# Fungus wars: basidiomycete battles in wood decay

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**Abstract:** Understanding the mechanisms underlying wood decay basidiomycete community dynamics is crucial for fully understanding decomposition processes, and for modelling ecosystem function and resilience to environmental change. Competition drives community development in decaying woody resources, with interactions occurring at a distance, following physical contact, and through specialised relationships such as mycoparasitism. Outcomes of combative interactions range from replacement, where one mycelium displaces another, to deadlock, where neither combatant captures territory from the other; and a spectrum of intermediate outcomes (i.e. partial or mutual replacement) lie between these extremes. Many wood decay basidiomycetes coexist within a resource, in a complex and dynamic community, and new research techniques are focussing on spatial orientation of interactions in 3 dimensions, as opposed to historical two-dimensional research. Not only do interactions drive changes in species composition and thus wood decomposition rate, they also may have industrial applications in biocontrol of pathogenic or nuisance fungi, enzyme production, and in the production of novel antifungals and antibiotics. Altogether, fungal interactions are a fascinating and important field of study.

**Key words:** Antagonism, Basidiomycetes, Competition, Decomposition, Interactions, Wood decay.

## BACKGROUND TO INTERACTIONS

Wood decay basidiomycetes are central to the decomposition of recalcitrant lignocellulose, and thus to global carbon cycling. With approximately 80 Tg of carbon sequestered in woody biomass annually (Luyssaert *et al.* 2010, Bellassen & Luyssaert 2014), understanding the mechanisms underlying basidiomycete community dynamics is crucial for fully understanding decomposition processes, and for modelling ecosystem function and resilience to environmental change (Bardgett *et al.* 2008, Chapin *et al.* 2009, McGuire & Treseder 2010). Competition appears to be the most common type of interaction between wood decay basidiomycetes (Boddy 2000), and this drives community development in decaying woody resources. The distinction between interference competition, where one organism inhibits another, and exploitation competition, where one organism uses a resource and consequently reduces the availability to another, is not clear for wood decay fungi (Keddy 1989, Boddy 2000). Their mycelia colonise solid organic resources and utilise the nutrients within, so competition for territory and nutrients cannot be divorced (Boddy & Hiscox 2017). Interactions can occur at a distance, following contact at the hyphal level (mycoparastism), or following contact at the mycelial level (Boddy 2000).

## Antagonism at a distance

Antagonism at a distance, including both attack and defence, impedes invasion of colonised territory by a competitor mycelium without mycelia actually making contact. Mycelia may produce volatile or diffusible organic compounds (VOCs and DOCs), or alter the pH of the territory they inhabit, which inhibits competitor growth and acts as defensive and attacking mechanisms (Heilmann-Clausen & Boddy 2005, Hynes *et al.* 2007). Many fungi produce mono- and sesquiterpenes, and aromatic compounds, some of which possess antifungal activity (Viiri *et al.* 2001, Hynes *et al.* 2007, El Ariebi *et al.* 2016). Reactions to VOCs and DOCs vary depending on the combination of species involved, and include altered spore germination and changes in mycelial morphology and enzyme activity (Rayner *et al.* 1994, Heilmann-Clausen & Boddy 2005). In some cases mutual inhibition of both competitors may occur (Boddy 2000), yet in others mycelial growth may be stimulated (Evans *et al.* 2008). Defences include physical barriers, for example pseudosclerotial plates, comprising narrow bands of melanised tissue which surround the territory occupied by the fungus (Rayner & Boddy 1988).

## Interactions at the hyphal level

Interactions at the hyphal level include mycoparasitism and hyphal interference. Mycoparasitic relationships occur when one mycelium gains nutrition directly from another (Jeffries 1995). Some mycoparasites are biotrophic, deriving nutrition from living mycelia in a complex and specialised association between mycoparasite and host. The host remains relatively healthy, but suffers a loss of fitness due to abstraction of nutrients by the mycoparasite (Jeffries 1995). In contrast, necrotrophic mycoparasites cause death of the host mycelium and utilize nutrients from the dead or dying hyphae. These necrotrophs tend to have a broad host range and utilise unspecialised parasitic mechanisms (Jeffries 1995). In some cases, mycoparasitism may function as a temporary strategy to gain the territory of a competitor, following which the mycoparasite will switch to obtaining nutrition through wood decomposition, for example *Lenzites betulina*, which is parasitic on *Trametes* species (Rayner *et al.* 1987). To a certain extent, all wood decay basidiomycete species behave as necrotrophs during antagonistic interactions, because they utilise the mycelium of a displaced competitor for nutrition when capturing its territory.

