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Opinion Article

Armed and dangerous – Chemical warfare in wood decay communities

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ABSTRACT

Fungal community structure and development in decaying woody resources are largely dependent on interspecific antagonistic interactions that determine the distribution of territory – and hence the nutrients within – between different individuals occupying that resource. Interactions are mediated by antagonistic mechanisms, which determine the combative outcome: either deadlock, where neither mycelium loses any territory, or replacement, where one mycelium displaces the other. These mechanisms function aggressively and/or defensively, and include changes in primary metabolism and growth, as well as secondary metabolite production and stress mitigation responses. This chemical warfare may occur as a constitutive defence through modification of the territory occupied by an individual, and the deposition of antimicrobial compounds within. Following detection of a competitor, the metabolite and enzymic profile of a mycelium alters both qualitatively and quantitatively, and different mechanisms may be stimulated when confronted with different competitors. Biotic and abiotic factors, even small alterations, can affect the deployment of these antagonistic mechanisms, altering the general hierarchy of combative ability between species and making it impossible to predict outcomes with certainty. Here we explore recent advances in our understanding of combative interactions between wood decayers, and explain why future research priorities involving the application of emerging biochemical and molecular technologies must focus on interactions in more ecologically realistic and meaningful scenarios.
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1. Introduction

Understanding the dynamics of decomposer community development is essential for modelling carbon cycling and other ecosystem functions, and the resilience of these processes to environmental change (e.g. McGuire and Treseder 2010). Fungal competition in decaying woody resources is effectively competition for territory and the nutrients within, and encompasses both interference and exploitation competition; fungi exhibit the former by inhibiting other organisms and limiting their access to resources, and the latter by sequestering nutrients within the territory they occupy, hence preventing other organisms from using them (Boddy and Hiscox 2016). In general, fungal competition can be divided

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into primary resource capture, where a fungus colonises previously unoccupied territory, and secondary resource capture, where a fungus captures territory from fungi that have already colonised a resource (Boddy 2000). Success in primary resource capture is determined by efficient dispersal mechanisms, rapid growth rate, and the ability to use easily accessible nutrients (R-selected characteristics; Boddy 2000). Success in secondary resource capture depends on aggressive and/or defensive antagonistic mechanisms (C-selected), or at very late stages of decomposition, the ability to tolerate abiotic/biotic stress and disturbance (S-selected and R-selected; Boddy 2000).

The ultimate outcome of combative interactions can either be deadlock, where neither fungus loses any territory, or replacement, where one fungus displaces the other. Between these extremes lies a spectrum of outcomes, including partial replacement of one fungus by another, or mutual replacement, where both fungi capture territory from each other (Boddy 2000). These combative interactions can be mediated at a distance, following contact at the level of individual hyphae (e.g. hyphal interference and mycoparasitism, see Boddy and Hiscox 2016), or following contact at the mycelial level. The establishment of physical contact between two competing mycelia, often called 'gross mycelial contact', results in the induction of antagonistic mechanisms in one or both competitors. Competing mycelia undergo changes in morphology, secondary metabolite production, pigment deposition, accumulation of reactive oxygen species, and alterations in enzyme activity (see Section 2). These changes may function aggressively and/or defensively against a competitor, and different mechanisms may be stimulated when confronted with different competitors (Eyre *et al.* 2010). The majority of this review will concentrate on mycelial interactions, as they are the most frequently observed interaction type within wood decay communities.

2. Antagonistic mechanisms

Constitutive defence and antagonism at a distance

Constitutive defences function to impede the invasion of colonised territory by a competitor mycelium. Certain species modify the territory they occupy to make it less hospitable for invaders, for example lowering water potential or pH (Boddy *et al.* 1985; Tudor *et al.* 2013). Some fungi produce pseudosclerotial plates, thin shells of melanised tissue completely surrounding the territory they occupy, which maintain the conditions within, and can also act as a physical barrier against invasion (Rayner and Boddy 1988; Fig. 1A). Further, fungi produce, and perhaps accumulate, inhibitory secondary metabolites, which can slow or halt the extension of competitors (Heilmann-Clausen and Boddy 2005; Fig. 1B and C). These secondary metabolites span a variety of chemical classes; different species tend to produce a characteristic metabolite profile, although this is partly dependent on their growth conditions (Lemfack *et al.* 2013; Fig. 1D and E). Inhibitory effects of both diffusible and volatile organic compounds (DOCs and VOCs, respectively) have been demonstrated for fungi growing in wood blocks, across soil, and in artificial agar media (Heilmann-Clausen and Boddy 2005; El Ariebi *et al.* 2016). DOCs have local antagonistic potential (e.g. in scenarios where they can accumulate or diffuse through substrata), whereas VOCs can act over greater distances and in heterogeneous environments. Whilst these chemical defences may help protect against invasion by most competitors, adaptive relationships occur where certain species are attracted to the metabolite profile emitted by a competitor, with certain VOC/DOC profiles stimulating competitor growth (Evans *et al.* 2008). Similarly, territory modification may provide an advantage for invading fungi with analogous preferences.

Morphological changes

Changes in mycelial morphology are most dramatic in areas in direct contact with the competitor: the interaction zone. Hyphae may aggregate to form barrages which physically block invasion by competitors, or to form invasive replacement fronts or cords (linear aggregations of hyphae) to penetrate competitor defences (Fig. 2A–C). Morphological structures may differ between regions of the same interaction front, indicating that antagonistic mechanisms are deployed in response to local stimuli (Rayner *et al.* 1994). Morphological changes during interactions are associated with changes in gene expression compared to non-interacting mycelia (Table 1). For example, cytokinesis-related proteins and 1,3-beta glucan synthase were upregulated in *Trametes versicolor* during antagonism with *Stereum gausapatum*, indicating increases in cell division and cell wall formation or alteration (Eyre *et al.* 2010). This was concomitant with a downregulation of chitin synthase expression in *S. gausapatum*; the decrease in growth of this fungus may be associated with its eventual replacement by *T. versicolor* (Eyre *et al.* 2010).

Melanin deposition is often associated with morphological changes at interacting hyphal fronts, and may be wall-bound or extracellular, often visible as pigmentation (Rayner *et al.* 1994). Melanins are formed by the oxidative linkage of aromatic metabolites into complex heteropolymers which alter hyphal hydrophobicity, and confer structural strength by strengthening cell-to-cell adhesion (Bell and Wheeler 1986). Similarly, hydrophobin proteins, which are involved in forming attachments in aggregating cells and have been linked to the formation of aerial hyphae and cell wall assembly, increase in expression in both competitors during interactions between *Phlebiopsis gigantea* and *Heterobasidion parviporum* (Adomas *et al.* 2006). Hydrophobins may also have a role in sealing off hyphae damaged by antagonistic processes, preventing loss of cytoplasm from surrounding compartments. A similar role has been suggested for the protein HEX-1 (hexagonal protein 1) which is upregulated in *Schizophyllum commune* during interactions with *Trichoderma viride* (Ujor *et al.* 2012). HEX-1 is a major component of the Woronin body, which functions to plug septa (the junctions between different hyphal compartments) and seal off damaged hyphae (Collinge and Markham 1987).

