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Figure 1. Typical understory vegetation in the Swedish boreal forest consisting of the dwarf shrubs *Empetrum hermaphroditum, Vaccinium myrtillus, V. vitis-idaea* and the feather mosses *Hylocomium splendens* and *Pleurozium schreberi*. Photo by Paul Kardol.

Boreal forests in a warmer world

How soil ecosystems shift in response to warming and changes in understory vegetation

Jonathan R. De Long, Ellen Dorrepaal, Paul Kardol, Marie-Charlotte Nilsson, Laurenz M. Teuber and David A. Wardle

Boreal forests are important for global carbon (C) storage. Therefore, it is crucial to understand how the boreal forest will respond to climate change.

Predictable changes in the understory vegetation occur with post-fire succession and these changes have important consequences for ecosystem functioning.

However, little is known regarding how increased temperatures could interact with the major understory plant functional groups (i.e., mosses and shrubs) in boreal forests of contrasting successional age.

We assessed how soil microbes and nematodes and litter decomposition and nutrient release were affected by interactions between successional stage, warming, moss removal and shrub removal.

Soil microbes responded to interactions between successional stage, warming and plant functional groups, while mosses and shrubs were the predominant drivers of soil nematodes, litter decomposition and nutrient release.

These results demonstrate that in the short term, the direct effects of warming and successional stage can impact upon soil microbes, but may play a relatively minor role in controlling soil ecosystem processes and functioning in the boreal forest. However, as the climate warms, temperature and its indirect effects via changes to mosses and shrubs will likely alter soil nematode communities and litter decomposition, thereby potentially altering C storage and nutrient cycling.

Global temperatures are expected to rise by 1–3 °C by the end of this century. Warmer temperatures will likely lead to changes in the soil community and temperature-driven processes such as litter decomposition, nutrient cycling and carbon (C) storage. Current theory predicts that increasing temperatures will accelerate decomposition, which may create a positive feedback with climatic warming as more CO_2 is released into the atmosphere. However, a great deal of uncertainty remains concerning how other environmental conditions such as interactions with the understory vegetation (i.e., mosses and shrubs, Figure 1) might modify the effects of increased temperature on soil organisms and decomposition. Therefore, investigating the direct effects of warming on the soil community and litter decomposition, together with its interaction with understory vegetation, is essential to understanding how soil organisms and decomposition and the processes they control will be altered as climate change advances.

