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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_2 emissions. However, wet boreal ecosystems underlain by permafrost are often CH_4 sources, and permafrost thaw could ultimately result in drier soils that consume CH_4, thereby offsetting some of the greenhouse warming potential of soil CO_2 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.

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^2 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 (Schuur *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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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 ~1.5 °C (Moritz *et al.* 2002), and are expected to warm by 4–7 °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.

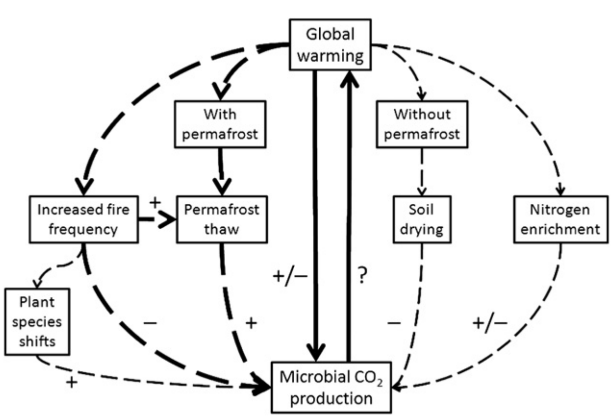

Fig 1 – Predicted direct and indirect effects of global warming on microbial CO_2 production in boreal ecosystems, based on data from laboratory and field studies. The integrated effect of global warming will depend on the relative strength of each effect, and the distribution of permafrost in boreal forests. We predict that the strongest effects will be derived from permafrost thaw and increased fire frequency. Permafrost thaw should increase microbial CO_2 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_2 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