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Effects of pre-colonisation and temperature on interspecific fungal interactions in wood

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ABSTRACT

Understanding the effects of changing abiotic conditions on assembly history in wood decay communities is especially important with predicted environmental changes. Interspecific interactions drive community development, so it is important to understand how microclimatic environment affects outcomes of interactions between species from different successional stages in *natural* substrata. Interactions between eight wood decay fungi were performed in beech (*Fagus sylvatica*) wood at seven temperatures (12–30 °C), and in soil microcosms and wood that had been pre-colonised for different lengths of time. The hierarchy of combative ability could be altered by changes in temperature: at higher temperatures early secondary colonisers were able to outcompete usually later colonising cord-forming species. Length of pre-colonisation had a species-specific effect on combative ability, probably attributable to biochemical changes rather than the state of decay of the resource. Abiotic variables have clear effects on fungal interactions, underlining the importance of stochastic factors in fungal community succession.

1. Introduction

Saprotrophic decay fungi dominate primary wood decomposition in temperate woodlands, and are key determinants of carbon sequestration and nutrient cycling (Boddy and Watkinson, 1995; Hättenschwiler et al., 2005; Baldrian and Lindahl, 2011). Competition between mycelia for territory and the resources within is central to their ecology, and antagonistic interactions occur where there is overlap between the niches of different species or strains (Boddy, 2000). Apart from the very early and very late stages of decomposition, or under high environmental stress, community composition is determined by these antagonistic interactions. Antagonism is mediated through morphological changes such as the production of barrages and invasive cords, and metabolic changes such as the upregulation and secretion of antifungal toxins, metabolites, and oxidative enzymes (Boddy, 2000; Baldrian, 2004; Heilmann-Clausen and Boddy, 2005; Hiscox et al., 2010). Interactions either result in replacement of one mycelium by another, or deadlock, where neither mycelium can gain territory from the other, although a variety of outcomes can occur between these extremes (Boddy, 2000).

Depending on the timing of their development, the fungal community can be categorised into primary, secondary, late secondary, and end-stage colonisers. Primary colonisers are often ruderal or specialised opportunists which arrive as spores, many of which will have been latently present as endophytes within functional sapwood (Parfitt et al., 2010). The primary colonisers usually cause limited decay before they are replaced by early secondary colonisers, which likely arrive at the resource as spores and cause more extensive decomposition and utilisation of the resource (Boddy, 2000). These are in turn replaced by more combative 'later' secondary colonisers and end-stage colonisers, often arriving at the resource as mycelial cords, which are linear aggregations of hyphae

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that grow out of colonised resources, foraging for new ones (Holmer and Stenlid, 1993; Boddy and Heilmann-Clausen, 2008; Fricker and Bebber, 2008; Boddy et al., 2009). There is a general hierarchy of combative ability where primary colonisers are the least combative and late secondary colonisers the most, but these relationships are not always transitive, and certain species may outcompete others in some situations due to their tolerance of specific environmental stresses rather then through combative ability (Boddy, 2000; Boddy and Heilmann-Clausen, 2008).

Both biotic and abiotic factors have been shown to affect the progress and outcomes of interactions (e.g. invertebrate grazing, gaseous regime, water potential, substrate quality; Boddy et al., 1985; Griffith and Boddy, 1991; Crowther et al., 2014; Venugopal et al., 2016). Temperature changes can reverse outcomes of interactions between cord-forming fungi in soil (Crowther et al., 2012; A'Bear et al., 2012; A'Bear et al., 2013), because different species display contrasting sensitivities and patterns of response (Boddy, 1983a; A'Bear et al., 2013). Temperature has also been shown to alter fungal assembly history in mixed communities (Toljander et al., 2006). Temperature optima for wood decay basidiomycetes vary between species, although most are mesothermic with minimum, optimum, and maximum temperatures for growth around 5, 25, and 40 °C (Cartwright and Findlay, 1958; Magan, 2008). Fungal decomposition rates increase with temperature to similar optima (Boddy, 1986; A'Bear et al., 2012; Venugopal et al., 2016). Investigations into the effects of temperature on interactions have mostly used small shifts in temperature, and have not studied interactions between competitors from different successional stages.

Different species of fungi decompose wood at different rates and in different ways. An extreme example of this is the difference between white and brown rot fungi, which use different enzymatic processes to attack lignin to access bound cellulose and hemicellulose (Eastwood et al., 2011). However, even between white rot species, the relative proportion and location of substrates used will vary, due to differences in production and specificity of oxidative enzymes (Tuor et al., 1995; Worrall et al., 1997). Further, production and deposition of secondary metabolites differs between species, or different species may maintain a specific water potential or pH within the resource (Heilmann-Clausen and Boddy, 2005; Woodward and Boddy, 2008). Within a decaying woody resource, there would be patches of the resource in different states of structural and chemical modification, due to historical occupancy by different species (Pyle and Brown, 1999; Kubartova et al., 2012). These alterations of the resource may affect the ability of a competitor to invade the resource, and are thought to be partly responsible for determining succession and assembly history within decomposing wood (Hiscox et al., 2015). In theory, the longer a mycelium has inhabited a resource, the greater the alteration of the resource and the more difficult it would be for a competitor to invade. For example, it was found that increasing the duration of colonisation of resources by *Gloeophyllum trabeum* increased its ability to outcompete the more combative *Irpex lacteus* (Song et al., 2015). Conversely, nutrients within the resource will be depleted with increasing colonisation time, making the resident mycelium less able to mount metabolically costly antagonistic mechanisms to resist invasion or capture new territory.

The aim of this work was to investigate the effect of ambient temperature and length of colonisation on the combative abilities of eight wood decay fungi in natural substrata. Interactions were set up in beech wood blocks, to simulate conditions within a piece of decaying wood where two mycelia from adjacent regions encounter each other. Interactions were also set up in soil microcosms (colonisation length experiment only), to simulate the interactions between mycelial cords and remote resources. Firstly, the effect of temperature was investigated by incubating interacting blocks at seven temperatures spanning 12–30°C; we hypothesise that different species will vary in their temperature optima, and their ability to tolerate temperature stress, which will lead to changes in interaction outcomes at different temperatures. Secondly, interactions were set up between blocks that had been pre-colonised for short (2 or 3 months) or long (9 or 12 months) periods; we hypothesise that the longer a species has inhabited a resource, the more it will have depleted the nutrients within, so that combative ability decreases as colonisation time increases.

