



Review paper

Size matters: What have we learnt from microcosm studies of decomposer fungus–invertebrate interactions?



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ABSTRACT

The ongoing research 'boom' in soil ecology has been advanced by a widespread use of laboratory experiments to investigate mechanisms that could not be unravelled with field observations alone. Interactions between soil fungi and invertebrates have received considerable attention due to their trophic and functional importance in belowground systems. Saprotrophic cord-forming basidiomycete fungi are major agents of primary decomposition in woodland ecosystems, where they are also an important source of nutrition for fungal-feeding soil invertebrates. A plethora of microcosm experiments, with their main benefit being that they enable most variables to be kept constant while just a few are manipulated, have provided detailed insights into the ecology of fungus–invertebrate interactions. This review identifies important trends from this body of work (including a meta-analysis of grazing effects on fungal growth and wood decomposition) and explores the extent to which these patterns are supported by the few related experiments conducted in more complex mesocosm and field systems. Grazing in microcosms reduced fungal growth and increased decomposition, but with interaction-specific magnitude, reflecting invertebrate feeding preferences for different fungi. Macro-invertebrates (woodlice and millipedes) had stronger effects than micro- (e.g. nematodes) and meso- (e.g. collembola) invertebrates. This greater grazing pressure generally increased enzyme activities beneath mycelia during interactions in which wood decay was increased. Top-down effects of fungal-feeding can be extrapolated to more complex systems, but only for macro-invertebrates, particularly woodlice. Soil enzyme activity was stimulated, in microcosms and more complex systems, by short-term or low intensity grazing, but reduced when large areas of mycelium were removed by high-intensity grazing. Effects of differential fungal palatability on invertebrate populations are evident in microcosm studies of collembola. These bottom-up effects can be extrapolated more broadly than top-down effects; fungal community dominance determined collembola abundance and diversity, in mesocosms, and woodlouse abundance in the field. Using, as a case study, a series of experiments conducted at a range of scales, mechanisms underlying potential climate change effects on grazing interactions and decomposition are also explored. Biotic effects on decomposer community functioning are heterogeneous, depending on fungal dominance and the density of key macro-invertebrate taxa.

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1. Introduction

Microcosms (artificial, simplified systems used to simulate the behaviour of natural ecosystems, under controlled conditions) have long been used in ecology to increase scientific understanding of natural processes. Many ecological research questions are not tractable with observational field studies alone, so experimentation

is used to provide insights into otherwise inaccessible interactions and mechanisms (Lawton, 1995, 1996; Stewart et al., 2013). The recent and ongoing research 'boom' in soil ecology has been facilitated by a widespread use of laboratory experiments to overcome limitations to mechanistic understanding imposed by the particularly complex and opaque nature of the belowground environment (e.g. De Deyn et al., 2003; Bradford et al., 2007, 2010; de Vries et al., 2012). Soil has traditionally been considered as a 'black box' of decomposers – a single trophic level through which aboveground life is ultimately recycled (Sugden et al., 2004). Mechanistic understanding of biotic regulation of decomposition and nutrient cycling is one of the primary goals of soil ecologists, particularly

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given the potential for global warming to disrupt the balance of carbon exchange between the biosphere and the atmosphere (Knorr et al., 2005; Wall et al., 2008). A major use for model laboratory systems, with the benefit of being able to keep most variables constant and manipulate just a few, is the investigation of how biotic interactions moderate ecological responses to climate change.

Terrestrial decomposition and nutrient cycling is primarily regulated by soil micro-organisms (fungi and bacteria). Interactions between soil microbes and invertebrates receive attention as a consequence of their trophic and functional significance within belowground food webs. In forest ecosystems, a globally significant carbon store (1240 Pg; Lal, 2005), basidiomycete fungi are the main agents of primary decomposition (Hättenschwiler et al., 2005). Their powerful enzymatic capabilities make them one of very few taxa capable of breaking down the more complex and recalcitrant components of soil organic matter, such as lignin and cellulose (Lindahl et al., 2002; Snajdr et al., 2011). A major ecological grouping of basidiomycete fungi, the saprotrophic cord-formers, produce dynamic networks of foraging mycelium which ramify at the interface between soil and litter (fallen leaves and woody debris), linking woody resources and reallocating nutrients over large distances (Boddy et al., 2009). The large biomass and high nutrient status (low C:N relative to organic matter) of mycelium, as a component of the first trophic level in the decomposer food web, makes it vulnerable to grazing by soil invertebrates (Boddy and Jones, 2008). Grazing can influence mycelial development and activity in decomposition and nutrient cycling, reflecting invertebrate body size, population density and differential fungal palatability (Hedlund and Augustsson, 1995; Kaneko et al., 1998; Crowther and A'Bear, 2012). A plethora of microcosm experiments, and a limited number of manipulations in more complex systems, have investigated in detail the effects of decomposer fungus–invertebrate interactions on fungal growth or biomass, wood decomposition, soil enzyme activities and grazer population dynamics.