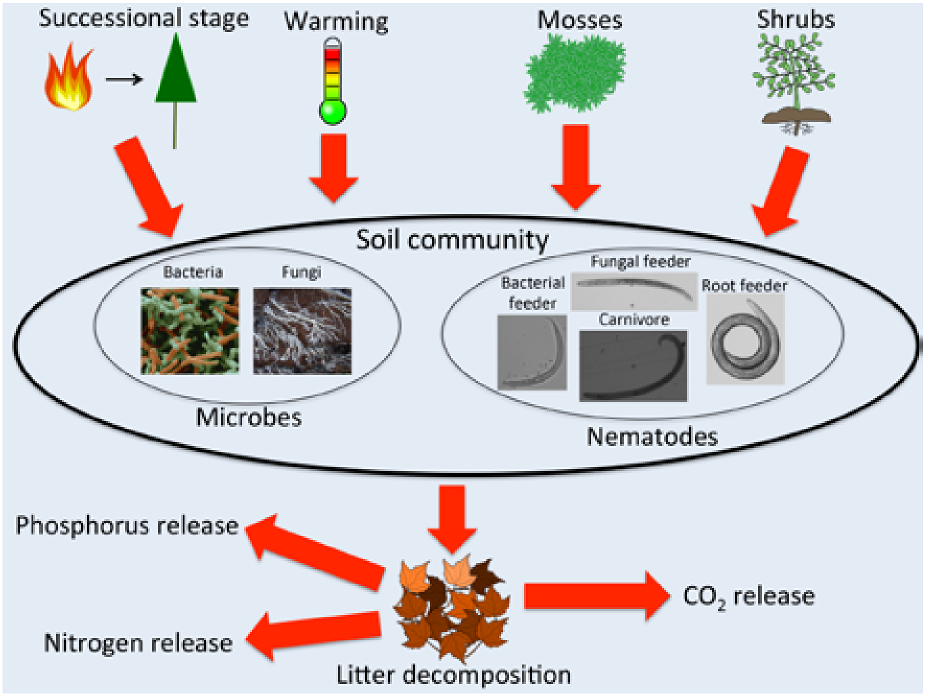

Figure 2. Conceptual diagram depicting how successional stage, warming, feather mosses and dwarf ericaceous shrubs impact upon the soil community. Changes to the soil community have the potential to alter litter decomposition processes, which controls the release of carbon dioxide into the atmosphere and also makes nitrogen and phosphorus available to plants and microbes.

Who cares about rotting plants?

Atmospheric CO_2, an important greenhouse gas, is transformed into plant biomass via photosynthesis. After plants die, their biomass begins to decompose. Plant tissues are broken down and CO_2 is released into the atmosphere and/or soil by decomposer organisms. Decomposition is the key process, which, after photosynthesis, determines how much C is stored in the soil.

In addition to releasing C from plant tissues, decomposition also controls the cycling of other nutrients that are important for ecosystem processes, namely nitrogen (N) and phosphorus (P). After C, N and P are two of the principle components of plant and animal tissue. The availability of both N and P controls the growth and productivity of plants, microbes and animals in the boreal forest.

Many different organisms in the soil affect decomposition, such as soil microbes (i.e., bacteria and fungi) and nematodes. Fungal-dominated energy channels in the soil are typically associated with slower decomposition and nutrient cycling rates, while bacterial-dominated energy channels generally lead to faster rates. Further, nematodes are the most abundant multicellular animals on the planet and occupy many niches in the soil food web (i.e., feeding upon fungi, bacteria, plants, other nematodes). Additionally, alterations to the composition of the nematode community can indicate shifts in nutrient input and decomposition. Therefore, understanding how different decomposer organisms respond to contrasting environmental conditions is crucial for making predictions of how C storage and N and P cycling will be altered by climate change (Figure 2).

Figure 3. Litter bags decomposing in one of the plots with shrub removal (left side) and moss and shrub removal (right side) located at one of the late successional stage boreal forest sites (N 65° 46' 27.17", E 19° 6' 20.37") used in this experiment. At the site shown, the last fire occurred in 1647. Photo by Paul Kardol.

The understory plant community: running the show in the boreal forest

Feather mosses and ericaceous dwarf shrubs are the two dominant plant functional groups in the boreal forest understory. The presence of mosses can accelerate decomposition by creating a microclimate more favorable to decomposer activity. Understory shrubs produce high quantities of litter, but the quality of this litter

