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## Mini-review

# Climate change feedbacks to microbial decomposition in boreal soils

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### ABSTRACT

Boreal ecosystems store 10–20% of global soil carbon and may warm by 4–7 °C over the next century. Higher temperatures could increase the activity of boreal decomposers and indirectly affect decomposition through other ecosystem feedbacks. For example, permafrost melting will likely alleviate constraints on microbial decomposition and lead to greater soil CO<sub>2</sub> emissions. However, wet boreal ecosystems underlain by permafrost are often CH<sub>4</sub> sources, and permafrost thaw could ultimately result in drier soils that consume CH<sub>4</sub>, thereby offsetting some of the greenhouse warming potential of soil CO<sub>2</sub> emissions. Climate change is also likely to increase winter precipitation and snow depth in boreal regions, which may stimulate decomposition by moderating soil temperatures under the snowpack. As temperatures and evapotranspiration increase in the boreal zone, fires may become more frequent, leading to additional permafrost loss from burned ecosystems. Although post-fire decomposition could also increase due to higher soil temperatures, reductions in microbial biomass and activity may attenuate this response. Other feedbacks such as soil drying, increased nutrient mineralization, and plant species shifts are either weak or uncertain. We conclude that strong positive feedbacks to decomposition will likely depend on permafrost thaw, and that climate feedbacks will probably be weak or negative in boreal ecosystems without permafrost. However, warming manipulations should be conducted in a broader range of boreal systems to validate these predictions.

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## Introduction

Boreal forests occupy 8–11% of the Earth's land surface and store a large fraction of global terrestrial carbon (Whittaker 1975). The boreal zone includes large regions of Alaska, Canada, Scandinavia, and Siberia for a total of 11.2–15.8 million km<sup>2</sup> worldwide (Chapin & Matthews 1993; Gower *et al.* 2001). Although estimates vary, these regions contain 60–110 Pg carbon (C) in plant biomass (Schlesinger 1977; Apps *et al.* 1993) and 90–230 Pg C in upland forest soil

(Schlesinger 1977; Post *et al.* 1982; Oechel & Billings 1992; Apps *et al.* 1993). Boreal peat soils are estimated to store an additional 420–455 Pg C (Gorham 1991). All of these values may be underestimates because they are based on surface soils (generally <1 m depth), and a recent analysis suggests that deep high-latitude soils may store >1670 Pg C, although this estimate also includes tundra ecosystems (Schoor *et al.* 2008). Overall, boreal soils probably contain at least 10–20% of the global total of ~2300 Pg soil C (Jobbágy & Jackson 2000).

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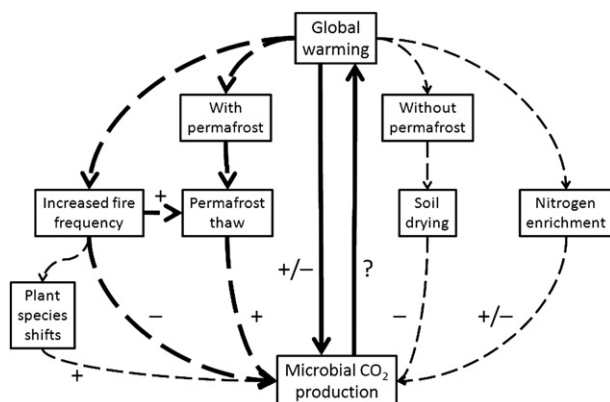
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Because there is so much C stored in boreal ecosystems, they have the potential to effect feedbacks between climate and the global C cycle. Increasing concentrations of greenhouse gases due to human activities are increasing global mean temperatures, and feedbacks in the climate system are expected to cause disproportionate warming at high latitudes (IPCC 2007). These systems have already warmed by  $\sim 1.5^\circ\text{C}$  (Moritz *et al.* 2002), and are expected to warm by  $4\text{--}7^\circ\text{C}$  in the next century (IPCC 2007). Warming of this magnitude is expected to alter many processes that affect C cycling in boreal ecosystems (McGuire *et al.* 2009). For example, climate warming may increase plant biomass and litter inputs if higher temperatures result in faster rates of plant growth and soil nutrient mineralization. Conversely, warmer temperatures may stimulate C losses from boreal soils through increased rates of decomposition. Carbon has accumulated in boreal soils primarily because cold temperatures and permafrost (perennially frozen soil) reduce decomposition rates relative to C inputs from primary production (Stokstad 2004). These thermal constraints are further reinforced by plant–soil feedbacks that lead to poor litter quality (Hobbie *et al.* 2000) and a high relative abundance of ectomycorrhizal fungi that may inhibit decomposition by saprotrophic fungi in boreal soils (Lindahl *et al.* 2002).

Given that boreal ecosystems contain 10–20 % of global soil C, climate change could have large impacts on global C balance through effects on decomposition. The decomposition of soil C is a biological process controlled primarily by micro-organisms such as fungi and bacteria (Swift *et al.* 1979). The direct and indirect effects of climate change will therefore mediate boreal C cycling through effects on decomposer communities, and

these interactions will be the focus of our review (Fig 1). Climate change may influence decomposer microbes directly through changes in temperature or precipitation (IPCC 2007). Indirect effects include changes in soil moisture due to increased evapotranspiration and melting of permafrost (Potter *et al.* 2001; Zimov *et al.* 2006; Schuur *et al.* 2008). If rates of decomposition increase, nutrient availability to decomposers may increase through faster rates of mineralization (Rustad *et al.* 2001). Climate may also indirectly affect microbial decomposers through changes in fire frequency and plant community composition (Kasischke & Stocks 2000; Hollingsworth *et al.* 2008); either of these changes may affect the chemical and physical environment for decomposition.

