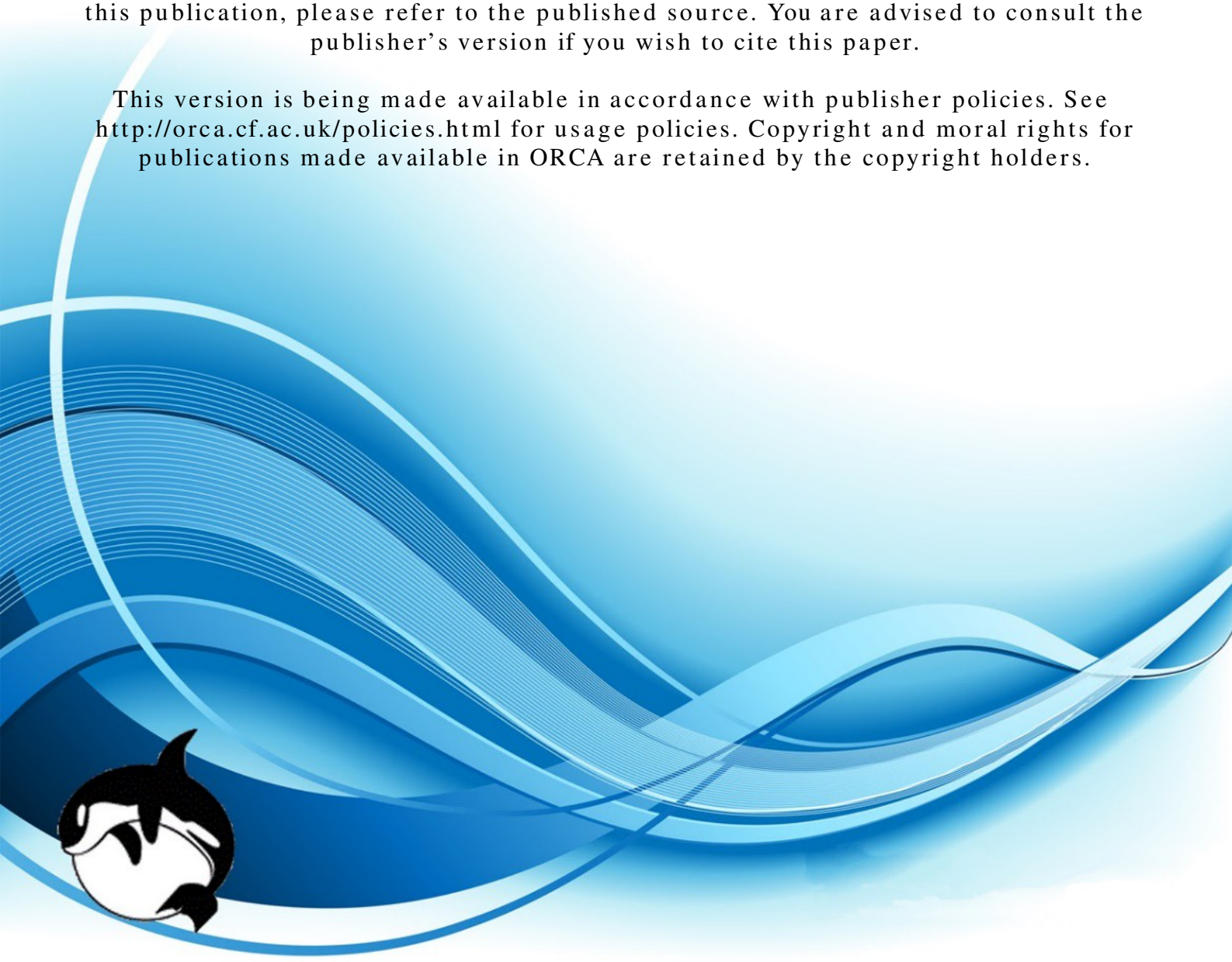

Inoculum volume effects on competitive outcome and wood decay rate of brown- and white-rot basidiomycetes