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## Interactions at the mycelial level

Larger scale mycelial interactions occur following the establishment of physical contact between competing mycelia, and involve the upregulation of antagonistic mechanisms in one or both competitors (Boddy 2000, Hiscox & Boddy 2017). Antagonistic mechanisms are most highly upregulated in the interaction zone, the area(s) of direct contact between competitors (Hiscox *et al.* 2010). Mycelia may undergo morphological changes, seen in agar culture and on the surface of soil, where hyphae aggregate to form barrages to physically block invaders, or replacement fronts or cords to invade competitor territory (Boddy 2000, Fig. 1). Profiles of VOCs and DOCs may alter qualitatively and quantitatively following mycelial contact, and toxic secondary metabolites may be produced (Evans *et al.* 2008, El Ariebi *et al.* 2016). Reactive oxygen species (ROS) also accumulate at interaction zones, although their current role in antagonism is unclear (Eyre *et al.* 2010). Activity of laccases and peroxidases are upregulated at interaction zones, where they most likely function to detoxify competitor VOCs and DOCs; other enzymes involved in detoxification are also upregulated during interactions such as glutathione-S-transferases (Baldrian 2004, Hiscox *et al.* 2010, Eyre *et al.* 2010, Arfi *et al.* 2013). Laccases may also be involved in pigment production through melanin polymerisation. Pigmentation is frequently observed at interaction zones, likely resulting from the synthesis of melanins via the oxidation of phenolic compounds, which results in pigmentation, to insulate hyphae from ROS, toxins, and hydrolytic enzymes (Bell & Wheeler 1986). Different antagonistic mechanisms may be stimulated during confrontations with different competitors (Eyre *et al.* 2010), and the ability of a mycelium to both deploy these mechanisms, and to resist those of its competitors, will ultimately determine its success during combat.

## OUTCOMES OF INTERACTIONS

The outcomes of combative interactions can either be replacement, where one mycelium displaces another, or deadlock, where neither combatant captures territory from the other. Between these two extremes, a spectrum of intermediate outcomes occur; for example, partial replacement, where one mycelium only partly displaces another before a deadlock is reached, and mutual partial replacement, where both fungi capture territory from each other. The actual time course of interactions varies between combinations of competitors, and the progress of replacement may be fast or slow, roughly correlated with the disparity in competitor combative abilities (Hiscox *et al.* 2015a). For example, the secondary coloniser *Trametes versicolor* replaced the primary coloniser *Biscogniauxia* sp. in beech wood blocks within 28 d, but took 56 d to replace the more combative *Heterobasidion annosum* (Fig. 2). Mycelia may remain in deadlock for an extended period of time before any replacement occurs (Hiscox *et al.* 2015a); this is evident during interactions between species growing in wood blocks, where there was a period of deadlock lasting at least 14 d in 67 % of combinations tested (Fig. 2).

Outcomes of interactions between the same combinations of fungi, even where the combatants are replicates of the same individuals, are not always consistent, even under apparently identical conditions. This is likely due to immeasurably tiny differences in initial conditions, which can affect the progress and outcomes of interactions (Huisman & Weissing 2001). These shifts in outcome are much less likely to occur where the relative difference in combative ability between competitors is high, since the more combative competitor has a higher probability of dominating despite differences in conditions (Huisman & Weissing 2001). Many different biotic and abiotic factors can affect the progress and outcomes of interactions. Changes in ambient temperature, water potential, invertebrate grazing, and relative concentrations of $O_2$ and $CO_2$ can all reverse interaction outcomes (including Boddy *et al.* 1985, Griffith & Boddy 1991, Crowther *et al.* 2011, A'Bear *et al.* 2013a, Venugopal *et al.* 2016), because different species display contrasting sensitivities and/or patterns of response to these variables (Hiscox *et al.* 2016). The amount of territory occupied by a mycelium affects its combative ability, with mycelia that occupy relatively larger territories being more successful than those occupying smaller territories (Holmer & Stenlid 1993). The duration of colonisation of a resource by a mycelium impacts combative ability in a species- and combination-specific manner; whilst the accumulated effects of resource utilisation and metabolite deposition by the resident mycelium may make it more difficult for a competitor to invade, nutrient depletion over time might make the resident mycelium less able to mount costly antagonistic mechanisms to resist invasion or capture new territory (Hiscox *et al.* 2016). Examples include *Gloeophyllum trabeum*, which was more able to outcompete *Irpex lacteus* with increasing colonisation time
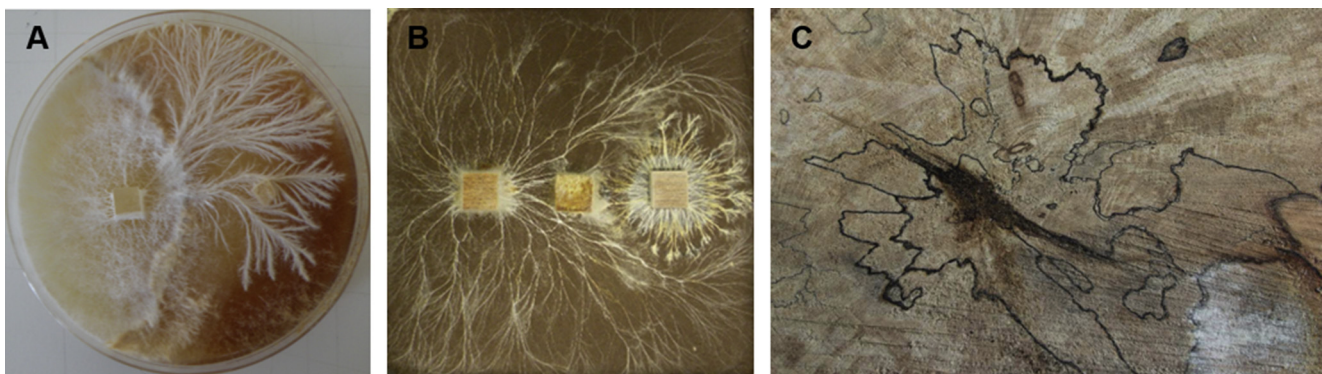