Since climate change will affect soil C decomposition directly and indirectly through microbial communities, the goal of this synthesis is to evaluate the feedbacks among climate change, microbes, and decomposition in boreal ecosystems. By understanding these feedbacks, we aim to improve models and predictions of boreal C storage and global climate in the coming decades. Specifically, we will address the following questions: (1) What is the diversity and distribution of decomposer microbes relevant for decomposition in boreal forests? (2) How do microbial communities and decomposition respond directly to temperature increase? (3) What are the responses to indirect climate feedbacks, such as permafrost thaw, soil drying, increases in fire frequency, increased nutrient mineralization, and changes in plant community composition? We conclude with a summary of predictions for boreal C storage in the face of climate change and recommendations for increasing the accuracy of uncertain predictions.



**Fig 1 – Predicted direct and indirect effects of global warming on microbial CO<sub>2</sub> production in boreal ecosystems, based on data from laboratory and field studies. The integrated effect of global warming will depend on the relative strength of each effect, and the distribution of permafrost in boreal forests. We predict that the strongest effects will be derived from permafrost thaw and increased fire frequency. Permafrost thaw should increase microbial CO<sub>2</sub> production owing to thicker active layers and drainage of water-saturated soils. More frequent fires may also lead to greater permafrost loss, but may reduce microbial CO<sub>2</sub> production due to declines in microbial biomass. Solid lines = direct effects; dashed = indirect. Thicker lines = stronger predicted effects.**

## Microbial abundance and community structure in boreal soils

Fungi are the most well-studied microbes in boreal soils, although bacteria and archaea may also act as decomposers (Thormann *et al.* 2004). Separating the contribution of each microbial domain to decomposition is challenging and has rarely if ever been quantified in any ecosystem. Fungi are assumed to be important for boreal decomposition because of their enzymatic potential to decompose recalcitrant forms of soil C and their tolerance of the acidic pH values typical of most boreal soils (Högberg *et al.* 2007). While there are many studies demonstrating that boreal fungi are important for decomposition (Lindahl *et al.* 2002; Virzo De Santo *et al.* 2002; Read *et al.* 2004; Allison *et al.* 2009; LeBauer 2010), there are few to support the assertion that bacteria and archaea are unimportant. It is therefore clear that more studies are warranted to determine the quantitative importance of fungi, bacteria, and archaea for decomposition in boreal soils.

Boreal soils contain a high diversity of saprotrophic and mycorrhizal fungi that participate in the breakdown of soil organic matter. Arbuscular mycorrhizas are present in many boreal ecosystems, but their role in decomposition is thought to be relatively minor (Read & Perez-Moreno 2003; Treseder *et al.* 2004; Treseder & Cross 2006), so they will not be considered further here. Many saprotrophic fungi found in boreal ecosystems produce extracellular enzymes capable of decomposing the major chemical compounds found in plant

litter and humus, such as cellulose, lignin, tannins, protein, and chitin (Lindahl & Finlay 2006; Allison *et al.* 2009; LeBauer 2010). Ericoid and ectomycorrhizal taxa also possess genes for oxidative and hydrolytic enzymes that may be expressed to decompose soil organic compounds (Read & Perez-Moreno 2003; Lindahl & Taylor 2004; Courty *et al.* 2005; Buée *et al.* 2007; Bödeker *et al.* 2009). Although they may not decompose soil C as effectively as saprotrophs on a per-biomass basis (Baldrian 2009), the high relative abundance of ericoid and ectomycorrhizal fungi in many boreal ecosystems suggests that they may be quantitatively important for soil C turnover (Lindahl *et al.* 2007, 2010; Allison *et al.* 2008; Talbot *et al.* 2008).

There is clear evidence that fungal community composition differs vertically through the soil profile. Wood decay fungi, especially brown-rot and white-rot basidiomycetes, colonize standing dead or fallen coarse woody debris (Berglund *et al.* 2005). In a boreal forest dominated by Scots pine, surface litter horizons were dominated by saprotrophic basidiomycetes and ascomycetes, whereas humus layers and mineral soils were dominated by ectomycorrhizal fungi (Lindahl *et al.* 2007, 2010). This segregation of fungal functional groups probably occurs because mycorrhizal fungi can access labile C from host plants in deeper soil layers where C availability may limit saprotrophs. However, ectomycorrhizal fungi occur throughout the soil profile, with different taxa found in organic versus mineral layers (Tedersoo *et al.* 2003).

Distributions and functions of boreal bacteria and archaea are not well understood. Studies based on phospholipid fatty acid (PLFA) data suggest that some boreal soils may be dominated by Gram-negative bacteria (Demoling *et al.* 2008), whereas others may be dominated by Gram-positive bacteria (Högberg *et al.* 2003). This latter study also found that the ratio of Gram-negative:Gram-positive bacteria declined with soil depth, from the F to the H horizon. In wetter bog environments, Jaatinen *et al.* (2007) found that Gram-negative bacteria dominated surface soils, and decreased relative to Gram-positive bacteria in deeper soil horizons in two of three Finnish study sites. They also found a relatively high abundance of actinobacterial PLFA markers in a mineral-rich bog site and suggested that these microbes may contribute to decomposition due to their ability to produce degradative enzymes. However, the functional roles of bacteria within these broad groups are highly diverse, so changes in bacterial community composition are difficult to link with decomposition rates. Fierer *et al.* (2007) have proposed a functional classification scheme for bacteria, but both oligotrophic and copiotrophic classes occur within the Gram-negative bacteria, so measurements of bacterial community composition must occur at finer taxonomic resolution than PLFA groups to be functionally relevant.

