RESEARCH ARTICLE

Interactive effects of warming and invertebrate grazing on the outcomes of competitive fungal interactions

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Abstract

Saprotrophic fungal community composition, determined by the outcomes of competitive mycelial interactions, represents a key determinant of woodland carbon and nutrient cycling. Atmospheric warming is predicted to drive changes in fungal community composition. Grazing by invertebrates can also exert selective pressures on fungal communities and alter the outcome of competitive fungal interactions; their potential to do so is determined by grazing intensity. Temperature regulates the abundance of soil collembola, but it remains unclear whether this will alter the top-down determination of fungal community composition. We use soil microcosms to explore the direct (via effects on interacting fungi) and indirect (by influencing top-down grazing pressures) effects of a 3 °C temperature increase on the outcomes of competitive interactions between cord-forming basidiomycete fungi. By differentially affecting the fungal growth rates, warming reversed the outcomes of specific competitive interactions. Collembola populations also increased at elevated temperature, and these larger, more active, populations exerted stronger grazing pressures. Consequently, grazing mitigated the effects of temperature on these interactions, restoring fungal communities to those recorded at ambient temperature. The interactive effects of biotic and abiotic factors are a key in determining the functional and ecological responses of microbial communities to climate change.

Introduction

Saprotrophic basidiomycete fungi are ubiquitous in temperate woodland soils where they are primary regulators of belowground nutrient cycling (Hättenschwiler *et al.*, 2005). By virtue of their lignocellulytic enzymes, these fungi are the major agents of litter decomposition in woodland soil and contribute substantially to the flux of CO_2 between terrestrial and atmospheric pools (Wardle *et al.*, 2004). Fungal communities, determined by the outcomes of competitive mycelial interactions (Crowther *et al.*, 2011a), are regulated by biotic (resource availability and selective grazing by invertebrates) and abiotic (including temperature and moisture) factors, both of which are likely to vary under projected global climate change scenarios (Jones *et al.*, 1998; He *et al.*, 2010). Species-specific enzyme production and respiration rates suggest that climate-induced changes in fungal community (specifically lignin-decomposing white rot basidiomycetes) composition will drive changes in nutrient cycling and influence carbon cycle feedbacks to climate change (Bardgett *et al.*, 2008; McGuire & Treseder, 2010). Despite this, and the fact that multiple drivers of microbial community change are likely to vary in concert, most climate change research, to date, has failed to address the effects of biotic and abiotic factors in combination.

Temperature plays a prominent role in regulating microbial growth and activity in the soil and litter horizons. Prolonged warming has been shown to exert selective pressures on fungal communities, favouring the development of fast-growing species and enabling them to replace less adaptable opponents (Castro *et al.*, 2010). Although yet to be shown in saprotrophic basidiomycete communities, species-specific growth responses of various cord-forming species to elevated temperature have been recorded in artificial agar media (Boddy, 1983a, b; Schoeman *et al.*, 1996). The contrasting fungal responses suggest that warming is likely to influence saprotrophic

communities directly, by differentially affecting fungal competitive abilities, but it may also have indirect effects, via changes in the soil biotic community (Jones *et al.*, 1998; Crowther *et al.*, 2011a).

In woodland ecosystems, fungi form the first trophic level in the decomposer food web and support a vast abundance of fauna (Pollierer *et al.*, 2009). Invertebrate 'grazing' is a key biotic driver of fungal community change, exerting selective pressures via two opposing mechanisms – stimulation of the least competitive fungus and removal of the dominant species (Crowther *et al.*, 2011a). Mycophagous collembola constitute a major component of soil mesofauna (in terms of biomass and ecosystem functioning) in temperate woodland soils (Rusek, 1998). Many species have the capacity to influence, or even halt, development of basidiomycete mycelia (Tordoff *et al.*, 2008; Crowther *et al.*, 2011b), but their potential to do so is determined by grazing intensity (Hanlon & Anderson, 1979; Kaneko *et al.*, 1998). Although previous studies (including those using the present study system; Crowther *et al.*, 2011a) have failed to reveal consistent effects of collembola on the outcomes of competitive fungal interactions, it is predicted that factors that contribute to increased collembola abundance will stimulate the top-down determination of fungal community composition (Kaneko *et al.*, 1998). At constant soil moisture, collembola populations are highly responsive to temperature, generally increasing in abundance in warmer soils (Haimi *et al.*, 2005; Day *et al.*, 2009). One such increase in the abundance of mycophagous collembola, *Folsomia candida*, was found to correlate with changes in soil microbial abundance, leading Jones *et al.* (1998) to speculate that climate-induced changes in invertebrate communities may drive shifts in fungal community compositions. If changes in atmospheric temperature affect the potential of soil collembola to modify fungal community composition and diversity, they are also likely to cause shifts in rates of fungus-mediated nutrient cycling and below-ground ecosystem functioning.