**Fig. 1.** **Fungal interactions in agar culture (A), across soil trays (B) and in wood (C)**. **A.** *Resinicium bicolor* (left) and *Phanerochaete velutina* (right) interacting on 2 % malt extract agar. *R. bicolor* can be seen producing mycelial cords. **B.** Wood blocks colonised with *P. velutina* (left), *Stereum hirsutum* (middle) and *Hypholoma fasciculare* (right) were placed onto trays of compacted non-sterile soil. *P. velutina* and *H. fasciculare* produced foraging mycelial cords. Pigmentation associated with antagonistic enzyme production surrounds the *H. fasciculare* colonised wood block. **C.** Fungal interactions within beech wood produce interactions zone lines and pseudosclerotial plates.
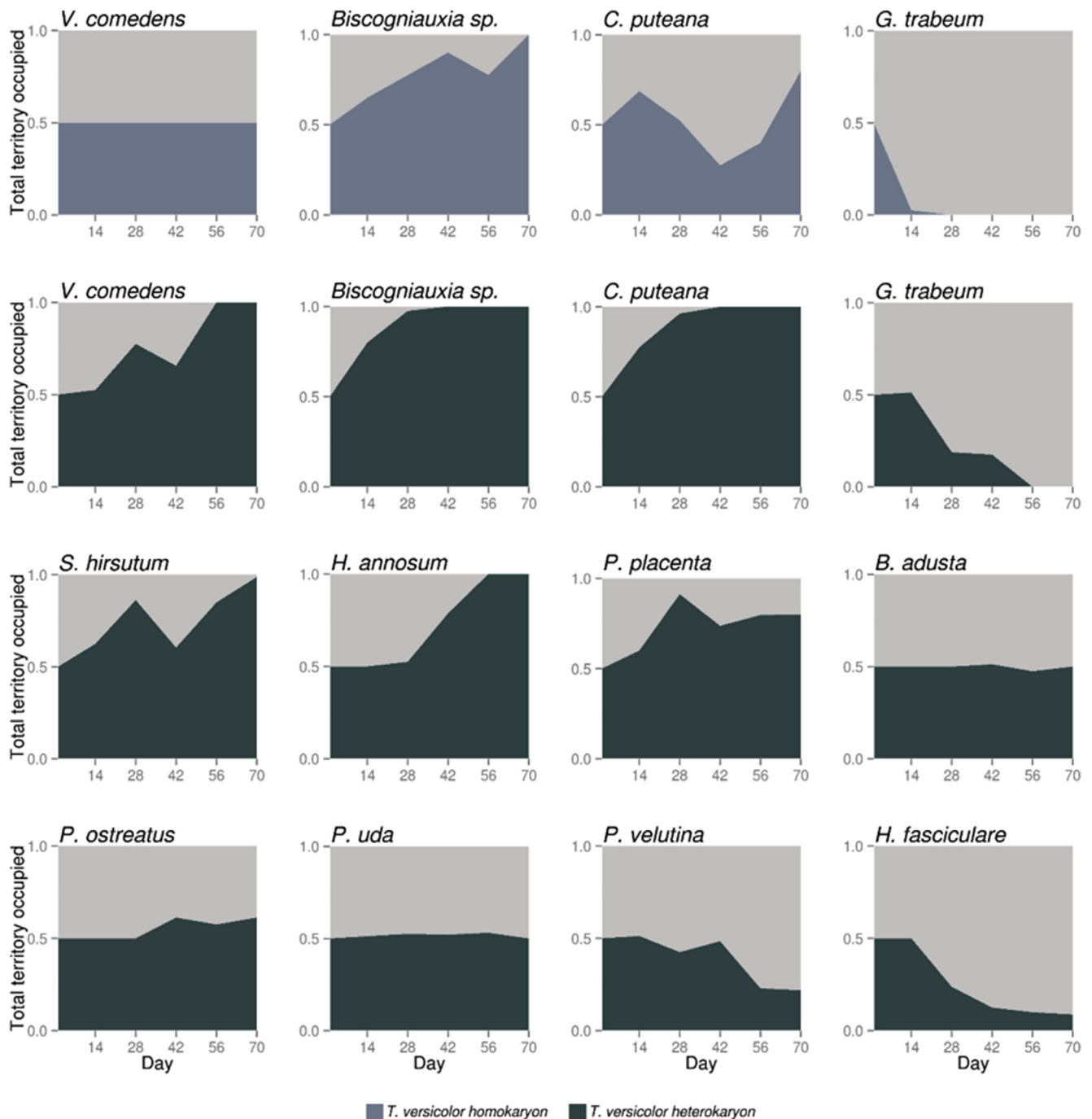
**Fig. 2. Changes in territory occupation by paired mycelia interacting in beech wood blocks.** Beech wood cubes (8 cm³) were pre-colonised by a single fungus, either *Trametes versicolor* or a competitor, and interactions between these mycelia established by pairing blocks together (see Supplementary Methods 1 for a detailed description). Interactions were harvested periodically over 70 d and reisolations taken from within the wood blocks to determine whether any replacement of one mycelium by the other had occurred. Interactions were established for both a homokaryotic and a heterokaryotic strain of *T. versicolor*. At the start, each mycelium occupied one block, which equates to 50 % of the total available territory per interaction. During the interaction between the *T. versicolor* heterokaryon and *Phlebia uda*, neither combatant captured any territory from the other, so at 70 d both mycelia still occupied 50 % of the total territory each. However, during the interaction between the *T. versicolor* heterokaryon and *Heterobasidion annosum*, from 28 d T. versicolor began to capture territory from (i.e. to displace) the *H. annosum* mycelium, resulting in complete replacement by *T. versicolor* by 56 d. In contrast, *Gloeophyllum trabeum* completely replaced the *T. versicolor* heterokaryon by 56 d.

