The ISME Journal (2012) 6, 1992–2001

www.nature.com/ismej

MINI REVIEW

Functional and ecological consequences of saprotrophic fungus–grazer interactions

Thomas W Crowther[1,2], Lynne Boddy[1] and T Hefin Jones[1]
[1]*Organisms and Environment Division, Cardiff School of Biosciences, Cardiff University, Cardiff, UK and*
[2]*Yale School of Forestry and Environmental Studies, Yale University, New Haven, CT, USA*

Saprotrophic fungi are key regulators of nutrient cycling in terrestrial ecosystems. They are the primary agents of plant litter decomposition and their hyphal networks, which grow throughout the soil–litter interface, represent highly dynamic channels through which nutrients are readily distributed. By ingesting hyphae and dispersing spores, soil invertebrates, including Arthropoda, Oligochaetae and Nematoda, influence fungal-mediated nutrient distribution within soil. Fungal physiological responses to grazing include changes to hydrolytic enzyme production and respiration rates. These directly affect nutrient mineralisation and the flux of CO_2 between terrestrial and atmospheric pools. Preferential grazing may also exert selective pressures on saprotrophic communities, driving shifts in fungal succession and community composition. These functional and ecological consequences of grazing are intrinsically linked, and influenced by invertebrate grazing intensity. High-intensity grazing often reduces fungal growth and activity, whereas low-intensity grazing can have stimulatory effects. Grazing intensity is directly related to invertebrate abundance, and varies dramatically between species and functional groups. Invertebrate diversity and community composition, therefore, represent key factors determining the functioning of saprotrophic fungal communities and the services they provide.
The ISME Journal (2012) **6,** 1992–2001; doi:10.1038/ismej.2012.53; published online 21 June 2012
Keywords: fungal communities; grazing; fungus–invertebrate interactions; ecosystem functioning; soil biodiversity

Introduction

Soil microbes are the primary regulators of terrestrial carbon and nutrient cycling. A powerful cocktail of lingocellulolytic enzymes, capable of the initial deconstruction of complex organic compounds, make saprotrophic fungi the dominant agents of plant litter decomposition in many terrestrial (primarily woodland) ecosystems (Baldrian and Valášková, 2008). During litter decomposition, the C:N ratio gradually decreases and inorganic nutrients are released into the surrounding environment (Lindahl *et al.*, 2002). This 'slow cycling of nutrients' maintains ecosystem stability, ensuring the retention of nutrients within late-succession soils (Fierer *et al.,* 2009). Saprotrophic fungi also contribute up to 90% of total heterotrophic respiration in woodland ecosystems (Cooke and Rayner, 1984) and are considered key regulators of soil carbon fluxes between the biosphere and atmosphere.

Saprotrophic fungi are continuously engaged in the search for fresh nutrients. Whereas some (termed resource-unit-restricted) disseminate to encounter new resources solely by production of propagules (spores or hyphal fragments), others (termed non-unit-restricted) extend as hyphae, and interconnect discrete organic resource units. Aggregations of hyphae (forming linear organs known as cords) enable some fungal species to extend vast distances (covering many m^2) at the soil–litter interface (Boddy, 2000). Their ability to translocate carbon, nitrogen and phosphorus throughout these cords means that saprotrophic fungi are important agents of nutrient redistribution in soil (Cairney, 2005).

Mycelial growth inevitably leads to encounters with antagonistic soil organisms. Invertebrates contribute extensively to the species and functional diversity within soils. Their classification is usually based on size (micro-, meso- or macrofauna) or functional group (Rusek, 1998). In terms of nutrient cycling, the most important are the arthropods, oligochaetes, molluscs and nematodes, the majority of which are primarily mycophagous (Pollierer *et al.*, 2009). Damage to hyphal compartments and faecal pellet production directly influence the release of labile nutrients into the surrounding soil (Boddy and Watkinson, 1995); an important process in the recycling of nutrients to plants (Bardgett and Chan, 1999). Invertebrate 'grazing' can also influence mycelial growth and physiology (Crowther *et al.*, 2011a, c). Given the prominent roles of saprotrophic fungi in nutrient decomposition and

Correspondence: T Crowther, Yale School of Forestry and Environmental Studies, Yale University, New Haven, CT 06511, USA.
E-mail: Thomas.Crowther@yale.edu

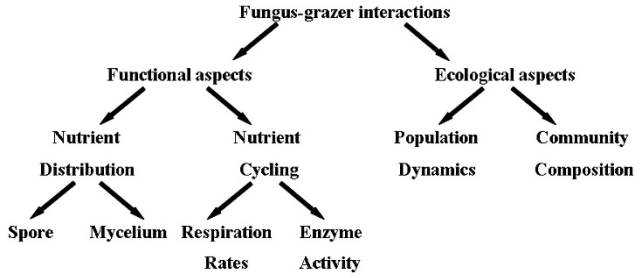

Figure 1 Breakdown of the key functional and ecological aspects of fungus–grazer interactions.

redistribution (Hättenschwiler *et al.,* 2005), grazing may represent the primary role of soil fauna in woodland ecosystem functioning.

The various mechanisms by which invertebrates and saprotrophic fungi interact (trophic and non-trophic) have been reviewed extensively (Lussenhop, 1992; Maraun *et al*., 2003). This review focuses on the consequences of grazing interactions on fungal functioning and community ecology (Figure 1). Specifically, it explores the effects of soil invertebrates on: (i) fungal-mediated nutrient distribution (via mycelia and spores); (ii) mycelial physiology and nutrient cycling (extracellular enzyme production and respiration); and (iii) fungal community composition and diversity.