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Abstract

Theory predicts that the energetic cost of competition between fungal mycelia might accelerate or retard the rate of wood decomposition, depending on various factors. To evaluate the effect of occupied territory on wood decay rate and competitive outcome, we set up a pairing competition experiment using beech wood blocks colonised by three brown-rot and three white-rot basidiomycetes. All white-brown combinations (totalling nine), and five ratios of wood volume (4:0, 3:1, 2:2, 1:3, 0:4) were performed. Pairings

were incubated in the dark at 20˚C for 3 months, and then competition outcome and wood weight loss were determined. Mycelia occupying larger territory were more competitive than mycelia occupying smaller territory. There were negative relationships between wood volume and percentage wood weight loss. Wood decay was slower at the competition front than at the rear of the wood blocks in some cases. These results suggest that wood volume (territory size) affects both competition outcome and wood decay rate in basidiomycete communities.

Keywords: antagonism; competition, mycelial interaction, wood decomposition

Introduction

Wood decay basidiomycetes are the major agents of lignocellulose decomposition in forest ecosystems, and thus have a central role in global carbon cycling (Rayner & Boddy 1988). Since more than 70 Pg carbon is estimated to be stocked in dead wood world-wide (Pan et al. 2010), understanding relationships between basidiomycete

community dynamics and wood decay is crucial for modelling and predicting ecosystem function under environmental change (Bradford et al. 2014).

Competition is the predominant type of interaction determining community development of wood decay basidiomycetes (Boddy 2000; Boddy & Hiscox 2016). With primary colonisers, competition is initially for unoccupied territory within wood, and then combat (antagonism) in defence of territory or acquirement of more territory. With later colonisers, competition is largely for space already occupied by decay fungi, i.e. combat. Outcome of combative interactions can be: replacement, where one fungus takes territory from another; deadlock, when neither fungus obtains additional territory; and even reciprocal replacement, where one fungus gains territory from the other in one region, but loses it elsewhere (Boddy 2000; Boddy & Hiscox 2016). There is a hierarchy of combative ability with later colonisers typically more combative than earlier colonisers, reflecting order of fungal succession in the dead wood decomposition process in natural ecosystems. Within this general hierarchy there are intransitive situations, i.e. species A replaces B, B replaces C, but C replaces A. This is probably due to species employing different antagonistic mechanisms (Hiscox et al. 2018). Also,

abiotic variables, such as temperature, water potential and state of decay, can affect the outcome (Wells & Boddy 2002; Hiscox et al. 2016, 2018), as can grazing invertebrates (Crowther et al. 2011, 2012), bacteria (Johnston et al. 2016), and the presence of other fungal competitors (Hiscox et al. 2017; O'Leary et al. 2018). Resource availability (territory) also influences outcome of interactions; even fungal species that are relatively weak competitors can sometimes replace stronger competitors if the former occupies more territory than the latter (Holmer & Stenlid 1993; Song et al. 2015).

Numerous laboratory studies have revealed that competitive interactions between wood decay basidiomycetes result in increased CO_2 efflux, and increased production of extracellular enzymes and secondary metabolites (Evans et al. 2008; Hiscox et al. 2010; Hiscox et al. 2015; El Ariebi et al. 2016; Maynard et al. 2017a, b; O'Leary et al. 2019). Thus, competition is clearly energetically expensive. Such energetic costs may be met by accelerated wood decay (Wells & Boddy 2002; Hiscox et al. 2015; O'Leary et al. 2019). However, interspecific interactions can sometimes retard decomposition (Toljander et al. 2006; Fukami et al. 2010; Hiscox et al. 2015) if a fungal mycelium allocates disproportionally more stored energy to competition (i.e. producing