2. Methods

2.1. Preparation of inocula

Eight native, beech (*Fagus sylvatica*)-inhabiting fungi (Table 1) from different stages of decay were used to colonise beech wood blocks. Blocks were either 20 × 20 × 10 mm (temperature experiment; colonisation length soil interactions experiment) or 20 × 20 × 20 mm (colonisation length wood interactions experiment; Fig. 1). Blocks were sterilised by autoclaving 3 times over 72 h, then placed onto cultures of single species on 0.5% malt agar (MA: 5 g l^{-1} malt extract, 15 g l^{-1} agar; Lab M, Lancs, UK) and incubated at 20 °C in the dark, following Hiscox et al. (2010a). Blocks were pre-colonised for either 3 or 12 months for wood block interaction experiments where blocks were paired by joining together (temperature experiment; colonisation length wood interactions experiment), or for either 2 or 9 months for soil microcosm experiments. Block densities, used as an indication of amount of decay, were determined destructively at the start of experiments as dry weight/fresh volume (g cm^{-3}; 15 replicates). Radial extension rates were determined for all species at all temperatures on 2% MA (5 replicates), by inoculating a 6 mm plug of agar plus mycelium centrally and measuring two diameters perpendicular to each other over 1–6 d.

2.2. Interactions between colonised blocks

Pre-colonised blocks were scraped free of adhering mycelium and paired with cut vessels touching (wood grain running in the same direction; Fig. 1). Blocks were held together using a sterile rubber band which was removed after 5 d. Paired blocks were placed directly onto perlite (25 ml; Homebase, UK) moistened with sterile distilled water to achieve a water potential of −0.012 kPa (determined by the method of Fawcett and Collins-George, 1967), in plastic 100 ml lidded pots (Cater4you, UK). The pots were incubated at 20 °C in the dark and watered fortnightly to maintain the water potential. A hole in the pot wall (1 × 2 mm diameter) covered in microporous surgical tape (3M, UK) allowed aeration. Interaction outcomes were determined by reisolation (length of interactions varied between experiments; Fig. 1). Blocks were split in half using a sterile chisel, perpendicular to the point of contact. Pieces of wood (2 mm^3) were excised approximately 2, 7, 12 and 17 mm from the point of contact, inoculated onto 2% MA and incubated at 21 °C until mycelia had emerged and could be identified morphologically. The proportion of the two blocks colonised by each species was estimated, and interaction outcomes recorded as deadlock, partial replacement or complete replacement. Final block densities were determined from the other half of the block as dry weight/fresh volume.

Interactions between wood blocks at different temperatures were established by pairing together blocks that had been colonised for 3 months (5 replicates per temperature), and incubating at 12, 15, 18, 21, 24, 27, or 30 °C in the dark (Fig. 1A). Interaction durations varied between temperatures, and were calculated using

Table 1
Details of species used. All strains are held within the Cardiff University culture collection. Cultures were obtained through isolation from wood or fruit bodies, and their identification subsequently confirmed by sequencing of the ITS rRNA region.

Name	Ecological role	Cord-former?	Strain	Source	Type of rot	
*Hypoxylon fragiforme**	Primary coloniser	No	HpfFF1	Beech wood isolation	White – selective	(Fackler et al., 2006)
Vuilleminia comedens	Primary coloniser	No	VcWVJH1	Beech wood isolation	White (type unknown)	
Trametes versicolor	Early seconday coloniser	No	TvCCJH1	Fruit body isolation	White – simultaneous	(Ortiz et al., 2013)
Stereum hirsutum	Early seconday coloniser	No	ShSS1	Beech wood isolation	White – selective	(Lee et al., 2007)
Bjerkandera adusta	Early seconday coloniser	No	BaSS1	Fruit body isolation	White – selective	(Ortiz et al., 2013)
Hypholoma fasciculare	Late secondary coloniser	Yes	HfDD3	Fruit body isolation	White (type unknown)	
Phanerochaete velutina	Late secondary coloniser	Yes	Pv29	Beech wood isolation	White – selective	(Ortiz et al., 2013)
Resinicium bicolor	Late secondary coloniser	Yes	Rb1	Beech wood isolation	White – simultaneous	(Hakala et al., 2004)

* indicates that this species is an ascomycete, all others are basidiomycetes.

relative changes in mean extension rate of all species at each temperature (an interaction duration of 84 d at 18 °C was used as a baseline). This led to interaction durations of 137 d at 12 °C, 102 d at 15 °C, 84 d at 18 °C, 69 d at 21 °C, 63 d at 24 °C, 57 d at 27 °C, and 91 d at 30 °C. *Resinicium bicolor* was not used in this experiment.

Interactions between blocks that had been pre-colonised for different lengths of time were established by pairing together blocks that had been colonised for 3 or 12 months in all combinations (5 replicates; Fig. 1B). Interaction outcomes were determined by reisolation after 84 d of incubation at 20 °C in the dark. *Hypoxylon fragiforme* and *R. bicolor* were not used in this experiment.

2.3. Interactions in soil microcosms

The cord-formers *Hypholoma fasciculare*, *Phanerochaete velutina* and *R. bicolor*, were paired against the non-cord-forming species *Trametes versicolor* and *Bjerkandera adusta* in soil microcosms (following Crowther et al., 2011). Briefly, soil was collected from deciduous woodland (Coed Beddick, Tintern, UK; 51° 41′ 48.37″ N, 2° 40′ 53.11″ W) to a depth of 20 cm. Soil was first sieved through a 10 mm mesh, air-dried, then sieved through a 2 mm mesh before being frozen for 12 h to prevent population explosions of invertebrates. Soil was moistened with distilled water to give a water potential of −0.012 kPa, then 200 g was compacted into 24 × 24 cm bioassay trays (Nunc, UK) to a depth of 5 mm. Pre-colonised wood blocks, scraped free of adhering mycelium, were positioned on the soil surface 9 cm from opposing corners on a diagonal line, ensuring a gap of 8 cm between competing blocks. The cord-forming species were added first and allowed to grow until the mycelial front reached 5–10 mm from the intended position of the competitor, at which point the non-cord-former-colonised blocks were added. Blocks were pre-colonised for either 2 or 9 months, and paired together in all combinations (Fig. 1C). Microcosms were incubated at 20 °C in the dark, and watered weekly to maintain the soil water potential. The blocks were harvested 4–6 weeks following addition of the competitor block, and the proportion of the non-cord-former wood block captured by the cord-former was determined by excision of wood chips onto 2% MA as described above.

2.4. Scoring of interaction outcomes

The outcome of each pairing was given a score, as an aid to comparison of combative ability (following Hiscox et al., 2010a): replacement of the focal competitor by an antagonist was assigned −2; partial replacement by the antagonist, -1; deadlock, 0; partial replacement of the antagonist by the focal competitor, +1; complete replacement by the focal competitor, +2. Mutual partial replacement (one occurrence in *P. velutina vs. H. fasciculare* at 15 °C; Supplementary Table 2) was scored the same as deadlock as net territory occupation remained the same. Combative scores were determined for each species at different temperatures, and for