Mycelial growth and propagule dissemination: redistribution of nutrients

Propagule dissemination

Grazing invertebrates can damage or destroy fungal propagules, but can also act as vectors, assisting in their dispersal. This can be passive— resulting from external adherence of propagules to invertebrate bodies or passage in guts —or active, when fungal propagules are carried in specialised sacs (for example, mycangia) on, or in, the invertebrate's body. Active dissemination often occurs where mutualistic symbiosis has evolved (for example, between the higher termites (Macrotermitinae) and basidiomycetes in the genus *Termitomyces* (Aanen and Boomsma, 2006), attine ants and basidiomycete *Attamyces, Leucoagaricus* and *Lepiota* (North *et al.,* 1997), and woodwasps (Siricidae) and *Amylostereum* (Basidiomycota) (Slippers *et al.,* 2003)). Passive dispersal of fungal propagules by oribatid mites (Renker *et al.,* 2005), earthworms (Moody *et al.,* 1996), collembola (Visser *et al.,* 1987) and enchytraeids (Hedlund and Augustsson, 1995) can also result in the vertical and horizontal redistribution of propagules within litter layers.

Passive transport via passage through invertebrate guts is not always successful; germination and subsequent development can be inhibited. Earthworm (*Lumbricus terrestris* and *Aporrectodea longa*) grazing, for example, reduced or prevented germination of several basidiomycete and ascomycete spores, but propagule survival varied between species; germination of ascomycete, *Chaetomium globosum*, spores was stimulated following ingestion by *A. longa* (Moody *et al.,* 1996). This specialised association conferred a selective advantage to the stimulated fungal species following grazing. Similar symbiotic interactions with termites (Mueller and Gerardo, 2002) and dipteran larvae (Nuss, 1982) have also been found to stimulate spore germination. For some fungi (for example, basidiomycete species of *Ganoderma*), passage of spores through invertebrate guts is essential to allow successful germination (Nuss, 1982).

Mycelial distribution

The extensive mycelial systems of non-unit-restricted fungi represent highly dynamic channels through which nutrients are translocated. Network growth and development are key processes in the redistribution of nutrients within woodland soils (Cairney, 2005). By severing mycelia and ingesting growing hyphal tips, mycophagous collembola can restrict mycelial extension (Tordoff *et al.,* 2006) and high-intensity enchytraeid and woodlouse grazing can completely remove foraging *Hirsutella rhossiliensis* and *Resinicium bicolor* systems, respectively (Jaffee *et al.,* 1997; Crowther *et al.,* 2011a). As well as limiting the ability of foraging basidiomycetes to encounter new resources, grazing also disrupts the translocation of carbon (Butenschoen *et al.,* 2007) and nitrogen (Tordoff *et al.,* 2011) through mycelial systems. These changes in nutrient partitioning affect the dynamics and spatial heterogeneity of forest floor nutrients.

Mycelial systems are highly dynamic and most species show distinct growth responses during grazing. Compensatory growth, analogous to that seen in plants during herbivory (McNaughton, 1983), is characterised by increased mycelial extension and branching of hyphae around thick basidiomycete cords. This may facilitate increased nutrient uptake by fine hyphae to counteract the negative effects of grazing (Bengtsson *et al*., 1993). It has also been interpreted as an 'escape response', increasing mycelial extension into uncolonised regions of soil (Hedlund *et al.,* 1991). These effects depend on grazing intensity. Compensatory growth is commonly associated with low-density collembola grazing (Figure 2), whereas growth is inhibited 'beyond a certain density threshold' (Crowther and A'Bear, 2012). By controlling grazer populations, predatory invertebrates can exert top–down control of fungal communities. Predation of mycophagous collembola (*Folsomia fimetaria*) by predatory mites (*Hypoaspis aculeifer*), for example, limited their grazing potential, indirectly stimulating growth and respiration rates of three soil ascomycetes (Hedlund and Ohrn, 2000). In contrast, factors (abiotic and biotic) contributing to increased collembola