Archaea also occur in boreal forest soils, and may contribute to decomposition through mineralization of labile organic matter in the rhizosphere. Crenarchaeota appear to be the dominant taxon in soil (Jurgens *et al.* 1997) and are known to occur in preferential association with mycorrhizal plant roots where they may metabolize plant exudates (Bomberg *et al.* 2003; Bomberg & Timonen 2009). Euryarchaeota have also been observed to associate with *Pinus sylvestris* mycorrhizas (Bomberg & Timonen 2007).

## Direct effect of warming on microbial processes and soil C cycling

A major concern with climate change in boreal regions is that rising temperatures will increase the metabolic rates of decomposer microbes, thereby mobilizing the large C stocks in boreal soils (McGuire *et al.* 2009). Temperature manipulations in boreal systems can provide information about the direct response of microbial communities and decomposition rates to climate warming. However, given their importance for the global C cycle, relatively few warming manipulations have been carried out in boreal ecosystems. In particular, we know of no experiments that have examined microbial responses to warming in the Siberian boreal zone or in boreal bogs which together store the majority of C in boreal ecosystems globally. Therefore our current knowledge is mainly restricted to the upland boreal forests of Alaska, Canada, and Scandinavia.

Warming manipulations in these boreal regions have yielded conflicting results (Table 1). In an Alaskan boreal forest underlain by permafrost, warming during three growing seasons resulted in a 20 % reduction in forest floor biomass, suggesting increased microbial activity and decomposition (Van Cleve *et al.* 1990). Several other studies have also found that soil respiration and possibly decomposition increase with warming, although these measurements cannot easily distinguish root and heterotrophic responses (Strömberg 2001; Bergner *et al.* 2004; Niinistö *et al.* 2004; Bronson *et al.* 2008). In contrast, some researchers have found negative soil respiration responses to warming (Allison & Treseder 2008), including Bronson *et al.* (2008), who observed that a positive response turned negative when air was warmed in addition to soil (Table 1). Although the mechanism for negative responses to warming is not entirely clear, concomitant declines in soil moisture or physiological stress on roots and soil microbes are possible explanations. Studies by Verburg *et al.* (1999) and Allison *et al.* (2010b) found no response of litter decomposition and soil respiration, respectively, to warming. For logistical reasons, most of the manipulations in Table 1 were carried out only during the growing season, but climate warming is expected to occur during the winter and to increase growing season length, which could result in greater warming responses on an annual basis (Strömberg 2001; Euskirchen *et al.* 2006).

Predicting the direct response of microbes and decomposition to warming is further complicated by potential changes in microbial community composition and physiology. Initial responses to higher temperature could change if warming causes microbes with different functional characteristics to become dominant in boreal soils. In addition, microbial communities could adapt to warming through physiological adjustments in rates of metabolism, or evolution of proteins with different thermal optima (Hochachka & Somero 2002; Bradford *et al.* 2008). All of these responses could contribute to altered sensitivities of key processes related to decomposition, such as extracellular enzyme catalysis and microbial respiration. Although there is some evidence that boreal soil respiration may adapt to warming (Strömberg 2001), there are as yet few studies of microbial community responses. Our work in recently burned and mature Alaskan boreal forests

**Table 1** – Summary of warming manipulations in boreal ecosystems

Site	Method	Duration	Soil warming	Air warming	Permafrost	Response variable	% Change	Comments	Reference
Washington Creek, AK, USA	Soil warming (resistance tape)	3 Growing seasons	8–10 °C	NA	Yes	Forest floor biomass	–20 %		Van Cleve et al. (1990)
Flakaliden, Sweden	Soil warming (heating cables)	6 Growing seasons	5 °C	NA	No	Soil respiration	+10 % to +20 %	Irrigated and fertilized	Strömgren (2001)
Delta Junction, AK, USA	Open top chamber	3 Growing seasons	0.9 °C	0.4 °C	No	Soil respiration	+20 %	Burned ecosystem	Bergner et al. (2004)
Mekrijärvi Research Station, Finland	Closed chamber	4 yr	2–4 °C	5 °C	No	Soil respiration	+27 % to +43 %	2 yr post-fire	Niinistö et al. (2004)
Thompson, Manitoba, Canada	Soil warming (heating cables) Soil warming + closed chamber	2 Growing seasons	3.1–4.5 °C	NA	No	Soil respiration	+11 % to +24 %	Irrigated; <i>Pinus sylvestris</i> in chambers	Bronson et al. (2008)
Delta Junction, AK, USA	Closed chamber	3 Growing seasons	0.5 °C	ND	No	Soil respiration	–22 %	Irrigated; <i>Picea mariana</i> in chambers	Allison & Treseder (2008)
CLIMEX: Risdalsheia, Norway	Soil warming (heating cables)	2 yr	3–5 °C	NA	No	Litter mass loss	No change	Possible drying effect	Verburg et al. (1999)
Delta Junction, AK, USA	Closed chamber	3 Growing seasons	1.2 °C	ND	No	Soil respiration	No change	Burned ecosystem	Allison et al. (2010b)
James Bay, Quebec, Canada	Open top chamber	2 yr	–1 °C (cooling)	1–2 °C	No	Litter mass loss	0 % to –3 %	7 yr post-fire	Dabros & Fyles (2010)

has shown relatively little change in fungal community composition after 2–3 growing seasons of warming, although there was a 50 % reduction in microbial biomass in the mature forest site (Bergner et al. 2004; Allison & Treseder 2008; Allison et al. 2010b).