extracellular enzymes and secondary metabolites to reduce activities of competitor) than to wood decay (i.e. production of enzymes for wood decay) (Woodward & Boddy 2008; Gessner et al. 2010). There is some evidence that highly intransitive communities comprising weak competitors exhibit positive diversity-function relationships, whereas weakly intransitive communities comprising strong competitors exhibit negative relationships (Maynard et al. 2017a). However, what determines positive and negative effects of fungal competition on wood decay is poorly understood. In the present study, we focus on the effects of resource availability on fungal competition and wood decay. We hypothesised that competition accelerates wood decay rate in smaller territory than in larger territory (hypothesis 1). If competition costs equal amount of energy in both of the competitors, mycelia occupying smaller territory may use up their resources relatively faster (i.e. decay faster) than mycelia occupying larger territory to obtain a similar absolute amount of carbon and energy (Hughes & Boddy 1994, 1996).

Interspecific differences in extracellular enzyme production is another important factor affecting competition and wood decay, since they are crucial to both activities (Baldrian 2004; Chi et al. 2007; Hiscox et al. 2010; Hiscox & Boddy 2017). Though the

situation is more complex, wood decay basidiomycetes were traditionally categorized into two distinct but evolutionally related functional groups: white-rot and brown-rot fungi according to their extracellular enzyme profiles (Floudas et al. 2012; Nagy et al. 2015). Lignin, a recalcitrant carbon matrix, can be decomposed by white-rot fungi, often simultaneously with carbohydrates (cellulose and hemicellulose). In contrast, brown-rot fungi remove carbohydrates, but the majority of lignin remains (Riley et al. 2014), thus they do not need to allocate energy for breaking down lignin, and are predicted to be energetically more efficient in wood decomposition than are white-rot fungi, allowing brown-rot fungi to allocate more energy to competition. Thus, it is hypothesized that competition may have a smaller effect on wood decomposition by brown-rot fungi than by white-rot fungi. To test this second hypothesis, white- and brown-rot basidiomycete species were compared in the experiment.

Materials and methods

Preparation of colonised wood blocks

Wood blocks colonised by three brown- and three white-rot basidiomycetes (Table 1) were prepared by incubating 2 x 2 x 2 cm beech wood blocks on colonised 0.5 % malt extract agar (MA: 5 g l^{-1} malt extract, 15 g l^{-1} agar; Lab M, Kances, UK) at 20˚C in the dark for 3 months (following Hiscox et al. 2015). Isolates were chosen to display a range of interaction outcomes. The initial wood density of the colonised blocks was determined as dry weight/fresh volume (10–12 replicates, destructively sampled). There were no significant differences in wood density, percentage weight loss, and water content between the blocks colonised with different species at the start of the experiment (0.53 g cm^{-3}; df = 5, $F = 2.357$, $P = 0.0507$; Fig. S1).

Microcosm competition experiment

Four pre-colonised blocks, scraped free of surface mycelia, were arranged linearly with cut vessels touching and held together with a sterile rubber band which was removed after 1 week. Competitions were set up in all white-brown combinations (totalling 9 combinations). For each combination, five inoculum:volume ratios were

established (Fig. 1): (1) all of the four blocks were inoculated with a white-rot species (W4_B0, control); (2) three blocks with a white- and one block with a brown-rot species (W3_B1); (3) both of the white- and brown-rot species with two blocks each (W2_B2); (4) one block with a white-rot species and three blocks with a brown-rot species (W1_B3); (5) all of the four blocks with a brown-rot species (W0_B4, control). Seven replicates were prepared for each treatment. Combined blocks were placed directly onto perlite (60 ml; medium grade, 3–6 mm) moistened with sterile distilled water to achieve a water potential of –0.012 MPa, in 400 ml plastic pots with lids (DK8900, toppac, Denmark). Four holes (1 mm diameter) covered in microporous surgical tape (3M, Bracknell, UK) allowed aeration. The pots were incubated at 20˚C in the dark for another 3 months, and watered every 2 weeks to maintain moisture.