Changes in metabolism

The processes involved in antagonism are energetically expensive. Increases in respiration and nutrient acquisition

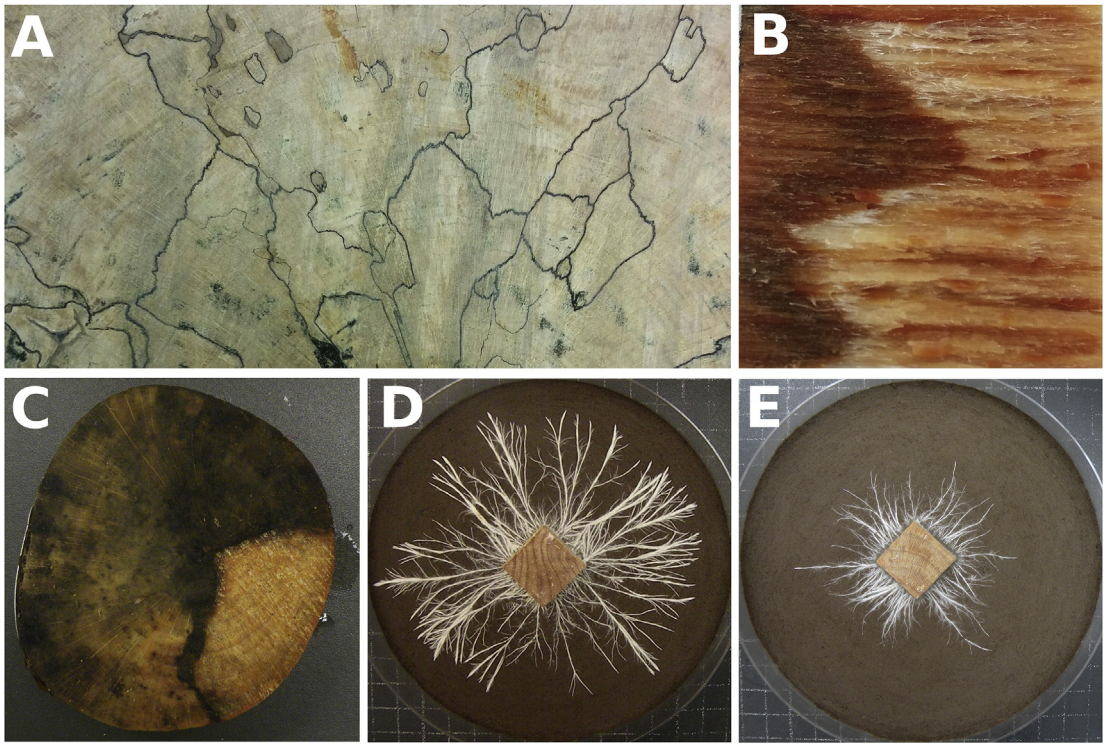

Fig. 1 – A: Cross section of a decaying beech trunk showing the mosaic structure of the decay community within. Dark lines are pseudosclerotial plates (PSPs) demarcating the territory of different individuals. B: Transverse section of a beech wood block colonised with *Coniophora puteana* (left, darkly pigmented) and *Trametes versicolor* (right, lightly pigmented). *T. versicolor* will eventually replace *C. puteana*. C: Decaying beech disk colonised by two main competitors, one highly pigmented and the other non-pigmented. D: *Resinicium bicolor* growing across soil, under exposure to the VOCs produced by bare soil. E: *R. bicolor* growing under exposure to VOCs from self-pairings of *R. bicolor*. Images D and E adapted from El Ariebi *et al.* (2016).

may occur to fund these processes; for example, production of invasive mycelial cords by a competitor is associated with increases in respiration (Hiscox *et al.* 2015a). Increased expression of genes encoding key components of the glycolytic pathway, glyceraldehyde-3-phosphate dehydrogenase (GAPDH) and phosphoglucomutase, were detected in *P. gigantea* during combat with *H. parivporum*, and also in *T. versicolor* during interactions with *Bjerkandera adusta* (Table 1; Adomas *et al.* 2006; Eyre *et al.* 2010). Increased production of cellulases, phosphatase and chitinases, both at interaction zones and throughout competing mycelia, implies upregulation of nutrient acquisition to support increased energetic demands (Table 2 and references within). The concurrent reduction in biomass accumulation during interactions between *Pycnoporus coccineus* and *Coniophora puteana* supports the theory that this increased nutrient acquisition functions to fund antagonistic mechanisms rather than mycelial growth (Arfi *et al.* 2013).

The mycelium of a displaced competitor is utilised by the victor; metabolism and respiration increased in regions where one mycelium had captured the territory of another, concomitant with increases in activity and expression of genes whose products likely function to recycle the mycelium of the displaced competitor (Lindahl and Finlay 2006; Ujor *et al.* 2012; Arfi *et al.* 2013; Hiscox *et al.* 2015a; Karlsson *et al.* 2016). Changes in activity of proteases likely function to hydrolyse competitor cell walls and contents, and increased expression of an array of genes encoding aspartyl proteases, serine-like proteases, and endochitinases have been detected during antagonistic interactions (Ujor *et al.* 2012; Arfi *et al.* 2013). Further, genes whose products are involved in carbohydrate and nitrogen metabolism were significantly upregulated in mycelia of *T. versicolor* during interactions where it replaced *S. gausapatum* or deadlocked with *Bjerkandera adusta* (i.e. where it captured or maintained territory), but not during interactions where *T. versicolor* was itself replaced by *Hypholoma fasciculare* (Eyre *et al.* 2010).

Several metabolites related to stress mitigation are upregulated during antagonism, including cyclophilins, protein chaperones and heat shock proteins, which are known to function in stress tolerance by maintaining protein stability and enhancing folding (Adomas *et al.* 2006; Eyre *et al.* 2010; Ujor *et al.* 2012). The disaccharide trehalose also functions as a protein- and membrane-stabiliser, and accumulates in stressed mycelia (Ocon *et al.* 2007). Reductions in trehalose phosphorylase content of *S. commune* during interactions with *T. viride* suggests preservation of trehalose by decreasing its catabolism by this enzyme (Ujor *et al.* 2012). Sugar alcohols increase during interactions, possibly with a similar function in stress tolerance (Table 3).