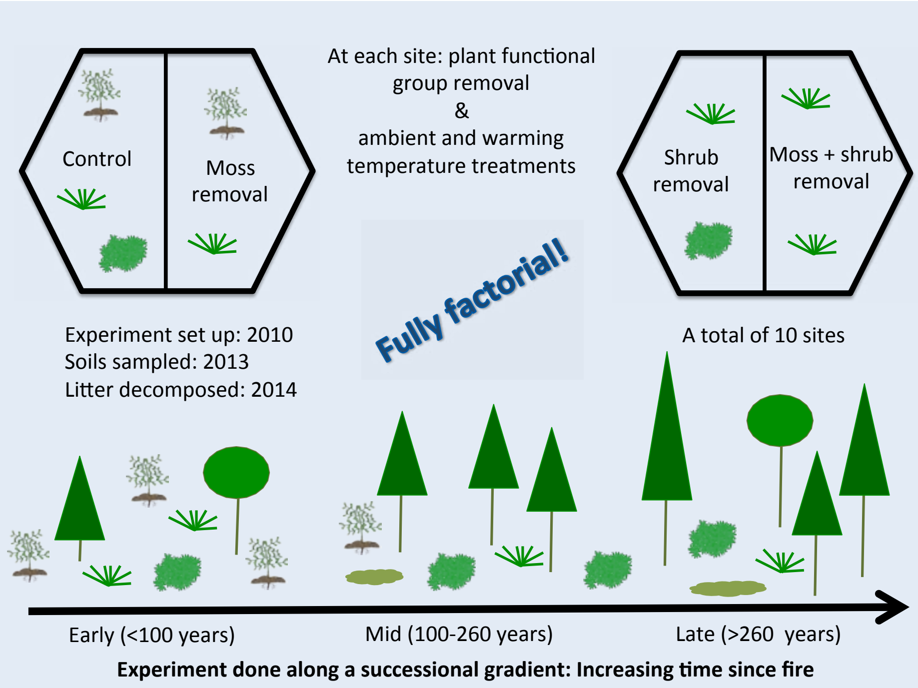

Figure 4. Diagram showing the experimental design. Plots were divided in half and randomly assigned to one of eight full-factorial combinations of warming, shrub removal and moss removal treatment. Across all ten sites, this yielded a total of 80 subplots.

varies between species and therefore can affect decomposition rates by influencing decomposer community composition and activity.

Post-fire succession in the boreal forest
Forest fire caused by lightning strike is one of the strongest abiotic drivers of boreal forest ecosystem function on decadal to centennial timescales. However, fire suppression in Fennoscandia over the past two centuries has decreased wildfire prevalence, although fire is expected to increase in sparsely populated boreal regions (Russia, Canada and Alaska) as climate change advances. Increasing time since fire in the boreal forest is associated with lower plant-available N and shifts in the vegetation from faster growing, nutrient acquisitive species with litter that decomposes quickly to slower growing, nutrient conservative species with litter that decomposes slowly.

An interactive experimental design
The field sites used in this study were located near Arvidsjaur in northern Sweden. We used ten sites along a fire-driven boreal forest chronosequence that varied in time since last stand replacing fire from 48 to 368 years. The present experiment involved plant functional group removals and warming treatments using open top chambers (OTCs) along this chronosequence (Figure 3). Functional group removal experiments are useful for understanding how different plant groups affect ecosystem processes. OTCs generally raise average air temperatures by approximately 1–2 °C during the growing season. At each site, four hexagonal plots were established. Each plot was divided into two subplots and randomly assigned to one of eight full-factorial combinations of warming, shrub removal and moss removal treatments (Figure 4). This design allowed us to look at interactions between successional stage, temperature, moss removal and shrub removal. Soil samples were taken from each subplot and used to measure microbial and nematode community composition. Further, bags containing the litter of three common boreal vascular plant species were placed in each subplot and allowed to decompose for one year before they were analyzed for mass loss, N loss and P loss.

What we found
Successional stage, warming, moss removal and shrub removal all interacted to drive the soil microbial community. Warming interacted with successional stage and moss and shrub removal to favor bacterial-based energy channels, particularly in early successional stage forests. Bacterial-based energy channels are known to promote faster decomposition and nutrient release, which could impact upon the amount of C stored in the soil. However, the nematode community was the most responsive to moss and shrub removal, with successional stage and warming rarely generating significant effects. Most nematodes were positively affected by the presence of mosses and shrubs, particularly plant and fungal feeders (Figure 5). These results demonstrate that care must be taken to consider the response of each soil guild when making predictions about the impacts of future climate change on the decomposer community in boreal forest soils.