(Song *et al.* 2015), and *Trametes versicolor*, which was far less combatively successful against a range of competitors as colonisation time increased (Hiscox *et al.* 2016).

## RELATIVE COMBATIVE ABILITY

In communities of wood decay basidiomycetes, there is a general hierarchy where primary colonisers are often the least combative and some of the later stage colonisers the most.

Primary colonising species are adapted to capturing territory in uncolonised resources, possessing ruderal (R-selected) characteristics of rapid germination, rapid mycelial extension, and rapid commitment of biomass to spore production (Boddy & Hiscox 2017). Competition between primary colonisers occurs as mycelia expand and encounter other developing mycelia. Secondary colonisers capture territory by displacing mycelia already resident within the resource; their success in colonisation depends on their ability to use lignocellulose and on their competitive/combative ability (C-selected; Boddy & Hiscox

2017). These secondary colonisers may in turn be replaced by more combative later secondary (sometime referred to as tertiary) colonisers. At the very latest stages of decomposition of the resource, or under stressful environmental conditions at any stage (e.g. desiccation, water saturation, presence of inhibitory wood extractives), tolerance of the stress (S-selected) becomes a major determinant of colonisation success, either solely or in combination with R- and/or C-selected characteristics (Boddy & Heilmann-Clausen 2008).

Hierarchies of combative ability between wood decay basidiomycetes have been compared to a sports league, with species varying in their attack and defence capabilities. For example, *Stereum hirsutum* and *Phlebia centrifuga* have good defensive abilities, and can resist invasion from otherwise highly combative fungi, but both are poor attackers and are unable to capture territory from most fungi, sometimes even including weak competitors (Boddy & Rayner 1983, Hiscox *et al.* 2015a). Again, similar to a sports league, the outcome of a confrontation can be considerably altered by abiotic conditions, which can allow teams at the top of the table sometimes to be beaten by those lower down (Boddy 2000). Indeed, the combative hierarchy is not rigid, and interaction outcomes are often intransitive (non-hierarchical, species A beats B, and B beats C, but C beats A), presumably resulting from different combinations of attack and defence traits, with different opponents varying in susceptibility to different mechanisms (Laird & Schamp 2006, Hiscox & Boddy 2017). Intransitivity is likely to promote species coexistence within resources, due to the resulting cyclic competition structure (Laird & Schamp 2006, Hiscox *et al.* 2017).