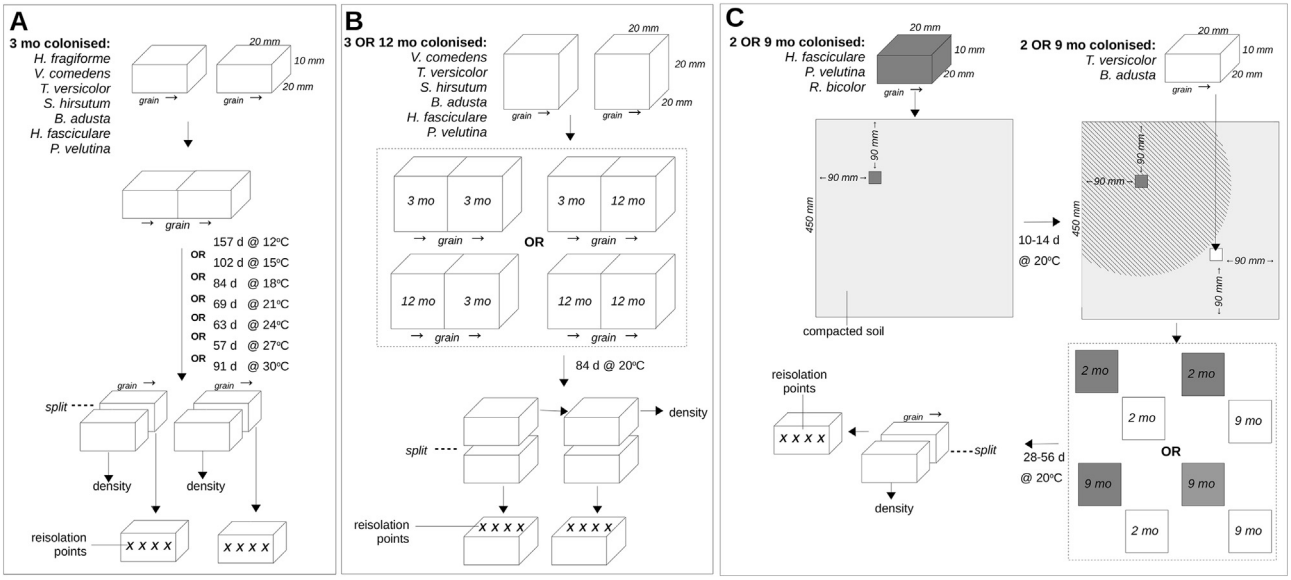

Fig. 1. Experimental set up of interactions. (A) Wood block interactions at different temperatures. (B) Interactions in wood blocks that had been pre-colonised for either 3 or 12 months (mo). (C) Interactions in soil microcosms between cord-formers and non-cord-formers that had been pre-colonised for either 2 or 9 months.

different lengths of pre-colonisation, by addition of scores from all interaction combinations normalised to the total number of interactions performed.

2.5. Image analysis

Images of the soil microcosms were taken every 3–10 d following addition of the competitor block (see Supplementary Table 1 for details). Images were processed using ImageJ (National Institute of Health, USA). Hyphal coverage (cm^2) was determined as the number of white pixels in a binary image, following manual thresholding to remove soil from the images.

2.6. Statistical analysis

Statistical analyses were carried out using R (R Core Team, 2014) or Minitab (v17; Coventry, UK), and graphs were generated using the R package ggplot2 (Wickham, 2009). The initial densities of colonised blocks, and undecayed wood, were compared using one-way ANOVA and Tukey–Kramer *a posteriori* analysis. These tests were also used to compare density loss over the course of the experiment during different interactions, and following interactions at different temperatures. A chi square test was performed to determine differences in the proportion of interaction outcomes between different treatments for each species over all interaction combinations (colonisation length and temperature experiment analysed separately). This was performed separately for species interacting in wood blocks and in soil microcosms. Outcomes between individual interaction combinations at different temperatures were compared using binary logistic regression (if 2 outcome categories occurred), or nominal logistic regression (if > 2 outcome categories occurred). Individual pairings were excluded from analyses if contamination affected >40% of the replicates for a particular treatment. Changes in hyphal area over time between different interactions were compared using a linear mixed-effects model with Tukey–Kramer *a posteriori* comparisons using the R package multcomp (Hothorn et al., 2008), and effects of repeated measurements were controlled for by using biological replicate as a random effect.

3. Results

3.1. Extension rate and decay at different temperatures

For all species the extension rate on agar (Fig. 2A) and decay rate of wood (Fig. 2B) at different temperatures were positively correlated ($t_{46} = 4.8774$, $P < 0.0001$). Patterns of change in extension and decay rates at different temperatures were not smooth or linear. In general, decay rate and extension rate of *T. versicolor*, *Stereum hirsutum* and *B. adusta* increased with temperature (although *T. versicolor* extension rate and *B. adusta* decay rate decreased from 27 to 30 °C; Fig. 2A and B). Neither extension nor decay rate of *H. fasciculare* altered much at temperatures between 12 and 21 °C or 27–30 °C, but there was a sharp increase in decay rate at 24 °C. *P. velutina* extension rate was similar between 21 and 27 °C, but decreased at 30 °C; however, the decay rate of *P. velutina* increased at 27 °C relative to lower temperatures (no data for this species at 30 °C; Fig. 2A and B). *Vuilleminia comedens* extension rate peaked at 24 °C, but decay rate did not show a similar pattern, with highest rates at 21 and 27 °C and a dip in decay rate at 24 °C. *H. fragiforme* effected little decay at any temperature, but extension rate on agar increased with temperature up to 24 °C.

3.2. Initial decay states of wood pre-colonised for different lengths of time

All of the species used caused a significant ($P < 0.05$) decrease in wood block density after all colonisation periods, with the exception of *H. fasciculare* after 3 months (Fig. 2C). There were no significant differences ($P > 0.05$) in the % weight loss between 2 and 3 months pre-colonisation, with the exception of *H. fasciculare* (Fig. 2C). Similarly, there were no significant differences ($P > 0.05$) in the % weight lost between 9 and 12 months, excepting *H. fasciculare* and *T. versicolor* which actually lost more weight in the set of blocks colonised for 9 months than the set colonised for 12 months (Fig. 2C). Decay increased between the 'short' and 'long' pre-colonisation periods for the wood interactions (3 or 12 months) and the soil interactions experiments (2 or 9 months) in all species; however this increase was not significant ($P > 0.05$) for *T. versicolor* between 3 and 12 months pre-colonisation, for *S. hirsutum* between 3 and 12 months pre-colonisation, nor for *R. bicolor* between 2 and 9 months pre-colonisation. The smaller blocks used for the soil interactions experiments (2 or 9 months pre-colonisation) lost weight relatively faster than the larger blocks used for the wood interactions experiment (3 or 12 months pre-colonisation), with weight loss rates of 0.83 mg cm^{-3} d^{-1} and 0.52 mg cm^{-3} d^{-1} respectively (across all pre-coloniser treatments).

3.3. Outcomes of interactions in beech wood blocks at different temperatures

For *H. fragiforme*, *T. versicolor* and *B. adusta*, overall combative ability increased as temperature increased (Table 2A; Fig. 3A), although caution must be taken with *H. fragiforme* as it displayed a slight increase in ability at 30 °C only. Conversely, for *H. fasciculare* and *P. velutina*, overall combative ability generally decreased as temperature increased (Table 2A; Fig. 3A). No significant ($P > 0.05$) differences in combative ability of *V. comedens* or *S. hirsutum* were detected at different temperatures (Table 2A). For all species, the proportion of interactions resulting in deadlock or partial replacement decreased as temperature increased. In some combinations, outcomes at 21 °C were inconsistent with those at adjacent temperatures.