Aside from direct manipulations, climate gradients can also provide insight into ecosystem responses to warming. Consistent with the prediction that warming will lead to soil C loss, Kane et al. (2005) used a climate and productivity gradient in Alaskan black spruce forests to show that soil organic C stocks decrease with increasing soil temperature, particularly in mineral horizons. Across a climate gradient spanning –1 °C to –5 °C mean annual temperature in boreal peatlands of northern Manitoba, Camill & Clark (1998) assessed the relative importance of regional climate versus local factors in controlling permafrost dynamics, which strongly influence soil C storage. This study showed that local factors such as topography, aspect, and vegetation communities mediated the response of permafrost to regional temperature. The importance of local processes may help explain why direct manipulations of temperature at single sites often yield conflicting results (Table 1).

### Direct effect of precipitation change on microbial processes and soil C cycling

Increased atmospheric moisture content due to regional warming in the high latitudes will likely lead to increased precipitation in most boreal ecosystems. In the Eurasian boreal zone, nearly all climate models predict increased precipitation, particularly in winter (IPCC 2007). Most models also predict increased autumn and winter precipitation in the North American boreal zone, with relatively small changes in summer precipitation (IPCC 2007). Increased winter precipitation will fall as snow, which will likely increase snow depth and potentially moderate the temperatures experienced by soil microbes during winter. In alpine forests, winters with deeper snowpack are associated with increased soil temperatures and greater soil CO<sub>2</sub> efflux (Monson et al. 2006). Although deeper snowpack may stimulate decomposition, the effects of increased snowmelt and rainfall are less certain and may depend on soil hydrology. Decomposition is more likely to respond positively to increased precipitation in soils with better drainage and more frequent moisture limitation compared to poorly drained soils with anaerobic conditions (Rapalee et al. 1998; Preston et al. 2006). Overall, it appears that decomposition responses to precipitation increase will be positive, but interactions with temperature, soil hydrology, snow dynamics, and vegetation change will likely mediate the response.

### Indirect effects of warming on microbial processes and C cycling

Aside from the direct effects, climate change in the boreal zone will likely lead to indirect feedbacks that also have the potential to affect microbial communities and rates of C loss (Fig 1). In some cases, these indirect effects may be more

important than the direct response to warming. A major challenge in predicting boreal responses to climate change is estimating the magnitude and direction of these feedbacks. Therefore we focus the remainder of this review on indirect effects resulting from climate change in the boreal zone.

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## Permafrost thaw

Permafrost exerts a strong influence over C balance in high-latitude ecosystems (Carrasco *et al.* 2006; Zimov *et al.* 2006; Schuur *et al.* 2008; Ping *et al.* 2010). Permafrost soils often store large amounts of C because low temperatures and limited diffusion of oxygen and solutes constrain the activity of microbial decomposers in frozen soil. Furthermore, permafrost impedes soil drainage, leading to waterlogging and low oxygen availability in surface soil horizons. If permafrost melts under warmer conditions, all of these constraints could be alleviated, resulting in a rapid release of stored soil C (Schuur *et al.* 2008).

In the boreal zone, permafrost thaw is likely to represent an important but spatially heterogeneous feedback to microbial activity and decomposition. Unlike tundra ecosystems, permafrost is not found in all boreal soils, and permafrost feedbacks will not occur in many boreal systems. Overall, we estimate that 40–55 % of the boreal zone is underlain by permafrost (Fig 2). This estimate is based on the boreal forest extent from Larsen (1980) and the distribution of permafrost extent from Brown *et al.* (1998). Based on these distributions, we visually estimated the fraction of the boreal zone underlain by continuous, discontinuous, sporadic, isolated, and no permafrost. These classes represent 90–100 %, 50–90 %, 10–50 %, 0–10 %, and 0 % permafrost coverage, respectively. We then calculated the average permafrost coverage for the whole boreal zone, weighted by the fraction of boreal forest in each permafrost class. Our range of estimates (40–55 %) is based on using the low versus high limit of coverage for each permafrost class.

In boreal forests with permafrost, microbial feedbacks to decomposition under climate warming are likely to be strong. The boreal zone encompasses the southern boundary of permafrost extent, so permafrost soils in this region may become destabilized with relatively little warming. In the mineral horizon of an Alaskan boreal forest, the relative abundance of fungi was lower in permafrost soils compared to non-permafrost soils, whereas the potential activity of polyphenol oxidase enzyme was greater (Waldrop & Harden 2008). At a single Alaskan site with permafrost, abundances of bacteria and fungi were lower in permafrost than in the overlying active layer (Waldrop *et al.* 2010). Chemical analyses at this site also indicated that organic compounds in permafrost are relatively labile. Overall, these results suggest that decomposition of permafrost C is limited by low microbial activity, but high potential enzyme activity and an abundance of available C could result in rapid losses of soil C following permafrost thaw (Freeman *et al.* 2001, 2004). This conclusion is supported by radiocarbon measurements of soil respiration in the arctic which suggest large losses of C greater than 50 yr old from melted permafrost soils (Schuur *et al.* 2009).

Although increased soil CO<sub>2</sub> emissions following permafrost thaw would provide a positive feedback to climate warming, changes in CH<sub>4</sub> cycling could provide a negative feedback. Methane is a potent greenhouse gas produced through anaerobic decomposition and microbial reduction of CO<sub>2</sub>. Whereas upland boreal soils can be a sink for methane, bogs and waterlogged soils underlain by permafrost can be methane sources (Whalen *et al.* 1991; Whalen & Reeburgh 1996; Burke *et al.* 1997; Gullede & Schimel 2000; Panikov & Dedysh 2000; Kim *et al.* 2007). Therefore conversion of permafrost to non-permafrost soils could ultimately reduce the amount of CH<sub>4</sub> emitted from boreal soils, although CH<sub>4</sub> emissions could increase during the thaw process, which may take several decades (Nykänen *et al.* 1998; Kim & Tanaka 2003). In Alaskan tundra, transition to drier conditions occurred within 50 yr of permafrost thaw (Schuur *et al.* 2009), and in Finland, conversion from wetland to forest vegetation occurred within 50 yr after mires were drained (Laine *et al.* 1995).

