Fungal ecology: principles and mechanisms of colonization and competition by saprotrophic fungi.

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SUMMARY

Decomposer fungi continually deplete the organic resources they inhabit, so successful colonisation of new resources is a crucial part of their ecology. Colonisation success can be split into (1) the ability to arrive at, gain entry into, and establish within a resource, and (2) the ability to persist within the resource until reproduction and dissemination. Fungi vary in their life-history strategies, the three main drivers of which are stress (S-selected), disturbance (ruderal, or R-selected), and incidence of competitors (C-selected); however, fungi often have combinations of characteristics from different strategies. Arrival at a new resource may occur as spores or mycelium, with successful entry and establishment (primary resource capture) within the resource largely dependent on the enzymatic ability of the fungus. The communities that develop in a newly available resource depend on environmental conditions, and in particular the levels of abiotic stress present (e.g. high temperature, low water availability). Community change occurs when these initial colonisers are replaced by species that are either more combative (secondary resource capture), or better able to tolerate conditions within the resource, either through changing abiotic conditions or due to modification of the resource by the initial colonisers. Competition for territory may involve highly specialised species-specific interactions, such as mycoparasitism, or may be more general; in both cases combat involves changes in morphology, metabolism, and ROS production, and outcomes of these interactions can be altered under different environmental conditions. In summary, community development is not a simple ordered sequence, but a complex ever-changing mosaic.

INTRODUCTION

Decomposer fungi, by their very nature, continually deplete the organic resources in which they grow and feed. They therefore rely on continual successful spread to new resources. In terrestrial ecosystems resources are distributed heterogeneously in space and time (1, 2). They are often discrete, ranging in size from small fragments, e.g. bud scales, to large tree trunks, though discrete leaves *en masse* can form a continuous layer on the forest floor. The processes of arrival and spread are thus crucial to the success of saprotrophic fungi. Following arrival at a resource, their competitive ability will determine whether they are successful in colonization and, also, how long they retain that territory. Colonization and competition are the main focus of this paper, and are discussed separately below, largely drawing on wood decay fungi for illustrative examples.

In view of the large number of decomposer fungi, and the variety of organic material that is available for them potentially to feed on, it is not surprising that they have evolved a range of different life history strategies to cope with the environment they inhabit, the three major drivers being: stress (S-selected), disturbance (R-selected or ruderal), incidence of competitors (C-selected), or a combination of these (3-5). Characteristics defining these life-history strategies are given in Table 1. These strategies are relative depending on the communities being considered, and they also vary in different stages of the life cycle, or between regions of the same mycelium exhibiting different physiological states. The wood decaying basidiomycete *Phlebia radiata*, for example, has a rapidly extending aseptate mycelial margin, that can utilize only simple carbon sources and does not recognise antagonists (R-selected characteristics), whereas the more mature septate mycelium is able to use the lignocellulose complex and is antagonistic to other mycelia (C-selected characteristics) (6). Thus, taxa should not usually be classified *per se* as having a specific life history strategy, but their behaviour in a particular context can be defined by these terms. Further, fungi often have combinations of characteristics from different strategies (R-C, R-S, C-S or R-C-S; Figure 1).

COLONIZATION

Arrival

Most fungi can only spread between resources by producing asexual spores, sexual spores or sclerotia. These fungi are termed resource-unit-restricted, as opposed to non-resource-unit-restricted fungi that grow out of resources and spread as mycelium. Spores can enable rapid spread, sometimes over many kilometres (7-11), though most basidiospores, for example, land within a few metres of the basidiocarp that produced them (9,11). Spores, however, usually contain only small food reserves, and the chance of landing on a suitable new resource, with an appropriate environment for germination and growth is small if spread by wind or rain, though greater if transported by animal vectors (5, 12). Sclerotia often contain larger food reserves, and allow survival in time, though spread is more limited than for most other spore types (13). Thick-walled chlamydospores also enable survival in time, e.g. the wood decaying basidiomycetes *Botryobasidium* spp., *Hyphodontia paradoxa*, *Piptoporus quercinus* and *Trechispora* spp., allowing them to survive severe abiotic stress, e.g. desiccation (see 5 and references therein).

Though the inoculum potential of an individual spore is small, it can be considerably increased if genetically identical spores, e.g. conidia, germinate close to one another. Germ tubes home in on each other and fuse to form a network (14). In contrast, when spores are genetically different, and hence somatically incompatible, competition is likely to result (15). When basidiospores germinate, the mycelia that develop are usually homokaryotic. It is generally thought that this homokaryotic stage is short-lived, and that mycelia soon (within hours or days of germination) encounter a suitable conspecific and, following a successful mating, become heterokaryotic. However, even common fungi such as *Trametes versicolor* and *Heterobasidion annosum* can sometimes remain homokaryotic for several years (11, 15-17), and rare species, e.g. *Hericium* spp., might be expected to remain homokaryotic for much longer (18). Homokaryotic and heterokaryotic mycelia do not necessarily behave the same in terms of growth rate, decay ability, competitive ability etc., though there does not

seem to be a general trend where one is better (has higher 'fitness') than the other (19 and references therein).

In contrast to arrival as spores, arriving as mycelium allows the fungus to draw upon a much larger supply of nutrients (20). Mycelial spread can be as individual hyphae, albeit sometimes forming dense mycelia or fronts, or as hyphae aggregated to form linear organs - mycelial cords and rhizomorphs (2, 21, 22). Some leaf litter decay fungi can form large patches, e.g. *Collybia* spp. and *Marasmius* spp., or 'fairy rings', e.g. *Clitocybe nebularis* (20, 23). These patch formers colonise individual fallen leaves, but spread by mycelial growth from one leaf to another as if the litter layer was one large continuous resource. In contrast to mycelial patches, that exhibit no particular pattern, fairy rings comprise a 30 – 40 cm wide annulus of mycelium which is highly polar growing outwards from an initial site of establishment, death of older mycelium forming a central zone devoid of the fairy ring-former (20, 23).

The mycelial systems of those fungi that produce linear organs of aggregated hyphae are very different from others. The structure of the linear organs covers a spectrum of complexity, from simple loose aggregations, through to hyphae highly aggregated to form cords, e.g. *Hypholoma fasciculare*, *Megacollybia platypylla*, *Phallus impudicus*, *Phanerochaete velutina* form cords with a thick outer rind that are differentiated internally, in contrast to the thick-walled melanised rhizomorphs of *Armillaria* spp. (21, 22, 24, 25). Rhizomorphs grow from the tip, whereas cords tend to form behind an actively growing front of individual hyphae. When mycelia grow out from a resource they exhibit different branching patterns which vary between species, and depend on many biotic and abiotic factors including size, quality and states of decay of the resource, soil type, micro-climatic environment, antagonistic fungi and other microbes, and grazing invertebrates (12, 20, 26, 27) Some can be considered short-range foragers, with highly dense hyphae and mycelia, yielding mass fractal dimension close to 2 in 2-dimensions, e.g. *H. fasciculare* (27; Figure 2A). They are likely to be

successful in encountering small organic food resources. Others are longer-range foragers with more open systems and a lower mycelial mass fractal dimension, e.g. *P. velutina* and *Resinicium bicolor* (Figure 2B&C). Even longer-range-forages have a mass fractal dimension of close to 1, e.g. rhizomorphs of *Armillaria* spp. (27).

When mycelia of cord-forming species encounter new resources they are able to exert considerable 'inoculum potential' for colonisation, being able to draw on nutrient reserves from the mycelial network which gives them considerable advantage over spores. If colonisation of the newly encountered resource is successful there is often reallocation of mycelial biomass, with thickening of cords interconnecting the original and new resource, and regression of non-connecting mycelium (2). Thus a network of cords interconnecting woody resources develops on the forest floor, and can operate a 'sit-and-wait' strategy colonising wood when it falls onto the network as well as an 'active-search' strategy (12). These networks can be extensive, though dynamic, covering many m^2 or even hectares; networks of rhizomorphs of *Armillaria* spp. constitute the largest organisms on the planet (20, 28-32). While in temperate and boreal forests such mycelial networks are confined to the forest floor, in tropical forests similar networks are found both on the floor and in the canopy (33), in the latter case catching small leaf litter and wood components before they reach the forest floor.

Entry and establishment

Plant tissues that have recently died are usually colonised initially by endophytic fungi already present, and/or by prolifically sporing R-selected species, which happened to arrive first (34, 35); so at early stages the absence of species commonly considered to be later colonisers reflects arrival time rather than an inability to colonise newly available plant tissues. On the forest floor, arrival by mycelium can, however, sometimes happen early on if the resource is located on or close to an active mycelia patch or network of mycelial cords.