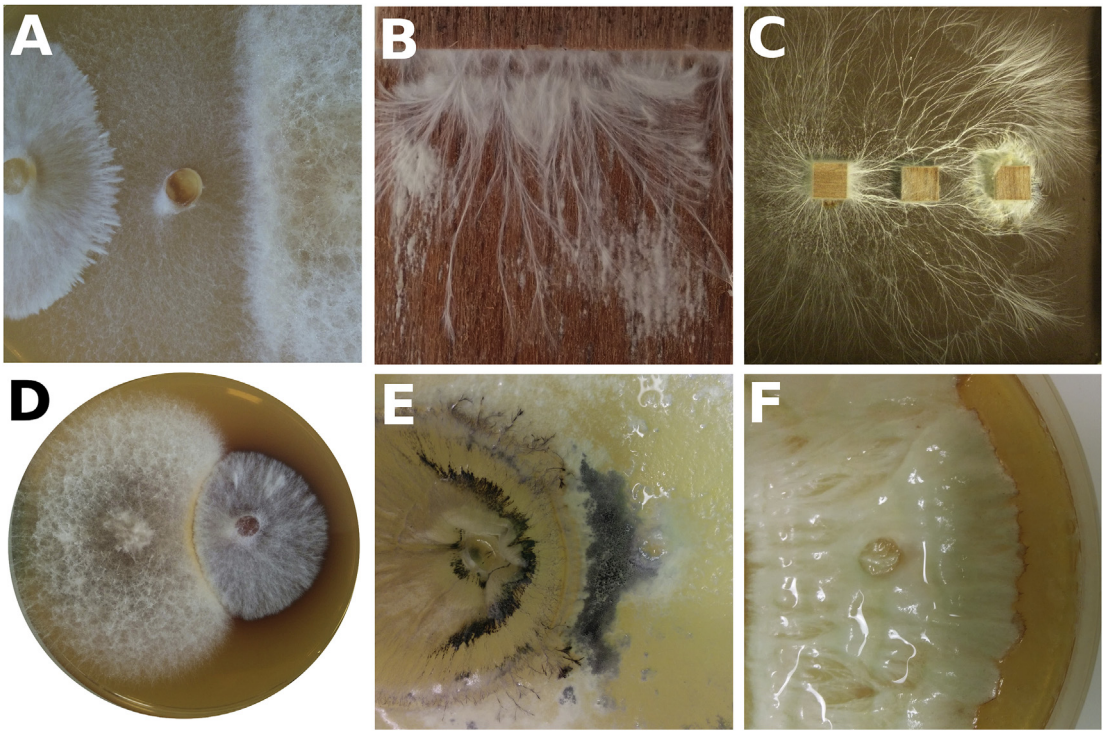

Fig. 2 – A: Three-way interaction between *Hypholoma fasciculare* (left), *Trametes versicolor* (middle), and *Stereum hirsutum* (right) on 2 % malt agar. A barrage was formed at the interaction zone between *T. versicolor* and *S. hirsutum*, and cords of *H. fasciculare* are beginning to encroach over *T. versicolor*. B: Interaction between *T. versicolor* (bottom) and *H. fasciculare* (top) in beech wood blocks. Cords of *H. fasciculare* are overgrowing the block colonised by *T. versicolor*. Interestingly, at this stage of the interaction, no replacement of *T. versicolor* had occurred, although it would later be completely replaced by *H. fasciculare*. C: Interaction between cord systems of *P. velutina* (left) and *H. fasciculare* (right) with a beech wood block colonised by *T. versicolor* (middle), across soil. Cords of *P. velutina* have overgrown the *T. versicolor* block, and are beginning to attack the *H. fasciculare* block, resulting in the eventual replacement of both competitors. D: *S. hirsutum* (left) interacting with *H. fasciculare* on 2 % malt agar which has been supplemented with a dye that forms a purple colour when oxidised by laccase; *H. fasciculare* produced laccase at the colony margins but *S. hirsutum* did not. E: Accumulation of ROS (superoxide) during interaction between *Kretschmaria deusta* (left) and *T. versicolor* on 2 % malt agar; ROS levels are highest in interaction structures. F: Peroxidase activity is highest at the edge indicated by brown dye of the invading front during interaction between *T. versicolor* (left) and *Eutypa spinosa* (right). Staining techniques used in D–F were taken from Silar (2005).

Secondary metabolite production

Profiles of VOCs and DOCs alter both quantitatively and qualitatively during antagonism (Table 3 and references within). Compounds that were constitutively produced may be up- or downregulated, and additional compounds are often made. For example, production of dimethylbenzoic acid by *S. gausapatum* increased when confronted with *T. versicolor*, and the terpenoid α-myrcene was detected, which was not present in the VOC profile of either competitor during solo growth (Evans *et al.* 2008). Interaction specific VOCs are frequently terpenoids, predominantly sesquiterpenes (El Ariebi *et al.* 2016), which have bioactive properties, such as antifungal activity (Abraham 2010). Secondary metabolites may be actively toxic to one or both competitors, possibly through disruption of metabolic processes, a trait referred to as 'metabolic interference'. The fungi producing these metabolites may either have resistance to their own toxins, or sacrifice their own mycelium in the region of production. The reduction in biomass accumulation during interactions between *P. coccineus* and *C. puteana* may partly result from self-inhibition of *P. coccineus* by its own antifungal toxins (Imtiaj and Lee 2007; Arfi *et al.* 2013).

Enzyme activity and ROS

In addition to alteration of activities of enzymes involved in nutrient acquisition (see Sub-section Changes in metabolism), interacting fungi often produce extracellular enzymes to attack competitor mycelium directly, e.g. cell wall-hydrolysing chitinases and glucanases (Lindahl and Finlay 2006). Enzymes involved in generation of reactive oxygen species (ROS), such as NADPH oxidases, laccase (phenoloxidase) and peroxidases, are sometimes upregulated (Eyre *et al.* 2010; Fig. 2D and F). ROS accumulate at interaction zones (Fig. 2E) and may have a toxic function by causing oxidative damage to competitor mycelia (Tornberg and Olsson 2002;

Table 1 – Genes & proteins changing in expression during interactions. R, replacement. References in footnotes.

Mechanism	Name/class	Up/down regulated	Focal species	Competitor	Substrate	Eventual outcome	Ref
Detoxification	Cystathione gamma-lyase	Down	*Physisporinus sanguinolentus*	*Heterobasidion annosum*	Hagem agar + cellophane	Inhibition of *H. annosum*	1
	Cytochrome c oxidase subunit 1	Down	*Trametes versicolor*	*Stereum gausapatum*	Malt agar	R by *T. versicolor*	2
	Cytochrome P450	Down	*Pycnoporus coccineus*	*Coniophora puteana*; *Botrytis cinerea*	Malt-yeast extract broth (MYEB)	R by *P. coccineus*	3
	Cytochrome P450	Down	*T. versicolor*	*S. gausapatum*	Malt agar	R by *T. versicolor*	2
	Serine/threonine protein kinases	Down	*P. coccineus*	*C. puteana*; *B. cinerea*	MYEB	R by *P. coccineus*	3
	Killer toxin resistant gene	Up	*P. sanguinolentus*	*H. annosum*	Hagem agar + cellophane	Inhibition of *H. annosum*	1
	Glutathione-S-transferase	Up	*P. coccineus*	*B. cinerea*	MYEB	R by *P. coccineus*	3
	Dihydrolipoamide acetyltransferase	Up	*P. coccineus*	*B. cinerea*	MYEB	R by *P. coccineus*	3
	Zinc-binding oxidoreductase	Up	*P. coccineus*	*B. cinerea*	MYEB	R by *P. coccineus*	3
	Predicted short-chain-type dehydrogenase	Up	*P. coccineus*	*B. cinerea*	MYEB	R by *P. coccineus*	3
	Kynurenine 3-monooxygenase	Up	*P. coccineus*	*B. cinerea*	MYEB	R by *P. coccineus*	3
	Aldo/keto reductase	Up	*P. coccineus*	*B. cinerea*	MYEB	R by *P. coccineus*	3
	Predicted short-chain-type dehydrogenase	Up	*P. coccineus*	*B. cinerea*	MYEB	R by *P. coccineus*	3
	Zinc-binding oxidoreductase	Up	*P. coccineus*	*B. cinerea*	MYEB	R by *P. coccineus*	3
	Glycosyl transferase	Up	*Schizophyllum commune*	*Trichoderma viride*	PDA	R by *T. viride*	4
	Short-chain dehydrogenase/reductase	Up	*T. viride*	*S. commune*	PDA	R by *T. versicolor*	4
	Oxidoreductase	Up	*T. versicolor*	*S. gausapatum*	Malt agar	R by *T. versicolor*	2
	Superoxide dismutase	Up	*Trichoderma aggressivum*	*Agaricus bisporus*	Malt broth + compost extract	R by *T. aggressivum*	5
Nutrient acquisition and growth	Fimbrin	Down	*P. sanguinolentus*	*H. annosum*	Hagem agar + cellophane	Inhibition of *H. annosum*	1
	Chitin synthase	Down	*P. coccineus*	*B. cinerea*	MYEB	R by *P. coccineus*	3
	1,3-Beta-glucan synthase	Up & Down	*T. versicolor*	*S. gausapatum*	Malt agar	R by *T. versicolor*	2
	Cytokinesis-related protein	Up	*T. versicolor*	*S. gausapatum*	Malt agar	R by *T. versicolor*	2
	Guanylate kinase	Up	*T. aggressivum*	*A. bisporus*	Malt broth + compost extract	R by *T. aggressivum*	5
	Actin depolymerase	Up	*T. aggressivum*	*A. bisporus*	Malt broth + compost extract	R by *T. aggressivum*	5
Primary metabolism	Mitochondrial inner membrane protein	Down	*P. sanguinolentus*	*H. annosum*	Hagem agar + cellophane	Inhibition of *H. annosum*	1
	Mitochondrial protein	Down	*P. gigantea*	*H. parviporum*	Hagem agar	R by *P. gigantea*	6
	ATP-binding cassette	Down	*P. gigantea*	*H. parviporum*	Hagem agar	R by *P. gigantea*	6
	Triosephosphate isomerase	Down	*S. commune*	*T. viride*	PDA	R by *T. viride*	4
	Trehalose phosphorylase	Down	*S. commune*	*T. viride*	PDA	R by *T. viride*	4
	Sugar transporter	Down	*T. versicolor*	*S. gausapatum*	Malt agar	R by *T. versicolor*	2
	ABC transporter	Down	*T. versicolor*	*S. gausapatum*	Malt agar	R by *T. versicolor*	2
	Succinyl-CoA synthetase	Up	*H. parviporum*	*P. gigantea*	Hagem agar	R by *P. gigantea*	6
	Mitochondrial protein	Up	*H. parviporum*	*P. gigantea*	Hagem agar	R by *P. gigantea*	6
	GAPDH	Up	*P. gigantea*	*H. parviporum*	Hagem agar	R by *P. gigantea*	6

