



## Warming alters routing of labile and slower-turnover carbon through distinct microbial groups in boreal forest organic soils

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### ABSTRACT

Our understanding of the mechanisms driving the response of soil organic carbon (SOC) pools to warming, though critical for predicting climate feedbacks, remains limited. Here we report results from a warming experiment using O-horizon soils from two mesic, boreal forest sites with contrasting climate regimes. We replaced extant Oi soil horizons, or litterfall C, with another coniferous Oi possessing a distinct  $\delta^{13}\text{C}$  signature, and tracked the net incorporation of the replaced Oi and, by difference, Oea-C into soil microbial phospholipid fatty acids (PLFA) following 120-day incubations at 15 °C and 20 °C. We demonstrate how regional climate (site effects) and experimental warming (temperature effects) influence microbial incorporation of Oi versus slower-turnover Oea SOC pools. Microbial biomass, estimated from total PLFA, increased by 32–60% with temperature and was 20–42% higher within soils from the warmer versus cooler site, congruent with increased mineralization in those soils. The proportion of Gram-positive bacterial PLFA-C derived from Oi-C more than doubled and coincided with a reduction in the incorporation of Oi-C into fungal relative to bacterial PLFA with warming and in soils from the warmer site. Mirroring the relative decrease in fungal incorporation of Oi-C, warming led to an increase of 22–31% in the proportion of fungal PLFA-C derived from the Oea-C, consistent with the increased incorporation of this slower-turnover SOC pool in soils from the warmer site. The increase in microbial biomass and shift in routing of Oi and Oea pools through PLFA indicate that warming preferentially increases fungal mineralization of more slow-turnover C pools in these boreal organic soils. Shifts in microbial substrate routing and biomass increases with warming observed here underscore the potential importance of changing proportions of microbial biomass remnant contributions to SOC pools with climate warming.

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### 1. Introduction

Climate warming is linked to increased mineralization rates of soil organic carbon (SOC; Lloyd and Taylor, 1994; Kirschbaum, 1995; Davidson and Janssens, 2006; Sierra et al., 2012) with some studies

suggesting greater relative increases in mineralization of more complex, slow-turnover SOC pools (Hartley and Ineson, 2008; Craine et al., 2010; Janssens and Vicca, 2010; Li et al., 2012). Even small increases in mineralization of Earth's large reservoir of relatively slow-turnover SOC would represent a significant positive feedback to climate warming, a fact that has prompted many studies of soil warming. Multiple challenges have hampered attempts to develop a mechanistic understanding of the influence of warming on microbial substrate choice and associated patterns of mineralization, however. These challenges include: (1) tremendous variation in the composition and associated reactivity of multiple SOC substrates, (2) potential changes in microbial structure and function with warming, and (3) changing physical and environmental soil attributes such as organo-mineral interactions, nutrient availability, and soil moisture with temperature (Davidson and Janssens, 2006; Conant et al., 2011). Some of these features may govern differences between apparent temperature sensitivities of

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decay and those at least qualitatively predicted by enzyme kinetics (Davidson and Janssens, 2006; Bradford and Watts, 2010; Conant et al., 2011), but the mechanisms controlling the varied response of soil C processing to warming remain unclear.

Any mechanistic study attempting to unravel these mysteries must consider the longevity of any observed effects of warming to project their potential ramification on climate feedbacks (Janzen, 2004). *In situ* warming experiments are useful for quantifying SOC responses to warming on time scales of years (Oechel et al., 2000; Luo et al., 2001; Rustad et al., 2001; Melillo et al., 2002), but are difficult to extrapolate across more expansive time scales relevant for anthropogenic climate change. Differences in the turnover and geochemical attributes of soil organic matter profiles across natural temperature gradients (Trumbore et al., 1996; Leifeld et al., 2009; Li et al., 2012) highlight the utility of such gradients for understanding more long-term influences of climate on soil organic matter characteristics. The multiple factors that vary in addition to mean annual temperature (MAT), however, often make it difficult to determine the physical or biological processes responsible for varying soil composition across climate gradients (Nakatsubo et al., 1997; Steinberger et al., 1999). Coupling investigations of soils from varying climate regimes with laboratory investigations of the same soils can permit insight into the biogeochemical processes responsible for changes in soil organic matter pools with climate warming on longer time scales (Fissore et al., 2009; Wu et al., 2009; Schindlbacher et al., 2010).

