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Effects of isopod population density on woodland decomposer microbial community function

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Trophic interactions between heterotrophic soil microbes and grazing soil invertebrates influence decomposer community composition and function. Cord-forming basidiomycete fungi are primary agents of woody litter decomposition in temperate forests. In laboratory experiments, grazing by woodlice (Isopoda) is an important factor limiting the biomass and functioning (decomposition and extracellular enzyme production) of cord-forming fungi, but its significance in the field has hitherto not been studied. Field populations of the woodlouse, *Oniscus asellus*, were manipulated ('reduced' [zero] or standardised at 'current' [28 m^{-2}] or 'double' [56 m^{-2}] density) in delimited plots inoculated with different fungi (un-inoculated, *Hypholoma fasciculare* or *Phanerochaete velutina*) and the effects on the microbial decomposer community assessed after 6 and 12 months. *Oniscus asellus* population density was reduced after 12 months in comparison to the standardised numbers at start. Significant differences between population densities remained, but varied between fungal inoculation treatments. Fatty acid analysis revealed *O. asellus* as a true generalist; markers for plants, fungi and bacteria were consistently abundant in storage lipids. Seasonal effects on microbial biomass and function were strong. Although woodlouse population density neither affected fungal biomass nor microbial community composition (ergosterol and soil phospholipid fatty acids), it influenced enzyme activities, depending on the inoculated fungus. Woodlice significantly reduced leucine aminopeptidase and lignin-degrading peroxidase activities, only in un-inoculated plots. In contrast, the highest woodlouse population density increased beech (*Fagus sylvatica*) wood decomposition and leucine aminopeptidase activity in *P. velutina*-inoculated plots. Increased enzyme activity and decomposition is likely a stress response, reflecting increased production of specific enzymes to provide the energy for mycelial repair and growth responses to grazing. Effects of grazing on fungal biomass and activity will be strongest at microsites of woodlouse aggregation and where forest floor woodlouse population densities are high.

1. Introduction

Terrestrial carbon and nutrient cycling is primarily regulated by soil-inhabiting bacteria and fungi. Microbial and invertebrate faunal populations are linked; as well as increasing resource availability for decomposer microbes by litter shredding, soil macro-arthropods also feed on the microbial decomposers, directly affecting their biomass and activity (Lavelle, 1997; Zimmer and Topp, 1999; Wardle, 2006). Altered relative abundance of different microbial species, due to selective grazing by soil invertebrates, is an important mechanism structuring fungal and bacterial communities (Rønn et al., 2002; A'Bear et al., 2013c; Crowther et al., 2013). The production of extracellular enzymes responsible for the breakdown of lignin and cellulose makes basidiomycete fungi the main agents of primary decomposition in temperate forest ecosystems (Hättenschwiler et al., 2005; Baldrian and Valášková, 2008). Some of these fungi, which form mycelial cords, extend from colonised woody resources and form large networks of mycelium which retain and translocate nutrients (Boddy, 1999; Fricker et al., 2008). The higher nutrient status (low C:N) of fungal mycelium, relative to organic matter, makes it an attractive source of nutrition to soil invertebrates (Boddy and Jones,

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2008). As a consequence of the large size and biochemical defences of fungal mycelia, the capacity for grazers to influence mycelial biomass and activity usually reflects invertebrate body size, population density and species–specific feeding preferences (Kaneko et al., 1998; Crowther et al., 2011a; Crowther and A'Bear, 2012).

Competitive dominance of decomposer basidiomycete mycelium reduces soil microfungal abundance and diversity (Crowther et al., 2013). This, in turn, limits mycophagous soil mesofauna (e.g. collembola) abundance because the size and biochemical defences of basidiomycete mycelium may make them less palatable (A'Bear et al., 2013a). Macrofauna (e.g. woodlice), with their larger body size and greater metabolic requirements, are more able to exploit basidiomycete fungal mycelia (Crowther and A'Bear, 2012). As a consequence of their longer lifecycles, effects of fungal palatability on macrofauna population density have not been assessed by short-term grazing studies. Taxon-specific population responses to field carbon and nutrient amendment have been reported, none of which mirrored microbial biomass change (Scheu and Schaefer, 1998). Woodlice, even at low density, consistently reduce mycelial biomass and exert selective pressures strong enough to alter the outcomes of competitive interactions (Crowther et al., 2011a; A'Bear et al., 2013b,c). Extensive mycelial ingestion by a widely distributed woodlouse species (*Oniscus asellus*, Isopoda) has been shown to reduce soil extracellular enzyme activities and increase collembola abundance by releasing the more easily ingested microfungi from competitive suppression (Crowther et al., 2013). Their capacity to maintain high fungal diversity and mycophagous mesofaunal abundance has led to woodlice being suggested as keystone grazers in temperate woodland soil (Crowther et al., 2013). As the rate of fungal utilisation of colonised wood depends, at least in part, on extra-resource biomass (Bebber et al., 2011), extensive mycelial ingestion may reduce resource decay as well as the potential for decomposition (enzyme activities) in soil.