(continued on next page)

Table 1 (*continued*)

Mechanism	Name/class	Up/down regulated	Focal species	Competitor	Substrate	Eventual outcome	Ref
	GAPDH	Up	*T. viride*	*S. commune*	PDA	R by *T. viride*	4
	Glutamine synthetase	Up	*P. gigantea*	*H. parviporum*	Hagem agar	R by *P. gigantea*	6
	Endopolygalacturonase	Up	*P. gigantea*	*H. parviporum*	Hagem agar	R by *P. gigantea*	6
	$Ca2^{+}$-dependent phospholipid-binding protein	Up	*P. coccineus*	*B. cinerea*	MYEB	R by *P. coccineus*	3
	GTPase effector	Up	*P. coccineus*	*B. cinerea*	MYEB	R by *P. coccineus*	3
	Two-component phosphorelay intermediate	Up	*P. coccineus*	*B. cinerea*	MYEB	R by *P. coccineus*	3
	Glycoside hydrolase family 13 protein	Up & Down	*T. versicolor*	*S. gausapatum*	Malt agar	R by *T. versicolor*	2
Protein metabolism	Peptide N-myristoyl transferase	Down	*P. gigantea*	*H. parviporum*	Hagem agar	R by *P. gigantea*	6
	Amino acid transporters	Down	*P. coccineus*	*B. cinerea*	MYEB	R by *P. coccineus*	3
	Alpha-ketoglutarate dependent xanthine dioxygenase	Down	*T. versicolor*	*S. commune*	Malt agar	R by *T. versicolor*	2
	Ubiquitin	Up	*H. parviporum*	*P. gigantea*	Hagem agar	R by *P. gigantea*	6
	Cyclophilin	Up	*P. gigantea*	*H. parviporum*	Hagem agar	R by *P. gigantea*	6
	Probably E3 ubiquitin protein ligase	Up	*S. commune*	*T. viride*	PDA	R by *T. viride*	4
	Aspartyl protease	Up	*T. viride*	*S. commune*	PDA	R by *T. viride*	4
	Ubiquitin activating enzyme	Up	*T. versicolor*	*S. gausapatum*	Malt agar	R by *T. versicolor*	2
Secondary metabolite production	Phenylalanine ammonia lyase	Up	*S. commune*	*T. viride*	PDA	R by *T. viride*	4
Stress mediation	Hydrophobins 2 & 3	Down	*P. gigantea*	*H. parviporum*	Hagem agar	R by *P. gigantea*	6
	Hydrophobin 1	Up	*P. gigantea*	*H. parviporum*	Hagem agar	R by *P. gigantea*	6
	Heat shock protein 90	Down	*P. gigantea*	*H. parviporum*	Hagem agar	R by *P. gigantea*	6
	REcA homolog rah1	Up	*H. annosum*	*P. sanguinolentus*	Hagem agar + cellophane	Inhibition of *H. annosum*	1
	HEX1	Up	*S. commune*	*T. viride*	PDA	R by *T. viride*	4
	Cyclophilin A-1	Up	*S. commune*	*T. viride*	PDA	R by *T. viride*	4
	Spermine synthetase	Down	*T. aggressivum*	*A. bisporus*	Malt broth + compost extract	R by *T. aggressivum*	5
	Maintenance of telomere capping protein 2	Down	*T. aggressivum*	*A. bisporus*	Malt broth + compost extract	R by *T. aggressivum*	5
Transcription/translation	Mago nashi like protein	Down	*P. sanguinolentus*	*H. annosum*	Hagem agar + cellophane	Inhibition of *H. annosum*	1
	RNA helicase	Down	*P. coccineus*	*B. cinerea*	MYEB	R by *P. coccineus*	3
	Transcriptional regulator	Down	*T. viride*	*S. commune*	PDA	R by *T. viride*	4
	Transcriptional repressor	Up	*H. annosum*	*P. sanguinolentus*	Hagem agar + cellophane	Inhibition of *H. annosum*	1
	40S ribosomal protein	Up	*T. versicolor*	*S. gausapatum*	Malt agar	R by *T. versicolor*	2
	60S ribosomal protein	Up	*P. gigantea*	*H. parviporum*	Hagem agar	R by *P. gigantea*	6
	60S acidic ribosomal protein	Up	*T. aggressivum*	*A. bisporus*	Malt broth + compost extract	R by *T. aggressivum*	5
	60S ribosomal protein L20A	Up	*T. versicolor*	*S. gausapatum*	Malt agar	R by *T. versicolor*	2
	ExoRNase	Up	*S. commune*	*T. viride*	PDA	R by *T. viride*	4
	Transcriptional regulator	Up	*S. commune*	*T. viride*	PDA	R by *T. viride*	4
	RNA polymerase	Up	*S. commune*	*T. viride*	PDA	R by *T. viride*	4
	eIF-5A	Up	*S. commune*	*T. viride*	PDA	R by *T. viride*	4

Elongation factor II	Up	*T. viride*	*S. commune*	PDA	R by *T. viride*	4
DNA binding protein SART-1	Up	*T. versicolor*	*S. gausapatum*	Malt agar	R by *T. versicolor*	2
Pre-mRNA splicing factor 38B	Up	*T. versicolor*	*S. gausapatum*	Malt agar	R by *T. versicolor*	2
Bifunctional preprotein translocase	Up	*S. commune*	*T. viride*	PDA	R by *T. viride*	4
Glycine-rich RNA binding protein	Up & Down	*T. versicolor*	*S. gausapatum*	Malt agar	R by *T. versicolor*	2

1, Iakovlev *et al.* (2004)†; 2, Eyre *et al.* (2010)†; 3, Arfi *et al.* (2013)†; 4, Ujor *et al.* (2012)†; 5, O'Brien *et al.* (2015); 6, Adomas *et al.* (2006)†.
† Present in main references. Other references found in supporting document 1.