Entry and establishment in an un-colonised dead organic resource, be it following arrival as spores or mycelium, will depend largely on the enzymatic ability of the fungus. If the fungus has the enzymatic capacity to use compounds available within the resource it will colonise, establish and remain present until it is (1) ousted by another species, (2) inhibited or killed by adverse abiotic conditions, (3) uses up the food supply, or (4) is triggered to fruit or grow out of the resource in search of others. If the fungus exits the resource by fruiting it may or may not commit all of its mycelial biomass to reproduction, depending on its life strategy (see above). Timing of production of reproductive structures also depends on life strategy, ruderal (R-selected) species committing themselves rapidly and prolifically to reproduction, others (C- or S-selected) tending to reproduce later in life, and not usually committing all of their mycelial biomass to reproduction (Table 1). Fungi that are able to exit by mycelial spread (those with C- and S-selected characteristics), do so at different times following colonisation, with the exact timing varying depending on species, other biotic and abiotic factors, and on the relative size/nutrient status of the resource compared with other resources in the network (2).

During colonisation simple compounds are typically used first followed by more recalcitrant cellulose, hemicellulose and lignin. Colonisation of the non-lignified tissues is relatively easy for mycelia, but woody tissues are more challenging. In wood most rapid spread is usually along vascular tissues; tangential and radial spread necessitates boring through lignocellulose in the cell walls (35). Plant anatomy results in the characteristic often longitudinally extensive decay columns seen in wood (Figure 3).

Community development

Communities that develop initially depend on the environmental conditions when the resource becomes available for colonisation, ranging between low environmental stress, where fungi with R-selected characteristics dominate initially, to high stress, e.g. due to extreme abiotic variables, where species that dominate have appropriate S-selected characteristics often combined with some R-

selected characteristics (3, 5; Figure 4). High stress conditions include heartwood of trees containing allelopathic compounds, extreme temperature of hot deserts and Arctic, Antarctic and alpine tundra, and the desiccating conditions of tree canopies. Though some of the initial fungal colonisers will have the enzymatic ability to completely break down the resource that they are colonising, most are usually replaced sooner or later by other species, when abiotic conditions worsen (stress aggravation) or improve (stress alleviation), when the habitat is disturbed or when competition/combat (see next section) with other fungi ensues (Figure 1). Changes to the abiotic conditions occur due to changes in microclimate, but are also brought about by fungi altering the physical and chemical environment as they metabolise the resource they are colonising (see next section). Disturbance occurs when resources are suddenly made available (enrichment disturbance) or when part or all of the resident mycobiota is destroyed, e.g. following fire. Competition/combat occurs when the expanding territory of fungi in freshly available resources overlaps, and when new colonisers arrive at a resource via spores or mycelial spread.

So, communities of primary, secondary and late secondary (or tertiary) colonisers develop. Community development is not a simple ordered sequence, but a complex ever-changing mosaic. The general order of colonising species – succession - has been determined in many types of organic substrata, but three-dimensional structure has been mostly studied in decaying wood, because the mosaic of different individual fungi is clear to see at all but the earliest and latest stages of community development (Figure 5A). Since organic substrata are opaque, they have to be destructively sectioned to reveal the individual decay columns. The patterns revealed can be mapped, isolations can be made onto agar media and subsequently identified, or DNA can be directly extracted from wood, and the three-dimensional community determined (Figure 3; Figure 5A). Isolation onto agar has the benefit that isolates of the same species can be paired to determine, in the case of basidiomycetes, whether the isolates are the same genotype/individual, based on somatic incompatibility (11, 36). The same can be done with ascomycetes, but different individuals/genotypes can sometimes belong to the same vegetative compatibility (VC) group (36, 37), so the situation is not so clear cut. Experimental

pairings can also be made between different species to give indications of relative combative ability, which can aid understanding of community development pathways.

Sectioning is destructive, so patterns of community development cannot be followed in an individual organic substratum, but rather must be inferred by analysing many units at different stages of decay. Extracting DNA samples from substrata, e.g. by collecting sawdust from holes drilled into wood, can reveal species composition (e.g. 38). Such samples could be extracted at different times to reveal a temporal sequence of colonisation but, of course, sampling may alter abiotic conditions in the resource and/or allow different fungi to colonise. Presence of fruit bodies provides a vague idea of fungi present, and has been used to infer colonisation sequence. Sequences of fruit bodies occurring on dung is an early cautionary tale (see 39). The order in which fruit bodies appear and disappear is largely related to their simplicity: mucorales, e.g. *Mucor*, *Pilaria* and *Pilobolus* are usually visible within a few days, declining after a week; after 5-6 days fruit bodies of discomycetes, e.g. *Ascobolus* and *Coproboia* spp., are evident; these are joined fruiting after 9 – 10 days by pyrenomycetes and loculoascomycetes, e.g. *Sordaria* and P*odospora*; finally basidiomycetes, e.g. *Coprinus*, *Stropharia* and *Paneolus* fruit. The fungi are, however, often already present in the dung when it is deposited or colonise very early. Some species have evolved adaptations to passage through the gut, and may even be able to germinate and grow whilst still within the near-anaerobic conditions of herbivore rumens; *Sporormiella minima*, for example, begins to grow before sheep dung is deposited, allowing it to colonise and fruit much more quickly than other species with similarly complex fruit bodies (40).

In wood, the order of fruit body appearance depends, to some extent, on the order within succession, but also on the ecological strategy, fungi with S- and C-selected characteristics tending to fruit sporadically and much later in their lifecycles. However, fruit bodies of some species repeatedly and sometimes almost exclusively follow those of other specific species (41-44). For example, *Antrodiella hoehnelii* almost always fruits following *Inonotus nodulosus* and *I. radiatus*, while *Hericium*

coralloides fruits following *Inonotus obliquus*, *I. cuticularis* or *Fomes fomentarius* on angiosperm wood in Central Europe and Scandinavia (41, 43). This has led to the idea of predecessor-successor relationships and priority effects.

The order in which species arrive at a resource, i.e. the assembly history, affects the composition and development of the community which follows. When earlier colonising species affect the colonisation success of species that arrive later, whether as spores or mycelium, they are described as exerting priority effects (45, 46). Such effects can be stimulatory or inhibitory. Wood decay fungi again provide good examples: they change the resource they occupy both chemically and physically by utilising different components of the wood cell wall, making nutrients available, altering wood chemistry, pH and water content. This can prevent some species from capturing territory, acting as a sort of constitutive defence (35), or, can select for certain species that prefer the altered environment (44, 47-50). The actual presence of a certain species can make a resource easier to colonise by specific fungi, for example, wood colonized by *Trametes* species may be more attractive to *Lenzites betulina* than is other wood, since the latter is temporarily mycoparasitic (see next section) on the former and can gain easy access via the mycelium of its host (51). Once *L. betulina* has taken over the territory occupied by *Trametes* spp., it operates other antagonistic mechanisms (see next section) to defend and gain territory from other fungi. Similary, *Trametes gibbosa* is temporarily mycoparasitic on *Bjerkandera adusta* (51). Priority effects are common in the development of wood decay communities (e.g. 45, 46, 49, 52-55), although they may be less evident in the later stages of decay (56).

COMPETITION

Competition is the negative effect that one organism has on another by using up, or inhibiting access to, a resource of limited availability (57). When one organism inhibits the other and limits access to resources it is termed interference competition, whereas when one organism depletes a resource, consequently reducing its availability, it is termed exploitation competition (57). The sequestration of

nutrients by mycelia growing through soil, hence preventing other fungi from using them, is an example of exploitation competition. However, when saprotrophic basidiomycetes and xylariacious ascomycetes are growing in and feeding on solid organic resources, e.g. wood and leaf litter, the distinction between exploitation competition and interference competition is not clear, and cannot sensibly be divorced from each other (58). This is because these fungi compete to obtain and defend 3-dimensional territory within the organic resource; within the territory the resources can be used at the fungus' 'leisure'. Thus, competition for nutrients is effectively brought about by competition for territory/space.

Fungal competition in organic resources is often divided into: (1) primary resource capture, when a fungus colonises and gains influence over previously unoccupied territory/resource; and (2) secondary resource capture, when a fungus captures territory from fungi that have already colonised a resource (3, 58). Another aspect to secondary resource capture is defence of territory from potential invaders. R-selected characteristics favour primary resource capture, whereas success in secondary resource capture depends on combative/antagonistic mechanisms (predominantly C-selected characteristics). Combative/antagonistic interactions can occur at a distance and following contact, comprising mycoparasitism and larger scale mycelial interactions.

Antagonism at a distance

Antagonism between fungi can occur in the absence of mycelial contact, through the production of volatile and diffusible organic compounds (VOCs and DOCs respectively; 59). Fungi produce a wide range of these so-called 'secondary' metabolites, spanning a variety of chemical classes, from short-chain alcohols and ketones to aromatic compounds and terpenes (60-62). Different species tend to produce a characteristic metabolite profile (63, 64), although this profile can be perturbed by growth substrate, pH, culture age, and temperature (65-67).

Whilst DOCs have antagonistic potential in circumstances where they can accumulate or diffuse through substrata (i.e. locally), VOCs function in much more heterogeneous environments and can act over greater distances (68, 69). Mycelia exposed to the DOCs or VOCs of a competitor exhibit altered spore germination, mycelial morphology, foraging behaviour, and enzyme production (47, 67, 68, 70-72). For example, the extension rate of *Trametes versicolor* was reduced when grown on media containing DOCs from *Fomes fomentarius* cultures (Figure 5B&C), and the extension of *Phallus impudicus* cords across soil was reduced as a result of exposure to VOCs from *Hypholoma fasciculare* (Figure 5D&E; 67). The antagonistic potential of VOC and DOC profiles depends on the chemical composition of that profile and the susceptibility of the combatants; effects of VOCs and DOCs may be stimulatory, and function as attractants to competitors, mycoparasites, or invertebrates (47, 72).