Mechanistic understanding of the trophic interactions occurring between decomposer cord-forming fungi and mycophagous soil fauna has been based mainly on microcosm (few-species interactions) and occasionally mesocosm (natural communities subjected to simple biotic manipulations) studies, always at relatively small spatial scales, under controlled abiotic conditions (Tordoff et al., 2008; Crowther et al., 2011a,b, 2013; A'Bear et al., 2012, 2013a). Whether the strengths of interactions revealed in these systems can be extrapolated to the greater spatial and temporal scales, and abiotic variability of field conditions remains unexplored. Populations of mycophagous macrofauna, including woodlice, are predicted to increase in temperate regions as they become warmer and wetter due to climate change (David and Handa, 2010). The capacity for field woodlouse populations to regulate decomposer community structure and function will determine their potential to moderate climate-induced stimulation of decomposition and CO_2 efflux from temperate forest soil (A'Bear et al., 2014a).

This study investigates the influence of woodlouse (*O. asellus*) population density on the biomass, composition and functioning of soil microbial communities, and the abundance and diversity of mycophagous micro-arthropods (collembola and oribatid mites), in a saprotrophic basidiomycete-dominated woodland decomposer community. A field experiment was established to test four specific hypotheses: (1) Woodlouse population density and diet will be affected by fungal species dominance in the decomposer community. Using fatty acids as biomarkers enables animal feeding strategies in the field to be defined (Ruess et al., 2005, 2007; Chamberlain et al., 2005). Increasing woodlouse population density will: (2) reduce fungal biomass and the ratio of fungi to bacteria; (3) increase mycophagous micro-arthropod abundance and diversity; and (4) reduce extracellular enzyme activity and fungal-mediated beech (*Fagus sylvatica*) wood decomposition (due to fungal biomass reduction). Wood decomposition can be measured directly, whereas the potential for decomposition in soil is indicated by extracellular enzyme activities (Sinsabaugh et al., 2008; Henry, 2012).

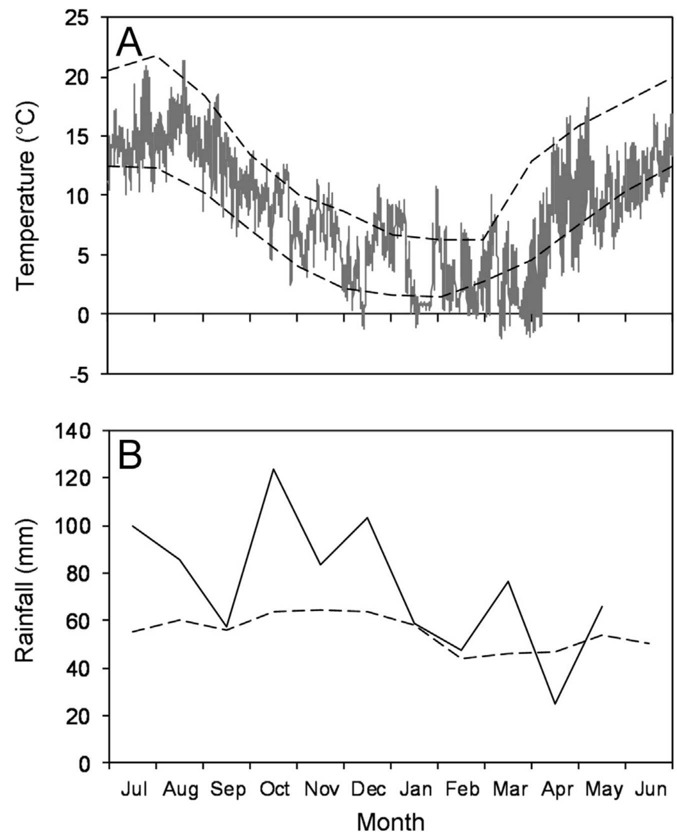

Fig. 1. Hourly temperature (A) and monthly rainfall (B) at the field site (Wytham Woods) during the experimental period (July 2012–June 2013). Dashed lines represent the 100 year monthly averages; maximum and minimum for temperature (data from Met Office).

2. Materials and methods

2.1. Experimental design

The influence of woodlouse (*O. asellus* Linnaeus, Isopoda) population density on decomposer community dynamics and functioning, in a saprotrophic basidiomycete-dominated temperate woodland soil, was investigated in a field experiment. Nine treatments were derived from the factorial crossing of three fungal treatments (un-inoculated, or inoculated with *Hypholoma fasciculare* (Huds: Fr.) Kummer or *Phanerochaete velutina* (DC: Pers.) Parmasto) with three woodlouse population density ('reduced', 'current' or 'double') treatments. Eight replicate blocks (3 × 3 m) contained nine plots (1 m^2) to which treatments were assigned at random. Woodlouse diet, microbial biomass and community composition, mycophagous micro-arthropod (collembola and oribatid mites) populations, extracellular enzyme activities and *in situ* decomposition of fungus-colonised beech (*F. sylvatica*) wood were assessed.

2.2. Experimental set-up and sampling

The experiment was established in a beech stand within Wytham Woods (Savill et al., 2010; Oxfordshire, UK; NGR 445355,