To date, understanding of the biotic and abiotic factors affecting the competitive fungal interactions has been restricted by the high complexity and opacity of the soil environment. Recently, two-dimensional (2-D) soil microcosms have been used as model systems, ensuring that fungal cords grow at the soil surface as they do in natural woodland environments where they extend at the soil-litter interface (Boddy, 2000). These systems can provide a mechanistic understanding of specific decomposer interactions, ensuring that the effects of invertebrates are not masked by the huge diversity of other soil inhabiting biota. The present study uses 2-D microcosms to explore the potential of atmospheric warming to influence the outcomes of competitive interactions between saprotrophic fungi and the degree of top-down determination of fungal community composition by the common collembola, *F. candida*. Two predictions were tested: (1) differential effects of elevated temperature on competing fungal species will reverse the outcomes of specific fungal interactions in soil; and (2) at elevated temperature, higher grazing intensity (resulting from larger *F. candida* populations; Haimi *et al.*, 2005; Day *et al.*, 2009) will increase the potential of collembola to influence the outcomes of competitive mycelial interactions.

Materials and methods

Experimental design

A multi-factorial soil microcosm design was used to investigate the outcomes of competitive fungal interactions between three cord-forming basidiomycete fungi (*Resinicium bicolor*, *Hypholoma fasciculare* and *Phanerochaete velutina*) under ambient (15 °C) and elevated (18 °C) temperatures and in the presence and absence of collembola, *F. candida*. All interacting fungi are ubiquitous in temperate UK woodlands, forming large mycelial cord systems at the soil –litter interface (Boddy, 2000). As well as being a good model species, *F. candida* is known to feed directly on cord-forming basidiomycetes. Fast generation times also mean that *F. candida* populations are highly responsive to changes in atmospheric temperature, with direct consequences for grazing pressures (A'Bear *et al.*, 2012). Ambient conditions were based on early-autumn temperatures beneath the litter horizon in UK temperate woodland (Boddy, 1983a, b), and a temperature rise of 3 °C was used to mimic predicted warming over the next century under a high emission scenario (IPCC, 2007). All treatments (three fungal interactions × two temperatures × two grazing treatments) were replicated five times, as were invertebrate-only controls at each temperature.

Fungal culturing and inoculum preparation

Hypholoma fasciculare (Huds.: Fr.), *R. bicolor* (Abertini & Schwein.: Fr.) and *P. velutina* (DC.: Pers.) (Cardiff University Fungal Genetic Source Collection) were subcultured in 9-cm, non-vented Petri dishes on 2% malt extract agar (MEA; 15 g L^{-1} Lab M agar no. 2, 20 g L^{-1} Munton and Fiston malt). Freshly felled beech (*Fagus sylvatica*) wood was cut into blocks (2 × 2 × 1 cm), stored at −18 °C before being soaked in deionized water (DH_2O) and autoclaved at 121 °C for 20 min in sealed autoclave bags. Sterilized blocks were then added to fungus-colonized Petri dishes. These were sealed and incubated in a dark CT room at 16.5 °C for 3 months prior to experimental use.

Collembola culturing

Folsomia candida Willem 1902 (Cardiff University Culture) were cultured in 0.9 L plastic containers on a medium of 5% activated charcoal (Sigma, Poole, UK), and 95% plaster of Paris (Minerva Dental, Cardiff, UK) and fed weekly on dried baker's yeast (Spice of Life, Cardiff, UK). Cultures were stored in a dark cupboard at 18 °C and moistened weekly using DH_2O. Before introduction into experimental microcosms, adult collembola were size-selected (200–400 μm diameter) using a series of metal sieves and starved for 24 h in fresh plaster of Paris pots. Sixty adults were added to each experimental microcosm. This represents a low estimate of collembola field densities (Petersen & Luxton, 1982) but has been shown to be appropriate in microcosms where collembola are restricted to 2-D rather than the 3-D soil environments (Crowther & A'Bear, 2012).