Mycoparasitism

Mycoparasitic relationships occur when one mycelium gains nutrition directly from another (35). The mycoparasite may cause the death of the host mycelium and utilise nutrients from the dead or dying hyphae (necrotrophy), or it may derive nutrition from living mycelia (biotrophy). There is a spectrum of relationships between these extremes, and some fungi may grow biotrophically on certain hosts but necrotrophically on others (73). Not only do fungi parasitise other mycelia, but they can also parasitise fruiting bodies, spores and sclerotia (73).

Biotrophic mycoparasitic relationships are complex, controlled, and specialised associations between mycoparasite and host. Biotrophic mycoparasites have a narrow host range, and the mycoparasite is frequently dependent on the host for survival; for example, *Coniothyrium minitans* is an obligate mycoparasite of certain *Sclerotinia* and *Botrytis* species, and lacks a free-living saprotrophic stage (74). The establishment of biotrophic associations requires high specificity in recognition between the host and the mycoparasite (73). The associations are relatively non-destructive, with the cytoplasm of the host remaining relatively healthy, but abstraction of nutrients

from the host results in reduction in host biomass, often causes distortion of host hyphae, and has adverse effects on host sporulation (73, 75, 76). Three subdivisons of biotrophic mycoparasitism have been described based on physiological characteristics. Firstly, the intracellular biotrophs function by the entire thallus entering and developing within the host cells, and absorbing nutrients directly from the host cytoplasm. Secondly, haustorial biotrophs penetrate host cell walls by the production of appressoria, and the development of specialised absorbtive branches (haustoria) which invaginate the host plasma membrane. Host nutrients are abosrbed across the plasma membrane into the haustorium. Thirdly, fusion or contact biotrophs produce specialised hyphae which closely adpress to the host hyphae and form channels or micropores in the host cell wall, allowing the biotroph plasmalemma to fuse with that of the host and absorb nutrients directly from the host cytoplasm (37, 76).

Necrotrophic mycoparasites tend to have a broad host range and utilise relatively unspecialised, destructive parasitic mechanisms. For many necrotrophs parasitism is more opportunistic than biotrophy and, as mentioned above, can even be temporary, providing the parasite with a means of access a different food source. As with biotrophic mycoparasites, the necrotrophs can be subdivided based on their physiological relationship with the host. Non-invasive necrotrophs make contact with, or grow very close to (within a few micrometres), host hyphae which they attack by a process known as 'hyphal interference'. The mycoparasite secretes non-enzymic diffusible toxins, which cause impaired membrane function resulting in lysis of organelles, invagination of the plama membrane, and eventual death of the hyphal compartment (73). Death of the whole mycelium may occur if multiple contacts are made. In contrast, invasive necrotrophs coil around and penetrate host hyphae (73). Contact and recognition of a host often stimulates production of specialised structures on the mycoparasite cell wall, with which it binds to host hyphae (77). The mycoparasite produces antifungal metabolites and lytic enzymes to disrupt host cytoplasm, resulting in vacuolation and lysis of hyphal walls and organelles. For example, vigorous necrotrophs in the genus *Trichoderma* secrete antibiotic peptides called peptaibols, which disrupt cytoplasmic membranes causing hyphal leakage and eventual cell death, and they also secrete cell-wall degrading chitinases and proteases (78).

Larger scale mycelia interactions: antagonistic mechanisms

For saprotrophic fungi, the territory occupied by a mycelium is also its nutrient source, and as such mycelia attempt to maximise their territory by replacing other mycelia and defending themselves from replacement. This is clearly seen in communities of wood decay fungi; the territories occupied by different mycelia in decaying wood are often delineated by pigmented barriers, or 'pseudosclerotial plates', which are the interfaces between competitors (Figure 5A; 58). The establishment of physical contact between two competing mycelia, often termed 'gross mycelial contact', results in large-scale changes in the growth, gene expression, and metabolite production in both competitors, and the induction of antagonistic mechanisms. The outcomes of antagonistic interactions range from replacement of one competitor by another, to deadlock, where neither species can capture any territory from the other (58). Between these extremes are partial replacement, where one species is able to capture some but not all of the opponent's territory, and mutual replacement, where one species obtains some of the territory formerly occupied by the other and, simultaneously, *vice versa.* Outcomes are determined by the relative abilities of the opponents to capture and defend territory, and different species may exhibit different 'strategies' during combat, displaying traits that may benefit them in attack and/or defence (79). Some fungi are good at both attack and defence, whereas others are good at one of these but not the other. For example, the secondary coloniser *Stereum hirsutum* is relatively poor at gaining new territory in decaying beech wood, but can defend the territory it occupies against more combative later secondary colonisers such as *H. fasciculare* and *P. velutina* (49). Further, the progress and outcomes of interactions can be altered and even reversed by changing environmental conditions, such as invertebrate grazing, gaseous regime, water availability, and temperature (79-82).

Morphological changes: Antagonistic mechanisms utilised by mycelia to attack or defend against competitors include morphological changes, production of enzymes and toxins, detoxification of

competitor toxins, and alteration of metabolic rate. Changes in mycelial morphology are most dramatic in areas in direct contact with the competitor - the interaction zone. Hyphae may aggregate to form defensive barrages to physically block invaders, or to form invasive replacement fronts or cords to penetrate competitor defences (Figure 5F-H; 58). Different types of hyphal assemblage can be found in different regions of the same interaction front, indicating that antagonistic mechanisms are deployed dynamically and in response to local stimuli (68). Changes in morphology during interactions are reflected in changes in expression of genes involved with cell division, cellular transport, and cytoskeleton rearrangement compared to non-interacting mycelia (83-85).

Secondary metabolite production: Profiles of VOCs and DOCs alter quantitatively and qualitatively during interactions, often involving production of interaction-specific compounds not produced by either competitor during growth alone (66-68, 72, 86-88; Table 2). Interaction-specific VOCs are often identified as terpenoids, frequently sesquiterpenes (66, 67, 87). Many sesquiterpenes are known to be bioactive, displaying antifungal activity, or functioning as attractants or repellants to fungi and invertebrates (61, 91, 92). Some compounds that were produced constitutively may be up-regulated following contact with a competitor (Table 2), for example the production of a potentially antifungal quinolinium-type compound by *H. fasciculare* doubled during interactions with *Trametes versicolor* compared to during growth alone (72).

Accumulation of ROS: Reactive oxygen species (ROS) accumulate at interaction zones, although their exact role is unclear (Figure 5G; 84, 93, 94). ROS may be produced by one or both competitors to generate a toxic oxidative environment, and increases in potential sources of ROS, such as increases expression of genes encoding NADPH oxidase, and increases in peroxidase and phenoloxidase activity, have been detected at interaction zones (84, 94, 95). Increases in expression of genes encoding catalase and putative DNA repair proteins have also been detected at interaction zones, which suggests attempts by the mycelium to mitigate ROS toxicity and repair oxidative

damage (83, 84). However, a direct role for ROS toxicity during interactions between wood decayers seems unlikely since these fungi are adapted to tolerate the oxidative stress caused by activity of their own ligninolytic enzymes. Instead, ROS accumulation may be incidental, and occur as a result of disruption of cellular metabolism caused by other antagonistic mechanisms. Alternatively, increases in ROS levels may function as a defence signalling response similar to that in plants, for example, triggering biosynthesis of pigment (94, 96). Increases in another potential signalling compound, nitric oxide (NO), have also been detected during interactions between *Phellinus morii* and *Inonotus obliquus*, triggering the production of antifungal phenylpropanoid metabolites (97).

Oxidative enzyme activity: Activities of peroxidases and phenoloxidases (laccases) are also up-regulated at interaction zones (19, 83, 95; Table 3). This may function to increase decomposition and could be associated with increased utilisation of the resource during combat. However, laccases and peroxidases are also secreted in response to stress, and could function during interactions to detoxify competitor VOCs and DOCs (19, 85). Other enzymes involved in detoxification are also up-regulated during interactions, for example increases in expression of genes encoding oxidoreductases, aldo/ketoreductases, and glutathione-S-transferases were detected in *Trametes versicolor* and *Pycnoporus coccineus* during interactions with various competitors (84, 85). Laccases may also function to wall off and protect hyphae during interactions through production of melanin, which insulates hyphae from ROS, toxins, temperature extremes, and hydrolytic enzymes, and may also have direct antibiotic properties (106, 107). Pigmentation is frequently observed at interaction zones (Figure 5H), and whilst there is some indication that this is the result of deposition of DOCs, this may also be the result of melanisation (72).