## MULTIDIMENSIONAL INTERACTIONS

Wood decay basidiomycetes coexist with many other species within a resource, in a complex and dynamic community. The mosaic structure of these communities is commonly visible in cross-sections of decaying branches or logs, as different mycelia often stain the wood in different ways, or surround themselves with melanised barriers called pseudosclerotial plates. Most interactions' research has focused on pairwise combinations due to the challenges of working with multispecies systems. However, pairwise combinations are not always accurate predictors of outcomes of multispecies interactions, and outcomes are often less consistent in systems with multiple competitors (Hiscox *et al.* 2017). On the few occasions that multispecies interactions have been studied they have usually been conducted within 2-dimensional systems (Schoeman *et al.* 1996; Boddy & Abdalla 1998, White *et al.* 1998, Sturrock *et al.* 2002, A'Bear *et al.* 2013b, Toledo *et al.* 2016, Maynard *et al.* 2017). For example, Toledo *et al.* (2016) compared three-species interactions with pairwise interactions in agar culture revealing differences in outcomes due to additional competition and the positioning of individuals within the three-species system, and A'Bear *et al.* (2013b) assessed the effects of elevated temperature and invertebrate grazing on three-way fungal interactions across 2-dimensional soil trays. The spatial orientation of competitors, especially whether or not a competitor is surrounded by others, also affects outcomes in wood block interactions (White *et al.* 1998; Hiscox *et al.* 2017). Multispecies interactions may result in increased species coexistence within the resource (Hiscox *et al.* 2017). For example, pairwise interactions in beech wood blocks

between the primary coloniser *Stereum gausapatum*, *T. versicolor*, and the late secondary coloniser *Hypholoma fasciculare*, resulted in replacement of *S. gausapatum* by *T. versicolor*, and replacement of both competitors by *H. fasciculare* (Fig. 3). However, when all three species interacted simultaneously, either as 3-, 9-, or 27-block cube assemblages, *T. versicolor* retained approximately 20 % of the total territory available (80 % colonised by *H. fasciculare*; Fig. 3). Overall, the increased species diversity and inconsistency of outcomes resulting from multispecies interactions makes community development within decaying woody resources very difficult to predict.