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## Soil drying

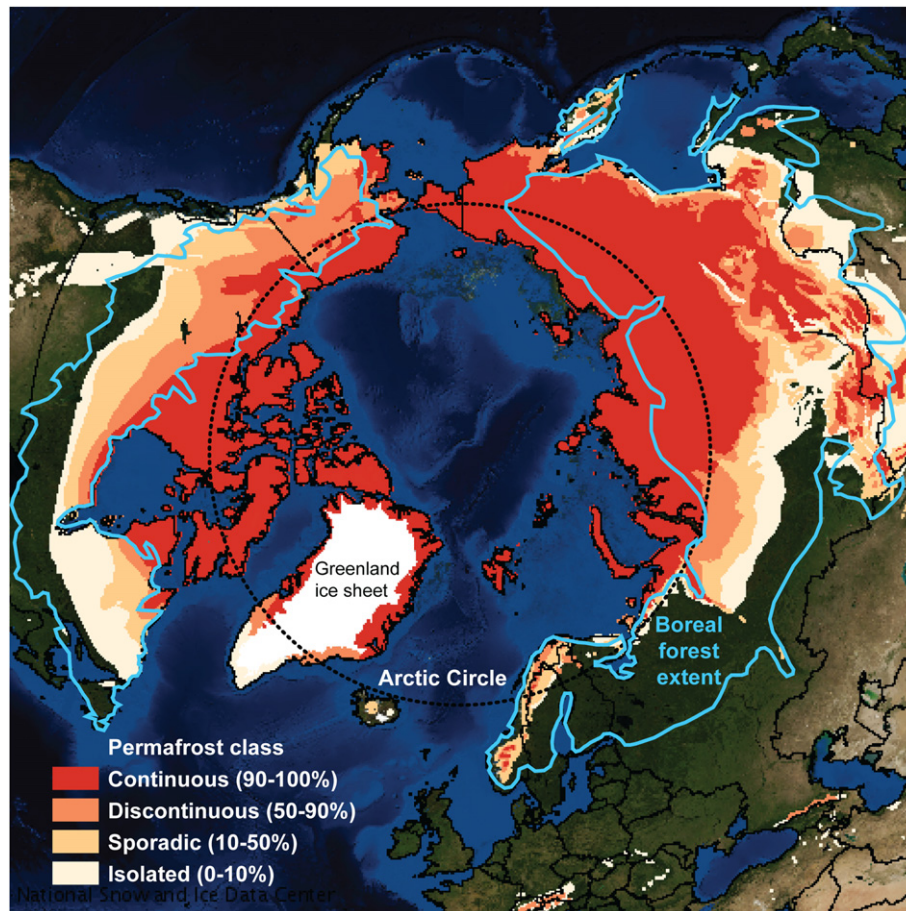
Climate warming in boreal ecosystems will likely lead to increased rates of evapotranspiration and substantial soil drying, particularly in surface horizons. However, the effect of reduced soil moisture on decomposition rates will probably depend on the initial moisture and permafrost status of the soil (Fan *et al.* 2008). Drying may inhibit microbial activity in well-drained upland boreal soils, but stimulate microbial decomposition in poorly drained and permafrost soils. These changes are important because wetter soils tend to store more C and support lower rates of decomposition (Trumbore & Harden 1997; Rapalee *et al.* 1998; Preston *et al.* 2006; Ping *et al.* 2010).

Evidence from warming manipulations generally supports the prediction that decomposition in relatively dry soils tends to respond negatively to additional drying. Soil C cycling in boreal sites that were not irrigated or underlain by permafrost generally showed weak or negative responses to warming and involved indirect drying effects (Table 1; Allison & Treseder 2008; Allison *et al.* 2010b). In contrast, drying of a Finnish boreal fen resulted in a threefold increase in soil respiration, increases in microbial biomass, and a shift in microbial community composition toward fungal taxa (Jaatinen *et al.* 2008). However, it should be noted that the effect of drying on CH<sub>4</sub> emissions from wet soils is likely to be negative (Nykänen *et al.* 1998), so positive CO<sub>2</sub> feedbacks from drying boreal wetlands may be partially countered by negative feedbacks from reduced CH<sub>4</sub> emissions.

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## Changes in fire regime

Each year, wildfires consume an average of ~110,000 km<sup>2</sup>, or ~1 %, of the boreal forest in Asia and North America, implying a fire return interval of ~100 yr (Giglio *et al.* 2006). Although there is large inter-annual variation (Wein & MacLean 1983), modelling studies in Canadian boreal forest suggest that fire may consume ~10–30 % of NPP based on long-term averages



**Fig 2 – Extent of northern boreal forest (blue lines) adapted from Larsen (1980) overlain on permafrost distributions adapted from Brown et al. (1998) and the National Snow and Ice Data Center, Atlas of the Cryosphere ([http://nsidc.org/data/atlas/atlas\\_info.html](http://nsidc.org/data/atlas/atlas_info.html)).**

for C loss through burning (Harden et al. 2000). Warmer temperatures and potential soil drying in the boreal zone may lead to increases in fire frequency, intensity and extent (Kasischke et al. 1995; Kasischke & Stocks 2000; Kasischke & Turetsky 2006).