At the end of the experiment, blocks were separated and split in half, perpendicular to the side of contact, using a sterile chisel. Pieces of wood (2 mm^3) were excised approximately 2, 7, 12, and 17 mm from the side of contact, placed onto 2 % MA and incubated at 20˚C until mycelium had emerged and could be identified morphologically. The competition outcomes were recorded as deadlock (where neither of the white- or

brown-rot fungi invaded wood blocks of the competitor), white replaced (where white-rot fungi invaded wood blocks initially colonised by brown-rot fungi), brown replaced (where brown-rot fungi invaded wood blocks initially colonised by white-rot fungi), and reciprocal replacement (where the white-rot fungus invaded territory of a brown-rot competitor in one region, and *vice versa* in another region). Replacement recorded here includes both complete replacement, where the incumbent species was completely replaced in all parts of the wood block or the partial replacement, where it was only replaced from part of the wood blocks. Final wood densities were determined from the other half of the block as dry weight/fresh volume. Weight loss (%) was calculated as:

% Weight loss = (initial density – density after the experiment)/initial density x 100

Total weight loss from the wood initially occupied by a fungus, and whose territory was not captured, was estimated by averaging the weight loss from each of the individual blocks.

Data analysis

All statistical analyses were conducted using R software (R Core Team 2018). A chi square test was performed using the pwr package to determine differences in the proportion of competition outcomes between different ratios of inoculum volume for each species combination. Among the four outcomes recorded (i.e. brown replaced, deadlock, reciprocal replacement, and white replaced), we selected 'white replaced' to be tested by a chi square test because this outcome was the most commonly recorded in the majority of the combinations, except for *Vuilleminia comedens* vs. *Fomitopsis pinicola*. Block weight losses were compared using non-parametric tests because of the lack of homogeneity of variance between treatments (Bartlett test, $P > 0.05$). Steel Dwass tests were performed for multiple comparisons among different volume ratios within each combination or among wood blocks within each volume ratio treatment using script provided by S. Aoki (http://aoki2.si.gunma-u.ac.jp/R/Steel-Dwass.html, accessed 10 June 2019). Wilcoxon tests were used for pairwise comparisons between the two wood blocks in W2_B2 combinations.

Results

Competition outcomes

White rot fungi replaced brown-rot fungi in 106 (of 189) pairings, brown-rot fungi replaced white-rot fungi in 64 pairings, there was deadlock in 18 pairings, and there was reciprocal replacement in one pairing (Fig. 2). *Hypholoma fasciculare* replaced *Coniophora puteana* and *Laetiporus sulphureus* regardless of the volume ratio of their wood blocks. *Trametes versicolor* and *F. pinicola* also replaced *C. puteana* and *V. comedens*, respectively, regardless of the volume ratio. In the combinations of *T. versicolor* vs. *F. pinicola*, and *V. comedens* vs. *C. puteana*, outcome of interactions varied significantly depending on the volume ratio of wood blocks; white-rot fungi (*T. versicolor* and *V. comedens*) tended to replace brown-rot fungi more frequently when they had a larger volume of wood blocks.

Wood decay rate

On average, control wood blocks (pure cultures) lost 11.4% of their weight after the

3 month during which the interaction experiment ran, and decay rate was significantly different among the six fungal species (Fig. 3). *T. versicolor* was the fastest decayer and *H. fasciculare* the slowest. Decay rates of the sets of four competition wood blocks were not significantly different from one or sometimes both of the control sets of four wood blocks of the two competitors (Fig. 4).

In replacement interactions decay was a result of the initial incumbent and the replacing species. It was not possible to aportion the amount of decay between the two. So, we also analysed the effect of competition and wood volume when data of 'replaced' wood blocks were removed from the analyses (Fig. 5). *V. comedens* decayed wood more rapidly when competing with *C. puteana* than when growing alone, particularly when *V. comedens* had the smallest wood volume (W1_B3) (Fig. 5A). No other combinations showed effects of competition and wood volume on wood decomposition rate.