Energy expenditure during interactions: Antagonism is energetically expensive. Production of invasive mycelial cords by one or both competitors is associated with increases in respiration, indicating that this requires up-regulation of metabolic processes (49). Enhancement of nutrient

acquisition through increased production of cellulases and phosphatases occurs at interaction zones and throughout the competing mycelia (85, 103, 104). The concurrent reduction in biomass accumulation during interactions between *P. coccineus* and *Coniophora puteana* suggests that this increased nutrient acquisition functions to fund antagonistic mechanisms rather than mycelial growth (85). Metabolism was also found to increase in newly captured territories (i.e. regions where a mycelium had replaced a competitor), and it is likely that the observed increases in activity and gene expression of proteases and chitinases in these regions function to recycle the mycelium of the displaced competitor (85, 89, 105, 108). Similary, genes whose products are involved in carbohydrate and nitrogen metabolism were up-regulated in *T. versicolor* mycelium during interactions where it replaced competitors, but not during interactions where it was outcompeted (84).

CONCLUSIONS

Fungal community development within decaying resources is ultimately driven by the abiotic conditions the resource is subjected to, and the local pool of potential colonising species. Fungi have evolved different life-history strategies to exploit different niches during community development within decaying resources, although certain species may often have combinations of characteristics from different strategies, or vary in their strategy during different stages of the life cycle or in different contexts. The communities that develop in newly available resources depend on the levels of abiotic stress present; this determines which of the latently present colonisers, and which of those that arrive as spores or via mycelial spread from local species pools, are most likely to establish within the resource. Changing abiotic conditions, modification of the resource by colonisers, and arrival of more combative species drive shifts in community composition, and in some cases the assembly history determines subsequent community development. Acquisition of previously colonised resources by more combative species is achieved through the deployment of antagonistic mechanisms, which can begin before mycelia establish physical contact through production of volatile and diffusible organic compounds. Interacting mycelia undergo a slew of morphological and biochemical changes, which may be aggressive or defensive in function, and the changes that occur differ depending on the

combination of species involved. Interaction outcomes, and thus community change, are determined by the relative combative abilities of the fungi involved, but these outcomes can be altered or even reversed under different environmental conditions.

Many questions remain to be answered for us to fully understand the processes underlying community development of saprotrophic fungi. Firstly, how far do spores spread, and how do they manage to establish within resources that are already colonised; what exactly is the success rate of a spore? Perhaps communities within decaying resources are determined through all initial stages of decay by propagules that are latently present; emerging sequencing technologies will allow a much more comprehensive profile of latent colonisers to assess the extent of their contribution to community development. Further, how strong are priority effects, and how resilient are these pathways of community development global environmental change? Finally, utilisation of emerging molecular and biochemical approaches will allow better understanding of the mechanisms involved in antagonism or facilitation within decay communities, which drive changes in community composition throughout the decomposition process.

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References

1. Boddy L. 1984. The microenvironment of basidiomycete mycelia in temperate deciduous woodlands, p 261-289. *In* Jennings DH, Rayner ADM (ed), *Ecology and Physiology of the Fungal Mycelium.* Cambridge University Press, UK.

2. Boddy L. 1999. Saprotrophic cord-forming fungi: meeting the challenge of heterogeneous environments. *Mycologia* **91:**13-32.

3. Cooke RC, Rayner ADM. 1984. Ecology of saprotrophic fungi. Longman, New York.

4. Pugh GJF, Boddy L. 1988. A view of disturbance and life strategies in fungi. Proc Roy Soc B **94:**3-11.

5. Boddy L, Heilmann-Clausen J. 2008. Basidiomycete community development in temperate angiosperm wood, p 211-237. *In* Boddy L, Frankland J, van West P (ed), *Ecology of Saprotrophic Basidiomycetes.* Academic Press, Elsevier, London, UK.

6. Boddy L, Rayner ADM. 1983. Origins of decay in living deciduous trees: the role of moisture content and a re-appraisal of the expanded concept of tree decay. *New Phytol* **94:**623-641.

7. Vilgalys R, Sun BL. 1994. Assessment of species distributions in *Pleurotus* based on trapping of airborne basidiospores. *Mycologia* **86:**270-274.

8. Hallenburg N. 1995. Dispersal abilities and distributional patterns in Aphyllophorales, with emphasis on corticoid fungi. A*cta Universitatis Upsaliensis, Symbolae Botanicae Upsaliensis* **30:**95-100.

9. Nordén B, Larsson KH. 2000. Basidiospore dispersal in the old-growth forest fungus *Phlebia centrifuga*. *Nordic J Bot* **20:**215-219.

10. Hallenburg N, Küffer N. 2001. Long-distance spore dispersal in wood-inhabiting basidiomycetes. *Nordic J Bot* **21:**431-436.

11. Stenlid J. 2008. Population biology of forest decomposer basidiomycetes, p 105-122. *In* Boddy L, Frankland JC, van West P (ed), *Ecology of Saprotrophic Basidiomycetes.* Elsevier, Amsterdam.

12. Boddy L, Jones TH. 2007. Mycelial responses in heterogeneous environments: parallels with macroorganisms, p 112-140. *In* Gadd GM, Watkinson SC, Dyer P (ed), *Fungi in the Environment.* Cambridge University Press, UK.

13. Smith ME, Henkel TW, Rollins JA. 2014. How many fungi make sclerotia? *Fungal Ecol* **13:**211-220.

14. Read ND, Goryachev AB, Lichius A. 2012. The mechanistic basis of self-fusion between conidial anastomosis tubes during fungal colony initiation. *Fungal Biol Rev* **26:**1-11.

15. Coates D, Rayner ADM. 1985. Fungal population and community development in cut beech logs: 1. Establishment via the aerial cut surface. *New Phytol* **101:**153-171.

16. Garbelotto MM, Lee HK, Slaughter G, Popenuck T, Cobb FW, Bruns TD. 1997. Heterokaryosis is not required for virulence of *Heterobasidion annosum*. *Mycologia* **89:**2-102.

17. Redfern DB, Pratt JE, Gregory SC, Macaskill GA. 2001. Natural infection of Sitka spruce thinning stumps in Britain by spores of *Heterobasidion annosum* and long-term survival of the fungus. *Forestry* **74:**53-71.

18. Boddy L, Crockatt ME, Ainsworth AM. 2011. Ecology of *Hericium cirrhatum*, *H. coralloides* and *H. erinaceus* in the UK. *Fungal Ecol* **4:**163-173.

19. Hiscox J, Baldrian P, Rogers HJ, Boddy L. 2010. Changes in oxidative activity during interspecific mycelial interactions involving the white-rot fungus *Trametes versicolor*. *Fungal Genetics Biol* **47:**562-571.

20. Fricker MD, Bebber D. 2008. Mycelial networks: Structure and dynamics, p3-18. *In* Boddy L, Frankland J, van West P (ed), *Ecology of Saprotrophic Basidiomycetes.* Academic Press, Elsevier, UK.

21. Boddy L. 1993. Saprotrophic cord-forming fungi: warfare strategies and other ecological aspects. *Mycol Res* **97:**641-655.

22. Rayner ADM, Powell KA, Thompson W, Jennings DH. 1985. Morphogenesis of vegetative organs, p 249-279. *In* Moore D, Cassleton LA, Wood DA, Frankland JC (ed), *Developmental Biology of Higher Fungi*. Cambridge University Press, UK.

23. Dowson CG, Rayner ADM, Boddy L. 1989. Spatial dynamics and interactions of the woodland fairy ring fungus, *Clitocybe nebularis*. *New Phytol* **111:**699-705.

24. Thompson W, Rayner ADM. 1982. Structure and development of mycelial cord systems of *Phanerochaete laevis* in soil. *Trans Brit Mycol Soc* **81:**333-345.

25. Thompson W. 1984. Distribution, development and functioning of mycelial cord systems of decomposer basidiomycetes on the deciduous woodland floor, p 185-215. *In* Jennings DH, Rayner ADM (ed), *The Ecology and Physiology of the Fungal Mycelium.* Cambridge University Press, Cambridge.

26. Tordoff GM, Boddy L, Jones TH. 2006. Grazing by *Folsomia candida* (Collembola) differentially affects mycelial morphology of the cord-forming basidiomycetes *Hypholoma fasciculare*, *Phanerochaete velutina* and *Resinicium bicolor*. *Mycol Res* **110:**335-345.

27. Boddy L, Donnelly DP. 2008. Fractal Geometry and Microorganisms in the Environment, p 239-272. *In* Senesi N, Wilkinson KJ (ed), *Biophysical Chemistry of Fractal Structures and Processes in Environmental Systems.* John Wiley, Chichester, UK.

28. Thompson W, Rayner ADM. 1983. Extent development and functioning of mycelial cord systems in soil. *Trans Brit Mycol Soc* **81:**333-345.

29. Ferguson BA, Dreisbach TA, Parks CG, Filipo GM, Schmitt CL. 2003. Coarse-scale population structure of pathogenic *Armillaria* species in a mixed-conifer forest in the Blue Mountains of northeast Oregon. *Can J For Res* **33:**612–623.

30. Cairney JWG. 2005. Basidiomycete mycelia in forest soils: Dimensions, dynamics and roles in nutrient distribution. *Mycol Res* **109:**7-20.

31. Boddy L, Tordoff GM, Wood J, Hynes J, Bebber D, Jones TH, Fricker MD. 2006. Mycelial foraging strategies of saprotrophic cord-forming basidiomycetes, p 13-20. *In* Meyer W, Pearce C (ed), *8th International Mycological Congress Proceedings.* Medimond, Italy.