Consistent with observed variation in soil organic matter composition with latitude (Cannone et al., 2008), warming can induce proportionally greater increases in exo-enzyme activities associated with the breakdown of relatively slow-turnover SOC (Li et al., 2012). Changes with warming in microbially mediated SOC decay may also be linked to changes in the relative abundances of the microbial groups competing for resources liberated upon decay (Zogg et al., 1997; Andrews et al., 2000; Biasi et al., 2005; Zhang et al., 2005; Frey et al., 2008). Such shifts in microbial dynamics with warming could have significant implications for SOC decay as well as SOC formation. For example, phenol oxidases are effective catalysts for the decay of phenolic components, including those derived from lignin (Sinsabaugh, 2010). Activities of these and other oxidative enzymes apparently can increase to a greater degree than activities of hydrolytic enzymes with soil warming (Wallenstein, 2011; Li et al., 2012). These oxidative enzymes are generated primarily by fungi and actinobacteria in soil (Duran et al., 2002; Claus, 2003; Rabinovich et al., 2004; Kirby, 2005). It remains unclear, however, whether changes in exo-enzyme activities with temperature are linked to changes in activity of physiologically different microbial groups relevant to formation of SOC compounds derived from that community's biomass. This is despite the growing recognition of the large proportion of natural organic matter pools comprised of microbially-derived compounds (Ogawa et al., 2001; Tremblay and Benner, 2006), including SOC pools (Amelung et al., 2001; Simpson et al., 2007; Potthoff et al., 2008).

A recent study suggests that turnover of biomass derived from different microbial groups may not vary (Throckmorton et al., 2012). However, other work suggests that different microbial groups may contribute to the input, composition and turnover of SOC pools to varying degrees due in part to variation in their cell wall composition (Liang et al., 2008; Strickland and Rousk, 2010; Fernandez, 2011). For example, recent evidence suggests that chitin, a polymer of glucosamine and major fungal cell wall material, is quite labile (Fernandez, 2011). On the other hand, some sugars, including amino sugars associated with bacterial peptidoglycan, can be preferentially preserved relative to fungal glucosamine in soils (Amelung et al., 2001). To the extent that warming results in altered biomass production rates of distinct microbial groups, an

important and relatively unstudied response to soil warming may be shifts in relative abundances of microbially-derived compounds important for soil organic matter formation. Thus, much like the need to ascertain changes in plant inputs with climate warming (Kirschbaum, 2000; Gu et al., 2004), we need to constrain how microbial inputs to SOC pools may change. Insight into the potential for changes in sources of these inputs directly associated with soil warming, however, can be gained on shorter time scales by investigating the impact of warming on the activity or soil substrate use by relevant microbial groups.

Here we explore the influence of warming on routing of two SOC pools with distinct turnover rates through microbial groups exhibiting different physiologies and biogeochemical functions from two boreal forests with differing climate regimes. Tracing a unique C isotopic signature in replaced Oi sub-horizons added to soil mesocosms, we investigated the proportion of Oi material incorporated into bacterial and fungal phospholipid fatty acids (PLFA) during a 120 day warming incubation, versus SOC derived from deeper, slower-turnover Oea sub-horizons. Comparing these results with the respiratory and enzymatic data from these same incubations, as reported in Li et al. (2012), we addressed two questions: (1) does experimental warming induce changes in substrate routing through distinct microbial groups relevant to both SOC decay and formation? and (2) do changes in SOC routing with experimental warming match processes and geochemistry observed in soils native to a warmer forest relative to soils from an otherwise similar, but cooler, forest?

## 2. Study site description and context

Soil samples were collected from Salmon River (SR) and Grand Codroy regions of the Newfoundland and Labrador Boreal Ecosystem Latitudinal Transect (NL-BELT). This transect spans 5.5 degrees of latitude from the southwest corner of the island of Newfoundland to the most northern extent of balsam fir (*Abies balsamea* (L.) Mill.) dominated forests in central-eastern Labrador and has been delineated into four distinct regions (for map see Li et al., 2012). The NL-BELT, part of the Canadian Forest Service's (CFS) National Network of Latitudinal and Elevation Transects (NNLET), is a research platform established by the CFS in collaboration with the Newfoundland and Labrador Forestry Service to facilitate research focused on climate change impacts on boreal forest ecosystems. All four regions of the transect consist of forested study sites approximately 60–65 years old underlain by soils consisting of relatively thick (~10 cm) organic horizons and moderately well drained B horizons characterized as Orthic Humo-Ferric Podzols. The two sites exploited in this study, though similar in forest stand class and elevation (14.0 and 13.1 masl), differ primarily in temperature regime. For further site characteristics please see Li et al. (2012).

Working within the NL-BELT provides a platform for investigating warming impacts on a globally significant C pool – O horizons – in a region expected to experience 4–7 °C increases in temperature this century (IPCC, 2007). The high moisture exhibited by these mesic, C-rich forest soils mitigates the influence of substrate limitation on SOC warming responses enabling the isolation of temperature effects on microbial processes. Radiocarbon, elemental and stable isotopic composition of the soil profiles at these study sites suggest greater microbial processing rates and possibly greater loss of older and more slow-turnover SOC at the warmer site (Li et al., 2012). Furthermore, warming induced losses of slow-turnover Oea C via respiration and leaching as dissolved organic C to a greater extent than Oi C and also induced a greater relative increase in phenol oxidase activity as compared with enzymes associated with the use of more labile C substrates. Here, we explore mechanisms likely responsible for the patterns reported in

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