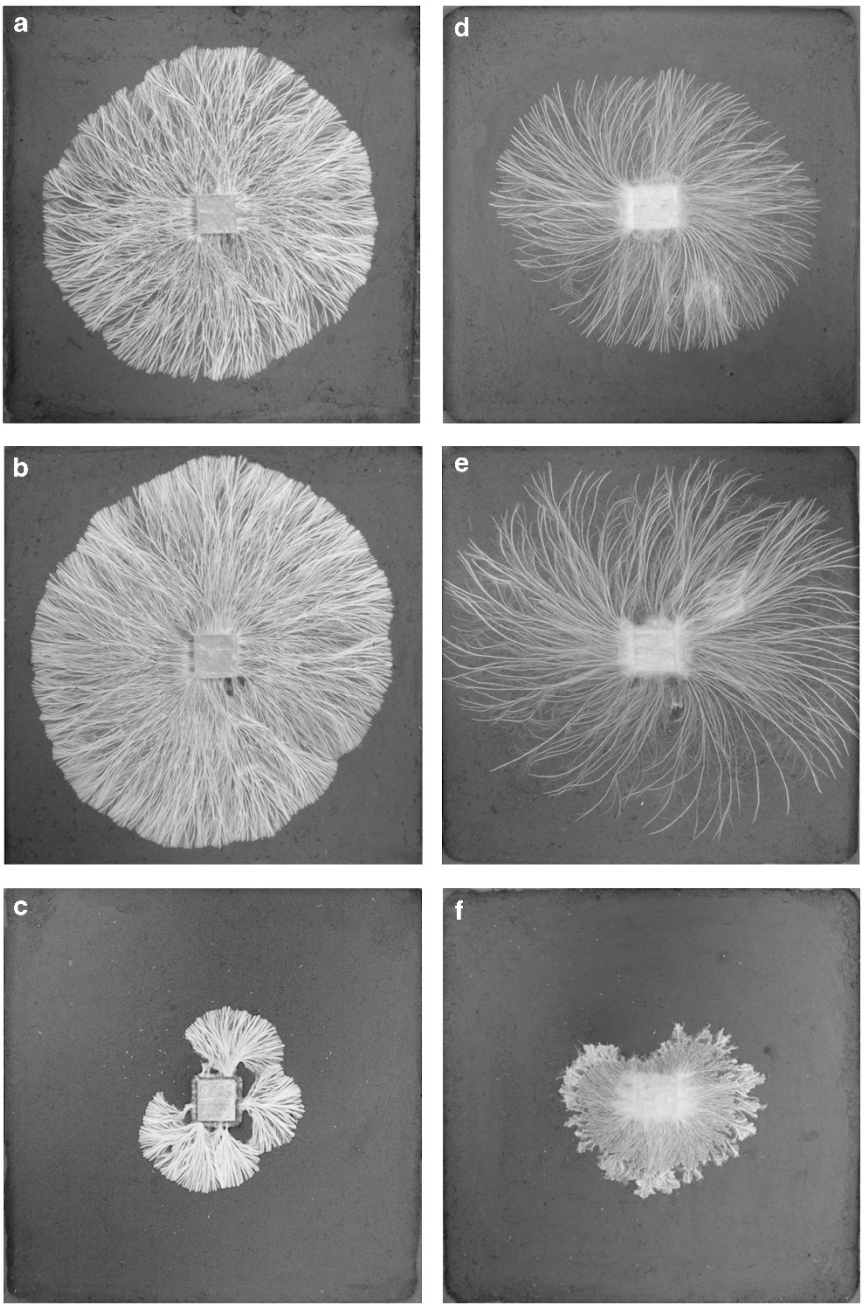

Figure 2 Digital images showing mycelia of *Hypholoma fasciculare* (**a**, **b**, **c**), and *Phanerochaete velutina* (**d**, **e**, **f**) during ungrazed (**a** and **d**), low intensity (**b** and **e**) and high intensity (**c** and **f**) *F. candida* grazing treatments following 10 days of growth from $2 \times 2 \times 1$ cm wood blocks on 24×24 cm soil trays. Low-intensity grazing (783 collembola m^{-2}) stimulated mycelial extension, whereas high intensity (1566 collembola m^{-2}) restricted growth of both fungi.

abundance often lead to reduced fungal biomass (Lenoir *et al.,* 2007).

Interspecific variation in invertebrate size, metabolic activity and feeding preference also leads to contrasting grazing pressures. This is apparent in the stark interspecific differences between collembola grazing effects (Tordoff *et al.,* 2008). Moreover, variation between invertebrate orders often outweighs that within orders. Macrofauna (isopods and millipedes) have a greater influence on basidiomycete growth than meso- and microfauna (Crowther *et al.,* 2011a). The capacity of larger invertebrates to sever thick cords and consume entire mycelia enables them to limit mycelial foraging (Crowther and A'Bear, 2012), whereas lower intensity grazing by smaller invertebrates often stimulated fungal growth (Crowther *et al.,* 2011b). The potential for mycelial networks to acquire new resources and redistribute nutrients, therefore, depends on both invertebrate density and community composition.

Physiological responses: decomposition and nutrient cycling

Enzyme production

Hydrolytic enzymes produced by saprotrophic fungi are responsible for the initial steps in the deconstruction of plant cell walls and the mineralisation of complex compounds into simple inorganic molecules (sugars, amino acids, NH_4^+, PO_4^{-3}, H_2O and CO_2) that can be assimilated by plants and microbes. Lignocellulolytic enzyme production by saprotrophic basidiomycetes colonising leaf litter increases during macrofauna (Scheu, 1993) and collembola (Parkinson *et al.,* 1979) activity. This may be attributed, in part, to litter comminution, but fungal physiological responses to grazing will also contribute to the enhanced nutrient mineralisation (Osono, 2007). Few studies have separated these indirect (litter comminution) and direct (mycelial physiological responses to grazing) effects, but in one such study, collembola (*Protaphorura armata*) grazing increased protease and α-amylase production by the zygomycete, *Umbelopsis isabellina,* growing in agar (Hedlund *et al.,* 1991). The nematode, *Panagrellus redivivus*, also stimulated protease production by the basidiomycete *P. velutina*, but induced the opposite effect while grazing on *Stereum hirsutum* (Dyer *et al.,* 1992). Species-specific fungal enzymatic responses have also been recorded in soil (Crowther *et al.,* 2011c). *Hypholoma fasciculare* and *P. velutina* (exhibiting fast, extensive growth), increased production of cellulolytic and phosphorolytic enzymes during macro-invertebrate grazing, whereas the slow-growing species, *R. bicolor,* reduced enzyme production, probably to conserve energy during mycelial disturbance (Figure 3). Contrasting enzymatic responses of fungal species suggest that the impacts of soil fauna on fungal-mediated nutrient mineralisation are dependent on fungal community composition.

As with mycelial distribution, grazer effects on fungal enzyme production are dependent on grazing intensity. Macrofauna had a greater influence than meso- or microfauna on the production of eight hydrolytic enzymes (associated with C-, N- and P-cycling) by basidiomycete networks in soil (Crowther *et al.,* 2011c). Although the nature of enzymatic responses were fungal species-specific, it was generally the high-intensity grazing associated with larger invertebrates that initiated the changes in fungal physiology.

Decomposition and respiration

Enzymatic responses of saprotrophic fungi will have direct consequences for wood and leaf-litter decomposition. Generally, invertebrate activity is thought to stimulate litter decomposition (Bardgett, 2005) although, as with enzyme production, few studies have distinguished between direct and indirect grazer effects. When restricted to feeding on extra-resource mycelia growing in soil, collembola affect the abilities of fungi to decompose wood resources (Tordoff *et al.,* 2008). These effects vary between fungal species; during grazing, *H. fasciculare* showed increased rates of wood decay, whereas the opposite was true of *R. bicolor* (Crowther *et al.,* 2011b). This difference is directly related to opposing enzymatic responses of these two fungal species during grazing.

