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Potential impacts of climate change on interactions among saprotrophic cord-forming fungal mycelia and grazing soil invertebrates

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ABSTRACT

Climate change has the potential to alter the activity of, and interactions among, saprotrophic fungi and soil invertebrate grazers, with implications for decomposer community composition, ecosystem regulation and carbon feedback. We reviewed the impacts of experimentally manipulated temperature, CO₂ concentration and soil moisture content on saprotrophic cord-forming basidiomycete growth and function, and on the abundance of soil micro-invertebrates (nematodes) and meso-invertebrates (collembola, mites and enchytraeids). In warmer and wetter conditions, mycelial growth and mycophagous invertebrate abundance are likely to increase. Grazers may either consume the extra mycelial biomass or amplify the temperature effect by stimulating fungal growth. Grazing can stimulate or inhibit decomposition of colonised woody resources and extracellular enzyme production. Future empirical study should partition saprotrophic fungi from the general microbial biomass, with particular attention focussed on enzyme activity and decomposition. Understanding how biotic and abiotic factors interact to regulate saprotrophic fungal activity is crucial to strengthen our predictive capacity regarding decomposition and carbon feedback under climate change.

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Introduction

Organic carbon decomposition by soil biota generates an annual global release of 60 Pg (10^{15} g) C to the atmosphere (almost 10 times that of fossil fuel emissions); this is balanced by the approximately equal quantity absorbed through primary production (Lal 2008). Shifts in this balance, mainly due to changes in ambient climate, have potentially far-reaching implications for CO₂ feedback and atmospheric gaseous composition. By 2100, atmospheric CO₂ concentration is predicted to reach 540–970 ppm, accompanied by globally differential temperature increases in the range 1.1–6.4 °C (IPCC 2007). Precipitation and the frequency of extreme events are also expected to increase, with less certainty regarding

magnitude. Although key drivers of ecosystem processes (Wardle *et al.* 1998; Bradford *et al.* 2002), soil microbes and invertebrates are not explicitly considered in models predicting impacts of climate change on CO_2 feedbacks via, for example, decomposition and soil respiration (Cao & Woodward 1998; Cox *et al.* 2000; Wall *et al.* 2008). This is primarily a consequence of belowground food web complexity, the general neglect of the significance of soil interactions in climate feedback predictions, and the dearth of understanding of the direct and indirect effects of climate change in soil (Bardgett *et al.* 2008).

Impacts of projected climatic scenarios on aboveground communities and trophic interactions (e.g. plants and their insect herbivores) have been well-studied and thoroughly

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reviewed (e.g. Bezemer & Jones 1998; Bale *et al.* 2002; Harsch *et al.* 2009; Hooper *et al.* 2012). Although soil biotic activity exerts a strong influence on the composition, structure and functioning of aboveground communities (De Deyn *et al.* 2003; van der Heijden *et al.* 2008), relatively little is known about the impacts of climate change on belowground community activity and functioning. Any influence on decomposition, nutrient cycling and soil organic matter (SOM) dynamics will be of crucial importance in determining ecosystem-level responses to climate change at both regional and global scales (Heimann & Reichstein 2008).

Saprotrophic fungi, in particular, are important regulators of spatial and temporal variation in nutrient availability, SOM dynamics and the sensitivity of decomposition to abiotic variables (Yuste *et al.* 2011). Basidiomycetes dominate primary decomposition in forest ecosystems (Hättenschwiler *et al.* 2005), a globally significant terrestrial carbon store (1240 Pg C; Lal 2005). A major ecological grouping of these fungi form extensive mycelial cord networks, mainly restricted to the woodland soil–litter interface, which link organic resources and conservatively retain and re-allocate nutrients (Boddy 1993, 1999). Decomposition rates are determined by fungal community composition, ecophysiological relationships with abiotic variables, and interactions with other biota.