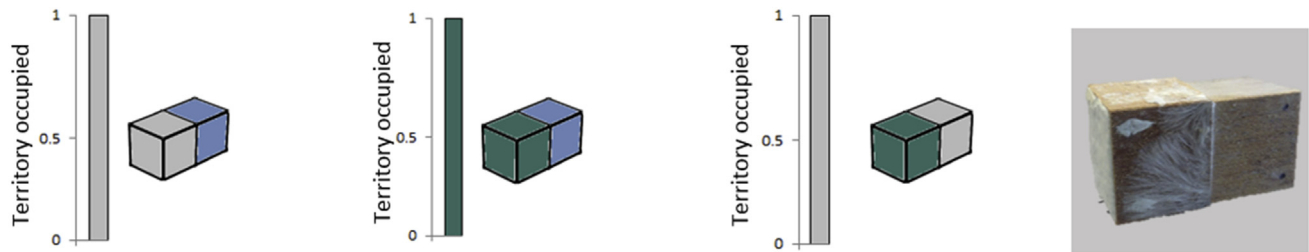## ECOLOGICAL SIGNIFICANCE OF INTERACTIONS

### Fungal community development

The construction and maintenance of local communities through sequential, repeated immigration of species from the regional species pool is defined as community assembly (Fukami *et al.* 2010, Fukami 2015). The assembly history describes the order in which species arrive at and colonise the resource, and where the identity and abundance of species that arrive early in the assembly history affect the colonisation success of species that arrive later, this is termed a priority effect (Fukami *et al.* 2010, Ottosson *et al.* 2014). Interactions are central to fungal succession and community development, and they determine priority effects, which have been repeatedly shown to occur within wood decay communities (including Fukami *et al.* 2010, Ottosson *et al.* 2014, Hiscox *et al.* 2015b). Primary colonising species rely on ruderal characteristics to maximise their capture of uncolonised territory, and by arriving at the resource early, they limit the amount of resources available to other species (niche preemption), resulting in inhibitory priority effects (Fukami 2015). Later stages of community development involve displacement of an earlier colonist through antagonistic mechanisms, and priority effects at this stage are driven by competitive ability and modification of the resource (Fukami 2015). Wood decay fungi modify the territory they inhabit through alteration of water content, pH, selective utilisation of different components, and production of secondary metabolites (Heilmann-Clausen & Boddy 2005, Stokland *et al.* 2012, El Ariebi *et al.* 2016). Termed niche modification, these alterations can act as a constitutive defence and inhibit the ability of incoming species to capture territory. However, they may instead select for species that are adapted to such conditions (van der Wal *et al.* 2013, Fukami 2015, Hiscox *et al.* 2015a), and in some cases certain predecessor species are almost exclusively succeeded by a specific individual species (Ottosson *et al.* 2014).
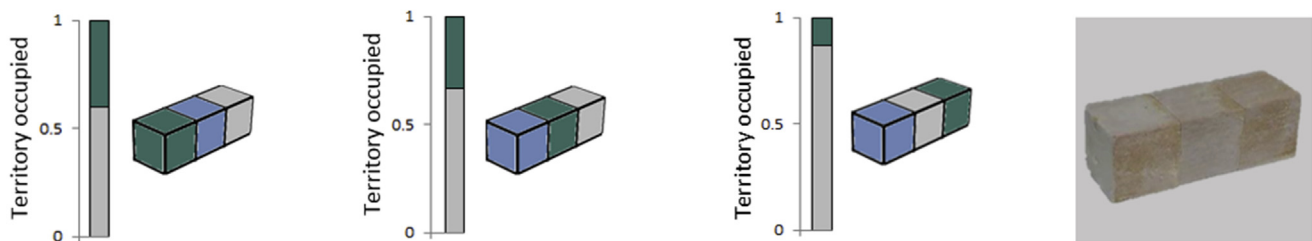
### Ecosystem processes

The central role of wood decay fungi in decomposition and carbon cycling means that interaction-mediated changes in community structure can impact these crucial ecosystem processes. Different species of fungi vary in the components of the resource that they decompose (e.g. white vs. brown rot fungi), and the rate at which they effect this decomposition (Worrall *et al.* 1997, Eastwood *et al.* 2011, Stokland *et al.* 2012, Hiscox *et al.* 2016). Mixed species
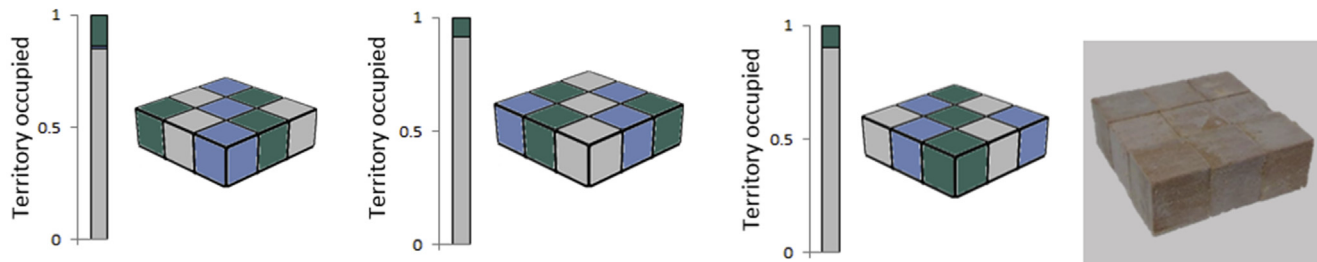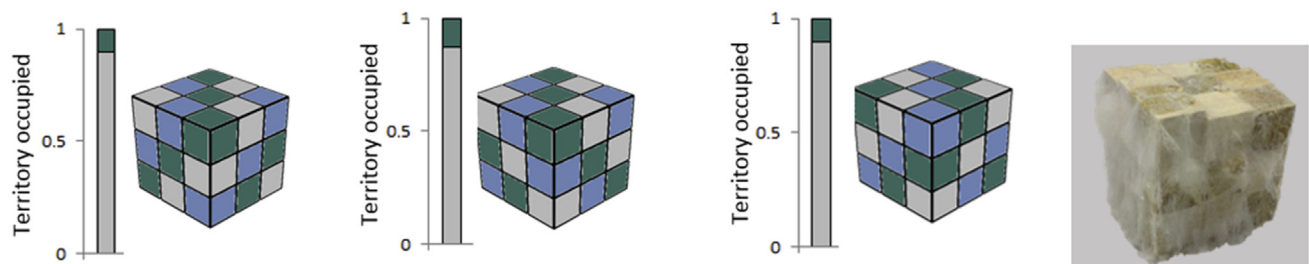
**Fig. 3. Multidimensional fungal interactions**. Beech wood cubes (2 cm$^3$) were pre-colonised by a single fungus, either *H. fasciculare*, *T. versicolor* or *S. gausapatum*, and interactions between these mycelia established by joining blocks in pairs, 3-, 9- or 27-block assemblages (see Supplementary Methods 2 for a detailed description). Interactions were harvested 154 d after interaction set up and replacement of one mycelium by another determined by reisolations taken from within the wood blocks. 9-block assemblages consisted of 3 blocks pre-colonised by each fungus and were arranged in spatial patterns with the constraint that no two blocks containing the same species were touching. 27-block assemblages consisted of 9 blocks pre-colonised by each fungus and were arranged in a 3 × 3 × 3 lattice of various spatial patterns with the constraint that blocks containing the same species did not touch. In pair-wise interactions there was a transitive hierarchical order of *H. fasciculare* > *T. versicolor* > *S. gausapatum*, where *T. versicolor* fully replaced *S. gausapatum*, and both competitors were fully replaced by *H. fasciculare*. During interactions between all three species simultaneously, however, *T. versicolor* retained territory and coexistence was promoted for a longer time.