Silar 2005), but their role(s) remain unclear, and accumulation may be an incidental result of the disruption of cellular processes caused by other antagonistic mechanisms, rather than active production. Fungi employ a range of molecular machineries to alleviate the effects of ROS and mitigate any oxidative damage during combat, such as increased expression of genes encoding catalase and putative DNA repair proteins (Iakovlev *et al.* 2004; Eyre *et al.* 2010). Increases in ROS levels may function as a defence response similar to that in plants (Silar 2005). Similarly, increases in another potential signalling compound, nitric oxide (NO), have also been detected during interactions between *Inonotus obliquus* and *Phellinus morii*, triggering production of antifungal phenylpropanoid metabolites (Zhao *et al.* 2015).

Activities of peroxidases and laccase (phenoloxidase) increase at interaction zones (Baldrian 2004), and are highly localised to this region (Hiscox *et al.* 2010). Laccase and peroxidases may be associated with increased utilisation of the resource during combat, or generation of ROS, but their main function is probably the extracellular detoxification of competitor VOCs and DOCs (Baldrian 2004; Hiscox *et al.* 2010), or in the formation of melanins (see Sub-section Morphological changes). In addition to their structural properties, melanins confer protection from ROS and toxins, and may also have antibiotic properties, as has been shown for wall bound melanins of *Phellinus weirii* (Haars and Hetterman 1980). However, the most important role of melanin is thought to be protection against hydrolytic enzymes; generally, the ability of hydrolytic enzymes to degrade fungal walls is inversely correlated with the melanin content of the wall (Bloomfield and Alexander 1967). Upregulation of intracellular detoxifying enzymes may constitute another line of defence: cytochrome monooxygenases, short-chain dehydrogenases/reductases, and glutathione-S-transferases have all been implicated in the intracellular detoxification of xenobiotics, and are upregulated during interactions (Table 1).

3. Outcomes of interactions

Fungi vary markedly in their combative ability, which is roughly related to their position within the successional community in decaying wood: primary colonisers are usually the weakest combatants, and the strongest are often later secondary colonisers (Hiscox *et al.* 2016). At the latest stages of decay, the ability to tolerate abiotic nutrient stress or disturbance by saproxylic invertebrates becomes a more important determinant of community composition than relative combative ability (Swift and Boddy 1984; Rayner and Boddy 1988). Within any particular system there is a hierarchy of combative ability, similar to a sports league (Boddy 2000). It is not a rigid hierarchy, and intransitive (non-hierarchical) relationships are common between wood decay fungi (Boddy 2000; Laird and Schamp 2006; Fig. 3). The simplest example of intransitive competition is the game of rock-paper-scissors, where rock is covered by paper, paper is cut by scissors, and scissors are blunted by rock. In spatially explicit interactions, such as those between fungi inhabiting decaying wood, the cyclical competition structure of intransitive interactions promotes species coexistence compared to combinations without

Table 2 – Enzymes changing in activity during interactions.

Enzyme	Function	Proposed role in interactions	Increase/decrease	Interaction (species) reported in	& substrate	Ref
Laccase	Degradation of lignin	Detoxification of competitor metabolites; pigment production; ROS generation	Increase	*Trametes versicolor vs. Stereum gausapatum*, *Bjerkandera adusta*, *Hypholoma fasciculare*, *Daldinia concentrica*	Malt agar	7
				T. versicolor vs. Trichoderma harzianum, *Acremonium sphaerospermum*, *Penicillium rugulosum*, *Escherichia coli*, *Endomyces magnusii*	CLN (cellulose low nutrient) broth	8
				Pleurotus ostreatus vs. Trichoderma harzianum, *Humicola grisea*, *P. rugulosum*, *E. magnusii*	CLN broth	8
				T. harzianum vs. 16 competitors	CLN broth	8
				Heterobasidion annosum vs. Resinicium bicolor	Hagem agar + cellophane	9
				T. verisicolor vs. T. harzianum	Defined low nitrogen broth (DLNB)	10
				Phellinus weirii vs. competitors	Malt agar	11
				Phlebia radiata, *Phlebia rufa*, *T. versicolor*, *Stereum hirsutum*, *P. velutina* and *H. fasciculare*	Malt agar	12
				Pleurotus sp., *Dichomitus squalens vs.* soil microbiota	Wheat straw & soil	13
				T. harzianum vs.Lentinula edodes	Yeast malt extract broth	14
				T. harzianum vs. competitors	Yeast malt extract agar	15
				Rhizoctonia solani vs. Pseudomonas fluorescens	Potato dextrose agar (PDA)	16
				Serpula lacrymans, *Coniophora puteuna*, *Trichoderma* spp., *Scytalidium*	Malt agar	17
				P. ostreatus vs. Ceriporiopsis subvermispora	Defined broth	18
				P. ostreatus vs. Phanerochaete chrysosporium	Neem hull waste, wheat bran, sugarcane bagasse	19
				H. fasciculare vs. Peniophora lycii	Malt agar & cellophane	20
				Marasmius pallescens vs. Marasmiellus troyanus	Defined broth	21
				Coprinopsis cinerea vs. Gongronella sp.	Defined medium	22
				Trametes maxima vs. Paecilomyces carneus	PDA + additives	23
			Decrease	*T. versicolor vs. Fomes fomentarius*	Malt agar	7
MnP	Degradation of lignin	Detoxification of competitor metabolites; pigment production; ROS generation	Increase	*T. versicolor vs. S. gausapatum*, *B. adusta*, *H. fasciculare*, *D. concentrica*, *F. fomentarius*	Malt agar	7
				Pleurotus sp., *D. squalens vs.* soil microbiota	Wheat straw & soil	13
				P. ostreatus vs. C. subvemispora or Physisporinus rivulosus	Defined broth	18
				P. ostreatus vs. Phanerochaete chrysosporium	Neem hull waste, wheat bran, sugarcane bagasse	19
				Marasmius pallescens vs. Marasmiellus troyanus	Defined broth	21
				Trametes maxima vs. Paecilomyces carneus	PDA + additives	23
Peroxidase	Degradation of lignin	Detoxification of competitor metabolites; pigment production; ROS generation	Increase	*Phellinus weirii vs.* competitors	Malt agar	11
				Phlebia radiata, *P. rufa*, *Coriolus versicolor*, *Stereum hirsutum*, *Phanerochaete velutina* and *Hypholoma fasciculare*	Malt agar	12
				Serpula lacrymans, *Coniophora puteuna*, *Trichoderma* spp., *Scytalidium*	Malt agar	17
LiP	Degradation of lignin	Detoxification of competitor metabolites; pigment production; ROS generation	Increase	*P. ostreatus vs. P. chrysosporium*	Neem hull waste, wheat bran, sugarcane bagasse	19

NAG	Chitin degradation	Attack of competitor cell walls, degradation after secondary colonisation	Increase	*T. versicolor vs. H. fasciculare*	Malt agar	7
				Fomitopsis pinicola, Coniophora arida, Hypholoma capnoides, R. bicolor	Spruce veneer	24
				Trichoderma aggressivum vs. Agaricus bisporus	PDA	25
			Increase (gene expression)	*R. solani vs. T. harzianum*	PDA	26
Acid phosphatase	Phosphate release	Increased nutrient acquisition	Increase	*T. versicolor vs. S. gausapatum, B. adusta, D. concentrica*	Malt agar	7
				H. fasciculare vs. P. velutina	Soil	27
α-Glucosidase	Cellulose degradation	Increased nutrient acquisition	Increase	*H. fasciculare vs. P. velutina*	Soil	27
Cellobiohydralase			Increase	*H. fasciculare vs. P. velutina*	Soil	27
β-Glucosidase			Increase	*T. versicolor vs. B. adusta*	Malt agar	7
Cellobiase			Increase	*T. verisicolor vs. T. harzianum*	DLNB	10