Microcosm preparation, inoculation and running

Soil, collected to a depth of 20 cm from deciduous woodland (Coed Beddick Enclosure, Tintern, UK (SO 52800 01800; 51°41′ 48.37″ N, 2°40′ 53.11″ W) was sieved on site through a 10-mm mesh. This soil was air-dried and sieved a second time through 2-mm mesh before being frozen for 24 h (−18 °C) to kill remaining fauna. Prior to addition to microcosms, soil was re-wetted (340 mL DH_2O kg $soil^{-1}$) providing a water potential of −0.012 MPa. Moistened soil (200 g) was then compacted and smoothed to a depth of 5 mm into 24 × 24 cm bio-assay dishes. Trays were incubated at constant temperatures, half at 15 °C (ambient) and half at 18 °C (elevated), at relative humidity of 70%.

Wood blocks were removed from cultures and the densities (dry weight/fresh volume; g cm^{-3}) of five blocks colonized by each fungal species determined at 0 days. These blocks were later used to estimate wood decay rates. Surface mycelia and agar were removed from the remaining blocks before being added to soil trays. Wood blocks colonized by opposing species were placed 8 cm apart on a diagonal line across each tray. Wood block addition dates were staggered, depending on the species-specific fungal growth rates (Crowther *et al.*, 2011a), to ensure that emerging mycelia met directly between the two wood blocks after approximately 4-cm growth. Once opposing mycelia in 50% of trays for each fungal interaction, at each temperature, had met for 2 days, collembola were introduced onto un-colonized regions of soil. Trays were then stacked in polythene bags to reduce water loss and microcosms were re-wetted with DH_2O weekly to a constant weight. After 63 days (9 weeks), the experiment was concluded. Each wood block was cut in half; one half was used for re-isolation and identification of colonizing fungi, and the second to determine final wood block density and estimation of wood decay rate (g cm^{-3} day^{-1}). Final collembola populations were estimated for each tray using Tullgren funnel extractions.

Image capture and analysis

To monitor changes in mycelial growth during competitive interactions, digital images were captured 0, 3, 7, 14, 21, 35, 49 and 63 days after collembola addition, using a Nikon Coolpix 57000 camera, at a height of 39.5 cm. Image analysis was carried out using IMAGEJ (National Institutes of Health). A 10-cm line was initially drawn against a ruler for calibration. Mycelial extent was measured as the mean length of four lines (30° apart), drawn from the centre of each wood block to mycelial tips through a 90° angle, in the direction of the opposing wood block following Crowther *et al.* (2011a). Extension rates (cm day^{-1}) were recorded for each interaction until mycelia of either fungus reached the opposing wood block.

Determination of interaction outcomes

On the soil, interaction outcomes were determined following Crowther *et al.* (2011a) by identifying which fungi had reached the opponent's wood block after 63 days. Outcomes were classified as: (1) replacement, where one fungus was killed and replaced by an opponent; (2) overgrowth, where one fungus was overgrown by another and regressed without being killed; and (3) deadlock, where neither species had gained territory (Supporting Information, Fig. S1). Replacement and overgrowth were recorded as being a 'win' for the aggressor, while deadlock or mutual replacement were recorded as 'draws'.

On the final day, wood chips were removed from newly cut surfaces of halved wood inocula and placed onto Petri dishes containing 2% MEA. These were incubated for 7 days at 18 °C, and emerging mycelia were identified visually. If both wood blocks from a single microcosm were colonized by a single fungus (i.e. one fungus had replaced its opponent and defended its own resource), the interaction was recorded as a 'win'. A 'draw' was recorded if wood blocks were colonized by different fungi (i.e. both fungi had been replaced).

Statistical analysis

A multinomial logistic regression model (MINITAB 15) was used to test for differences between the frequencies of the three possible interaction outcomes ('win' for fungus 'a',

'win' for fungus 'b' or 'draw') in grazed and un-grazed treatments, at ambient and elevated temperature. Binary logistic regression was used when only two outcomes were recorded for any given comparison.