communities sometimes exhibit increased decomposition rates compared to the component species growing alone, likely due to niche differentiation (resource partitioning) between species (Nielsen *et al.* 2011). However, this has only been reported for relatively species-poor communities (<10 species), probably resulting from the limited possibilities for resource partitioning and intense competition for space within the resource, and the redundancy in metabolic abilities (van der Wal *et al.* 2013). Inhibitory effects of multiple species on diversity-decomposition

rate may occur, however, when the effects if interspecific interactions are stronger than the effects of complementarity (Nielsen *et al.* 2011). The metabolic cost of mounting antagonistic mechanisms against multiple competitors is suggested as resulting in less metabolic energy available for allocation to decomposition processes (Wells & Boddy 2002, Fukami *et al.* 2010).

It is not only the assemblage of species present, but the interaction processes occurring between these species that

determines the decomposition rate of a resource. However, no negative effects of interactions on decomposition rate were found during pairwise interactions in beech wood blocks between *T. versicolor* and various competitors, and in half of the combinations investigated, decay rate was significantly greater than would be expected based on decay rates of the competitors during solo growth (Fig. 4). This implies that either decomposition of the resource is upregulated to fund metabolically costly antagonistic mechanisms, or that resource partitioning between the two competitors enabled much more rapid decay by the successor in the captured territory. Measurements of fungal respiration during antagonism in beech wood detected a significant increase in $CO_2$ evolution as soon as pairings were established in only two of the ten pairings investigated; this was associated with morphological changes in one or both mycelia (invasive cord formation), and can be attributed to the metabolic cost of these changes (Hiscox *et al.* 2015a). However, in four of the remaining eight pairings an increase in respiration occurred only after replacement of one competitor by another had begun, which is more likely attributable to the successor utilising the predecessor mycelium for nutrition, or due to resource partitioning enabling more rapid decay by the successor (Hiscox *et al.* 2015a).

## APPLICATIONS OF INTERACTIONS

Highly combative fungi have potential as biocontrol agents of pathogenic and nuisance fungi by effectively displacing and/or outcompeting them. *Trichoderma* spp. are the most commonly used fungi for wood protection, and inhibit wood decay fungi through a mixture of mycoparasitism and production of anti-fungal metabolites (Susi *et al.* 2011). Their broad spectrum inhibitory activity makes them ideal for protecting freshly felled wood and service timber from invasion by decay fungi (Boddy 2000). Other biocontrol agents have a much more specific mode of action. For example, *Phlebiopsis gigantea* is commonly used to protect pine and Norway spruce (*Pinus sylvestris* and *Picea abies*, respectively) stumps from colonisation by *Heterobasidion annosum*, at least partly through hyphal interference (Berglund & Rönnberg 2004).