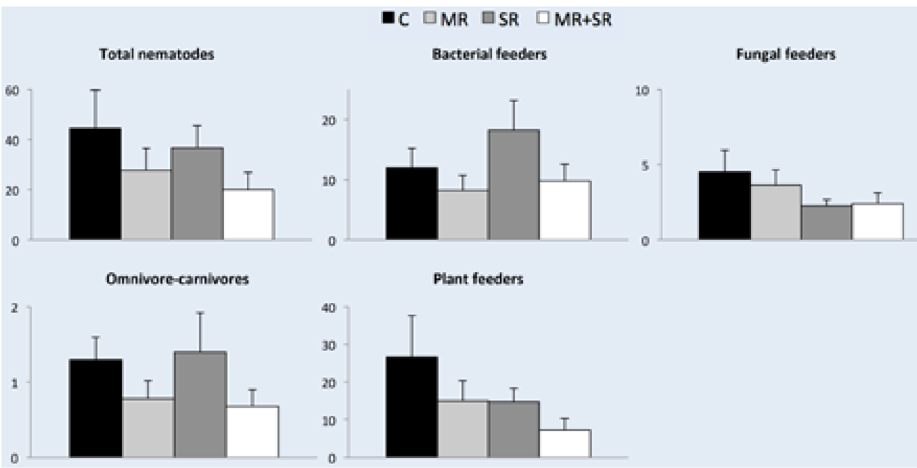

Figure 5. Measurements of total nematodes, bacterial feeders, fungal feeders, omnivore/carnivores and plant feeders in control (C), moss removal (MR), shrub removal (SR), and moss + shrub removal (MR+SR) plots. Data are means plus standard error bars (C, MR, SR, MR+SR: n=20) and expressed as nematodes per gram dry weight soil.

On the other hand, the litter species identity, as well as moss removal and shrub removal, were the primary drives of decomposition. The removal of mosses generally reduced litter mass loss and increased litter P loss, while shrub removal tended to increase litter mass loss. However, litter N loss was unaffected by the removal of either mosses or shrubs. Successional stage and warming generally had few effects on litter decomposition. This indicates that, in the short term, mosses and shrubs may play a larger role than warming and successional stage in determining litter decomposition and nutrient release rates in the boreal forest.

"... care must be taken to consider the response of each soil guild when making predictions about the impacts of future climate change on the decomposer community in boreal forest soils."

Implications and future directions

As climate change advances, moss cover is expected to decrease, while shrub cover is expected to increase. Our results suggest that lower moss cover will decrease litter decomposition but increase nutrient fluxes, while increasing shrub cover will likely decrease litter decomposition and reduce nutrient fluxes. Additionally, changes to the soil community structure do not always equate to predictable changes in litter decomposition. Further, climate-induced changes to understory vegetation will probably impact upon forest productivity, C storage, and nutrient cycling. Given the broad global distribution of shrubs and mosses in the understory of boreal forests, the results of this study are likely relevant throughout the boreal region. Our results underscore that considering the direct and indirect impacts of mosses and shrubs is necessary for developing more reliable predictions about how soil organisms and the decomposition and nutrient release processes that they drive in boreal forests will respond to advancing climate change ■

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Keywords
Boreal forest, carbon storage, litter decomposition, global climate change, nematodes, nutrient cycling, plant functional group removal, post-fire succession, soil microorganisms.

Read more

- **De Long, J.R., Dorrepaal, E., Kardol, P., Nilsson, M.-C., Teuber, L.M. & Wardle, D.A. 2015.** Contrasting responses of soil microbial and nematode communities to warming and plant functional group removal across a post-fire boreal forest successional gradient. Ecosystems, 19, 339–355.
- **De Long, J. R., Dorrepaal, E., Kardol, P., Nilsson, M.-C., Teuber, L.M. & Wardle, D.A. 2016.** Understory plant functional groups and litter species identity are stronger drivers of litter decomposition than warming along a boreal forest post-fire successional gradient. Soil Biology and Biochemistry, 98, 159–170.

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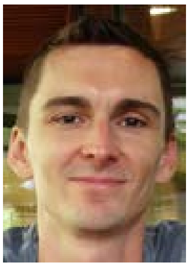

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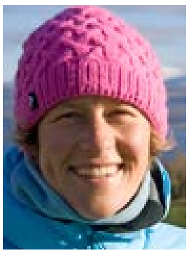

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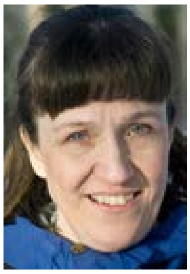

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