While the importance of invertebrate density on extracellular enzyme production remains unexplored, effects can be seen on fungal-mediated litter decomposition. By reducing fungal biomass and activity, high-density collembola populations reduce wood decay rates (Tordoff *et al.*, 2006, 2008),

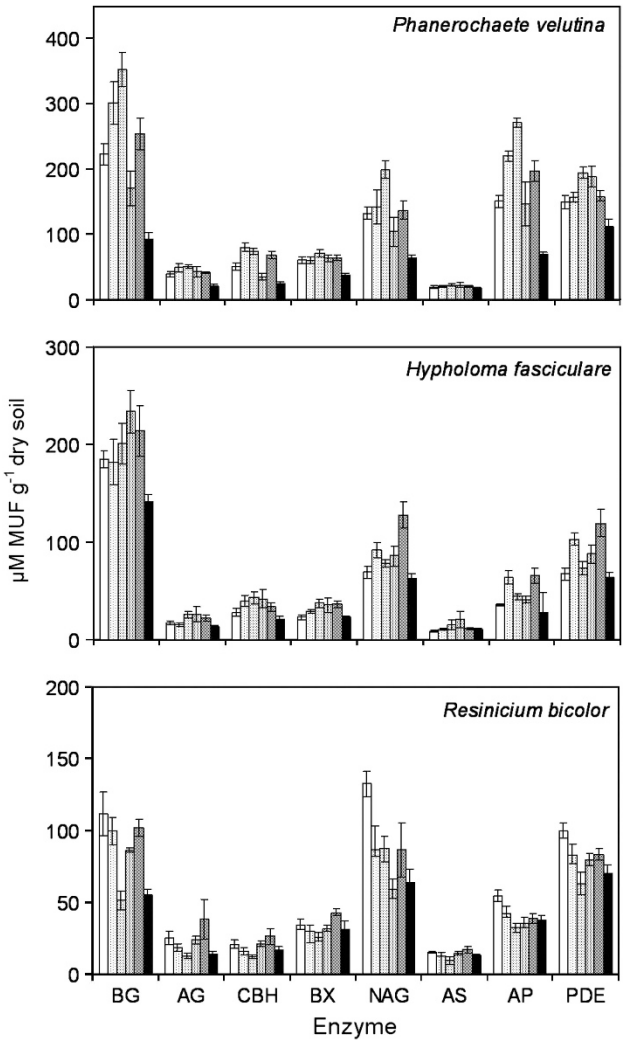

Figure 3 Activities of 1,4-β-glucosidase (BG), 1,4-α-glucosidase (AG), cellobiohydrolase (CBH), 1,4-β-xylosidase (BX), arylsulfatase (AS), *N*-acetylglucosaminidase (NAG), a acid phosphatase (AP) and phosphodiesterase (PDE) enzymes in soil colonised by *Phanerochaete velutina, Hypholoma fasciculare* and *Resinicium bicolor.* Mean and s.e. are shown for each enzyme activity during fungus-only control (□), *F. candida* (⊡), *O. asellus* (⊠), *Blaniulus guttulatus* (▦) and *Panagrellus redivivus* (▩) grazing treatments as well as uncolonised soil (■). Figure was modified from Crowther *et al.* (2011c).

but lower intensity grazing can stimulate fungal nutrient uptake from wood (Crowther *et al.,* 2011a). This reflects the contrasting effects of micro- and macrofauna on fungal-mediated wood decay. Heavy grazing on extra-resource mycelia by the woodlouse, *O. asellus*, reduced the decomposition of *R. bicolor*-colonised wood, whereas less intense nematode, *P. redivivus*, grazing stimulated decay rates, although this effect was not statistically significant (Crowther *et al.,* 2011b).

During decomposition, CO_2 is released from litter resources via microbial respiration, which is directly related to biomass and enzyme activity (Table 1); at high densities collembola reduce fungal respiration rates (Bardgett *et al.,* 1993), whereas low-intensity grazing stimulates CO_2 production (Hanlon and Anderson, 1979). This density-dependent trend is also found during enchytraeid (Hedlund and Augustsson, 1995) and oribatid mite (Kaneko *et al.,* 1998) grazing. Although the importance of invertebrate species identity is as yet unknown, the clear parallels between mycelial enzyme activity and respiration suggest that macrofauna are likely to be particularly important in influencing the fungal-mediated flux of carbon between the terrestrial and atmospheric carbon pools.

Fungal community structure

The majority of soil fauna are generalists, capable of exploiting a variety of microbial resources within highly diverse and heterogeneous environments (Setälä *et al.,* 2005). Indiscriminate feeding can have major consequences for fungal species richness. Wicklow and Yocom (1982) found that the number of coprophilous fungal species on rabbit faeces was reduced during grazing by sciarid fly, *Lycoriella mali*, larvae. By ingesting entire microfungi (1–100 μm), indiscriminate grazers reduced the amount of competition between fungi and remaining fungi were 'released' from competitive stress. This led to increased rates of organic matter decomposition. Via this process, indiscriminate grazers can alter the cycling of nutrients and efflux of CO_2 from soil.

Despite their polyphagous nature most mycophagous fauna display distinct feeding preferences for nutritious or palatable fungi (Maraun *et al.*, 2003). Preferential grazing can exert selective pressures on fungal communities, favouring the growth of less palatable species. This process is particularly important during early stages of fungal succession as late-succession fungi are often less susceptible to grazers (Lussenhop, 1992). Selective grazing by *F. candida* on primary saprotrophs led to faster replacement by secondary saprotrophs on spruce and fir needles (Klironomos *et al.,* 1992). By restricting the less competitive species, collembola facilitated fungal succession in decaying litter. Grazers also regulate this process by an opposing mechanism; stimulation of the dominant competitor. In soil microcosms grazing by *F. candida* stimulated growth of the dominant species, *P. velutina*, over its opponent, *H. fasciculare* (Rotheray *et al.*, 2011). This supported previous studies where collembola reinforced the outcomes of competitive mycelial interactions, stimulating fungal species turnover but not eventual species composition (Parkinson *et al.*, 1979; McLean *et al.*, 1996).

