subarctic birch forest in northern Sweden. Fungal guild composition (a), mass remaining (b), fungal biomass (c) and respiration rate (d) of five organic substrates incubated for 3 years in mesh bags in plots with or without exclusion of tree roots and associated fungi by permanent barriers (trenching). All plots had an understory of ericoid dwarf shrubs. Substrates in (a), (c) and (d) had been incubated for 3 years. Significant effects of substrate type (S), root exclusion (E), incubation duration (Time) and their interactions are indicated by * $P < 0.05$, ** $P < 0.01$ or *** $P < 0.001$. Full statistical results are available in Tables S8 and S9. Note the truncated y-axis in (b). FL: forest litter; HL: heath litter; FH: forest humus; HHu: upper heath humus; HHI: lower heath humus; DM = dry mass. Error bars indicate ± 1 standard error of the mean, $n = 5-6$.

depth in forest humus also indicates more active mycorrhizal N recycling, as mycorrhizal fungi fractionate the N pool and preferentially pass ¹⁵N-depleted N to the plant host (Högberg *et al.* 1996). The higher concentrations of dissolved organic pools in the forest humus further suggest high activities of trees and associated mycorrhizal fungi, as these pools have been directly linked to photosynthetic and root activity, rather than saprotrophic decomposition, in a girdling study (Giesler *et al.* 2007). The elevated C-to-N ratios of dissolved pools towards the forest also support selective uptake of organic N by ectomycorrhizal trees (Northup *et al.* 1995). Mycorrhizal mycelial growth was 10 times higher, and fungal biomass approximately double, in the forest compared to the heath. It thus appears plausible that losses of organic matter during

nutrient mobilization/mining by certain ectomycorrhizal fungi hamper C sequestration in the organic soil of forested sites. A strong stimulatory effect of tree photosynthesis on decomposition in this region has also been suggested based on observations of decreased soil respiration after tree girdling (Parker *et al.* 2020), decreased enzyme activities after defoliating moth attacks (Sandén *et al.* 2020) and decreased respiration from old organic pools in periods of low birch activity (Hartley *et al.* 2012).

Ectomycorrhizal fungi with ‘short-distance’ mycelium, particularly *Inocybe* and *Tomentella* species, dominated communities in the heath and shrub humus. Short-distance exploration types commonly dominate in environments with relatively high inorganic N levels (Lilleskov *et al.* 2002; Sterkenburg

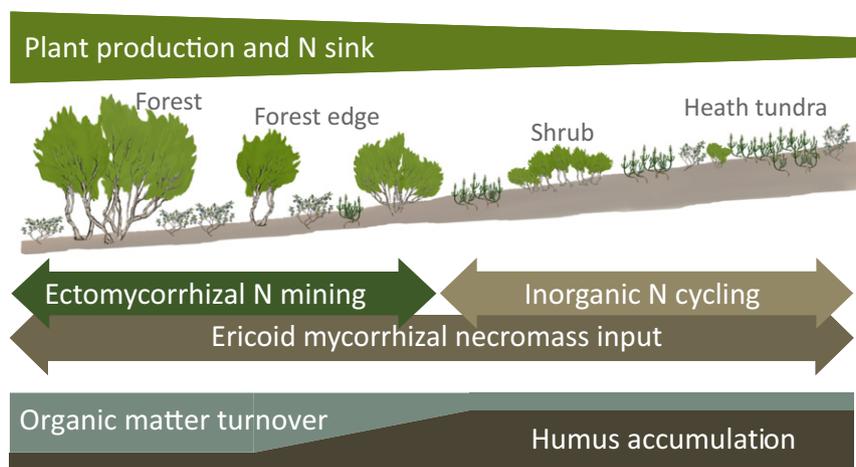


Figure 6 Conceptual diagram of treeline gradient. Arctic downy birch forms the forest line and associates with an ectomycorrhizal fungal community with the capacity to decompose soil organic matter when mining for nitrogen (N). This results in faster organic matter turnover and smaller total humus stocks in the forest than in shrub and heath ecosystems above the forest line. Ericoid mycorrhizal plants and fungi contribute to soil organic matter build-up in all vegetation types along this gradient. The lower decomposition capacity and lack of trees supporting ectomycorrhizal N mining above the forest line facilitate bacterial-driven inorganic N cycling.