Mycelial extension rates of both fungi in each interaction were compared across temperature and grazing treatments using two-way analysis of covariance (ANCOVA; General Linear Model; MINITAB 15) with time as a covariate. For each fungal treatment and invertebrate-only controls, collembola populations were compared between temperatures using one-way analysis of variance (ANOVA; R version 2.10.1). Wood decay rates of both fungi in each interaction were then compared across grazing and temperature treatments using two-way analysis of variance (ANOVA; R version 2.10.1). In each test, data not meeting assumptions of ANOVA [normally distributed (Anderson-Darling Test) and variances equal (Levene's Test)] were log transformed. Individual treatments were compared using Tukey's pairwise comparison.

Results

Outcomes of interactions in soil

At 15 °C, and in the absence of grazing, there was a clear hierarchy of fungal dominance (*R. bicolor* < *H. fasciculare* < *P. velutina*). A temperature increase of 3 °C was, however, sufficient to alter significantly (logistic regression; $G = 7.44$, $P = 0.039$) the outcome of interactions between *R. bicolor* and *P. velutina* (Fig. 1a). Stimulated growth rates of the former at 18 °C (ANCOVA, temperature × time; $F_{2,8} = 15.9$, $P = 0.005$) enabled it to replace *P. velutina* on soil and reach the opposing wood block by 35 days (Fig. S1e). The temperature change alone did not significantly ($P > 0.05$) affect the outcomes of any other interactions but stimulated extension rates of the *P. velutina* across *H. fasciculare* ($F_{2,8} = 11.21$, $P = 0.014$).

Collembola had no significant ($P > 0.05$) effect on the outcomes of any fungal interactions at 15 °C (Fig. 1). Population numbers in collembola-only control, and all fungal trays were, however, significantly ($P < 0.001$ in each case) increased at 18 °C (Fig. 2). Although, in the absence of collembola *R. bicolor* replaced *P. velutina* at 18 °C, selective grazing by these large *F. candida* populations reduced *R. bicolor* extension rates ($F_{2,8} = 7.52$, $P = 0.029$), enabling *P. velutina* to extend more rapidly ($F_{2,8} = 22.86$, $P = 0.002$) and reach the opposing wood block by 35 days (Fig. S1f). High-intensity grazing, therefore, reversed the outcome of this interaction at 18 °C ($G = 13.86$, $P = 0.001$), restoring the outcome to that observed at 15 °C (Fig. 1a). Although collembola reduced extension rates of both *P. velutina* ($F_{2,8} = 6.94$, $P = 0.03$)