Although numerous studies show selective collembola grazing, none have reported the complete reversal of mycelial interaction outcomes. Newell (1984a, b) provided some evidence that collembola grazing can alter the relative abundances of competing basidiomycetes in *Picea sitchensis* needle litter, but this did not lead to the complete replacement of a dominant species by a less competitive opponent. In most cases, the grazing pressures exerted by mesofauna are not strong enough, even at twice the recorded field densities, to alter fungal competitive abilities (McLean *et al.,* 1996). In contrast, macrofauna, can exert stronger top–down pressures on fungal community composition (Crowther *et al.,* 2011d). By ingesting entire *R. bicolor* mycelial systems the isopod, *O. asellus*, prevented the competitive exclusion of *H. fasciculare* and *P. velutina*. Nematodes (*P. redivivus*), also influenced the progression of fungal interactions, stimulating growth of the less competitive *H. fasciculare*, enabling it to overcome its opponent, *R. bicolor*. Thus, two opposing mechanisms (suppression of the dominant competitor and stimulation of the less competitive species) allow soil fauna to determine the outcomes of competitive mycelial interactions and regulate fungal community compositions in soil.

Perhaps the most extreme example of invertebrates influencing fungal community composition is found with the mutualistic symbiotic relationships of higher termites and ants with their respective basidiomycete symbionts. In both systems, the invertebrates maintain monocultures of the fungi by antibiotic secretions and physical grooming (North *et al.,* 1997; Aanen and Boomsma, 2006). Invertebrates also influence fungal community composition through differential survival of ingested spores. The stimulated germination of *C. globosum* spores following earthworm, *A. longa,* grazing exerted selective pressures on the resulting microbial community (Moody *et al.,* 1996). Although grazing will not influence the competitive abilities of germinating fungi, the short-term selective advantage and rapid establishment of stimulated species is a key process influencing fungal species composition and activity.

Comparisons with mycorrhizal fungi

Soil faunal grazing can influence the development of plant–mycorrhizal associations, as well as the transfer of nutrients between symbionts (Fitter and

Table 1 Effects of invertebrate grazing on fungal biomass and activity

Fungal taxon[a]	*Fungal species*	*Grazer taxon*	*Effects*			*Reference*
			Biomass	*Respiration*	*Enzyme production or decomposition*	
B	*Trametes versicolor*	Collembola	increased at low density	increased at low density		Hanlon and Anderson, 1979
			negative at high density	decreased at high density		
B	various	Collembola	decreased			Leonard and Anderson, 1991
B	*Phanerochaete velutina*	Nematoda	increased		increased	Dyer *et al.*, 1992
B	*Hypholoma fasciculare*	Collembola	increased at low intensity decreased at high intensity			Kampichler *et al.*, 2004
B	*Hypholoma fasciculare*	Collembola	decreased			Harold *et al.*, 2005
B	various	Collembola	decreased		decreased	Tordoff *et al.*, 2006
B	*Phanerochaete velutina*	Collembola	decreased			Wood *et al.*, 2006
B	*Phanerochaete velutina*	Collembola	decreased at high density	decreased at high density		Bretherton *et al.*, 2006
			increased at high density	increased at high density		
			increased following grazing			
B	various	Earthworm	decreased			Butenschoen *et al.*, 2007
B	various	Collembola	decreased		decreased	Tordoff *et al.*, 2008
B	*Phanerochaete velutina*	Collembola	decreased			Boddy *et al.*, 2010
B	various	Collembola	decreased			Boddy *et al.*, 2010
		Oribatid mite	neutral			
B	various	various	neutral effects of micro- and mesofauna		increased	Crowther *et al.*, 2011a
			decreased during macrofauna		increased	
B	various	various	neutral during micro- and mesofauna		increased at low intensity	Crowther *et al.*, 2011b
		Collembola	decreased during macrofauna		decreased at high intensity	
B	various	various	neutral during micro- and mesofauna		increased and decreased depending on fungal species	Crowther *et al.*, 2011c
			decreased during macrofauna		increased and decreased depending on fungal species	
A/B	various	Collembola	increased at low density decreased at high density	increased		Ineson *et al.* 1982
A/B	various	Collembola	increased at low density	increased at low density		Kaneko *et al.*, 1998
			decreased at high density	decreased at high density		
		Oribatida	increased at low density	increased at low density		
			decreased at high density	decreased at high density		
A	*Botrytis cinerea*	Collembola	increased at low density	increased at low density		Hanlon, 1981
			decreased at high density	decreased at high density		

Table 1 (Continued)

Fungal taxon[a]	*Fungal species*	*Grazer taxon*	*Effects*			*Reference*
			Biomass	*Respiration*	*Enzyme production or decomposition*	
A	*Phoma exigua*	Collembola	decreased	decreased		Bardgett *et al.*, 1993
A	various	Collembola	positive	increased		Bengtsson *et al.*, 1993
A	*Hirsutella rhossiliensis*	Enchytraeid	decreased			Jaffee *et al.*, 1997
A	various	Collembola	increased at low density	increased at low density		Hedlund and Ohrn, 2000
			decreased at high density	decreased at high density		
Z	*Mortierella isabellina*	Collembola	decreased	decreased		Bengtsson and Rundgren, 1983
			increased following grazing	increased following grazing		
Z	*Mortierella isabellina*	Collembola	increased		increased	Hedlund *et al.*, 1991
Z	*Mortierella isabellina*	Enchytraeid	increased at low density	increased at low density		Hedlund and Augustsson, 1995
			decreased at high density	decreased at high density		

[a]A, Ascomycota; B, Basidiomycota; Z, Zygomycota.

Sanders, 1992; Gange and Brown, 2002). A number of parallels can be drawn between the influence of grazers on saprotrophic and mycorrhizal systems: (i) spore ingestion can have positive and negative effects on spore distribution, depending on the grazer–fungus combination (Harinikumar and Bagyraj, 1994); (ii) severing of hyphae can restrict growth and nutrient translocation throughout hyphal networks (Klironomos and Kendrick, 1995); and (iii) grazing can have positive or negative effects on fungal activity (Gormsen *et al.,* 2004) with consequences for nutrient mineralisation and primary productivity. As with saprotrophic fungi, grazing effects are density dependent. High-intensity grazing generally reduces mycorrhizal activity, whereas low-intensity grazing can stimulate growth, directly increasing plant productivity (Klironomos and Ursic, 1998). Contrasting effects of earthworm and collembola populations suggest that effects are also taxon specific (Gormsen *et al.,* 2004).