Changes in fire dynamics are important because fires have dramatic impacts on decomposition, microbial communities, and other ecosystem properties. Initially, boreal fires mobilize large amounts of C from biomass and organic soils through combustion. During recovery from wildfire, further decomposition losses of C are hypothesized to occur due to elevated soil temperatures that can increase by 3–8 °C compared to unburned areas (Burke et al. 1997; Richter et al. 2000; O'Neill et al. 2002; Kim & Tanaka 2003; Treseder et al. 2004). Fires also lead to the formation of black carbon, which decomposes very slowly with turnover times on the order of millennia (Preston & Schmidt 2006; Kuzyakov et al. 2009). However, the net effect of black carbon on decomposition is unclear because it has been found to increase humus decay rates in boreal soils, potentially by providing a favorable physical substrate for microbial decomposers (Wardle et al. 2008).

Based on measurements of soil respiration per unit area, many investigators have concluded that decomposition increases following fire. In upland Canadian boreal forest,

Burke et al. (1997) found that total rates of soil respiration were maintained immediately following fire, then declined after 2 yr and subsequently recovered to pre-burn levels 7 yr after fire. They concluded that increased microbial respiration immediately after burning may have offset a decline in autotrophic respiration, but that substrate depletion limited microbial respiration after 2–5 yr. Kim & Tanaka (2003) found 22–50 % reductions in soil respiration rates 0–2 yr after fire in boreal forests of interior Alaska, but concluded that microbial respiration had increased based on the assumption that only 20 % of pre-burn soil respiration was microbial. Similarly, O'Neill et al. (2003) found that soil respiration was 40–50 % lower in recently burned black spruce forests in Alaska, but suggested that decomposition rates had increased by >3-fold based on a C balance model and prior lab incubation results (Richter et al. 2000; O'Neill et al. 2006). Similar conclusions were drawn based on data from a fire chronosequence in Siberian boreal forest (Sawamoto et al. 2000).

These reported increases in microbial respiration are difficult to reconcile with microbial community responses to fire, which are consistently negative. Burning removes surface soil horizons that are rich in labile C, halts plant root exudation, reduces substrate availability, and generates recalcitrant combustion products that may constrain microbial

decomposition (Certini 2005; Harden *et al.* 2006). Bergner *et al.* (2004) found lower rates of soil respiration and non-detectable fungal biomass in severely burned soils of boreal Alaska. Using a nearby set of fire chronosequence sites, Treseder *et al.* (2004) found that the diversity of bacteria and the abundance of ectomycorrhizal fungi required >15 yr to recover to pre-burn levels. Fungal biomass, polyphenol oxidase activity, and rates of lignin decomposition also declined significantly 5 yr after fire in these sites (Waldrop & Harden 2008). Declines in microbial biomass C, fungal hyphal length, and basal soil respiration from lab incubations were likewise found 0–2 yr after fire in Scandinavian boreal forests (Pietikäinen & Fritze 1996).

Large increases in microbial respiration following fire are therefore surprising given the concurrent declines in microbial biomass and function. To increase heterotrophic respiration, fire would have to dramatically increase soil mass-specific rates of decomposition to compensate for combustion losses of C from the soil profile, which would tend to reduce heterotrophic respiration on an area basis. There is some evidence for increased mass-specific microbial respiration in burned soils (O'Neill *et al.* 2006), but these results were based on lab incubations of humic soil from a single site that had burned two weeks earlier, and are inconsistent with the findings of Pietikäinen & Fritze (1996). Thus, it is not clear how long after fire increases in substrate quality and microbial decomposition persist, or if decomposition shows the same fire response under field conditions.

Since the decomposition potential of the microbial community appears to decline following fire, other mechanisms may be required to explain observed rates of soil respiration. One such explanation may be root respiration from burned plants—Czimczik *et al.* (2006) found that soil respiration was ~50 % lower in black spruce forest that burned recently in Canada, but <sup>14</sup>C signatures provided no indication of an increase in heterotrophic respiration. Instead, they concluded that respiration from the roots of burned black spruce trees could account for 50–80 % of soil respiration. Respiration from dying roots and associated mycorrhizas has also been shown to persist for ~1 yr after tree girdling (Bhupinderpal *et al.* 2003). These results suggest that other studies may have overestimated heterotrophic respiration following fire if they assumed that root respiration was zero. Nonetheless, even low rates of heterotrophic respiration will cause burned ecosystems to lose C until inputs from NPP begin to recover after several years (Bond-Lamberty *et al.* 2004).

Resolving the source of soil respiration and the rate of decomposition in burned boreal ecosystems is important for determining the ultimate feedback to global climate change. It has been hypothesized that decomposition following fire may release as much C as the fire itself (Richter *et al.* 2000). One implication of increased fire frequency is that a greater fraction of the boreal zone will be occupied by forests that have recently lost soil and biomass C but have not accumulated large humus stocks, resulting in lower levels of C storage (Kasischke *et al.* 1995; Wirth *et al.* 2002; Wardle *et al.* 2003). However, changes in albedo may cancel and even reverse the positive climate feedbacks associated with CO<sub>2</sub> release from boreal forest fires (Randerson *et al.* 2006). Therefore, the

magnitude as well as the sign of climate feedbacks arising from increased boreal fire frequency may depend on the amount of soil C mobilized by microbes, a parameter that remains uncertain. Addressing this uncertainty will require additional measurements of soil C stocks at high temporal resolution across fire chronosequences and concurrent assessment of the heterotrophic contribution to soil respiration.