When interaction pairings were considered individually, nine (out of 21) showed significant differences in outcomes at different temperatures (Table 3). Four pairings shifted from predominantly deadlock and partial replacement at 12 °C to complete replacement at 30 °C (pairings 1–3 & 6 in Table 3), whilst another two pairings showed complete reversal of interaction outcomes (i.e. the competitor effecting replacement switched) between 12 °C and 30 °C (pairings 4 & 8 in Table 3). Two pairings had different outcomes at both extremes of the temperature range used, compared to the outcomes at temperatures in the middle of the range; in one case complete replacement of one competitor by another was completely reversed at moderate temperatures, whereas in the other the replacement of one competitor by another was only partial, not complete (pairings 5 & 9 in Table 3). One pairing had consistent outcomes between 12 and 27 °C, but then a complete reversal at 30 °C (pairing 7 in Table 3). A further two pairings (*H. fragiforme vs. P. velutina*, and *B. adusta vs. P. velutina*) showed reversals in outcome at 30 °C compared to other temperatures, but were considered unreliable because each had only one replicate remaining due to *Trichoderma* sp. contamination (Supplementary Table 2). Contamination of blocks by *Trichoderma* sp. was most common at and above 24 °C (Supplementary Table 2).

Combative ability (score) was positively correlated with decay rate over all temperatures and species ($t_{46} = 2.2994$, $P = 0.02607$). No correlation ($t_{47} = 1.3673$, $P = 0.178$) was found between

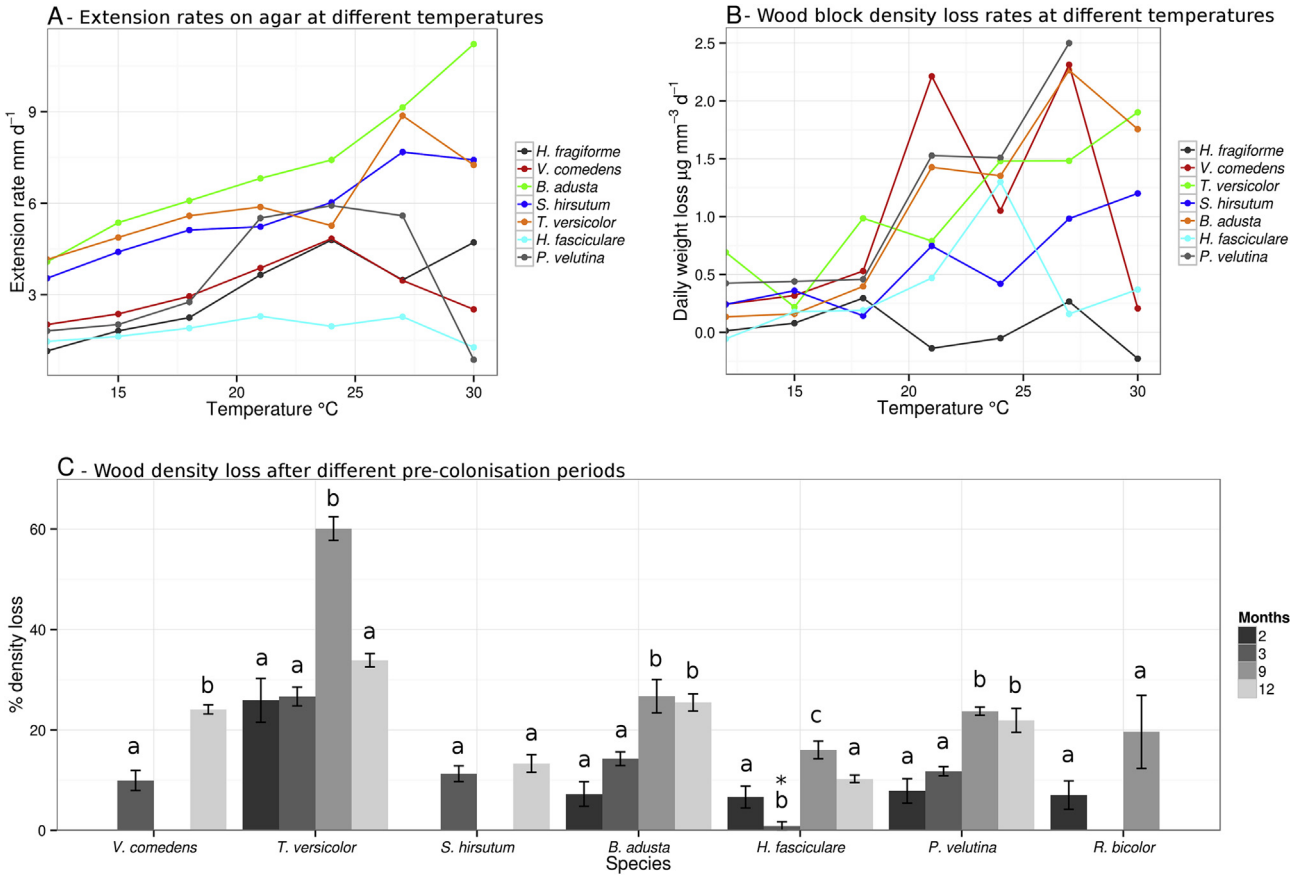

Fig. 2. Extension and decay rates at different temperatures and following different lengths of pre-colonisation. (A) Radial extension rates of fungi at seven temperatures spanning 12–30 °C (n = 5). (B) Daily weight loss of blocks colonised with different fungi at seven temperatures spanning 12–30 °C (n = 10); density loss given as a daily rate due to differences in experiment duration at different temperatures. (C) Density loss of wood blocks after different pre-colonisation periods at 20 °C (n = 15); density given as % loss relative to uncolonised wood; blocks pre-colonised for 2 or 9 months measured 2 × 2× 1 cm, whilst blocks pre-colonised for 3 or 12 months measured 2 × 2× 2 cm; bars indicate mean % density loss ± standard error of the mean; different letters indicate significant (P < 0.05) differences in % density loss between different pre-colonisation times.

combative ability and extension rate on agar. However, it is interesting to note that both the combative ability and extension rate on agar of *P. velutina* dropped sharply at 30 °C, despite no differences in decay rate at this temperature.

3.4. Outcomes of interactions in beech wood blocks at different states of decay

The profile of interaction outcomes for all species except *V. comedens* and *P. velutina* were significantly (P < 0.05) different between 3 and 12 months colonisation (Table 2B; Supplementary Table 3). For *T. versicolor*, *S. hirsutum*, and *H. fasciculare*, combative ability was negatively correlated with colonisation time, however, in *B. adusta* there was a positive correlation (Fig. 3B; Table 2B).