Invertebrate preference for saprotrophic over mycorrhizal fungi represents a clear difference between the effects of grazers on these two major fungal groups. When provided with a choice, invertebrates consistently prefer, and reproduce more successfully on, saprotrophic than mycorrhizal fungi (Gange, 2000). As a result, in complex, multi-species environments soil fauna commonly stimulate mycorrhizal growth by suppression of competing or inhibitory fungi (Klironomos and Kendrick, 1995). Plant pathogenic fungi are also generally preferred to mycorrhizal species, highlighting further the positive effects of grazers on plant productivity and mycorrhizal development (Lussenhop, 1992). Variation in the susceptibility of major fungal functional groups can lead to shifts in fungal community composition. Collembola grazing, for example, destabilised the saprotrophic fungal community, making it more susceptible to the negative effects of the competing arbuscular mycorrhizal species, *Glomus mosseae* (Tiunov and Scheu, 2005). Whereas changes in invertebrate communities are likely to have direct implications for saprotrophic fungi, the effects on mycorrhizal systems are likely to be more indirect.

Conclusions

There has been a growing interest in the role of soil biodiversity on terrestrial ecosystem processes (for example, soil nutrient availability and decomposition) and the related ecosystem services (primary productivity and soil carbon storage) they provide. Two trends pervading this review may help predict how invertebrate community structure and diversity affect saprotrophic fungal activity and functioning. These are underpinned by the fact that the biological and functional responses of saprotrophic fungi to grazing are intrinsically linked; increased mycelial growth is generally coupled with increased enzyme

production and respiration, and *vice versa*. First, the density-dependent impacts of grazing suggest that factors contributing to an increase in soil invertebrate abundance are likely to reduce the biomass of saprotrophic mycelial systems. This would decrease fungal-mediated nutrient translocation, mineralisation and CO_2 efflux into the atmosphere. In contrast, reducing soil faunal abundance is likely to stimulate mycelial respiration and soil nutrient availability. Second, taxon-specific effects suggest that macrofauna exert the strongest grazing pressures on mycelial systems. Predicted changes in the relative abundance of earthworms, isopods and millipedes as a result of climate and land use change (David and Handa, 2010) will be of particular importance because, even at low densities, these grazers have a dominant role in regulating mycelial activity. It may, as in aboveground systems, be functional group representation, rather than invertebrate species diversity, *per se*, that determines mycelial functioning in soil (Gessner *et al.,* 2010). The capacity of macrofauna to prevent the exclusion of less competitive fungi further highlights their importance in regulating microbial community composition and diversity which, in turn, affect woodland nutrient cycling.

In isolation, these functional consequences of grazing interactions are predictable, but these effects may be complicated by a myriad of other belowground interactions. As well as decomposing organic matter and increasing inorganic nutrient availability for plants, saprotrophic fungi also compete with plants and their mycorrhizal symbionts for these nutrients. Low-intensity grazing can stimulate fungal-mediated nutrient mineralisation with positive effects on plant growth (Bardgett and Chan, 1999), but it could also increase saprotrophic mycelial growth and nutrient uptake, eventually limiting primary productivity. Furthermore, understanding the top–down consequences of grazing on fungal growth and activity requires an appreciation of the concurrent bottom-up effects; invertebrate population responses to fungal resources will affect grazing intensities. Although detailed, microcosm-based manipulations have provided a good mechanistic understanding of these belowground interactions, this acquired knowledge must now be applied to more natural, multi-species environments to allow accurate predictions regarding the role of soil biodiversity on terrestrial ecosystem functioning.

References

Aanen DK, Boomsma JJ. (2006). Social-insect fungus farming. *Curr Biol* **16**: 1014–1016.

A'Bear AD, Boddy L, Raspotnig G, Jones TH. (2010). Non-trophic effects of oribatid mites on cord-forming basidiomycetes in soil microcosms. *Ecol Entomol* **35**: 477–484.

Baldrian P, Valášková V. (2008). Degradation of cellulose by basidiomycetous fungi. *FEMS Microbiol Rev* **32**: 501–521.

Bardgett RD. (2005). *The Biology of Soil*. Oxford University Press: Oxford.

Bardgett RD, Chan KF. (1999). Experimental evidence that soil fauna enhance nutrient mineralization and plant nutrient in montane grassland ecosystems. *Soil Biol Biochem* **31**: 23–33.

Bardgett RD, Frankland JC, Whittaker JB. (1993). The effect of collembolan grazing on fungal activity in differently managed upland pastures - a microcosm study. *Biol Fert Soil* **16**: 255–262.

Bengtsson G, Hedlund K, Rundgren S. (1993). Patchiness and compensatory growth in the fungus-Collembola system. *Oecologia* **93**: 296–302.

Bengtsson G, Rundgren S. (1983). Respiration and growth of a fungus, *Mortierella isabellina*, in response to grazing by *Onychiurus armatus* (Collembola). *Soil Biol Biochem* **15**: 469–473.

Boddy L. (2000). Interspecific combative interactions between wood-decaying basidiomycetes – a review. *FEMS Microbiol Ecol* **31**: 43–56.

Boddy L, Watkinson SC. (1995). Wood decomposition, higher fungi, and their role in nutrient redistribution. *Can J Bot* **73**: 1377–1383.

Boddy L, Wood J, Redman E, Hynes J, Fricker MD. (2010). Fungal network responses to grazing. *Fungal Genet Biol* **47**: 522–530.

Bretherton S, Tordoff GM, Jones TH, Boddy L. (2006). Compensatory growth of *Phanerochaete velutina* mycelial systems grazed by *Folsomia candida* (Collembola). *Microbl Ecol* **58**: 33–40.

Butenschoen O, Poll C, Langel R, Kandeler E, Marhan S, Scheu S. (2007). Endogeic earthworms alter carbon translocation by fungi at the soil-litter interface. *Soil Biol Biochem* **39**: 2854–2864.