Several empirical studies and reviews have assessed the value of experimentation at different scales (size and level of biotic and abiotic realism) in furthering ecological understanding of aboveground communities (e.g. plants: Korner, 1995; Messier et al., 2010; invertebrates: Roland and Taylor, 1997) and interactions (e.g. plant–insect: Heads and Lawton, 1983; host–parasitoid: Jones and Hassell, 1988), and ecosystem-level patterns and processes (e.g. Levin, 1992; Jones et al., 2000; Leuzinger et al., 2011). Opportunities to evaluate extrapolations from simplified to natural soil communities are rare, due to the varying nature of the research questions, experimental manipulations and measurements in studies conducted at different scales. This review aims to: (1) provide a synthesis of the effects of grazing interactions between saprotrophic cord-forming basidiomycete fungi and soil invertebrates on mycelial growth and functioning, and grazer population dynamics, in microcosms; and (2) explore the extent to which mechanisms revealed by microcosm studies are supported by recent experimentation in more complex systems. The latter includes mesocosms (isolated replicates of natural soil biotic communities), as well as the field. Grazing effects on mycelial growth and woody resource decomposition in microcosms are quantified here using meta-analysis, and related to fungal enzyme production, interspecific combative interaction outcomes and invertebrate populations. The assessment of extrapolation from microcosms to more complex systems includes a case study of a series of experiments performed to further mechanistic understanding of the potential influences of climate change on decomposer fungus–invertebrate interactions and ecosystem processes.

2. Decomposer fungus–invertebrate interactions in soil microcosms

2.1. Meta-analysis: responses of fungal growth and decomposition to grazing

Meta-analysis is used here as a tool for the calculation of effect sizes using data from published studies reporting the effects of grazing by soil invertebrates on growth rates and wood decomposition by individual saprotrophic cord-forming basidiomycete fungi. The included studies reported the effect of grazing (i.e. a grazed treatment relative to an un-grazed control) on an absolute measure of fungal growth (mycelial extension rate or hyphal coverage) and, in most cases, the decay rate of a fungus-colonised wood block. Although conducting the meta-analysis to provide a synthesis of a specific interaction mechanism limited the number of studies that could be included (Table S1), this approach enables the results generated to be compared with similar manipulations in more complex systems – a major aim of this review. In the source studies (Table S1), fungal mycelia emerged from pre-colonised beech (*Fagus sylvatica*) wood blocks and grew across the surface of compressed soil, where they were subjected to grazing by mycophagous invertebrates.

There were sufficient data to analyse the responses of four common fungal species (*Hypholoma fasciculare*, *Phallus impudicus*, *Phanerochaete velutina* and *Resinicium bicolor*) to grazing by a range of soil micro- (Nematoda: *Panagrellus redivivus*), meso- (Collembola: *Folsomia candida* and *Protaphorura armata*; Enchytraeidae: *Enchytraeus crypticus*; Oribatida: *Euzetes globulus*) and macro- (Diplopoda: *Blaniulus guttulatus*; Isopoda: *Oniscus asellus* and *Porcellio scaber*) invertebrates. Populations represented low estimates of field density (16,600 m⁻², 800–1000 m⁻² and 83 m⁻² for micro-, meso- and macro-invertebrates, respectively). If a study employed several population densities of the same invertebrate species, the density level most comparable with other studies was used. Control and treatment means, errors and replication (*n*) were recorded for each measurement. The natural logarithm of the response ratio (lnR) was used as the effect size metric to reflect relative changes in fungal growth or decomposition in response to grazing (Hedges et al., 1999). This was calculated as: $\ln R = \ln(X_T/X_C)$, where X_T and X_C are the treatment and control means, respectively. The logarithm linearises the metric so that deviations in the numerator and denominator are treated in the same way; this normalises the distribution. Positive values indicate an increase, and negative values a decrease, in the response variable due to grazing. Means and bootstrapped 95% confidence intervals (CI) of lnR were calculated in MetaWin 2.1 (Rosenberg et al., 2000) with *n* as the weighting function.

Direct mycelial grazing generally reduced fungal growth (mean lnR = -0.12; 95% CI: -0.19 to -0.07), but increased wood decomposition (mean lnR = 0.06; 95% CI: 0.02 to 0.09). The magnitude of responses for both parameters differed between fungus and invertebrate species (Fig. 1). Grazing, in general, did not significantly ($P \geq 0.05$) affect the growth of *P. impudicus* or wood decomposition by *R. bicolor* (Fig. 1). Whilst collembola (*F. candida* and *P. armata*) and macro-invertebrates (*B. guttulatus* and *O. asellus*) reduced mycelial growth, overall, only the latter exerted significant ($P < 0.05$) effects on decomposition (Fig. 1). The species-specific nature of interactions (Fig. 2) is, to some extent, masked in overall responses. The effects of invertebrate grazing on fungal growth and wood decomposition are likely to be intimately linked. In some cases, a large negative effect on fungal growth across soil was associated with a marked increase in wood decay rate (Fig. 2). As a consequence, the effect sizes for fungal growth and wood decay for specific interactions were negatively correlated, overall (Fig. 3).

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