32. Heaton L, Obara B, Grau V, Jones N, Nakagaki T, Boddy L, Fricker MD. 2012. Analysis of fungal networks. *Fungal Biol Rev* **26:**12-29.

33. Hedger, J. 1990. Fungi in the tropical forest canopy. *The Mycologist* **4:**200-202.

34. Osono T. 2005. Colonisation and succession of fungi during decomposition of *Swida controversa* leaf litter. *Mycologia* **97:**589-597.

35. Boddy L, Hiscox J, Gilmartin EC, Johnston S, Heilmann-Clausen J. 2017. Decay communities in angiosperm wood. *In* Dighton J (ed), *The Fungal Community.* Taylor, UK.

36. Malik M, Vilgalys R. 1999. Somatic incompatibility in fungi. In Structure and Dynamics of Fungal Populations (J. J. Worrall, ed.). Kluwer Academic Publishers, Dordrecht, pp. 123–138.

37. Watkinson S, Boddy L, Money N. 2015. *The fungi*, 3rd ed. Academic Press, UK.

38. Ovaskainen O, Nokso-Koivisto J, Hottola J, Rajala T, Pennanen T, Ali-Kovero H, Miettinen O, Oinonen P, Auvinen P, Paulin L, Larsson KH, Mäkipää R. 2010. Identifying wood-inhabiting fungi with 454 sequencing – what is the probability that BLAST gives the correct species? *Fungal Ecol* **3:**274-283.

39. Dix NJ, Webster J. 1995. Fungal Ecology. Chapman & Hall, London.

40. Richardson MJ. 2002. The coprophilous succession. *Fungal Diversity* **10:**101-111.

41. Niemelä T, Renvall P, Penttilä R. 1995. Interactions of fungi at late stages of wood decomposition. *Annales Botanici Fennici* **32:**141-152.

42. Holmer L, Stenlid J. 1997. Competitive hierarchies of wood decomposing basidiomycetes in artificial systems based on variable inoculum sizes. *Oikos* **79:**77-84.

43. Heilmann-Clausen J, Christensen M. 2004. Does size matter? On the importance of various dead wood fractions for fungal diversity in Danish beech forests. *For Ecol Manag* **201:**105-117.

44. Ottosson E. 2013. *Succession of wood-inhabiting fungal communities: diversity and species interactions during the decomposition of Norway Spruce.* Swedish University of Agricultural Sciences, Uppsala.

45. Fukami T, Dickie IA, Wilkie JP, Paulus BC, Park D, Roberts A, Buchanan PK. 2010. Assembly history dictates ecosystem functioning: evidence from wood decomposer communities. *Ecol Lett* **13:**675-684.

46. Ottosson E, Norden J, Dahlberg A, Edman M, Jonsson M, Larsson KH. 2014. Species associations during the succession of wood-inhabiting fungal communities. *Fungal Ecol* **11:**17-28.

47. Heilmann-Clausen J, Boddy L. 2005. Inhibition and stimulation effects in communities of wood decay fungi: exudates from colonized wood influence growth by other species. *Microbial Ecol* **49:**399-406.

48. Van der Wal A, Geydan TD, Kuyper TW, de Boer W. 2013. A thready affair: linking fungal diversity and community dynamics to terrestrial decomposition processes. *FEMS Microbiol Rev* **37:**477-494.

49. Hiscox J, Savoury M, Müller CT, Lindahl BD, Rogers HJ, Boddy L. 2015. Priority effects during fungal community establishment in beech wood. *ISME J* **9:**2246-2260.

50. Fukami T. 2015. Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Ann Rev Ecol Evol System* **46:**1-23.

51. Rayner ADM, Boddy L, Dowson CG. 1987. Temporary parasitism of *Coriolus* spp. by *Lenzites betulina*: a strategy for domain capture in wood decay fungi. *FEMS Microbiol Ecol* **45:**53-58.

52. Lindner DL, Vasaitis R, Kubartová A, Allmér J, Johannesson H, Banik MT. 2011. Initial fungal colonizer affects mass loss and fungal community development in *Picea abies* logs 6 years after inoculation. *Fungal Ecol* **4:**449-460.

53. Dickie IA, Fukami T, Wilkie JP, Allen RB, Buchanan PK. 2012. Do assembly history effects attenuate from species to ecosystem properties? A field test with wood-inhabiting fungi. *Ecol Lett* **15:**133–141.

562 **54. Pouska V, Svoboda M, Lepš J.** 2013. Co-occurrence patterns of wood-decaying fungi on *Picea*
563 *abies* logs: does *Fomitopsis pinicola* influence the other species? *Polish Journal of Ecology* **61:**119-
564 134.

565 **55. Hiscox J, Savoury M, Johnston SR, Parfitt D, Müller CT, Rogers HJ, Boddy L.** 2016.
566 Location location location: priority effects in wood decay communities may vary between sites.
567 *Environ Microbiol* doi: 10.1111/1462-2920.13141.

568 **56. Rajala T, Peltoniemi M, Hantula J, Mäkipää R, Pennanen T.** 2011. RNA reveals a succession
569 of active fungi during the decay of Norway spruce logs. *Fungal Ecol* **4:**437-448.

570 **57. Keddy PA.** 1989. Competition. Chapman and Hall, New York.

571 **58. Boddy L.** 2000. Interspecific combative interactions between wood-decaying basidiomycetes.
572 FEMS *Microbiol Ecol* **31:**185-194.

573 **59. Wheatley RE.** 2002. The consequences of volatile organic compound mediated bacterial and
574 fungal interactions. *Antonie van Leeuwenhoek* **81:**357-364.

575 **60. Rösecke J, Pietsch M, König WA.** 2000. Volatile constituents of wood-rotting basidiomycetes.
576 *Phytochem* **54:**747-50.

577 **61. Ladygina N, Dedyukhina E, Vainshtein M.** 2006. A review on microbial synthesis of
578 hydrocarbons. *Process Biochem* **41:**1001-1014.

579 **62. Lemfack MC, Nickel J, Dunkel M, Preissner R, Piechulla B.** 2013. mVOC: a database of
580 microbial volatiles. *Nucleic Acids Res* **42:**744-748.

581 **63. Fischer G, Schwalbe R, Möller M, Ostrowski R, Dott W.** 1999. Species-specific production of
582 microbial volatile organic compounds (MVOC) by airborne fungi from a compost facility.
583 *Chemosphere* **39:**795-810.

584 **64. Polizzi V, Adams A, Malysheva SV, De Saeger S, Van Peteghem C, Moretti A, Picco AM, De**
585 **Kimpe N.** 2012. Identification of volatile markers for indoor fungal growth and chemotaxonomic
586 classification of *Aspergillus* species. *Fungal Biol* **116:**941-53.

65. Schoeman MW, Webber JF, Dickinson DJ. 1996. The effect of diffusible metabolites of *Trichoderma harzianum* on in vitro interactions between basidiomycete isolates at two different temperature regimes. *Mycol Res* **100:**1454-1458.

66. Hynes J, Müller CT, Jones TH, Boddy L. 2007. Changes in volatile production during the course of fungal mycelial interactions between *Hypholoma fasciculare* and *Resinicium bicolor*. *J Chem Ecol* **33:**43-57.

67. El Ariebi N, Hiscox J, Scriven SA, Müller CT. 2016. Production and effects of volatile organic compounds during interspecific interactions. *Fungal Ecol* **20:**144-154.

68. Rayner ADM, Griffith GS, Wildman HG. 1994. Induction of metabolic and morphogenetic changes during mycelial interactions among species of higher fungi. *Biochem Soc Trans* **22:**389-395.

69. Wheatley R, Hackett C. 1997. Effect of substrate composition on production of volatile organic compounds from *Trichoderma* spp. Inhibitory to wood decay fungi. *Int Biodet Biodeg* **39:**199-205.

70. Strobel GA, Dirkse E, Sears J, Markworth C. 2001. Volatile antimicrobials from *Muscodor albus*, a novel endophytic fungus. *Microbiol* **147:**2943-2950.

71. Humphris SN, Bruce A, Buultjens E, Wheatley RE. 2002. The effects of volatile microbial secondary metabolites on protein synthesis in *Serpula lacrymans*. *FEMS Microbiol Lett* **210:**215-219.

72. Evans JA, Eyre CA, Rogers HJ, Boddy L, Müller CT. 2008. Changes in volatile production during interspecific interactions between four wood rotting fungi growing in artificial media. *Fungal Ecol* **1:**57–68.

73. Jeffries P. 1995. Biology and ecology of mycoparasitism. *Can J Bot* **73:**S1284–S1300.

74. Whipps JM, Bennett A, Challen M, Clarkson J, Coventry E, Muthumeenakshi S, Noble R, Rogers C, Sreenivasaprasad S, Jones EE. 2007. Control of sclerotial pathogens with the mycoparasite *Coniothyrium minitans*, p 223-241. *In* Vurro M, Gressel J (ed), *Novel Biotechnologies for Biocontrol Agent Enhancement and Management.* Springer, New York..