7, Hiscox *et al.* (2010)†; 8, Baldrian (2004)†; 9 Iakovlev and Stenlid (2000); 10, Freitag and Morrel (1992); 11, Li (1981); 12, White and Boddy (1992); 13, Lang *et al.* (1998); 14, Savoie *et al.* (1998); 15, Savoie *et al.* (2001); 16, Crowe and Olsson (2001); 17, Score *et al.* (1997); 18, Chi *et al.* (2007); 19, Verma and Madamwar (2002); 20, Rayner *et al.* (1994)†; 21, Gregorio *et al.* (2006); 22, Pan *et al.* (2014); 23, Cupul *et al.* (2014); 24, Lindahl and Finlay (2006)†; 25, Guthrie and Castle (2006); 26, Zeilinger *et al.* (1999); 27, Snajdr *et al.* (2011).
† Present in main references. Other references found in supporting document 1.

intransitivity (Laird and Schamp 2006; Hiscox *et al.* 2017). The mechanisms governing intransitive situations are unclear, but presumably result from different combinations of attack and defence traits, with different opponents varying in susceptibility to different mechanisms.

Fungi may utilise different antagonistic mechanisms against different competitors. Only 21 % of the transcripts overexpressed in *P. coccineus* were common between interactions with two competitors, suggesting that *P. coccineus* employs different pathways to eliminate different competitors (Arfi *et al.* 2013). However, whilst the transcripts themselves were different, they appeared to converge to similar functions (e.g. different isoforms of the detoxifying enzyme glutathione-S-transferase; Arfi *et al.* 2013). Further, different species exhibit different combative strengths; there are fungi that are good attackers, good defenders, both, or neither. In artificially inoculated wood blocks, *Stereum hirsutum* was good at defending its territory and resisting invasion, but unable to capture territory even from otherwise weak competitors (Boddy and Rayner 1983; Hiscox *et al.* 2015a).

Fungal interactions are dynamic and changes occur with time, the actual time course of interactions varies between competing fungi (Hiscox *et al.* 2015a). The time spent in each of the interaction 'stages' (e.g. deadlock or partial replacement) will vary between different combinations, and is roughly correlated with the disparity in competitor combative abilities (Hiscox *et al.* 2015a). For example, the highly combative *P. velutina* starts to replace *V. comedens* within seven days, but *T. versicolor* takes four weeks to begin replacing *V. comedens* (Hiscox *et al.* 2015a). Many different factors, both biotic and abiotic, can contribute to the progression or outcome of an interaction (Table 4). Small differences in abiotic conditions or physiological state may influence competitive outcomes, so it is impossible to predict the winner of interactions with certainty (Huisman and Weissing 2001).

The ability to translocate resources to the interaction zone from elsewhere in the mycelium is likely to be of major significance in the interplay of interactions (Lindahl and Olsson 2004). This is evidenced by the facts that: (1) outcomes of interactions sometimes depend on the relative size of the resources occupied by competing mycelium, fungi being more successful the larger the territory held (e.g. Holmer and Stenlid, 1993; Lindahl *et al.* 2001), implying that nutrients are moved from the bulk of the mycelium to the interaction front; and (2) radiotracer studies in mycelial cord systems have shown that carbon and phosphorous move to mycelial fronts and can be picked up by competing mycelia (Wells *et al.* 1995; Lindahl *et al.* 1999, 2001). Success in combat provides access to further resources, initially as nutrients from the mycelium of the displaced competitor, and subsequently from the substratum that it occupied. These acquired resources may be reallocated to support further combat, so there is positive feedback where the stronger combatant gets even stronger.

4. Ecological significance of interactions

Competitive interactions drive community change in wood decay communities, with community development resembling a complex, ever-changing mosaic, rather than a simple

Table 3 – Secondary metabolites produced during interactions.

Chemical class	Name	VOC/DOC	Interaction (species) reported in	Substrate	Change in production	Ref
Benzenoid	1-Hydroxy-3-methoxy-6-methylanthraquinine	DOC	*Stereum hirsutum vs. Coprinus micaceus*	Malt agar	Increases during interactions	28
	1,2-Dihydroxyanthaquinone	DOC	*Stereum hirsutum vs. Coprinus diseminatus*	Malt agar	Increases during interactions	28
	3-Amino-2, 6-dimethoxypyridine	DOC	*Nodulisporium* sp. intraspecific interaction	Potato dextrose agar (PDA)	Interaction specific	29
	3,5-Dimethlanisole	DOC	*Nodulisporium* sp. *vs. Pythium aphanidermatum*	PDA	Interaction specific	29
	4-Hydroxyphenyl ethanol	DOC	*Trichoderma viride vs. Schizophyllum commune*	PDA	Upregulated in *T. viride*	4
	5-Methyl,1,3-cyclohexadiene	VOC	*Trametes versicolor vs. Stereum gausapatum*	Malt broth	Interaction specific	30
	Dibutylbenzene	VOC	*T. versicolor vs. S. gausapatum*	Malt broth	Interaction specific	30
	Dimethylebenzoic acid, methyl ester	VOC	*T. versicolor vs. S. gausapatum*	Malt broth	Increases during interactions	30
	Indane	DOC	*Nodulisporium* sp. intraspecific interaction	PDA	Interaction specific	29
	Methoxybenzoic acid, methyl ester	VOC	*T. versicolor vs. S. gausapatum*	Malt broth	Increases during interactions	30
	Unidentified benzaldehyde	VOC	*T. versicolor vs. S. gausapatum*	Malt broth	Decreases in interactions	30
Carboxylic acid	2-Furanocaboxylic acid	DOC	*T. viride vs. Schizophyllum commune*	PDA	Upregulated in both	4
	2-Hydroxyglutaric acid	DOC	*T. viride vs. S. commune*	PDA	Upregulated in *T. viride*	4
	2-Methyl-2, 3-dihydroxypropanoic acid	DOC	*Stereum hirsutum vs. Coprinus micaceus*	Malt agar	Increases during interactions	28
	2,3-Dihydroxybutanoic acid	DOC	*S. hirsutum vs. C. micaceus*	Malt agar	Increases during interactions	28
	3-Hydroxypropanoic acid	DOC	*T. viride vs. S. commune*	PDA	Upregulated in both	4
	a-Amino butyric acid	DOC	*T. viride vs. S. commune*	PDA	Upregulated in *S. commune*	4
	Citramalic acid	DOC	*T. viride vs. S. commune*	PDA	Upregulated in *S. commune*	4
	Malic acid	DOC	*S. hirsutum vs. Coprinus diseminatus*	Malt agar	Increases during interactions	28
			T. viride vs. S. commune	PDA	Upregulated in *S. commune*	4
	Mandelic acid	DOC	*T. viride vs. S. commune*	PDA	Upregulated in both	4
	Pyruvic acid	DOC	*T. viride vs. S. commune*	PDA	Downregulated in *S. commune*	4
	Tropic acid	DOC	*T. viride vs. S. commune*	PDA	Upregulated in both	4
Sesquiterpene	Azulene-like	DOC	*Nodulisporium* sp. intraspecific interaction	PDA	Interaction specific	29
	Caryophyllene-like	DOC	*Nodulisporium* sp. intraspecific interaction	PDA	Interaction specific	29
	E-Germacrene D	VOC	*Hypholoma fasciculare vs. Resinicium bicolor*; *H. fasciculare vs. Phanerochaete velutina*; *P. velutina vs. R. bicolor*	Beech wood	Interaction specific	31