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## Changes in plant species composition

Changes in fire properties and climate may alter plant species composition in boreal forests which may in turn influence microbial decomposition. For example, increased fire frequency will increase the dominance of early-successional species such as grasses, forbs and deciduous trees in boreal ecosystems (Mack *et al.* 2008). The resulting differences in litter quality and chemistry among plant species may then affect litter decay rates (Anderson 1991) and levels of soil C storage. Many deciduous and early-successional plant species produce litter that decomposes more rapidly than the moss and coniferous litter produced in late-successional forests (Moore *et al.* 2005; Turetsky *et al.* 2008). Furthermore, dominance by early-successional species such as grasses could alter fungal community composition by favoring arbuscular over ectomycorrhizal fungi (Treseder *et al.* 2004). A shift toward arbuscular mycorrhizas may speed the accumulation of soil C through production of the fungal glycoprotein glomalin (Treseder *et al.* 2007) and through reduced decomposition by extracellular enzymes derived from ectomycorrhizal fungi (Read & Perez-Moreno 2003; Talbot *et al.* 2008). Although there is scant empirical evidence, it is also possible that arbuscular biomass decomposes more rapidly than ectomycorrhizal biomass, which would reduce soil C accumulation under early-successional plant species (Treseder & Allen 2000).

Climate-induced changes in vegetation communities are also expected to alter decomposition rates through litter and physical effects. After several decades, water table drawdown in Finnish peat bogs shifts the plant community toward woody plants that produce litter with slow decay rates (Laine *et al.* 1995; Straková *et al.* 2010). In Alaskan boreal forests, the presence of particular plant species such as black spruce (*Picea mariana*) and sphagnum moss are correlated with higher levels of soil organic C and potentially lower decomposition rates (Hollingsworth *et al.* 2008). Such differences may arise not only because of low litter quality, but also due to plant-induced changes in temperature and hydrology, such as shading from coniferous trees and soil insulation from mosses (Hollingsworth *et al.* 2008).

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## Feedbacks from increased nitrogen mineralization

If decomposition rates increase in a warmer climate, the nutrients bound up in organic matter may be released and increase nutrient availability for plants and microbes (Rustad *et al.* 2001; Hobbie *et al.* 2002). Higher nutrient levels could then

feedback to affect litter quality, microbial activity and rates of decomposition. Many of these feedbacks have been observed in warming manipulations around the globe, with average increases of 46 % for N mineralization and 19 % for plant productivity (Rustad *et al.* 2001). However, measurements of N cycling in boreal warming experiments are scarce, with only a few studies reporting changes in N availability. In the CLIMEX experiment in Norwegian boreal forest, whole-catchment warming increased nitrate and ammonium losses in runoff by 11 % and 60 %, respectively, although there were no apparent changes in litter decomposition rates (Lükewille & Wright 1997; Verburg *et al.* 1999). Similarly, available nitrate, ammonium, and phosphate increased by up to 34 %, 14-fold, and 60 %, respectively, in organic horizons of warmed black spruce soils in Alaska (Van Cleve *et al.* 1990). Soil potassium concentrations also increased, and foliar N concentrations were elevated by 38 %. In contrast, open top chambers did not increase nutrient supply rates in a Canadian boreal forest, possibly because the treatments were not effective at warming the soil (Dabros & Fyles 2010). Similarly, we have found relatively little effect of warming treatments on resin-available N and phosphorus in Alaskan boreal ecosystems (Allison & Treseder 2008; Allison *et al.* 2010b).

Although the effect of climate warming on nutrient availability is uncertain in boreal forests, many studies have examined the consequences of increased nutrient availability for microbial communities and decomposition. In general, these studies show that increased availability of nutrients (mainly N) strongly impacts microbial communities, but has inconsistent effects on decomposition. Mycorrhizal fungi are particularly sensitive to N availability, and frequently decline in response to N deposition and fertilization (Arnolds 1991; Brandrud & Timmermann 1998; Lilleskov *et al.* 2001). Certain nitrophilic taxa of mycorrhizas may persist under high N conditions (Boxman *et al.* 1998; Strengbom *et al.* 2001; Lilleskov *et al.* 2002), but overall abundance declines, possibly due to reductions in belowground C allocation by host plants (Högberg *et al.* 2003; Allison *et al.* 2008). There is some evidence for N-limitation of saprotrophic fungi from boreal forests, but only at relatively low levels of N addition (Allison *et al.* 2010a); high levels of N addition have been hypothesized to negatively affect decomposer fungi (Fog 1988). Demoling *et al.* (2008) found that fungal biomass and bacterial growth rates declined by >40 % in response to N addition in Swedish boreal forests. We observed a similar response in an early-successional boreal forest in Alaska, but no response of microbial biomass in an adjacent unburned forest (Allison *et al.* 2008, 2010a). However, both ecosystems showed significant changes in fungal community composition.

It is not yet clear how microbial responses to nutrients will affect decomposition processes in boreal forests. Studies from other ecosystems suggest that decomposition responses to N are variable and depend on many factors such as litter quality, ecosystem type and level of nutrient addition (Carreiro *et al.* 2000; Neff *et al.* 2002; Waldrop *et al.* 2004; Knorr *et al.* 2005). Long-term fertilization with N and phosphorus in the Alaskan arctic led to massive losses of C and N from the soil profile, accompanied by large changes in bacterial community composition (Mack *et al.* 2004; Campbell *et al.* 2010). Similar levels of N addition in an early-successional boreal site in

Alaska increased organic C-decomposition enzyme activities and litter decomposition rates, and appeared to cause substantial losses of soil C (Allison *et al.* 2010a). However, there was no evidence for increased rates of soil C loss through soil respiration at a nearby mature forest site (Allison *et al.* 2008). Other fertilization studies in Swedish and Finnish boreal forests imply that soil organic C decomposition slows down with N addition (Mäkipää 1995; Olsson *et al.* 2005). Together, the relatively weak response of nutrient mineralization to warming and the inconsistent response of decomposition to N addition suggest that indirect climate feedbacks involving nutrient availability will be relatively weak in boreal forests. However, fertilization experiments may be poor analogs for changes in nutrient availability under climate warming, since low levels of nutrient addition may have stronger or distinct impacts on C cycling relative to typical fertilizer levels (Allison *et al.* 2009).