611 **75. Lumsden R.** 2005. Mycoparasitism of soilborne plant pathogens, p 275-294. *In* Dighton J, White
612 J, Oudemans P (ed), *The fungal community: its organisation and role in the ecosystem.* Taylor Francis,
613 New York.

614 **76. Goh YK, Vujanovic V**. 2010. *Sphaerodes quadrangularis* biotrophic mycoparasitism on
615 *Fusarium avenaceum*. *Mycologia* **102:**757-762.

616 **77. Rosado V, Rey M, Codon AC, Govantes J, Moreno-Mateos MA, Benitez T.** 2007. QID74 cell
617 wall protein of *Trichoderma harzianum* is involved in cell protection and adherence to hydrophobic
618 surfaces. *Fung Gen Biol* **44:**950-964.

619 **78. Sharma P, Kumar PV, Ramesh R, Saravanan K, Deep S, Sharma M, Mahesh S, Dinesh S.**
620 2011. Biocontrol genes from *Trichoderma* species: a review. *African J Biotechnol* **10:**19898-19907.

621 **79. Crowther TW, Maynard DS, Crowther TR, Peccia J, Smith JR, Bradford MA.** 2015.
622 Untangling the fungal niche: the trait-based approach. *Frontiers Microbiol* **5:**2-12.

623 **80. Boddy L, Gibbon OM, Grundy MA.** 1985. Ecology of *Daldinia concentrica*: effect of abiotic
624 variables on mycelial extension and interspecific interactions. *Trans Br Mycol Soc* **85:**201-211.

625 **81. Griffith GS, Boddy L.** 1991. Fungal decomposition of attached angiosperm twigs. *New Phytol*
626 **117:**259-269.

627 **82. Hiscox J, Clarkson G, Savoury M, Powell G, Savva I, Lloyd M, Shipcott J, Choimes A,**
628 **Cumbriu XA, Boddy L.** 2016. Effects of pre-colonisation and temperature on interspecific fungal
629 interactions in wood. *Fungal Ecol* **21:**32-42.

630 **83. Iakovlev A, Stenlid J.** 2000. Spatiotemporal patterns of laccase activity in interacting mycelia of
631 wood-decaying basidiomycete fungi. *Microbial Ecol* **39:**236-245.

632 **84. Eyre C, Muftah W, Hiscox J, Hunt J, Kille P, Boddy L, Rogers HJ.** 2010. Microarray analysis
633 of differential gene expression elicited in *Trametes versicolor* during interspecific mycelial
634 interactions. *Fungal Biol* **114:**646-660.

85. Arfi Y, Levasseur A, Record E. 2013. Differential gene expression in *Pycnoporus coccineus* during interspecific mycelial interactions with different competitors. *Appl Environ Microbiol* **79:**6626-6636.

86. Peiris D, Dunn WB, Brown M, Kell DB, Roy I, Hedger JN. 2008. Metabolite profiles of interacting mycelial fronts differ for pairings of the wood decay basidiomycete fungus Ste*r*eum *hirsutum* with its competitors *Coprinus micaceous* and *Coprinus disseminatus. Metabolomics* **4:**52–62.

87. Chen Y, Huang J, Li Y, Zeng G, Zhang J, Huang A, Zhang J, Ma S, Tan X, Xu W, Zhou W. 2015. study of the rice straw biodegradation in mixed culture of *Trichoderma viride* and *Aspergillus niger* by GC-MS and FTIR. *Environ Sci Poll Res* **22:**9807-9815.

88. Sánchez-Fernández RE, Diaz D, Duarte G, Lappe-Oliveras P, Sánchez S, Macías-Rubalcava ML. 2016. Antifungal volatile organic compounds from the endophyte *Nodulisporium* sp. strain GS4dII1a: a qualitative change in the intraspecific and interspecific interactions with *Pythium aphanidermatum*. *Fungal Microbiol* **71:**347-364.

89. Ujor VC, Peiris DG, Monti M, Kang AS, Clements MO, Hedger JN. 2012. Quantitative proteomic analysis of the response of the wood-rot fungus *Schizophyllum commune* to the biocontrol fungus *Trichoderma viride*. *Lett Appl Microbiol* **54:**336-343.

90. Estrada AER, Hegeman A, Kistler HC, May G. 2011. In vitro interactions between *Fusarium verticillioides* and *Ustilago maydis* through real-time PCR and metabolic profiling. *Fungal Genet Biol* **48:**874-885.

91. Abraham WR. 2001 Bioactive sesquiterpenes produced by fungi: are they useful for humans as well? *Curr Med Chem* **8:**583-606.

92. Gao Y, Jin YJ, Li HD, Chen HJ. 2005. Volatile organic compounds and their roles in bacteriostasis in five conifer species. *J Integrative Plant Biol* **47:**499-507.

93. Tornberg K, Olsson S. 2002. Detection of hydroxyl radicals produced by wood-decomposing fungi. *FEMS Microbiol Ecol* **40:**13-20.

94. Silar P. 2005. Peroxide accumulation and cell death in filamentous fungi induced by contact with a contestant. *Mycol Res* **109:**137-149.

95. Baldrian P. 2004. Increase of laccase activity during interspecific interactions of white-rot fungi. *FEMS Microbiol Ecol* **50:**245-53.

96. Baxter A, Mittler R, Suzuki N. 2013. ROS as key players in plant stress signalling. *J Exp Bot* doi:10.1093/jxb/ert375.

97. Zhao Y, Xi Q, Xu Q, He M, Ding J, Dai Y, Keller NP, Zheng W. 2015. Correlation of nitric oxide produced by an inducible nitric oxide synthase-like protein with enhanced expression of the phenylpropanoid pathway in *Inonotus obliquus* cocultured with *Phellinus morii*. *Appl Microbiol Biotechnol* **99:**4361-4372.

98. Lang E, Nerud F, Zadrazil F. 1998. Production of ligninolytic enzymes by *Pleurotus* sp. and *Dichomitus squalens* in soil and lignocellulose substrate as influenced by soil microorganisms. *FEMS Microbiol Lett* **167:**239-244.

99. Verma P, Madamwar D. 2002. Production of ligninolytic enzymes for dye decolourisation by cocultivation of white rot fungi *Pleurotus ostreatus* and *Phanerochaete chrysosporium* under sold-state fermentation. *Appl Biol Biotechnol* **102:**109-118.

100. Cupul WC, Abarca GH, Carrera DM, Vázquez RR. 2014. Enhancement of ligninolytic enzyme activities in a *Trametes maxima-Paecilomyces carneus* co-culture: key factors revealed after screening using a Plackett-Burman experimental design. *Electronic J Biotechnol* **17:**114-121.

101. White NA, Boddy L. 1992. Extracellular enzyme localisation during interspecific fungal interactions. *FEMS Microbiol Letts* **1:**75-79.

102. Score AJ, Palfreyman JW, White NA. 1997. Extracellular phenoloxidase and peroxidase enzyme production during interspecific fungal interactions. *Int Biodet Biodeg* **39:**225-233.

103. Šnajdr J, Dobiášová P, Větrovský T, Valášková V, Alawi A, Boddy L. 2011. Saprotrophic basidiomycete mycelia and their interspecific interactions affect the spatial distribution of extracellular enzymes in soil. *FEMS Microbiol Ecol* **78:**80-90.

104. Freitag M, Morrell JJ. 1992. Changes in selected enzyme activities during growth of pure and mixed cultures of the white-rot decay fungus *Trametes versicolor* and the potential biocontrol fungus *Trichoderma harzianum*. *Can J Microbiol* **38:**317-323.

105. Lindahl BD, Finlay RD. 2006. Activities of chitinolytic enzymes during primary and secondary colonisation of wood by wood-degrading basidiomycetes. *New Phytolol* **169:**389-397.

106. Bell A A, Wheeler MH. 1986. Biosynthesis and functions of fungal melanins. *Ann Rev Phytopathol* **24:**411-451.

107. Henson JM, Butler MJ, Day AW. 1999. The dark side of the mycelium: melanins of phytopathogenic fungi. *Ann Rev Phytopath* **37:**447-471.

108. Jonkers W, Estrada AER, Lee K, Breakspear A, May G, Kistler HC. 2012. Metabolome and transcriptome of the interaction between *Ustilago maydis* and *Fusarium verticillioides in vitro. Appl Environ Microbiol* **78:**3656-3667.

Figure Legends

Figure 1. How R-C-S characteristics relate to r-K strategies

Figure 2. Foraging strategies of cord-forming basidiomycetes growing out of pre-colonised beech wood blocks across compacted soil. **A:** *Hypholoma fasciculare*, a short-range forager, produces highly dense hyphae and mycelia. **B:** *Phanerochaete velutina* is a longer-range forager, with a more open cord system. **C:** *Resinicium bicolor* has an even more open system than *P. velutina*, with thicker cords.

Figure 3. Sectioned beech trunk showing decay columns running longitudinally through the wood. Arrows indicate dark zone lines (pseudosclerotial plates) surrounding different decay columns.