Cairney JWG. (2005). Basidiomycetes mycelia in forest soils: dimensions, dynamics and roles in nutrient distribution. *Mycoll Res* **109**: 7–20.

Cooke RC, Rayner ADM. (1984). *Ecology of Saprotrophic Fungi*. Longman: London.

Crowther TW, A' Bear AD. (2012). Impacts of grazing soil fauna on decomposer fungi are species-specific and density-dependent. *Fungal Ecol* **5**: 277–281.

Crowther TW, Boddy L, Jones TH. (2011a). Species-specific effects of soil fauna on fungal foraging and decomposition. *Oecologia* **167**: 535–545.

Crowther TW, Boddy L, Jones TH. (2011d). Outcomes of fungal interaction are determined by soil invertebrate grazers. *Ecol Lett* **14**: 1125–1133.

Crowther TW, Jones TH, Boddy L. (2011b). Species-specific effects of grazing invertebrates on mycelial emergence and growth from woody resources into soil. *Fungal Ecol* **5**: 333–341.

Crowther TW, Jones TH, Boddy L, Baldrian P. (2011c). Invertebrate grazing determines enzyme production by basidiomycete fungi. *Soil Biol Biochem* **43**: 2060–2068.

David J, Handa IT. (2010). The ecology of saprophagous macroarthropods (millipedes, woodlice) in the context of global change. *Biol Rev* **85**: 881–895.

Dyer HC, Boddy L, Preston-Meek CM. (1992). Effect of the nematode *Panagrellus redivivus* on growth and enzyme production by *Phanerochaete velutina* and *Stereum hirsutum*. *Mycol Res* **96**: 1019–1028.

Fierer N, Strickland MS, Liptzin D, Bradford MA, Cleveland CC. (2009). Global patterns in belowground communities. *Ecol Lett* **12**: 1238–1249.
Fitter AH, Sanders IR. (1992). Interactions with soil fauna. In: Allen MF (eds). *Mycorrhizal Functioning*. Chapman and Hall: New York, pp 333–354.
Gange AC. (2000). Arbuscular mycorrhizal fungi, Collembola and plant growth. *Trends Ecol Evol* **15**: 369–372.
Gange AC, Brown VK. (2002). Actions and interactions of soil invertebrates and arbuscular mycorrhizal fungi in affecting the structur of plant communities. In: van der Heijden MGA, Sanders IR (eds). *Ecological Studies. Mycorrhizal Ecology*. Springer-Verlag: New York, pp 321–344.
Gessner MO, Swan CM, Dang CK, McKie BG, Bardgett RD, Wall DH *et al.* (2010). Diversity meets decomposition. *Trends Ecol Evol* **25**: 372–380.
Gormsen D, Olsson PA, Hedlund K. (2004). The influence of collembolans and earthworms on AM fungal mycelium. *Appl Soil Ecol* **27**: 211–220.
Hanlon RDG. (1981). Influence of grazing by collembola on the activity of senescent fungal colonies grown on media of different nutrient concentrations. *Oikos* **36**: 362–367.
Hanlon RDG, Anderson JM. (1979). Effects of collembola grazing on microbial activity in decomposing leaf litter. *Oecologia* **38**: 93–99.
Harinikumar KM, Bagyraj DJ. (1994). Potential of earthworms, ants, millipedes and termites for dissemination of vesicular-arbuscular mycorrhizal fungi in soil. *Biol Fertil Soil* **18**: 115–118.
Harold S, Toroff GM, Jones TH, Boddy L. (2005). Mycelial responses of *Hypholoma fasciculare* to collembola grazing: effect of inoculum age, nutrient status and resource quality. *Mycol Res* **109**: 927–935.
Hedlund K, Augustsson A. (1995). Effects of enchytraeid grazing on fungal growth and respiration. *Soil Biol Biochem* **27**: 905–909.
Hedlund K, Boddy L, Preston CM. (1991). Mycelial responses of the soil fungus *Mortierella isabellina* to grazing by *Onychiurus armatus* (Collembola). *Soil Biol Biochem* **36**: 591–599.
Hedlund K, Ohrn MS. (2000). Tritrophic interactions in a soil community enhance decomposition rates. *Oikos* **88**: 585–591.
Hättenschwiler S, Tiunov AV, Scheu S. (2005). Biodiversity and litter decomposition in terrestrial ecosystems. *Annu Rev Ecol Evol Syst* **36**: 191–218.
Ineson P, Leonard MA, Anderson JM. (1982). Effect of collembolan grazing upon nitrogen and cation leaching from decomposing leaf litter. *Soil Biol Biochem* **14**: 601–605.
Jaffee BA, Santos PF, Muldoon AE. (1997). Suppression of nematophagous fungi by enchytraeid worms: a field exclosure experiment. *Oecologia* **112**: 412–423.
Kampichler C, Rolschewski L, Donnelly DP, Boddy L. (2004). Collembolan grazing affects the growth strategy of chord-forming fungus *Hypholoma fasciculare*. *Soil Biol Biochem* **36**: 591–599.
Kaneko N, McLean MA, Parkinson D. (1998). Do mites and Collembola affect pine litter fungal biomass and microbial respiration? *Appl Soil Ecol* **9**: 209–213.
Klironomos JN, Kendrick WB. (1995). Stimulative effects of arthropods on endomycorrhizas of sugar maple in the presence of decaying litter. *Funct Ecol* **9**: 528–536.
Klironomos JN, Ursic M. (1998). Density-dependent grazing on the extraradical hyphal network of the *Arbuscular mycorrhizal* fungus, *Glomus intraradices*, by the collembolan, *Folsomia candida*. *Biol Fert Soil* **26**: 250–253.
Klironomos JN, Widden P, Deslandes I. (1992). Feeding preferences of the collembolan, *Folsomia candida*, in relation to microfungal successions on decaying litter. *Soil Biol Biochem* **24**: 685–692.
Lenoir L, Persson T, Bengtsson J, Wallander H, Wirén D. (2007). Bottom–up or top–down control in forest soil microcosms? Effects of soil fauna on fungal biomass and C/N mineralization. *Biol Fert Soil* **43**: 281–293.
Leonard MJ, Anderson JM. (1991). Grazing interactions between a Collembolan and fungi in a leaf litter matrix. *Pedobiologia* **35**: 239–246.
Lindahl BO, Taylor AFS, Finlay RD. (2002). Defining nutritional constraints on carbon cycling in boreal forests – towards a less 'phytocentric' perspective. *Plant Soil* **242**: 123–135.
Lussenhop J. (1992). Mechanisms of micro-arthropod-microbial interactions in soil. *Adv Ecol Res* **23**: 1–33.
Maraun M, Martens H, Migge S, Theenhaus A, Scheu S. (2003). Adding to 'the enigma of soil animal diversity': fungal feeders and saprotrophic soil invertebrates prefer similar food substrates. *Eur J Soil Biol* **39**: 85–95.
McLean MA, Kaneko N, Parkinson D. (1996). Does selective grazing by mites and collembola affect litter fungal community structure? *Pedobiologia* **40**: 97–105.
McNaughton SJ. (1983). Compensatory plant growth in response to herbivory. *Oikos* **40**: 329–336.
Moody SA, Piearce TG, Dighton J. (1996). Fate of some fungal spores associated with wheat straw decomposition on passage through the guts of *Lumbricus terrestris* and *Aporrectodea longa*. *Soil Biol Biochem* **28**: 533–537.
Mueller UG, Gerardo N. (2002). Fungus-farming insects: Multiple origins and diverse evolutionary histories. *Proc Natl Acad Sci USA* **99**: 15247–15249.
Newell K. (1984a). Interaction between two decomposer Basidiomycetes and a collembolan under Sitka spruce: distribution, abundance and selective grazing. Soil. *Biol Biochem* **16**: 223–233.
Newell K. (1984b). Interaction between two decomposer Basidiomycetes and a collembolan under Sitka spruce: grazing and its potential effects on fungal distribution and litter decomposition. *Soil Biol Biochem* **16**: 235–239.
North RD, Jackson CW, Howse PE. (1997). Evolutionary aspects of ant-fungus interactions in leaf-cutting ants. *Trend Ecol Evol* **12**: 386–389.
Nuss I. (1982). [Die Bedeutung der proterosporen: Schlufolgerungen aus untersuchungen an *Ganoderma* (Basidiomycetes)]. *Plant Syst Evol* **141**: 53–79.
Osono T. (2007). Ecology of ligninolytic fungi associated with leaf litter decomposition. *Ecol Res* **22**: 955–974.
Parkinson D, Visser S, Whittaker JB. (1979). Effects of collembolan grazing on fungal colonization of leaf litter. *Soil Biol Biochem* **11**: 529–535.
Pollierer MM, Langel R, Scheu S, Maraun M. (2009). Compartmentalization of the soil animal food web as indicated by dual analysis of stable isotope ratios ($^{15}N/^{14}N$ and $^{13}C/^{12}C$). *Soil Biol Biochem* **41**: 1221–1226.
Renker C, Otto P, Schneider K, Zimdars B, Maraun M, Buscot F. (2005). Oribatid mites as potential vectors for soil microfungi: study of mite-associated fungal species. *Microb Ecol* **50**: 518–528.
Rotheray TD, Chancellor M, Jones TH, Boddy L. (2011). Grazing by collembola affects the outcome of