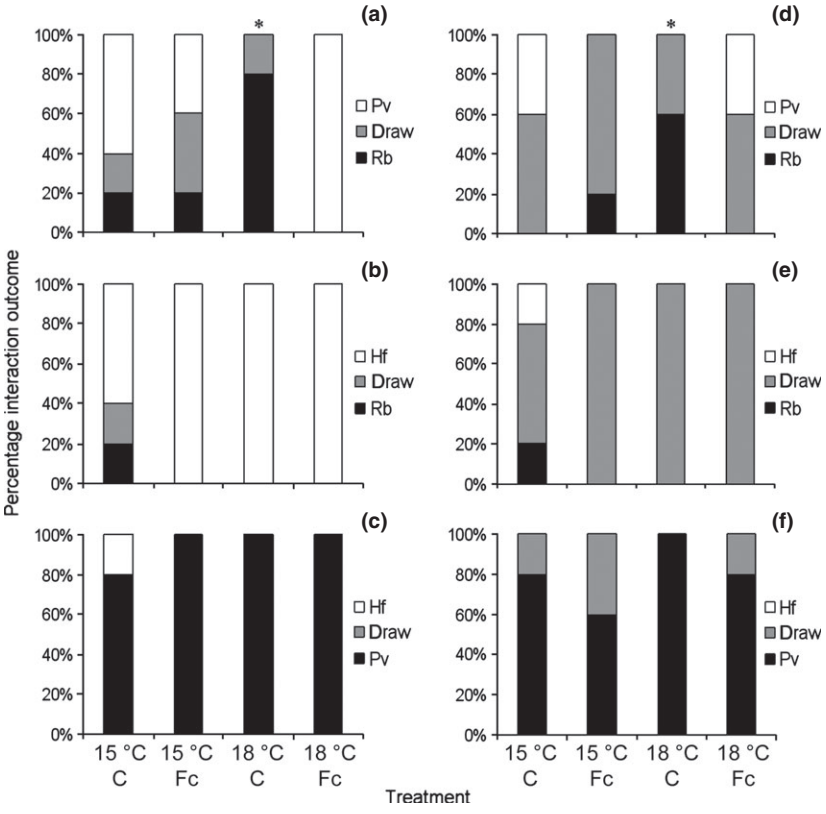

Fig. 1. Percentage outcomes of competitive fungal interactions ($n = 5$) between *Resinicium bicolor* (Rb), *Hypholoma fasciculare* (Hf) and *Phanerochaete velutina* (Pv) in soil (a, b and c) and wood blocks (d, e and f) during control (C) and *Folsomia candida* (Fc) grazing treatments at 15 and 18 °C. Stars indicate significant differences (logistic regression) compared with un-grazed controls at ambient temperature (*$P \leq 0.05$).

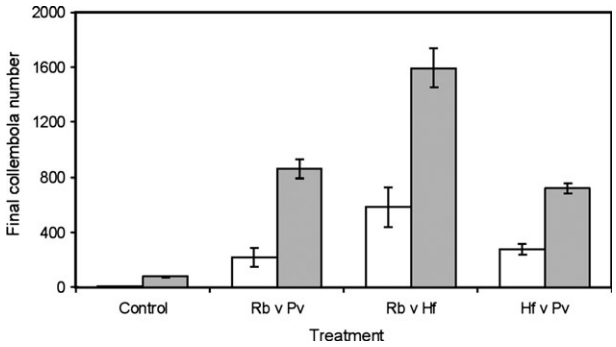

Fig. 2. Final population numbers (mean ± standard error) of living *Folsomia candida* extracted from invertebrate-only control, and all three fungal interaction (*Resinicium bicolor* vs. *Phanerochaete velutina* (Rb v. Pv), *R. bicolor* vs. *Hypholoma fasciculare* (Rb v Hf) and *H. fasciculare* vs. *P. velutina* (Hf v Pv)) trays at 15 °C (□) and 18 °C (■).

and *R. bicolor* ($F_{2,8} = 7.92$, $P = 0.021$) during interactions with *H. fasciculare* (Fig. 3), grazing had no significant ($P \geq 0.05$) effect on the extension rates of the latter, or outcomes of any other competitive interactions. Outcomes of all interactions at 15 °C in the absence of grazers were, therefore, the same as in the presence of collembola at 18 °C.

Wood block colonization

Generally, the colonization of wood blocks reflected the outcomes of interactions in soil. *Phanerochaete velutina*, for example, replaced *H. fasciculare* in the majority of replicates in each treatment (Fig. 1). Interactions involving *R. bicolor* were, however, not as straightforward as this species was rarely displaced from its original resource. As a result, when *R. bicolor* mycelium was replaced on soil, it often defended its original resource and the overall outcome was recorded as a 'draw' (where neither fungus was replaced in wood) (Fig. 1d, e). As in soil, elevated temperature shifted the outcome of interactions between *R. bicolor* and *P. velutina* in favour of the latter (from 60% draw to 60% *R. bicolor*; $G = 6.086$, $P = 0.048$; Fig. 1d). The interaction between *R. bicolor* and *H. fasciculare* was not significantly ($P > 0.05$) affected by the change in temperature.

As in soil, collembola exerted stronger selective pressures at 18 than at 15 °C (Fig. 1d). By selectively grazing *R. bicolor* on soil, *F. candida* significantly ($G = 6.086$, $P = 0.048$) increased the number of wood blocks colonized by *P. velutina* at 18 °C (Fig. 1d). This had no significant ($P > 0.05$) effects on either interaction involving *H. fasciculare*.