Soil invertebrates exert the strongest influence on decomposition where fungi are the dominant component of the microbial community (Wardle et al. 2004). The low C:N ratios of fungal cords and hyphae relative to plant-derived organic matter make mycelia an attractive nutritional source for soil invertebrates (Boddy & Jones 2008). Mycelial development and function can be markedly affected by invertebrate grazers, including nematodes (Dyer et al. 1992; Crowther et al. 2011a), oribatid mites (A'Bear et al. 2010), collembola (Kampichler et al. 2004; Tordoff et al. 2008), enchytraeids (Hedlund & Augustsson 1995), millipedes and woodlice (Crowther et al. 2011b, c). The dynamics of these interactions depend on the mycelial form and faunal community; cords may be ingested by macro-invertebrates, whereas individual hyphae will also be exploited by smaller invertebrates. Stimulation of mycelial growth can result from low intensity grazing by micro- and meso-invertebrates (Hedlund et al. 1991; Bretherton et al. 2006) but, more commonly, biomass is reduced, with macro-invertebrates often removing whole systems (Crowther & A'Bear 2012). Selective feeding on specific fungi can differentially affect the competitive abilities of interacting mycelia, influencing community composition (Newell 1984a, b; Crowther et al. 2011d).

Elevated temperature and high or low water availability have the potential to affect soil fungi and invertebrates both directly and indirectly. Given that CO₂ concentrations in soil are, at least, 10-fold higher than in the atmosphere (Lamborg *et al.* 1983; Lal 2008), belowground impacts of elevated CO₂ are generally assumed to be indirect, mediated by plant growth, rhizo-deposition and litter chemistry. The chemical content of wood and leaf litter could be affected by all of the abiotic variables considered here, with implications for decomposition activity of cord-forming mycelial systems. Elevated CO₂, in particular, reduces the nitrogen content and increases the C:N ratio and structural (e.g. lignin) content of litter (Cotrufo *et al.* 1994, 1998; Coûteaux *et al.* 1999; Norby *et al.* 2001). These responses reduce resource quality, often slowing the rate of decomposition, but could promote the dominance of lignocellulolytic cord-forming basidiomycetes due to their ability to decompose the structural components. Reduced quality of litter could further increase the relative palatability of nutritionally-conservative fungal mycelia to soil invertebrates, potentially increasing their influence on fungalmediated decomposition. Such direct and indirect climate change impacts on saprotrophic cord-forming fungi and their soil invertebrate grazers will influence the interactions between these organisms and the ecosystem processes they facilitate.

This review aims to identify: (1) trends in the responses of saprotrophic cord-forming fungi and soil invertebrate groups containing mycophagous members to experimentally manipulated abiotic variables; (2) implications of these responses for saprotrophic fungus-grazer interactions under climate change scenarios; and (3) future research priorities in terms of biotic and abiotic influences on saprotrophic fungal activity and functioning. The past 20 years has seen a body of literature emerge on the responses of potentially mycophagous soil micro-invertebrates (nematodes) and mesoinvertebrates (collembola, mites and enchytraeids) to experimental manipulation of temperature, CO₂, precipitation and drought; these data are synthesised using meta-analysis. This approach cannot be applied to saprotrophic fungi as they have rarely been partitioned from the rest of the fungal, or even microbial, biomass in studies on microbial responses to climate change. Ecophysiological relationships between saprotrophic cord-forming basidiomycetes and abiotic variables (e.g. temperature and water potential) have, however, been investigated and are considered. Other abiotic factors associated with climate change, such as increasing concentrations of methane (CH_4), ozone (O_3) and other gaseous pollutants (e.g. NO_x), will undoubtedly affect both fungi and fauna directly and indirectly, but as yet insufficient information is available in the literature to provide informative synthesis.

Impacts of climate change on saprotrophic cordforming mycelia

Climate change effects on plant productivity influence the composition and activity of soil microbial communities (Sadowsky & Schortemeyer 1997; Wolters et al. 2000). Elevated temperature (e.g. Zhang et al. 2005) and CO₂ concentration (e.g. Zak et al. 1993; Kandeler et al. 2008) have been reported to alter microbial community composition, favouring fungi. The extent to which this relates to the abundance and activity of cord-forming saprotrophs remains unclear. Climate-induced increases in belowground allocation of photosynthetic carbon are known to stimulate root colonisation by mycorrhizal fungi (Klironomos et al. 1997; Olsrud et al. 2010; Fransson 2012), which could account for the observed fungal dominance. There do not, however, appear to be any studies that partition biomass between saprotrophic and ectomycorrhizal mycelium. The ability of saprotrophic fungi to retain nutrients and, in the case of cord-forming fungi, to translocate them to different regions (Boddy 1993), confers a competitive advantage over other microbes when nitrogen availability is limited by

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