interspecific mycelial interactions of cord-forming basidiomycetes. *Fungal Ecol* **4**: 1–14.

Rusek J. (1998). Biodiversity of Collembola and their functional role in the ecosystem. *Biodiversity Conserv* **7**: 1207–1219.

Scheu S. (1993). Litter microflora-soil macrofauna interactions in lignin decomposition: a laboratory experiment with ^{14}C-labelled lignin. *Soil Biol Biochem* **25**: 1703–1711.

Setälä H, Berg PM, Jones TH. (2005). Trophic structure and functional redundancy in soil communities. In: Bardgett RD, Usher MB, Hopkins DW (eds). *Biological Diversity and Function in Soils*. Cambridge University Press: Cambridge, pp 236–249.

Slippers B, Coutinho TA, Wingfield BD, Wingfield MJ. (2003). A review of the genus *Amylostereum* and its association with woodwasps. *South Africa J Sci* **99**: 70–74.

Tiunov AV, Scheu S. (2005). Arbuscular mycorrhiza and Collembola interact in affecting community composition of saprotrophic microfungi. *Oecologia* **142**: 636–642.

Tordoff GM, Boddy L, Jones TH. (2006). Grazing by *Folsomia candida* (collembola) differently affects mycelial morphology of the chord-forming bacidiomycetes *Hypholoma fasciculare*, *Phanerochaete velutina,* and *Resinicium bicolor*. *Mycol Res* **110**: 335–345.

Tordoff GM, Boddy L, Jones TH. (2008). Species-specific impacts of collembola grazing on fungal foraging ecology. *Soil Biol Biochem* **40**: 434–442.

Tordoff GM, Chamberlain PM, Crowther TW, Black HIJ, Jones TH, Stott A *et al.* (2011). Nitrogen partitioning in the mycelia of *Phanerochaete velutina*: an investigation into the influence of collembola grazing using stable isotopes. *Soil Biol Biochem* **43**: 2338–2346.

Visser S, Parkinson D, Hassall M. (1987). Fungi associated with *Onychiurus subtenuis* (Collembola) in an aspen woodland. *Can J Bot* **65**: 635–642.

Wicklow DT, Yocom DH. (1982). Effect of larval grazing by lycoriella-mali diptera sciaridae on species abundance of coprophilous fungi. *Trans Br Mycol Soc* **78**: 29–32.

Wood J, Tordoff GM, Jones TH, Boddy L. (2006). Reorganization of mycelial networks of *Phanerochaete velutina* in response to new woody resources and collembola (*Folsomia candia)* grazing. *Mycol Res* **110**: 985–993.