Wood decay rates

Unlike mycelial extension rates, wood decay rates of all fungi were more affected by temperature than grazing (Fig. 2d, e, f). Decomposition rates by the most competitive fungus generally increased at 18 °C (*H. fasciculare* during interactions with *R. bicolor*: $F_{1,16} = 11.90$, $P = 0.003$; and *P. velutina* during interactions with

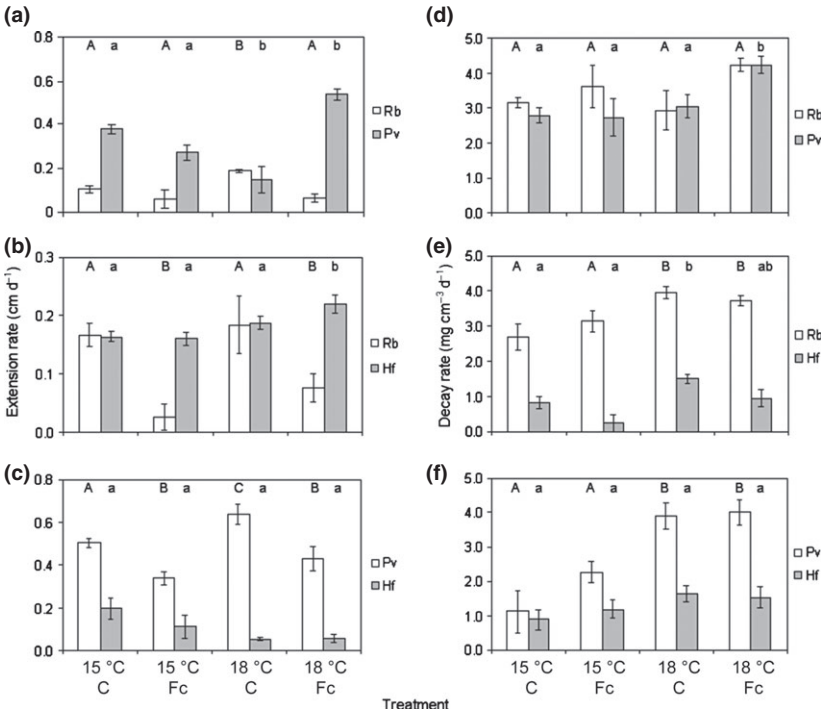

Fig. 3. Extension rates (a, b and c) and wood block decay rates (d, e and f) (mean ± standard error) of *Resinicium bicolor* (Rb), *Phanerochaete velutina* (Pv) and *Hypholoma fasciculare* JH (Hf) during competitive interactions under control (C) and *Folsomia candida* (Fc), grazing treatments at 15 and 18 °C. Different letters indicate significantly ($P \leq 0.05$; ANOVA; MINITAB 15) different extension and decay rates. Upper and lower case letters refer to different fungi and were analysed separately. *Y*-axis scales vary between graphs.

H. fasciculare: $F_{1,16} = 22.9$, $P < 0.001$) and the interactive effect of temperature and grazing stimulated *P. velutina* decomposition rates during interactions with *R. bicolor* ($F_{1,16} = 6.41$, $P = 0.022$). The presence of collembola alone did not significantly ($P > 0.05$) affect the decay rates of any fungus at ambient or elevated temperature (Fig. 2).

Discussion

Atmospheric temperature directly and indirectly affected the development and outcomes of competitive mycelial interactions. By differentially affecting the extension rates of competing fungi, warming enabled a formerly less competitive species (*R. bicolor*) to overcome its opponent (*P. velutina*) in soil and wood. These interaction outcomes also contrasted with those observed in a previous study at 20 °C (Crowther *et al.*, 2011a), highlighting the high temperature sensitivity of the system. At 15 °C, slow developmental rates of *R. bicolor* led to its replacement by both *H. fasciculare* and *P. velutina*, but increasing growth rates enabled it to displace *P. velutina* at 18 °C, and both opponents at 20 °C. Although the potential for climate change to influence microbial community composition is established (Kandeler *et al.*, 1998; Kampichler *et al.*, 1998; He *et al.*, 2010), this is the first study to show the temperature-induced reversal of competitive interaction outcomes between saprotrophic fungi in soil. Interspecific decomposition rates suggest that shifts in species composition could drive changes in nutrient turnover and the efflux of CO_2 from soil (Hättenschwiler *et al.*, 2005). *Resinicium bicolor*, for example, produces less cellulolytic enzymes and degrades wood at a slower rate than *P. velutina* when growing in isolation (Crowther *et al.*, 2011c). Promotion of the former at elevated temperature therefore suggests that, in these fungal communities, decomposition rates could fall under climate change scenarios. These effects may, however, be confounded by altered decomposition rates of the competing fungal species. Warming generally stimulated wood decomposition by the dominant fungal species, and this may override the effects of changing species compositions. Untangling the relative importance of these effects (changing species composition and fungal physiology) using long-term manipulations may prove an important step in understanding the effects of climate change on woodland nutrient cycling (McGuire & Treseder, 2010).