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## Interactive effects

As the boreal climate warms, direct and indirect effects will occur simultaneously, leading to the potential for interactions and additional feedbacks. Here we will focus mainly on feedbacks involving fire and permafrost that may be particularly strong and relevant for decomposition in boreal ecosystems. Fire is critical because it has rapid and dramatic effects on soil temperature, permafrost dynamics, microbial communities, vegetation communities and nutrient availability (Wein & MacLean 1983; Dyrness *et al.* 1986). Therefore fire leads to a cascade of additional indirect effects that may alter decomposition and C storage for decades. Similarly, permafrost melting—whether caused by fire or climate warming—also impacts biological communities, nutrient availability and C storage over the long term.

Fire appears to increase the sensitivity of boreal ecosystems to other environmental changes. For example, increased N availability had no effect on soil respiration in mature Alaskan boreal forest, but reduced soil C pools and ultimately soil respiration in an adjacent burned ecosystem (Allison *et al.* 2008; Allison *et al.* 2010a). Soil respiration in the burned ecosystem also showed an initial positive response to experimental warming, whereas the unburned system showed a negative response (Bergner *et al.* 2004; Allison & Treseder 2008). Increases in soil temperature also make recently burned ecosystems highly susceptible to permafrost thaw (O'Neill *et al.* 2002). These systems typically experience increases in active layer depth and reductions in soil moisture, leading to higher C losses through soil respiration (Brown 1983; Dyrness *et al.* 1986; Kasischke & Stocks 2000). Losses of permafrost and reductions in the depth of insulating organic horizons can then feedback positively to warmer, drier soils that support different vegetation communities and are more susceptible to future fire (Harden *et al.* 2000, 2006).

Whether due to fire or direct warming, permafrost loss will affect decomposition through other ecosystem feedbacks. For example, increased active layer depth and access of decomposer microbes to available forms of organic matter may stimulate nutrient mineralization more strongly than in non-permafrost soils (Van Cleve *et al.* 1990). Permafrost soils are



also associated with different vegetation communities. In Alaskan ecosystems, black spruce-sphagnum moss communities typically grow on permafrost soils and produce recalcitrant litter with slow decomposition rates (Kasischke & Stocks 2000). In contrast, white spruce (*Picea glauca*) and aspen (*Populus tremuloides*) communities are more common on drier, non-permafrost soils (Van Cleve & Yarie 1986) and may produce litter with higher decomposition rates. These systems may in turn be more susceptible to fire. Together these processes will likely lead to increased loss of soil C from boreal ecosystems.

## Conclusions

Climate change will clearly impact boreal ecosystems and decomposition processes through direct and indirect mechanisms. It is likely that feedbacks involving permafrost and fire will impact boreal microbes, decomposition and C storage most strongly. Within the boreal zone, permafrost soils may represent only ~50% of the land area, but they contain the vast majority of soil C stocks (Schuur *et al.* 2008). As a result, permafrost loss will have a dramatic impact on the C balance of boreal ecosystems, as predicted for tundra ecosystems as well. Increases in fire frequency will probably lead to further loss of permafrost, thereby accelerating a positive feedback to decomposition. However, the greenhouse warming impact of this decomposition feedback may be at least partly offset by long-term changes in albedo (Randerson *et al.* 2006) and reductions in the activity of decomposer microbes following fire (Waldrop & Harden 2008).

The boreal zone is large and heterogeneous, with permafrost absent from many southern and Scandinavian boreal forests (Fig 2). These regions will probably experience much weaker feedbacks to decomposition as a result of climate warming. Ecosystems on well-drained soils lacking permafrost may show small or negative responses to climate warming due to soil drying and moisture limitation of decomposer organisms. Decomposition in these systems may, however, respond positively to predicted increases in precipitation. Microbial communities may respond to vegetation shifts or changes in nutrient mineralization in both non-permafrost and permafrost soils, but the few studies that have examined these feedbacks suggest that they will be small relative to changes in permafrost and fire. One important implication of these conclusions is that global models need to account for the spatial distributions of fire and permafrost in the boreal zone in order to accurately predict C fluxes under climate change.

Although it will be helpful to revise models, we also emphasize that accurate predictions of global change feedbacks will require a greater empirical focus on undersampled regions of the boreal zone. Siberia contains by far the largest fraction of boreal land area and soil C, yet Siberian ecosystems have received much less attention in the literature than have Alaskan, Canadian and Scandinavian boreal forests. Warming manipulations should therefore be conducted in a wider range of ecosystems to better represent the heterogeneity within the boreal zone. It is problematic that only one of the warming studies in Table 1 was conducted on permafrost soils, and none

of them was located in Siberian boreal forest. Warming manipulations in peat bogs, which store a large fraction of boreal soil C (Gorham 1991), are similarly lacking. Integrating spatially resolved models with targeted empirical studies is absolutely essential for evaluating the mechanisms and feedbacks predicted to occur under global change in the boreal zone.

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