	Iso-longifolene	VOC	*H. fasciculare vs. R. bicolor*	Beech wood	Interaction specific	31
	α-Bulgarene	VOC	*H. fasciculare vs. R. bicolor*	Malt broth	Interaction specific	32
	α-Bulnesene	VOC	*H. fasciculare vs. P. velutina*; *R. bicolor vs. P. impudicus; P. veutina vs. P. impudicus*	Beech wood	Increases during interactions	31
			R. bicolor vs. P. velutina; *H. fasciculare vs. P. impudicus*		Decreases during interactions	
	α-Cadinene	VOC	*H. fasciculare vs. R. bicolor*	Malt broth	Increases during interactions	32
	α-Muurolene	VOC	*H. fasciculare vs. R. bicolor*	Malt broth	Interaction specific	32
	α-Selinene	DOC	*Nodulisporium* sp. intraspecific interaction	PDA	Interaction specific	29
	β-Chamigrene	VOC	*H. fasciculare vs. R. bicolor*	Beech wood	Interaction specific	31
	β-Selinene	DOC	*Nodulisporium* sp. *vs. Pythium aphanidermatum*	PDA	Interaction specific	29
	γ-Amorphene	VOC	*H. fasciculare vs. R. bicolor*	Malt broth	Interaction specific	32
	γ-Cadinene	VOC	*H. fasciculare vs. R. bicolor*	Beech wood	Interaction specific	31
	γ-Gurjunene	DOC	*Nodulisporium* sp. intraspecific interaction	PDA	Interaction specific	29
	γ-muurolene	VOC	*H. fasciculare vs. R. bicolor*	Malt broth	Interaction specific	32
Monoterpene	4-Carene	DOC	*Nodulisporium* sp. *vs. P. aphanidermatum*	PDA	Interaction specific	29
	a-Myrcene	VOC	*T. versicolor vs. S. gausapatum*	Malt broth	Interaction specific	30
	Limonene	VOC	*H. fasciculare vs. R. bicolor*	Beech wood	Interaction specific	31
			P. velutina vs. P. impudicus		Increases during interactions	
			P. velutina vs. R. bicolor		Decreases during interactions	
		DOC	*Nodulisporium* sp. *vs. P. aphanidermatum*	PDA	Interaction specific	29
	p-Cymene	DOC	*Nodulisporium* sp. *vs. P. aphanidermatum*	PDA	Interaction specific	29
	Pinene	VOC	*Trichoderma viride vs. Aspergillus niger*	Straw powder	Interaction specific	33
	Thujene	DOC	*Nodulisporium* sp. *vs. P. aphanidermatum*	PDA	Interaction specific	29
	Unidentified monoterpene	DOC	*Nodulisporium* sp. *vs. P. aphanidermatum*	PDA	Interaction specific	29
	γ-Terpinene	DOC	*Nodulisporium* sp. *vs. P. aphanidermatum*	PDA	Interaction specific	29
Sugar alcohol	Erythritol	DOC	*T. viride vs. S. commune*	PDA	Upregulated in *S. commune*	4
	Galactosylglycerol	DOC	*T. viride vs. S. commune*	PDA	Upregulated in *T. viride*	4
	Glycerol	DOC	*T. viride vs. S. commune*	PDA	Downregulated in *S. commune*	4
	Hexanetetrol	DOC	*T. viride vs. S. commune*	PDA	Upregulated in *S. commune*	4
	Meso-erythritol	DOC	*S. hirsutum vs. C. micaceus* and *C. disseminatus*	Malt agar	Increases during interactions	28
	Myo-inositol phosphate	DOC	*T. viride vs. S. commune*	PDA	Upregulated in *S. commune*	4
		DOC	*S. hirsutum vs. C. micaceus*	Malt agar	Increases during interactions	28
	Xylitol	DOC	*T. viride vs. S. commune*	PDA	Upregulated in *T. viride*	4

(*continued on next page*)

Table 3 (*continued*)

Chemical class	Name	VOC/DOC	Interaction (species) reported in	Substrate	Change in production	Ref
Ketone	3-Octanone	VOC	*H. fasciculare vs. P. velutina; R. bicolor vs. P. impudicus; P. veutina vs. P. impudicus*	Beech wood	Increases during interactions	31
			R. bicolor vs. H. fasciculare; H. fasciculare vs. P. impudicus		Decreases during interactions	
	Bicyclo-oct-6-en-3-one	DOC	*Nodulisporium* sp. intraspecific interaction	PDA	Interaction specific	29
Alkane	Alkanes (C7-C54)	VOC	*T. viride vs. Aspergillus niger*	Straw powder	Interaction specific	33
	Unidentified alkane	DOC	*Nodulisporium* sp. intraspecific interaction	PDA	Interaction specific	29
Pyridoxine	Pyridoxine	DOC	*S. hirsutum vs. C. micaceus*	Malt agar	Increases during interactions	28
			T. viride vs. S. commune	PDA	Upregulated in *S. commune*	4
Alcohol	2-Methyl-1-butanol	DOC	*Nodulisporium* sp. *vs. P. aphanidermatum*	PDA	Interaction specific	29
Aldehyde	2,3,4-Trihydroxybutanal	DOC	*T. viride vs. S. commune*	PDA	Upregulated in *T. viride*	4
Amino acid	Alanine	DOC	*T. viride vs. S. commune*	PDA	Downregulated in *S. commune*	4
Monosaccharide	N-Acetylglucosamine	DOC	*T. viride vs. S. commune*	PDA	Upregulated in *S. commune*	4
Nonadiyne	1,8-Nonadiyne	DOC	*Nodulisporium* sp. intraspecific interaction	PDA	Interaction specific	29

4, see Table 1; 28, Peiris *et al.* (2008); 29, Sanchez-Fernandez *et al.* (2016); 30, Evans *et al.* (2008)[†]; 31, El Ariebi *et al.* (2016)[†]; 32, Hynes *et al.* (2007); 33, Chen *et al.* (2015).
[†] Present in main references. Other references found in supporting document 1.

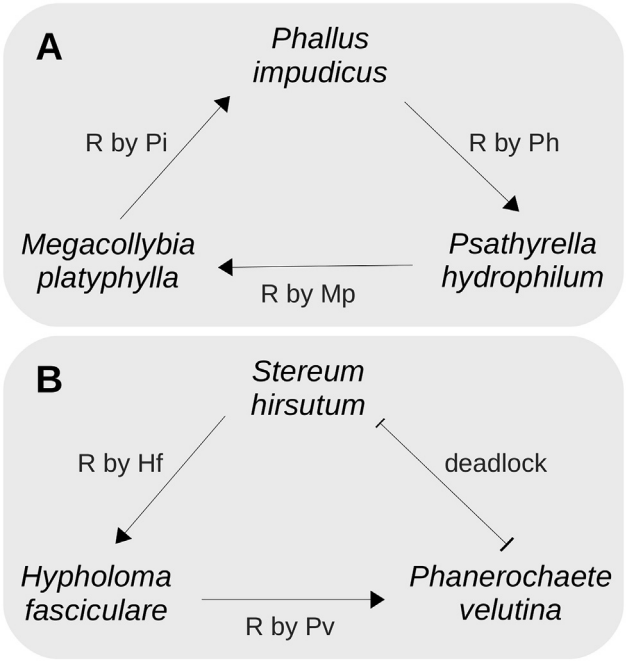

Fig. 3 – A: Intransitive hierarchy involving *Phallus impudicus* (Pi), *Psathyrella hydrophilum* (Ph), and *Megacollybia platyphylla* (Mp) during interactions on malt agar. *P. impudicus* was replaced by *P. hydrophilum*, *P. hydrophilum was* replaced by *M. platyphylla*, and *M. platyphylla* was replaced by *P. impudicus* (Chapela *et al.*, 1988). B: Non-linear hierarchy in combative behaviour between *P. velutina* (Pv), *H. fasciculare* (Hf), and *Stereum hirsutum* (Sh) during interactions in beech wood blocks. *P. velutina* deadlocked with *S. hirsutum*, and replaced *H. fasciculare*, and *S. hirsutum* was replaced by *H. fasciculare*. Although not truly intransitive, this type of non-linear hierarchy is common in wood decay communities.