et al. 2015). Their non-aggregated and hydrophilic mycelia are well adapted to take up nutrients from the soil solution by maximizing their active hyphal surface area (Lilleskov *et al.* 2002). A shift in mode of soil N cycling along the vegetation gradient was also evident from higher inorganic N pools and microbial N cycling potentials in the heath habitats. Abundant occurrence of ammonia-oxidizing bacteria (AOB), combined with higher concentrations of both ammonium and nitrate in the heath compared to the forested sites, indicates N mineralization and further transformation of ammonium to nitrate. Higher abundance of bacteria with denitrifying potential (*nosZ*), together with a lower DOC-to-nitrate ratio, in the heath habitats further indicate a more open N-cycle with genetic potential for both gaseous N losses and nitrate leaching. Thus, availability of N does not appear to be a primary constraint on growth and advancement of shrubs and trees above the current forest line. However, while more than two decades of experimental warming at the same heath indeed increased the cover of *Betula nana* (Campioli *et al.* 2012) and ecosystem respiration, the soil C stock remained unaffected (Ravn *et al.* 2017). Climate change-driven modification of tundra soils is a slow process, and better reconciliation of results from manipulative studies with observations along natural gradients is thus required to allow an integrative understanding of how initial transitional changes affect long-term trajectories of ecosystem development and feedbacks to climate.

Ectomycorrhizal fungi promote decomposition, while ericoid plants and fungi sustain belowground inputs

To experimentally test the capacity of tree roots and associated fungal communities to stimulate decomposition, we measured mass loss of five organic substrates incubated in forest plots from which tree roots were excluded, relative to mass loss in paired plots with living roots. Root exclusion largely removed ectomycorrhizal fungi, while other root-associated

fungi remained unaffected in accordance with the intact understory in the exclusion plots. Presence of living roots and associated ectomycorrhizal fungi led to more rapid mass loss of organic substrates, corroborating the idea that tree-associated ectomycorrhizal fungal communities take active part in decomposition (Sterkenburg *et al.* 2018), although our experimental design could not firmly distinguish direct ectomycorrhizal decomposition from stimulation of other decomposers (Parker *et al.* 2018; Gorke *et al.* 2019).

Faster initial mass loss of forest litter compared to heath litter corresponded to a lower C-to-N ratio of forest litter (L1 layer) and reflected general patterns among these litter types (Parker *et al.* 2018). In contrast, a more rapid initial mass loss of heath humus than of forest humus suggests that soil organic matter in heath tundra is of relatively high quality (Sjögersten *et al.* 2003), and that the higher organic matter accumulation in the heath was not caused by inherent chemical recalcitrance alone. These observations match with the steeper depth-wise decline in litter C-to-N ratio in the upper soil profiles of the forest, suggesting faster early stage litter decomposition driven by a more dominant and diverse community of saprotrophic Basidiomycota here.

However, while litter substrates continued to decrease in mass throughout the incubation, the mass of humus samples increased between years 1 and 3, particularly in plots where birch roots were excluded. This observation is consistent with the view that organic matter accumulation in deeper and older layers depends on the long-term balance between root-derived inputs (Clemmensen *et al.* 2013; Kyaschenko *et al.* 2018) and root-driven decomposition (Sterkenburg *et al.* 2018). Apparently, tree root exclusion removed the influence of ectomycorrhizal decomposers, while ingrowth by ericoid hair roots and associated fungi was retained and increased the organic matter mass in the bags. The importance of dead mycorrhizal mycelium as a major source of stable organic matter is supported