Figure 4. Fungal community development pathways in woody resources. Newly available wood (top) becomes progressively colonised, initially through primary resource capture in an open community stage where there is still unoccupied territory, until all territory becomes occupied, resulting in a closed community where further colonisation occurs as secondary resource capture. As the community moves from open to closed, combat becomes the driving force for change. Finally, communities in well-decayed wood are characterised by substrate modification and invasion by soil invertebrates. The ecological characteristics of the dominant organisms are indicated in boxes: R, ruderal; C, combative; S, stress-tolerant. Driving forces are indicated in italic, and direction of community change indicated by arrows. The community may be driven toward the left by stress aggravation, or to the right by stress alleviation, although destructive disturbance will drive the community towards species with R-selected characteristics.(Adapted from 5, 58).

Figure 5. Interspecific interactions fungi growing in natural and artificial media. **A:** Cross section of a decaying beech branch with dark zone lines (pseudosclerotial plates) surrounding competing mycelia. **B&C:** Growth of *Trametes versicolor* when exposed to the DOCs from uncolonised malt broth (control; **B**), or DOCs from *Fomes fomentarius* (**C**). **D&E:** *Phallus impudicus* cord systems growing across compacted soil when exposed to VOCs from uncolonised soil (control; **D**), or VOCs from *Hypholoma fasciculare* growing across soil (**E**). **F:** Interaction between *H. fasciculare* and *Resinicium bicolor* cord systems across compacted soil. **G:** Accumulation of reactive oxygen species (ROS) at the interaction zone between *Bjerkandera adusta* (left) and *T. versicolor* (left) on 2% malt agar (MA). ROS are stained purple using nitroblue tetrazolium (methods in 94). **H:** Three-way interaction between mycelia of *H. fasciculare* (left), *P. velutina* (centre), and *Stereum hirsutum* (right) growing on

2% malt agar (MA). *H. fasciculare* cords are beginning to encroach over the *P. velutina* mycelium, whilst *H. fasciculare* itself is overgrown by *P. velutina* cords. A thick barrage separates the mycelia of *S. hirsutum* and *P. velutina*, with a distinct orange/yellow band of pigment deposited in the agar at the regions of contact between the two mycelia.

Table 1. Characteristics defining the life-history strategies of ruderal (R), combative (C), and stress-tolerant (S) species.

	R	**S**	**C**
Characteristic features	Rapid growth; primary resource capture	Tolerance of specific stresses (e.g. temperature extremes, low water availability, extremely low or high pH, allelopathic chemicals)	Antagonistc ability against competitors
Growth rate	Rapid spore germination and growth	Sometimes slow	Not particularly slow
Enzymatic ability	Relatively narrow ability	Wide ability	Wide ability
Substrates utilised	Easily assimilable	More recalcitrant	More recalcitrant
Timing of reproduction	Early in life cycle	Later in life cycle, sometimes sporadic	Later in life cycle, sometimes sporadic
Commitment of biomass to reproduction	Rapid and substantial	Relatively low	Relatively low
Persistence within the resource	Low; easily replaced	Persistent while specific stress remains	Persistence depends on ability to capture and defend territory

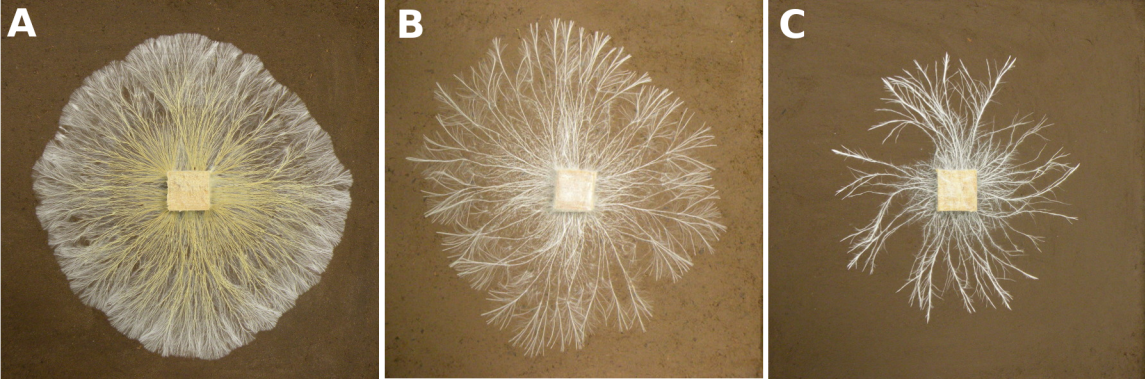
Table 2. Secondary metabolite production during antagonistic interactions. Select examples of the volatile and diffusible organic compounds (VOCs and DOCs respectively) that have been detected as changing in production during interspecific fungal interactions. Metabolites belong to a wide variety of chemical classes, and may increase or decrease in production during interactions relative to solo growth, or may be specific to the interaction. Interaction experiments were performed in a variety of substrates, including malt agar (MA) or broth, potato dextrose agar (PDA), beech wood, and straw powder.

Chemical class	Compound name	VOC/DOC	Change in production	Interaction (species) reported in & substrate	Reference
Benzenoid	1,2-dihydroxyanthaquinone	DOC	Increase	*Stereum hirsutum vs. Coprinus disseminatus on MA*	86
	5-Methyl,1,3-cyclohexadiene	VOC	Interaction specific	*Trametes versicolor vs. Stereum gausapatum in malt broth*	72
Carboxylic acid	Fusaric acid	DOC	Increases	*Ustilago maydis vs. Fusarium verticillioides on PDA*	90
	Malic acid	DOC	Increase	*S. hirsutum vs. C. disseminatus on MA; Trichoderma viride vs. Schizophyllum. commune on PDA*	86, 89
Sesquiterpene	α-bulnesene	VOC	Increases & decreases (depending on species involved)	*Hypholoma fasciculare vs. Phanerochaete velutina; Resinicium bicolor vs. Phallus impudicus; P. veutina vs. P. impudicus; R. bicolor vs. P. velutina; H. fasciculare vs. P. impudicus; all in beech wood*	67
	Selinene (α & β)	DOC	Interaction specific	*Nodulisporium sp. vs. Pythium aphanidermatum; Nodulisporium sp. intraspecific interaction; both on PDA*	88
Monoterpene	Pinene	VOC	Interaction specific	*T. viride vs. Aspergillus niger in straw powder*	87
	γ-terpinene	DOC	Interaction specific	*Nodulisporium sp. vs. P. aphanidermatum on PDA*	88
Sugar alcohol	Erythritol & Meso-erythritol	DOC	Increase	*T. viride vs. S. commune on PDA; S. hirsutum vs. Coprinus micaceus on MA; S. hirsutum vs. Coprinus disseminatus on MA*	86, 89
	Glycerol	DOC	Decreases	*T. viride vs. S. commune on PDA*	89
Ketone	3-octanone	VOC	Increases & decreases (depending on species involved)	*H. fasciculare vs. P. velutina; R. bicolor vs. P. impudicus; P. veutina vs. P. impudicus; R. bicolor vs. H. fasciculare; H. fasciculare vs. P. impudicus; all in beech wood*	67
	Bicyclo-oct-6-en-3-one	DOC	Interaction specific	*Nodulisporium sp. intraspecific interaction on PDA*	88
Alkane	Alkanes (C7-C54)	VOC/DOC	Interaction specific	*T. viride vs. A. niger in straw powder; Nodulisporium interspecific interaction on PDA*	87, 88
Alcohol	2-methyl-1-butanol	DOC	Interaction specific	*Nodulisporium sp. vs. P. aphanidermatum on PDA*	88
Aldehyde	2,3,4-Trihydroxybutanal	DOC	Increase	*T. viride vs. S. commune on PDA*	89

Table 3. Extracellular enzyme production during antagonistic interactions. Select examples of enzymes with changes in activity detected during interspecific fungal interactions relative to growth in solo cultures. Interactions were performed in a variety of substrates, including cellulose low nutrient (CLN) broth, malt agar (MA), potato dextrose agar (PDA), wheat straw, wheat bran-neem hull-sugarcane bagasse (WNS), low nitrogen (LN) broth, spruce veneer, or across soil. The interactions reported in represent a few examples, and only a fraction of the studies that have been performed are included in the table.