ordered sequence. The assembly history (the order in which species arrive at a resource) affects subsequent community composition and development. Wood decay fungi modify the territory they inhabit both chemically and physically, by altering water content, pH, or by the deposition of different secondary metabolites (as explained above). This niche modification may act as a sort of constitutive defence, or in certain cases, effectively select for species that are adapted to such conditions (Ottosson *et al.* 2014; Fukami 2015). When earlier colonising species affect the colonisation success of species arriving later, they are described as exerting priority effects (Ottosson *et al.* 2014; Fukami 2015). Such priority effects are common in wood decay communities (e.g. Fukami *et al.* 2010; Hiscox *et al.* 2015b), and there are examples of predecessor–successor relationships where certain species almost exclusively succeed a particular species (including Rayner *et al.* 1987; Heilmann-Clausen and Christensen 2004).

Since different species of fungi decompose wood at different rates, and in different ways, the species composition within a resource will ultimately determine its rate of decomposition (van der Wal *et al.* 2015). Further, interactions themselves directly affect decomposition rate through alteration of fungal respiration and resource utilisation; 60 % of interacting fungi increased total CO_2 evolution relative to non-interacting controls (Hiscox *et al.* 2015a). In the face of global climate change, the sensitivity of interaction outcomes to even slight changes in abiotic conditions, and the resultant changes in community structure, may have large effects on decomposition (Hiscox *et al.* 2016). Further, the carbon-use efficiency (CUE; the amount of fungal mycelium formed per amount of decomposed wood) of the wood decay community will likely alter under changing conditions, and thus affect the amount of CO_2 released into global cycles; decreases in CUE of artificial wood decay communities occurred with increasing community complexity under a fluctuating temperature regime (Toljander *et al.* 2006). Although quite large changes in conditions would have to occur to seriously disrupt the ecosystem function of wood decay communities, we predict that alterations in wood decay fungal combative hierarchies and community composition are inevitable in the near future.

5. Research priorities

Previous interactions research has focused on pairwise combinations, often in artificial resources. It is hugely important for future research to use multiple combatants simultaneously to ensure results are ecologically meaningful, since woody resources are colonised by a mixed species community. Pairwise combinations are not always accurate predictors of the outcomes of multispecies interactions (Huisman and Weissing 2001), and simultaneous exposure to multiple competitors may induce novel antagonistic mechanisms in a mycelium (El Ariebi *et al.* 2016). Studying interactions in artificial media may be convenient – and good for illustrating interaction processes, as shown in Fig. 2 – but interaction processes and outcomes in agar media can be totally different from those in natural substrates (Table 4), and the majority of research is now shifting towards using natural resources, which is more challenging but far more realistic.

Relatively few pairing combinations have been investigated using transcriptomic or proteomic approaches to date (Tables 1 and 2), although with the increasing affordability of emerging technologies this is likely to change. Results from transcriptomic or proteomic profiles of interacting mycelia would provide explanations for the roles of genes and proteins already identified as of importance during interactions. Using knockout or knockdown strains may also help elucidate some of the complex processes involved in these complex and intricate antagonistic relationships. Also of significant interest are the signalling processes involved during self- and non-self-recognition between hyphae, and the events that follow contact between two hyphae of different species. Publication of data – especially the large datasets that result from new technological approaches – from interactions experiments in global databases will facilitate sharing of information and allow more comprehensive comparisons to be undertaken. Altogether, exciting new insights into the

Table 4 – Variables affecting interaction outcomes.

Factor	Venue	Findings	Ref
Temperature	Wood	Combative ability of different species varied between temperatures, with early and late successional species more successful at lower temperatures, and mid successional species more successful at higher temperatures	34
	Soil	A temperature increase of 3 °C (15–18 °C) significantly altered the outcome of interactions between *Resinicium bicolor* and *Phanerochaete velutina*	35
	Soil	The fungal dominance hierarchy at ambient temperature (16 °C; *P. velutina* > *R. bicolor* > *Hypholoma fasciculare*) was altered by elevated temperature (20 °C; *R. bicolor* > *P. velutina* > *H. fasciculare*) in ungrazed systems	36
Invertebrate grazing	Soil	Grazing by collembola (*Folsomia candida*) at 18 °C but not 15 °C reversed the outcome of interactions between *R. bicolor* and *P. velutina*	35
	Soil	Grazing by collembola (*F. candida*) stimulated growth of the dominant species, *P. velutina*, over its opponent, *H. fasciculare*	37
	Soil	Grazing by woodlice (*Oniscus asellus*) and nematodes reversed outcomes of interaction between *R. bicolor*, *P. velutina*, and *H. fasciculare*	38
	Spruce and fir needles	Selective grazing by collembola (*F. candida*) of primary saprotrophs led to faster replacement by secondary saprotrophs on spruce and fir needles	39
	Soil	Woodlice (*O. asellus*) preferentially grazed *R. bicolor*, reversing the outcomes of interactions with *P. velutina* and *H. fasciculare* compared to ungrazed combinations. Grazing also reversed outcomes of interactions between *P. velutina* and *H. fasciculare*	36
	Sitka spruce needles	Selective grazing by collembola of the dominant fungus *Marasmius androsaceus* increased the relative abundance of the less palatable *Mycena galopus*	40
Relative size of mycelium/resource	Wood	Competitive success, measured as the replacement of the opposing fungus, was generally greatest for mycelia inhabiting sectors representing 92 % of a disc and smallest for 8 % sectors	41
	Wood	Competitive ability overrode effects of inoculum size	42
	Wood	*Gloeophyllum trabeum*, previously shown to lose in 'equal-footing' competition with *Irpex lacteus*, was able to win in two out of four types of wood when given higher inoculum potential	43
Quality of resources	Wood	*T. versicolor*, *S. hirsutum*, and *H. fasciculare*, combative ability was negatively correlated with colonisation time, however, in *B. adusta* there was a positive correlation	34
Venue	Wood vs. soil vs. agar	*H. fasciculare* replaced *Steccherinum fimbriatum* in agar culture under ambient conditions, but deadlocked with it when mycelial cords met in soil, and was itself replaced when paired in wood	44
Water potential	Agar	*Daldinia concentrica* was more combative at lower water potentials, whereas other species were less combative	45
Gaseous regime	Agar	*D. concentrica* was more combative at higher CO_2 concentrations, whereas other species were less combative	45

34, Hiscox *et al.* (2016)†; 35, Crowther *et al.* (2012); 36, A'Bear *et al.* 2(013); 37, Rotheray *et al.* (2011); 38, Crowther *et al.* (2011); 39, Klironomos *et al.* (1992); 40, Newell (1984); 41, Holmer and Stenlid (1993); 42, Holmer and Stenlid (1997); 43, Song *et al.* (2015); 44, Dowson *et al.* (1988); 45, Boddy *et al.* (1985)†.

† Present in main references. Other references found in supporting document 1.

mechanisms underlying antagonistic interactions can be expected in the near future.

Conflict of interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.fbr.2017.07.001.

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