by C-to-N ratios and C and N stable isotope signatures in the deep humus layers that matched those of mycelium (except for mycelial C-to-N in the forest, where humus was presumably selectively mined for N). Furthermore, interactions between plant-derived tannins and fungal necromass have been shown to stabilize microbial-derived C (Adamczyk *et al.* 2019). Read & Perez-Moreno (2003) argued that ericoid mycorrhizal fungi are generally better exploiters of organic resources than ectomycorrhizal fungi. Genome sequencing has confirmed the presence of a wide range of decomposer enzymes in ericoid mycorrhizal fungi (Martino *et al.* 2018). Our results, however, corroborate the proposal that ericoid mycorrhizal fungi and other root-associated Ascomycota, on balance, build, rather than decompose, organic stocks (Clemmensen *et al.* 2015). The association of root-associated Ascomycota with organic matter accumulation may be ascribed to their recalcitrant, often melanized tissues (Fernandez *et al.* 2019), combined with a lack of extracellular peroxidases, which are essential to unlock phenol-rich and structurally complex organic matter for further decomposition (Barbi *et al.* 2020) and which are only produced by Basidiomycota, including some ectomycorrhizal species (Lindahl & Tunlid 2015).

Paradox, conclusion and perspectives

Our decomposition experiment confirmed that the large stocks of organic matter that accumulate in tundra heaths in this region are more labile to decomposition than organic matter in birch forest in close proximity (Sjögersten *et al.* 2003). The data show that the smaller soil C stocks in the forest have been exposed to N mining, as indicated by their higher C-to-N ratios and steeper increase in $\delta^{15}\text{N}$ with depth, linked to the presence of certain groups of ectomycorrhizal decomposers. Contrary to our initial hypothesis, functional shifts in the fungal community were not related to mycorrhizal types, but to contrasting species composition among ectomycorrhizal fungi. Apparently, ectomycorrhizal decomposition outbalanced the greater plant productivity and organic inputs in the forest, restricting organic matter accumulation, while ericoid mycorrhizal plants and fungi elicited a larger deposition than loss of organic matter in the soil (Fig. 6). Although abundant, the ectomycorrhizal fungal species in the heath were unable to mediate a major turnover of the soil organic N pool, leading to the apparent paradox that large amounts of low C-to-N ratio organic matter accumulated and N mineralization was elevated, while the growth of heath plants remained limited. A plausible explanation for the current status in the vegetation gradient is that other biotic (e.g. competition) or climate-driven factors (e.g. length of growing season, extreme temperatures or limited snow cover) (Körner 1998; Mayor *et al.* 2017; Hagedorn *et al.* 2020) are the primary constraints on the upward expansion of birch forest and associated biota, rather than low N mineralization.

While it is important to quantify transient and long-term effects of climate change on above- and belowground processes to correctly predict feedbacks in tundra ecosystems (Smith & Shugart 1993; Chapin III *et al.* 2005; IPCC 2014), increased effort should also be made to understand the mechanisms

underlying these effects (Keuper *et al.* 2020). Here we propose a plant–soil feedback mechanism, driven by ectomycorrhizal symbiosis, that connects vegetation change to declining belowground C stocks across the advancing subarctic tree line. This mechanism predicts coordinated, interdependent patterns in vegetation and soil dynamics, resulting in decreased ecosystem C storage when heath tundra changes into forest (Fig. 6). Advancement of the forest boundary would promote an ectomycorrhizal fungal community with the capacity to release the large organic N reserves and favour tree growth, potentially leading to a strong, positive plant–soil feedback that accelerates tree expansion into former tundra and underpins a positive feedback of tundra to climate warming.

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AUTHORSHIP

KEC, BDL, RDF and AM initiated the project. KEC and BDL designed the studies. KEC carried out the field experiments and the fungal community work. MBD, BDL and KEC developed the bioinformatics pipeline. AM performed CN and stable isotope analyses. SH contributed quantitative PCR data. KEC analysed the data and wrote the first draft of the manuscript. All authors contributed to data interpretation and revisions.

COMPETING INTERESTS

The authors declare no competing interests.

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DATA AVAILABILITY STATEMENT

All data are available at DRYAD (<https://doi.org/10.5061/dryad.79cnp5htw>), apart from sequence raw data, which are archived at the Sequence Read Archive (www.ncbi.nlm.nih.gov/sra) with accession numbers PRJNA662779 and PRJNA662784.

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