Combative scores do not necessarily reflect changes in 'strategy' by different species at different states of decay. The increase in *B. adusta* combative ability from 3 to 12 months pre-colonisation resulted from better defensive capabilities (fewer replacements by competitors), despite the fact that its ability to effect replacement of competitors was less at 12 than at 3 months (Fig. 3B; Table 2B). The decrease in the combative score of *H. fasciculare* at 12 compared with 3 months resulted from decreased ability to replace competitors, with more interactions resulting in marginal outcomes (i.e. deadlocks and partial replacements), but its ability to withstand replacement did not alter. For *S. hirsutum*, the observed decrease in combative ability with increasing colonisation time resulted from a shift from interactions predominantly resulting in deadlock at 3 months, to predominantly resulting in replacement of *S. hirsutum* by competitors at 12 months. Similarly, the number of replacements of *T. versicolor* by competitors doubled at 12 compared with 3 months, concurrent with a decrease in the ability of *T. versicolor* to capture territory.

3.5. Effect of pre-colonisation time on outcomes of interactions in soil microcosms

Of the three cord-forming species used, only *P. velutina* showed a negative correlation between combative ability across soil and colonisation time (Fig. 3C; Table 2C; Supplementary Table 4). *H. fasciculare* increased in combative ability across soil between 2 and 9 months pre-colonisation, which is not consistent with results from mycelial interactions within wood blocks (Table 2C; Fig. 3C). *R. bicolor* also increased in combative ability across soil at 9 compared with 2 months, effecting more partial replacements of competitors (Table 2C; Fig. 3C). Results for the non-cord-formers *T. versicolor* and *B. adusta* were consistent between soil microcosms and wood block interactions: *T. versicolor* decreased in combative ability between 2 and 9 months, whereas *B. adusta* increased in combative ability (Table 2C; Fig. 3C).

The growth and hyphal coverage of *H. fasciculare* mycelial cords was not significantly different when extending from wood pre-colonised for 2 compared with 9 months, nor against either competitor (Fig. 4; Supplementary Table 5). During interactions between *R. bicolor* mycelium and *T. versicolor*, hyphal coverage on

Table 2
Proportion of interaction outcomes in each category over all interaction combinations in (A) wood blocks at different temperatures, (B) wood blocks at different states of decay, and (C) soil microcosms at different states of decay.

Species	Temperature °C	% of outcomes in each category					No. samples included (max = 30)	No. pairings included (max = 6)	Significance?			Direction of combative ability	Combative score
		R	PR	D	pr	r			X^2	df	P		
A													
H. fragiforme	12	0	0	0	0	100	30	6	13.98	6	0.03	↓	−200
	15	0	0	0	0	100	30	6					−200
	18	0	0	0	0	100	30	6					−200
	21	0	0	0	0	100	30	6					−200
	24	0	0	0	0	100	24	5					−200
	27	0	0	0	0	100	29	6					−200
	30	0	0	0	8	92	25	5					−192
V. comedens	12	17	0	13	13	57	30	6	31.85	24	0.1309	–	−93
	15	17	0	7	10	67	30	6					−110
	18	17	0	13	7	63	30	6					−100
	21	17	0	0	10	72	29	6					−121
	24	0	0	0	0	100	9	2					−200
	27	17	0	3	3	77	30	6					−123
	30	11	7	0	0	81	27	5					−133
T. versicolor	12	37	10	27	0	27	30	6	63.85	24	<0.0001	↓	30
	15	37	7	20	0	37	30	6					7
	18	37	0	33	3	27	30	6					17
	21	73	10	0	0	17	30	6					123
	24	44	4	0	0	52	25	5					−12
	27	43	3	7	0	47	30	6					−3
	30	83	0	0	0	17	30	6					133
S. hirsutum	12	20	3	23	10	43	30	6	32.02	24	0.1266	–	−53
	15	27	7	13	13	40	30	6					−33
	18	27	7	10	20	37	30	6					−33
	21	38	10	0	10	41	29	6					−7
	24	17	4	8	8	63	24	5					−96
	27	33	0	17	0	50	30	6					−33
	30	48	0	4	4	44	27	6					4
B. adusta	12	47	3	17	0	33	30	6	43.25	18	0.0007	↓	30
	15	50	3	13	0	33	30	6					37
	18	40	10	17	0	33	30	6					23
	21	50	0	0	0	50	30	6					0
	24	58	0	4	0	38	24	5					42
	27	68	0	7	0	25	28	6					86
	30	100	0	0	0	0	25	5					200
H. fasciculare	12	93	3	0	0	3	30	6	36.8	18	0.006	↑	183
	15	80	7	10	0	3	30	6					160
	18	83	3	0	0	13	30	6					143
	21	100	0	0	0	0	29	6					200
	24	79	3	3	0	14	29	6					134
	27	77	0	7	0	17	30	6					120
	30	56	4	4	0	37	27	6					41
P. velutina	12	63	3	20	0	13	30	6	95.71	24	<0.0001	↑	103
	15	73	3	17	3	3	30	6					140
	18	77	10	7	0	7	30	6					150
	21	66	0	0	0	34	29	6					62
	24	79	0	7	3	10	29	6					134
	27	79	0	21	0	0	29	6					159
	30	0	0	0	0	100	11	3					−200

B Species	Colonisation time	Percentage of outcomes in each category					No. samples included (max = 50)	No. pairings included (max = 10)	Significance?			Direction of combative ability	Combative score
		R	PR	D	pr	r			X^2	df	P		
V. comedens	3 months	0	0	19	2	79	47	10	3.3169	2	0.1904	–	−160
	12 months	0	0	23	7	70	44	9					−148
T. versicolor	3 months	24	0	39	17	20	41	10	21.84	4	0.0002	↑	−7
	12 months	6	4	34	16	40	50	10					−80
S. hirsutum	3 months	2	2	74	5	16	43	10	39.871	4	<0.0001	↑	−30
	12 months	5	2	33	2	57	42	10					−105
B. adusta	3 months	37	2	12	0	49	41	9	16.9383	3	0.00073	↓	−22
	12 months	26	13	28	0	33	46	10					0
H. fasciculare	3 months	71	0	8	0	21	48	10	20.7086	3	0.0001	↑	100
	12 months	52	5	19	0	24	42	10					62
P. velutina	3 months	88	6	6	0	0	50	10	4.5471	2	0.1029	–	182
	12 months	81	4	15	0	0	48	10					167

C Species	Colonisation time	Percentage of outcomes in each category					No. samples included (max for Pv/Hf/Rb = 20, for Tv/Ba = 30)	No. pairings included (max for Pv/Hf/Rb = 4, for Tv/Ba = 6)	Significance?			Direction of combative ability	Combative score
		R	PR	D	pr	r			X^2	df	P		
P. velutina	2 months	75	15	10	–	–	20	4	41.7517	2	<0.0001	↑	165
	9 months	44	56	0	–	–	18	4					144
H. fasciculare	2 months	16	53	32	–	–	19	4	23.1173	2	<0.0001	↓	84
	9 months	39	22	39	–	–	18	4					100
R. bicolor	2 months	0	6	94	–	–	18	4	4.9128	1	0.0267	↓	6
	9 months	0	17	83	–	–	18	4					17
T. versicolor	2 months	–	–	36	46	18	28	6	35.5449	2	<0.0001	↑	−82
	9 months	–	–	8	42	50	26	6					−142
B. adusta	2 months	–	–	45	17	38	29	6	20.586	2	<0.0001	↓	−93
	9 months	–	–	79	7	14	28	6					−36

Outcomes are defined as R, replacement of competitor by focal species; PR, partial replacement of competitor; D, deadlock; pr, partial replacement of focal species by competitor; r, complete replacement by competitor. Significant differences between profiles from interactions at different temperatures, or between profiles from interactions at different states of decay, were determined by multinomial regression. The number of replicates included are given for each species at each temperature or state of decay; these values may be less than the maximum possible (given in column header) because of loss of replicates due to contamination. If > 2/5 of the replicates from any given pairing were lost due to contamination that pairing was excluded from subsequent analyses and this table; this is given in the number of pairings included column (maximum possible given in column header). Full details of interaction outcomes are given in Supplementary Tables 2–4.