Grazing also influenced the outcomes of specific fungal interactions, but their potential to do so was temperature dependent. At ambient temperature, collembola could not alter the outcome of any fungal interactions. This is consistent with previous studies showing that, at current field densities, collembola grazing intensity is rarely strong enough to affect fungal community composition (McLean *et al.*, 1996; Kaneko *et al.*, 1998). The 3 °C temperature increase was, however, sufficient to stimulate collembola population growth in all fungal interactions. Increased *F. candida* reproduction rates are likely to have been coupled with increased metabolic activity in warmer soil (de Boer *et al.*, 2010). These larger, more active populations exerted stronger grazing pressures and the selective removal of *R. bicolor* (the dominant species at 18 °C, in the absence of grazers) eventually led to its replacement by *P. velutina*. Once again, this effect is in contrast with previous work conducted at 20 °C, where *F. candida* was unable to alter interactions between these fungi (Crowther *et al.*, 2011a). This further highlights the sensitivity of cord-forming basidiomycetes to subtle temperature changes. Although *R. bicolor* systems replaced *P. velutina* at both 18 and 20 °C, they were less resistant to high-intensity grazing at the lower temperature, enabling *F. candida* to remove mycelial cords and prevent the competitive exclusion of *P. velutina* in soil and wood. These interactive effects of biotic and abiotic factors provide the first empirical evidence to support the argument that climate-induced changes to invertebrate populations may indirectly drive shifts in microbial community composition and functioning (Jones *et al.*, 1998).

The increased top-down determination of fungal species composition at elevated temperature observed in the present study is the result of two factors: (1) increased grazing pressure exerted by larger collembola populations; and (2) temperature-induced promotion of the most palatable fungal resource. *Resinicium bicolor* is generally preferred to *P. velutina* by invertebrates, including *F. candida* (Tordoff *et al.*, 2008; Crowther *et al.*, 2011a). By stimulating growth of *R. bicolor*, the temperature change also increased the availability of the most palatable fungal resource, further increasing collembola grazing pressures (Crowther *et al.*, 2011b). These results must, however, be interpreted with caution as the effects observed in simplistic microcosm studies could be obscured by the complexity of the natural soil environment. It is possible that, in highly diverse soil communities, a similar temperature change may favour the development of various, less palatable species, with contrasting effects on grazing pressure. It is, however, evident that, by stimulating collembola population growth and altering their resource availability, changes in atmospheric temperature are likely to influence the top-down determination of fungal communities in woodland soil.

In combination, the direct and indirect effects of warming resulted in no net change in fungal species composition. While warming alone caused *R. bicolor* to replace *P. velutina*, the concurrent increase in grazing intensity restored the interaction outcome to that

observed at ambient temperature. Grazing, therefore, mitigated the effects of warming. Similar regulatory effects of mycpohagous fauna have been recorded previously in single fungus systems. Heavy grazing of extra-resource mycelia can limit fungal-mediated wood decay (Tordoff *et al.*, 2008; Crowther *et al.*, 2011d), potentially mitigating the positive effects of warming on soil carbon efflux (A'Bear *et al.*, 2012). Although these effects, recorded in simplistic 2-D microcosms, cannot accurately predict the responses of natural, highly diverse microbial communities, they can provide a valuable mechanistic understanding of the processes that regulate community structure and the processing of soil nutrients. Interactive effects of biotic and abiotic factors are likely to play a key role in determining microbial community composition and both should be considered in combination when exploring the effects of climate change on belowground ecosystem functioning.

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References

A'Bear AD, Boddy L & Jones TH (2012) Impacts of elevated temperature on the growth and functioning of decomposer fungi are influenced by grazing collembola. *Glob Change Biol*, in press DOI: 10.1111/j.1365-2486.2012.02637.x.

Bardgett RD, Freeman C & Ostle NJ (2008) Microbial contributions to climate change through carbon cycle feedbacks. *ISME J* **2**: 805–814.