Enzyme		Function	Proposed role in interactions	Change in activity	Interaction (species) reported in & substrate	Reference
Laccase (phenoloxidase)		Degradation of lignin	Detoxification of competitor metabolites; pigment production; ROS generation	Increase	*e.g. Trametes versicolor vs. Stereum gausapatum on MA; Humicola grisea vs. Trichoderma harzianum in CLN broth; Pleurotus sp. vs. Dichomitus squalens on wheat straw*	19, 95, 98
				Decrease	*e.g. T. versicolor vs. Fomes fomentarius on MA*	19
Peroxidase	Manganese peroxidase	Degradation of lignin	Detoxification of competitor metabolites; pigment production; ROS generation; enhanced nutrient uptake	Increase	*e.g. Trametes maxima vs. Paecilomyces carneus on PDA; Pleurotus ostreatus vs. Phanerochaete chrysosporium in NWS; T. versicolor vs. S. gausapatum on MA*	19, 99, 100
	Lignin peroxidase			Increase	*e.g. Pleurotus ostreatus vs. Phanerochaete chrysosporium in NWS*	99
	General peroxidase			Increase	*e.g. Phlebia radiata vs. Phlebia rufa on MA; Serpula lacrymans vs. Coniophora puteana on MA*	101, 102
Cellulase	β-glucosidase	Cellulose degradation	Enhanced nutrient uptake	Increase	*e.g. T. versicolor vs. Bjerkandera adusta on MA*	19
	α-glucosidase			Increase	*e.g. H. fasciculare vs. P. velutina on soil*	103
	Cellobiohydralase			Increase	*e.g. H. fasciculare vs. P. velutina on soil*	103
	Cellobiase			Increase	*e.g. T. versicolor vs. T. harzianum in LN broth*	104
N-acetyl glucosaminidase (chitinase)		Chitin degradation	Attack of competitor cell walls, degradation after secondary colonisation	Increase	*e.g. T. versicolor vs. Hypholoma fasciculare on MA; Fomitopsis pinicola vs. Resinicium bicolor on spruce veneer*	19, 105
Acid phosphatase		Phosphate release	Enhanced nutrient uptake	Increase	*e.g. T. versicolor vs. Daldinia concentrica on MA; H. fasciculare vs. Phanerochaete velutina on soil*	19, 103

increasing competition/combat
increasing disturbance
C
R-C
C-S
R
R-C-S
R-S
S
increasing stress
increasing disturbance
increasing competition/combat
increasing stress
r
K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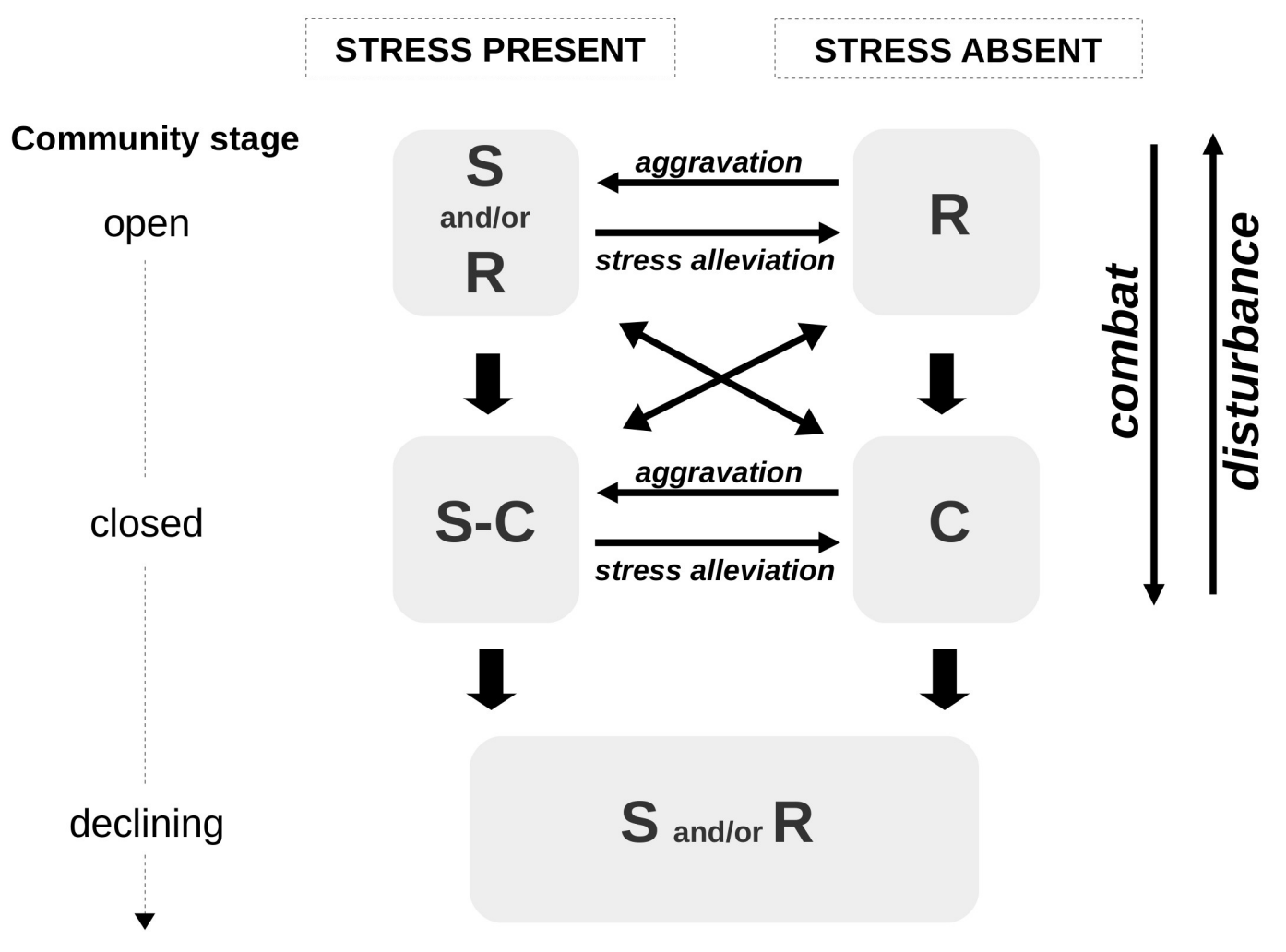
STRESS PRESENT
STRESS ABSENT
Community stage
open
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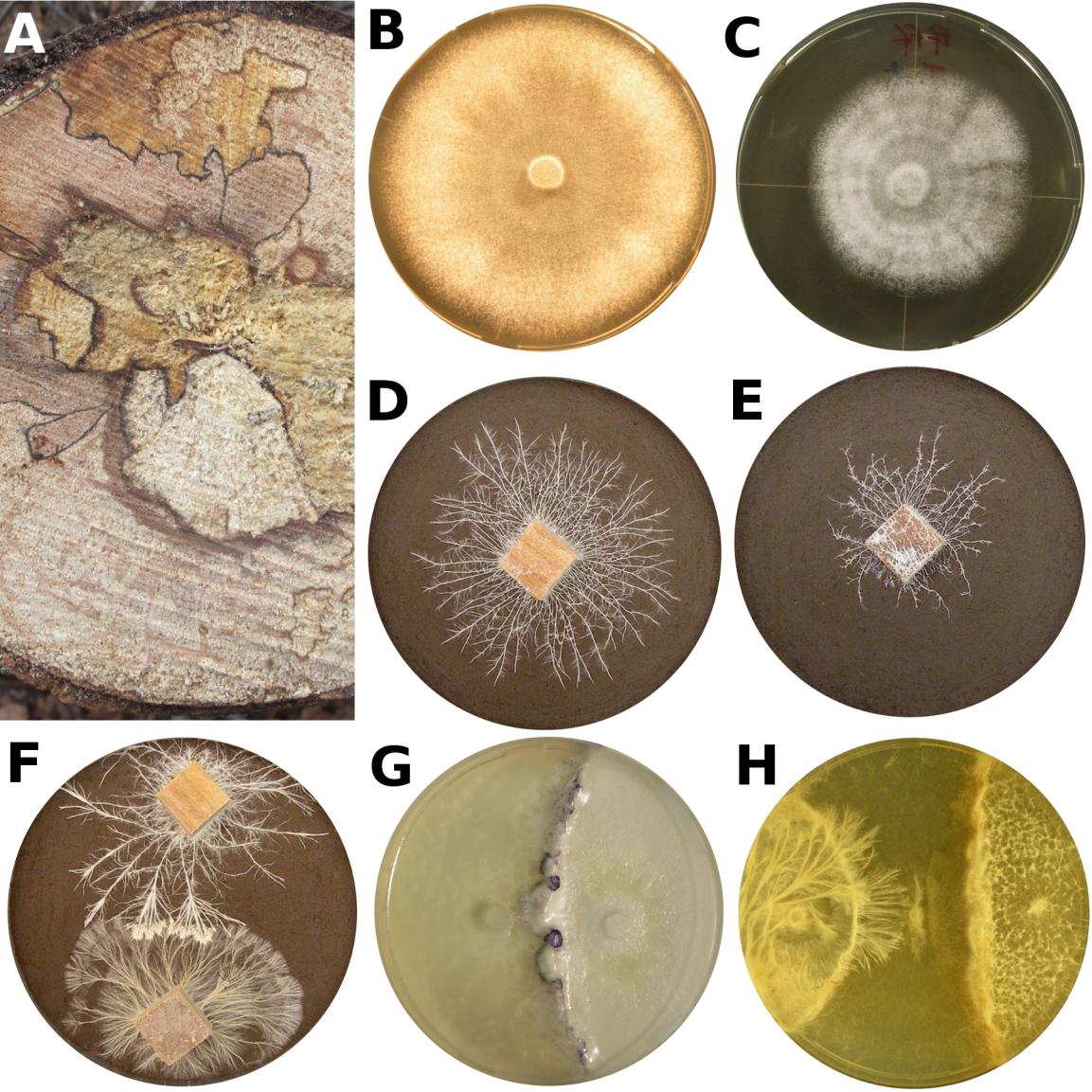
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