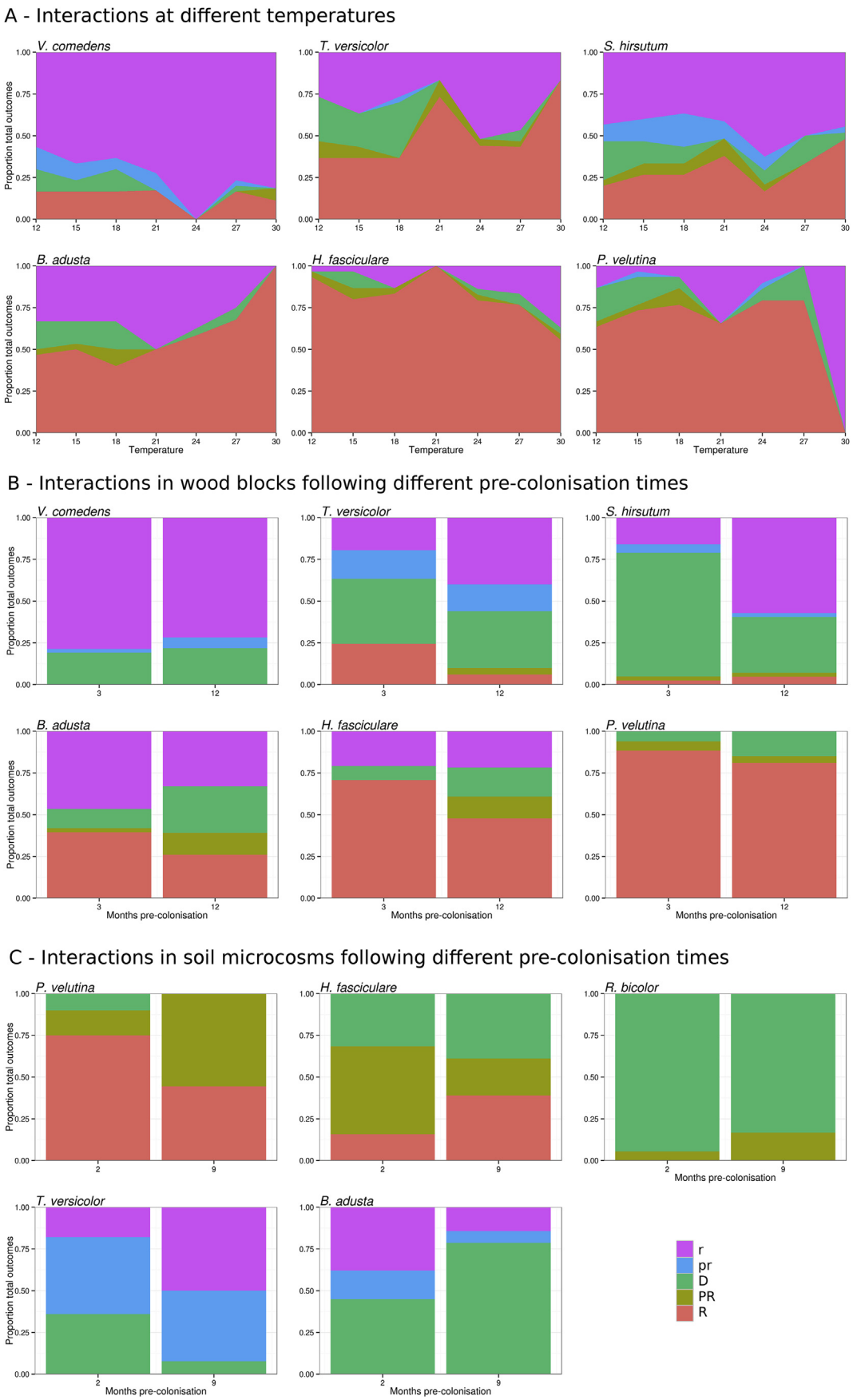

Fig. 3. Proportion of outcomes in different categories for individual species, over all interactions conducted, between (A) different temperatures, (B) 3 and 12 months colonisation in wood block interactions, and (C) 2 and 9 months colonisation in soil microcosm interactions. R, replacement of competitors by focal species; PR, partial replacement of competitors by focal species; D, deadlock; pr, partial replacement of focal species by competitors; r, complete replacement of focal species by competitors.

Table 3
Individual pairings where there were significant changes in outcomes at different temperatures.

	Interaction	Outcomes														Pattern/Comments
		12 °C		15 °C		18 °C		21 °C		24 °C		27 °C		30 °C		
1	*V. comedens vs. S. hirsutum*	r1 D3 pr1	*	r3 pr2	*†	r3 pr2	*†	pr3 r1	*	–		r	†	r	†	Gradual partial reversal of outcome (predominantly D to r)
2	*V. comedens vs. T. versicolor*	r1 D1 pr3	*	r2 D2 pr1	*†‡	D4 r1	†	r	‡	–		D1 pr1 r3	*†‡	r	‡	Gradual partial reversal of outcome (predominantly pr to r)
3	*B. adusta vs. T. versicolor*	D	*	D4 R1	*	D4 PR1	*	**r**	†	R	‡	R	‡	R	‡	Gradual partial reversal of outcome (D to R)
4	*B. adusta vs. H. fasciculare*	r	*	r	*	r	*	r	*	D1 r4	*	D2 r3	*	R	†	Gradual total reversal of outcome (r to R)
5	*S. hirsutum vs. T. versicolor*	r	*	r4 pr1	*†	r4 D1	*	pr3 r2	†	pr1 r4	*†	r	*	r	*	Different outcomes at extreme vs. moderate temp's
6	*S. hirsutum vs. P. velutina*	D4 pr1	*†	D3 pr1 r1	*†	pr3 r1 D1	*	**R**	‡	PR1 D2 r1	*†	D	†	R3	‡	Gradual partial reversal of outcome (predominantly D to R)
7	*T. versicolor vs. H. fasciculare*	r	*	r	*	r	*	r	*	r	*	r	*	R	†	Swift reversal of outcome at 30 °C
8	*T. versicolor vs. P. velutina*	D2 r3	*	r	*	r3 D1 R1	*	**R**	†	R2 r3	*	D1 r4	*	R	†	Gradual reversal of outcome (D/r to R)
9	*H. fasciculare vs. P. velutina*	R4 r1	*†	r1 D2 R1 PR1	*†‡	R1 r4	*‡$	r4	‡$	R1 r4	*‡$	r	$	R3	†	Different outcomes at extreme vs. moderate temp's