In W3_B1 combinations of *V. comedens* competing with *C. puteana*, the central block (block# II) of the three *V. comedens* blocks decayed significantly more rapidly than the block on either side (Fig. 5A). In wood blocks of *L. sulphureus* in W1_B3 combinations competing with *T. versicolor*, the block at the further side from the

interaction front decayed significantly more rapidly than the block at the interaction front (block# II) (Fig. 5B). Weight losses in those wood blocks of *V. comedens* and *L. sulphureus* were, however, not significantly different from that of any control wood blocks of the focal species ($P < 0.05$, Steel Dwass test). Thus the data indicated heterogeneous wood decay within a mycelium under competition, but did not indicate any stimulation or reduction in wood decay in these mycelia.

Discussion

We confirmed that the size of the wood volume occupied affects the outcome of competition and percentage decay rate of the wood. Interestingly, there were sometimes differences in percentage decay rate at different locations within occupied wood territory only in the competition microcosms.

Effect of territory size on competition outcome

As is often the case, the later secondary coloniser (*H. fasciculare*) was more combative than early secondary colonisers (*T. versicolor*, *F. pinicola*, *L. sulphureus*), which in turn were more combative than primary colonisers (*V. comedens*, *C. puteana*) (Fig. 2). Also, as predicted by previous work (Holmer & Stenlid 1993; Sturrock et al. 2002; Song et al. 2015; O'Leary et al. 2018), when generally poorer competitors occupied larger territory, their combative success improves (Fig. 2). This is probably attributable to the fact that the fungi occupying larger wood volumes have larger available energy for defensive and antagonistic mechanisms. Previous studies have shown that antagonism has energetic costs for production of thickened hyphal mats, enzymes and increased production of secondary metabolites (Boddy et al. 1989; Evans et al. 2008; Hiscox et al. 2010; Hiscox et al. 2015; El Ariebi et al. 2016; Maynard et al. 2017a, b; O'Leary et al. 2019). Nevertheless, a very strong competitor, such as *H. fasciculare*, was still able to replace other competitors occupying larger territory (1:3) even when *H. fasciculare* occupied the smallest (Fig. 2), as seen with the strong competitor *Antrodiella citrinella* in an earlier study (Holmer & Stenlid 1997).

Effect of competition and wood volume on wood decay rate

There was a negative relationship between wood volume and percentage wood weight loss (Fig. 5) as predicted by our hypothesis 1. However, since we did not test monocultures in different territory volumes, we could not say whether this negative relationship between wood volume and decay is due to the competition or not. In general, mass loss rate of smaller wood blocks is expected to be greater than that of larger ones if the decomposer organisms utilize the same amount of carbon per unit time (Yoneda 1982, 1985; Hughes & Boddy 1996). In the present study, the total energetic cost may be similar in all combinations of volume because the area of interaction front was unified to 4 cm^2 in all treatments. Further, greater surface area:volume ratio of smaller wood blocks can accelerate gaseous exchange between the inside and outside of the block compared to that of a larger block, which may stimulate decomposition (Harmon et al. 1986, 1995).

Interestingly, in two cases (*V. comedens* blocks coupled with *C. puteana*; *L. sulphureus* blocks coupled with *T. versicolor*), decay rate was significantly different among the three individual blocks of the same fungus within each experiment (Fig. 5).

Decay rate in the ‘central’ wood blocks was greater than in the blocks closest to and furthest from the interaction front. It is not surprising that decay rate varies depending on position within a mycelium because hyphal physiological activity differs in different regions of a mycelium (Zhang et al. 2016). Although previous studies have reported elevated activities of some oxidative enzymes and cellulases at the interaction front of competing wood decay basidiomycetes (Baldrian 2004; Hiscox et al. 2010; Boddy & Hiscox 2016), the present study suggests that these enzymes may not be directly associated with wood decay, because wood decomposition was not accelerated at the interaction front. As discussed previously, these enzymes activated at the interaction front may be for defensive or attacking aspects of combat, such as removing active oxygen species produced due to the physiological stresses for competition (Baldrian 2004; Iakovlev et al. 2004; Hiscox & Boddy 2017). Whether the relative difference in wood decay is restricted to the interaction front or occurs over a wider area may be affected by competition strategies of fungi. If a fungus relies mainly on physical defense or using only diffusible metabolites for competition, interactive response by the competitor may be restricted to the area directly touching the antagonist. However, if a