Increases in enzyme production during interactions may have potential for use in paper manufacture. Traditional pulping uses chemicals and/or mechanical processes to treat wood chips and separate the cellulose fibres within, incurring high waste treatment and energy costs. The ligninolytic enzymes secreted by white rot fungi could be utilised to 'biopulp' the wood chips, and increased enzyme yields during combat suggests that fungal co-cultures would be even more effective in this application (Chi *et al.* 2007). Similarly, the increased enzyme yields and differences in degradative abilities make interactions an attractive solution for potential bioremediation of recalcitrant xenobiotic compounds (Ijoma & Tekere 2017). Fungi are celebrated producers of antimicrobial compounds, and interactions are known to stimulate the production of secondary metabolites which may have antifungal and antibacterial properties (El Ariebi *et al.* 2016). Interactions could be a potential goldmine of novel antibiotics, with different combinations of competitors often stimulating production of specific – or possibly unique – compounds.
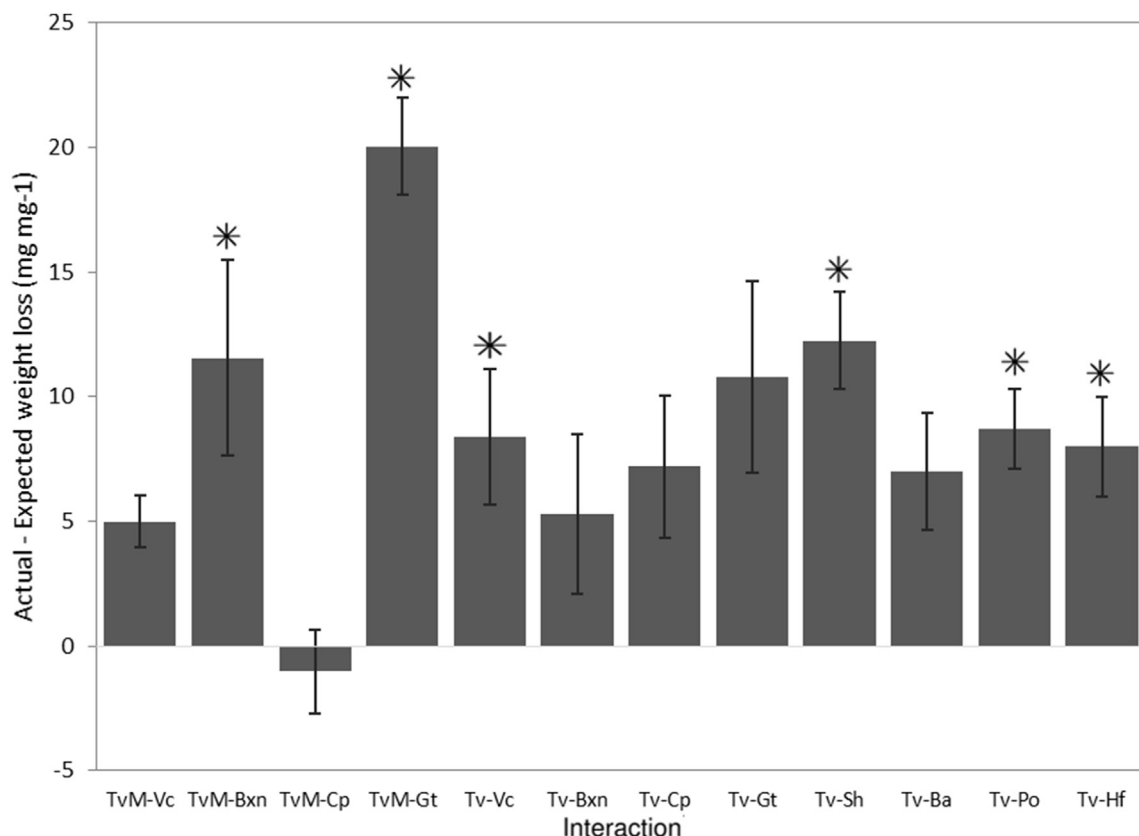


**Fig. 4. Changes in decomposition rate of inhabited resources following fungal interactions**. Beech wood cubes (8 cm$^3$) were pre-colonised by a single fungus, either *Trametes versicolor* (TvM: homokaryon; Tv: heterokaryon) or a competitor, and interactions between these mycelia established by pairing blocks together (see Supplementary Methods 3 for a detailed description). Interactions were harvested after 70 d and the density determined for all blocks as dry weight per unit fresh volume (g cm$^3$). Based on decay rates determined for each species growing individually, and the replacement rate of interacting mycelia, an expected density loss could be calculated for each interaction. Six interactions experienced significantly greater losses in density than was expected, indicating an increase in decay rate during these pairings. The bars show the mean of 5 replicates ± 95 % confidence interval. * indicates actual density loss minus expected density loss was significantly ($P < 0.05$) different to 0.

## CONCLUSIONS

Antagonistic interactions between wood decay basidiomycetes drive fungal community development in decaying woody resources, and range from the highly specialised (e.g. mycoparasitism) to relatively unspecialised. Outcomes of these interactions are affected by external variables, and the response varies depending on the conditions and species involved. Further, combative hierarchies exist, although intransitivity is common within these hierarchies, presumably resulting from different species possessing different combinations of attack and defence traits. There has been a recent shift in the focus of research from *in vitro* experiments on artificial media, to large-scale multidimensional studies in natural resources; the results from these experiments are exciting and give insight into the ecological significance of interactions. Not only are wood decay basidiomycete interactions important to carbon and nutrient cycling, their potential for producing novel antimicrobial metabolites promises exciting future developments in this field.

## APPENDIX A. SUPPLEMENTARY DATA

Supplementary data related to this article can be found at https://doi.org/10.1016/j.simyco.2018.02.003.

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