Different symbols indicate a significant ($P < 0.05$) difference in the proportion of outcomes occurring at different temperatures; the same symbol at different temperatures indicates no significant differences ($P > 0.05$) between proportions of outcomes at these temperatures. R, replacement by the competitor listed on the left hand side; PR, partial replacement by the competitor on the left; D, deadlock; pr, partial replacement by the competitor on the right hand side; r, replacement by the competitor on the right hand side. Where outcomes are underlined, this indicates a deviation in the pattern of outcomes relative to the neighbouring temperatures. Number of replicates performed for each pairing at each temperature was 5, where no number is given all 5 replicates had the same outcome, and different numbers indicate the number of replicates recorded for each outcome class (in some cases total number of replicates may not add up to 5 because of losses due to contamination).

the soil surface was lower where interactions involved *T. versicolor* in wood pre-colonised for 9 compared to 2 months, although differences were only sporadically significant (Fig. 4). During interactions between *R. bicolor* and *B. adusta*, by 27–30 d after addition of the block containing *B. adusta* there was significantly ($P < 0.05$) higher hyphal coverage of soil by *R. bicolor* emanating from wood pre-colonised for 2 months *vs. B. adusta* in wood pre-colonised for 2 months compared to all other decay state combinations (Fig. 4). This was not reflected in the interaction outcomes, which were deadlock for all combinations, i.e. *R. bicolor* did not ingress into any *B. adusta* pre-colonised wood (Table 2C).

Hyphal coverage on soil of *P. velutina*, emanating from blocks pre-colonised for 9 months, decreased relative to other combinations 11 d after the cords encountered blocks pre-colonised with *T. versicolor* for 9 months. However, by the end of the experiment there were no differences in hyphal coverage between all interaction combinations, and the extent of replacement of *T. versicolor* was similar (Fig. 4; Table 2C; Supplementary Table 5). During interactions between *P. velutina* mycelial systems and wood blocks pre-colonised with *B. adusta*, hyphal coverage of *P. velutina* emanating from blocks pre-colonised for 2 months, interacting with *B. adusta* in blocks pre-colonised for 9 months, was significantly lower than in at least one other combination from 11 d onwards. Conversely, hyphal coverage of *P. velutina* emanating from blocks pre-colonised for 9 months, interacting with *B. adusta* in blocks pre-colonised for 2 months, was significantly higher than all other combinations from 11 d onwards (Fig. 4).

4. Discussion

Both temperature and length of pre-colonisation affected the combative ability of wood decay fungi, and altered the interaction outcomes in almost half of the species combinations studied. These factors are thus highly important in determining fungal community composition and development, which will have implications for the rate of decay of resources, and ultimately the carbon turnover in woodland ecosystems (Woodward and Boddy, 2008). In general, the expected combative hierarchy was upheld: later secondary colonisers (*P. velutina*, *H. fasciculare*, *R. bicolor*) were more combative than early secondary colonisers (*T. versicolor*, *B. adusta*, *S. hirsutum*), which in turn were more combative than primary colonisers (*V. comedens*, *H. fragiforme*). However, as temperatures increased, the combative abilities of later secondary colonisers decreased whilst that of early secondary colonisers increased or remained the same, shifting this hierarchy in favour of the early secondary colonisers. The effect of pre-colonisation length on combative ability was less straightforward, with different species exhibiting different responses independent of their position in the successional community.

Combative ability at different temperatures is linked to optima for growth: the extension and decay rates for the cord-forming later secondary colonisers decreased at higher temperatures, concurrent with their decreased combative ability. Conversely, the extension and decay rates of the early secondary colonisers continued to increase at higher temperatures, and so did their combative ability. The lower temperature optima of cord-forming species concurs with previous studies (Boddy, 1983a; Dowson et al., 1988; Wells and Boddy, 1995; A'Bear et al., 2013), and may indicate an adaptation to more exposed conditions: mycelial cords grow through the litter layer, so cord-formers would need to be able to withstand lower winter temperatures than early secondary colonisers, which would be relatively insulated within wood (Boddy, 1999).

Of the twenty-one interaction combinations studied, nine exhibited changes in outcomes at different temperatures, which can mostly be explained by differences in temperature optima between the competitors. Complete reversals in interaction outcomes occurred relatively rarely, but could be caused by as little as a 3°C change. The predicted range of global temperature increase due to climate change is 0.3–4.8 °C by 2100 (IPCC, 2014), so if even half this estimate is realised then significant changes in fungal community composition, and hence possibly ecosystem function, would be expected. Seasonal fluctuations in temperature may also result in shifts in community structure. Currently, temperatures