fungus also uses volatile compounds (VOC), response by the competitor might be observed over a wider area in the outer wood blocks. Fungal VOC production is strongly dependent on fungal species and the combination of species pairings (Boddy & Hiscox 2016; O'Leary et al. 2019; Mali et al. 2019). The fungal species tested in the present study are all known to produce some sesquiterpenes, esters, ketones, alkenes, and aldehydes (Fäldt et al. 1999; Rapior et al. 2000; Hynes et al. 2007; O'Leary et al. 2019). Effects of those VOCs on fungal wood decomposition could be tested experimentally.

Differences between white-rot and brown-rot fungi

In contrast to our hypothesis 2, we did not detect any clear difference between brown- and white-rot fungi in the competition-wood decay relationship, which instead depended on individual species and species combinations. Previous studies reported that exposure to different competitors may induce different antagonistic mechanisms in a mycelium (El Ariebi et al. 2016; O'Leary et al. 2019). Such a flexible response of each fungal species to different competitors may make the total response profiles complex,

and hide potential differences between brown- and white-rot fungi. Other experimental approaches, e.g. competition under highly stressful conditions, where fungi have to pay larger costs to cope up with the stress, may make the fungal trade off for energy allocation more severe and thus may be able to make the fungal competition-wood decay relationship clearer. This would be an interesting experiment for the future research.

Further, fungal preference for wood species (Purahong et al. 2019) may also have potential effects on the results of the competition outcome because of the tree species-specific volatile and diffusible secondary compounds, which have growth inhibition/stimulation effects on fungi (Heilmann-Clausen & Boddy 2005). Among the strains used in the present study, *H. fasciculare* and *T. versicolor* are predominantly found on beech dead wood (Heilmann-Clausen et al. 2014), whereas *V. comedens* and *L. sulphureus* are more common on oak (*Quercus* species.) (Boddy 1983; Lindner & Banik 2008), and *C. puteana* and *F. pinicola* on conifers such as spruce (*Picea* species) and pine (*Pinus* species) (Kubart et al. 2016; Fukasawa & Matsuoka 2015). Future studies would benefit from using a larger number of fungal species and strains from focal tree

species to find overarching ecological patterns.

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Figure legends

Fig. 1. Experimental set up of competitions.

Fig. 2. Proportion of competition outcomes in different combinations of fungal species and volume ratio of wood blocks. Chi-square and *P* values shown above some of the plots indicate the results of chi-square tests comparing occurrence frequency of replacement of brown-rot fungi by white-rot fungi.

Fig. 3. Decay rate of wood blocks colonised by pure cultures of three white-rot and three brown-rot fungi (controls) during the 3-months competition period. Boxplots show median, quartiles, minimum and maximum values. Different letters indicate significant ($P < 0.05$, Steel Dwass test) difference between different volume ratio of wood blocks within a combination.

Fig. 4. Decay rate of wood blocks in different combinations of fungal species and volume ratio of wood blocks during the 3-months competition period. Boxplots show median, quartiles, minimum and maximum values. Different letters indicate significant ($P < 0.05$, Steel Dwass test) difference between different volume ratio of wood blocks within a combination. N = 28 for every boxplots.

Fig. 5. Decay rate of wood blocks that maintained the originally inoculated fungus after the 3-months competition period. Boxplots show median, quartiles, minimum and maximum values. Different uppercase letters indicate significant ($P < 0.05$, Steel Dwass test) difference between different volume ratio of wood blocks within a combination. Different lowercase letters indicate significant ($P < 0.05$, Steel Dwass test) difference between different wood block# within a volume ratio. Numbers shown below the boxplots indicate sample number. (A) wood blocks of white-rot fungi: (B) wood blocks of brown-rot fungi. The reason why some combinations lack boxplots is that all blocks inoculated with a focal species were replaced by the competitor in these combinations.