Boddy L (1983a) Microclimate and moisture dynamics of wood decomposing in terrestrial ecosystems. *Soil Biol Biochem* **15**: 149–157.

Boddy L (1983b) Effects of temperature and water potential on the growth rates of wood-rotting basidiomycetes. *Trans Br Mycol Soc* **80**: 141–149.

Boddy L (2000) Interspecific combative interactions between wood-decaying basidiomycetes. *FEMS Microbiol Ecol* **31**: 185–194.

Castro HF, Classen AT, Austin EE, Norby RJ & Schadt CW (2010) Soil microbial community responses to multiple experimental climate change drivers. *Appl Environ Microbiol* **76**: 999–1007.

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) Outcomes of fungal interactions are determined by soil invertebrate grazers. *Ecol Lett* **14**: 1134–1142.

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

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

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

Day TA, Ruhland CT, Strauss SL, Park J, Krieg ML, Krna MA & Bryant DM (2009) Response of plants and the dominant microarthropod, *Cryptopygus antarcticus*, to warming and contrasting precipitation regimes in Antarctic tundra. *Glob Change Biol* **15**: 1640–1651.

de Boer TE, Holmstrup M, van Straalen NM & Roelofs D (2010) The effect of soil pH and temperature on *Folsomia candida* transcriptional regulation. *J Insect Physiol* **56**: 350–355.

Haimi J, Laamanen J, Penttinen R, Raty M, Koponen S, Kellomaki S & Niemela P (2005) Impacts of elevated CO_2 and temperature on the soil fauna of boreal forests. *Appl Soil Ecol* **30**: 104–112.

Hanlon RDG & Anderson JM (1979) Effects of collembola grazing on microbial activity in decomposing leaf litter. *Oecologia* **38**: 93–99.

Hättenschwiler S, Tiunov AV & Scheu S (2005) Biodiversity and litter decomposition in terrestrial ecosystems. *Annu Rev Ecol Evol* **36**: 191–218.

He Z, Xu M, Deng Y, Kang S, Kellogg L, Wu L, Van Nostrand JD, Hobbie SE, Reich PB & Zhou J (2010) Metagenomic analysis reveals a marked divergence in the structure of belowground microbial communities at elevated CO_2. *Ecol Lett* **13**: 564–575.

IPCC (2007) Climate change 2007: synthesis report. *Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (Core Writing Team, Pachauri RK & Reininger A, eds), pp. 104. IPCC, Geneva, Switzerland.

Jones TH, Thompson LJ, Lawton JH *et al.* (1998) Impacts of rising atmospheric carbon dioxide on model terrestrial ecosystems. *Science* **280**: 441–443.

Kampichler C, Kandeler E, Bardgett RD, Jones TH & Thompson LJ (1998) Impact of elevated CO_2 concentration on soil microbial biomass and activity in a complex, weedy field model ecosystem. *Glob Change Biol* **4**: 335–346.

Kandeler E, Tscherko D, Bardgett RD, Hobbs PJ, Kampichler C & Jones TH (1998) The response of soil microorganisms and roots to elevated CO_2 and temperature in a terrestrial model ecosystem. *Plant Soil* **202**: 251–262.

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.

McGuire KL & Treseder KK (2010) Microbial communities and their relevance for ecosystem models: decomposition as a case study. *Soil Biol Biochem* **42**: 529–535.

McLean MA, Kaneko N & Parkinson D (1996) Does selective grazing by mites and collembola affect litter fungal community structure? *Pedobiologia* **40**: 97–105.

Petersen H & Luxton M (1982) A comparative analysis of soil fauna populations and their role in the decomposition process. *Oikos* **39**: 287–388.

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.

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

Schoeman MW, Webber JF & Dickinson DJ (1996) The effect of diffusible metabolites of *Trichoderma* on in-vitro interactions between basidiomycete isolates at two temperatures. *Mycol Res* **100**: 1454–1458.

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

Wardle DA, Bardgett RD, Klironomos JN, Setälä H, van der Putten WH & Wall DH (2004) Ecological linkages between aboveground and belowground biota. *Science* **304**: 1629–1633.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Digital images showing examples of three possible outcomes of mycelial interactions in soil: replacement (a), overgrowth (b) and deadlock (c).

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