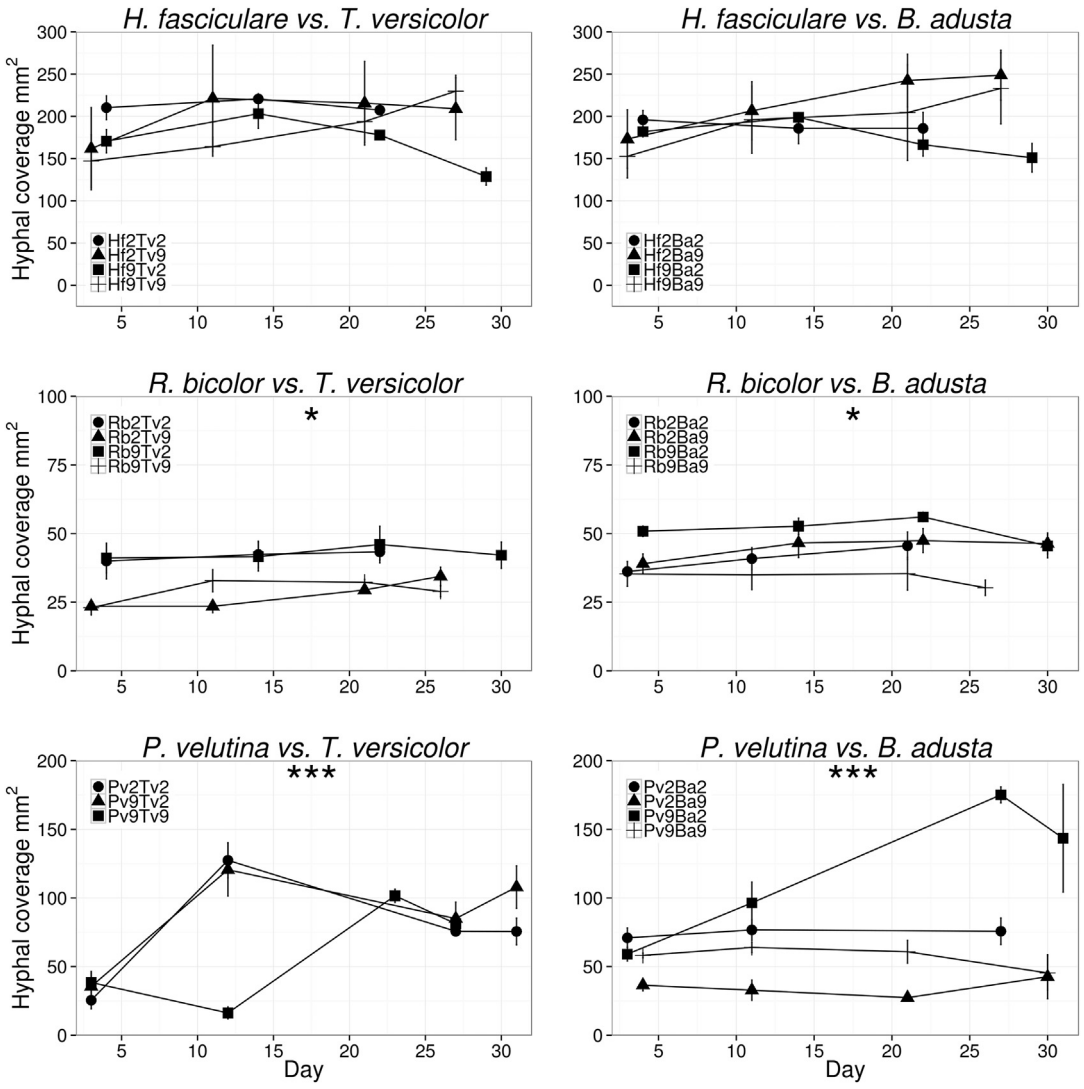

Fig. 4. Changes in hyphal coverage of cord forming fungi during interactions between combatants at different decay states in soil trays. Hyphal coverage of cord formers over the time course of the interaction was measured at 4 time points, detailed in Supplementary Table 1. Points indicate the mean hyphal coverage (n = 5) ± standard error of the mean. Hf, *H. fasciculare*; Tv, *T. versicolor*; Ba, *B. adusta*; Rb, *R. bicolor*; Pv, *P. velutina*; 2, 2 month colonised block; 9, 9 month colonised block. Significant differences in the changes in hyphal coverage between different interactions at one or more time points are indicated as: *, $P < 0.05$; ***, $P < 0.001$ (see Supplementary Table 5 for further detail).

within United Kingdom woodlands rarely exceed 20 °C, and fluctuate within the range at which the combative hierarchy of cord-formers > early secondary colonisers > primary colonisers is maintained (Boddy, 1983b). However, this hierarchy may regularly be challenged in the face of predicted extreme weather events (IPCC, 2014).

As temperature increased, interaction outcomes became more extreme: fewer deadlocks and partial replacements were recorded. This could be an effect of temperature stress reducing the ability of a competitor to mount defences, but it could indicate that the outcomes had not fully resolved at lower temperatures. In this case, using relative growth rate on agar may not be a good determinant of the length of time needed for interactions to resolve themselves at different temperatures. In five wood block interactions the outcomes at 21 °C seem anomalous in that they defy a trend established across the other six temperatures; three of these interactions show 21 °C outcomes that match those at 30 °C. These anomalies are possibly the result of temperature variation in the incubator used for the 21 °C interactions, or due to uneven colonisation of wood blocks, or an artefact of low replicate numbers. Rates of contamination of wood blocks were highest at 24 °C, and rarely occurred at lower temperatures. Contamination was mostly attributable to *Trichoderma* sp., and the increased susceptibility of wood decayers to this mycoparasite at higher temperatures is likely linked to its optimal growth temperature of 25–30 °C (Singh et al., 2014).

Changes in combative ability following different pre-colonisation lengths were species-specific and not associated with the position of a species in the successional community. Neither were they consistent between wood block interactions and soil microcosm interactions. Patterns were more nuanced than can be summarised by combative scores: for example, the increased combative score of *B. adusta* in wood that had been pre-colonised for longer reflected its increased ability to withstand replacement, whilst it was actually less successful at replacing competitors. It is likely that the longer a mycelium inhabits a resource, the more chemical and physical modifications it causes, making conditions less optimal for potential invaders and acting as a constitutive defence. Modifications may include depletion of key nutrients, alteration of pH and/or water potential, or accumulation

of secondary metabolites (Worrall et al., 1997; Boddy and Heilmann-Clausen, 2008; Tudor et al., 2013).

For most of the species used here, longer (9 or 12 months) periods of pre-colonisation resulted in wood blocks that were more decayed than shorter periods (2 or 3 months). However, this was not the case for *T. versicolor* and *S. hirsutum* where no significant density loss was detected for blocks pre-colonised between 3 and 12 months. Both of these species were much less combative after longer periods of pre-colonisation, perhaps suggesting depletion of one or more key nutrients necessary to support continued decomposition of the resource and the increased metabolic demand imposed by antagonism (Hiscox et al., 2015a). Conversely, when *T. versicolor* was inoculated into smaller blocks for 2 or 9 months (rather than the larger cubes colonised for 3 and 12 months), it caused extensive decay. In general, the smaller blocks decayed relatively more rapidly than the larger blocks, possibly because the greater surface area:volume ratio of the smaller blocks allowed increased oxygenation of tissues (Harmon et al., 1986, 1995).

Differences in colonisation length of resources did not lead to changes in the dynamics of mycelial cord development in the soil microcosms, although the success of new resource invasions by these cords was affected in a combination-specific manner. Hyphal coverage of soil by cord-forming fungi was not affected by the pre-colonisation length of the resource inhabited by the cord-former, implying that there were either ample nutrients available even after longer pre-colonisation periods, or that nutrients were acquired from the soil. However, hyphal coverage was affected by certain interactions, similar to previous findings for cord-forming fungi (Boddy and Donnelly, 2001). *P. velutina* and *R. bicolor* both showed greater hyphal coverage in successful interactions (i.e. where territory was captured from the non-cord-former) compared to unsuccessful interactions (i.e. where no territory was captured from the non-cord-former block). This may suggest that unsuccessful interactions required more energy expenditure by the cord-former, leaving them with less to use for increasing the size of their cord network than during/following successful interactions.

5. Conclusions

Abiotic variables are important modifiers of the outcome of fungal interactions within wood, and between mycelial cords and fungi already established in wood. Microclimate is of key importance, with relatively small changes in ambient temperature altering interaction outcomes and thus the assembly history of the decomposer community. Predicted global warming will likely lead to shifts in fungal community structure, and thus the decomposition rates of woody resources, the extent of which will depend on the actual temperatures achieved and the degree of annual and shorter term temperature fluctuations. Assembly history is also affected by the pre-colonisation length of the resources in which interactions occur, likely due to factors associated with duration of colonisation, and accumulation or depletion of metabolites, rather than the extent of decay itself, at least during early stages of the decay process like those studied here.

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Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.funeco.2016.01.011.

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