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Environmental fluctuations facilitate species co-existence and increase decomposition in communities of wood decay fungi

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Abstract A fluctuating environment may facilitate co-existence of species, and high species richness may be important for maintaining ecosystem processes under changing environmental conditions. A positive relationship has been found between species richness and primary production in many experiments, and there is now an increasing interest whether similar relationships also apply to microorganisms and decomposition. Basidiomycete fungi are the primary decomposers of wood with the functional groups brown and white rot fungi, which differ with respect to decay strategy. In this study, 16 species of boreal wood decay fungi, 8 brown rot fungi and 8 white rot fungi, were assembled in artificial communities. The aims were to study species persistence, wood decomposition and metabolic efficiency in fungal communities of increasing levels of species richness under constant and fluctuating temperature regimes. Species persistence was generally low, but temperature fluctuations facilitated co-existence of species. Decomposition was highest at intermediate diversity levels under the fluctuating temperature regime. Metabolic efficiency, estimated as the amount of fungal mycelium formed per amount of degraded wood, decreased with increasing community complexity under the fluctuating temperature regime. Brown and white rot fungi differed in decomposition rates and metabolic efficiency, but no synergistic effects were found where the two functional groups were mixed. This study demonstrates how niche differentiation in a variable environment may act to maintain diversity and function. In our experiment, differences in functional responses to the varying temperature rather than resource partitioning between brown and white rot fungi had significant effects. Niche differentiation is likely to be particularly important in maintaining species diversity in communities of wood decaying fungi, which are known from previous studies to be characterised by intense competition, and where otherwise metabolically costly interactions lead to species exclusion and dominance by highly competitive species.

Keywords Basidiomycetes · Fluctuating environment · Metabolic efficiency · Species richness · Wood decomposition

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Introduction

A fluctuating environment may facilitate co-existence of species (Naeem and Li 1997; Petchey et al. 1999; Chesson 2000) and high species richness may be important for maintaining ecosystem processes under changing environmental conditions (Yachi and Loreau 1999; Mulder et al. 2001). Many ecological experiments have displayed positive relationships between species richness and primary production (Naeem et al. 1994; Tilman et al. 1996; Hector et al. 1999). Niche complementarity among species and functional groups has been suggested as the principal mechanism behind this effect (Tilman et al. 1996) but, in communities artificially assembled from a species pool, there may also be a higher likelihood for highly productive species to be included in high-diversity treatments (Huston 1997). The relationship between species richness and primary production is relatively well studied, while less attention has been given to relationships between microbial species richness and decomposition (Loreau et al. 2001; Hättenschwiler et al. 2005). Recently, it has been shown that litter decomposition rates may be positively correlated with

species richness in bacteria (Wohl et al. 2004) and soil fungi (Setälä and McLean 2004; Tiunov and Scheu 2005).

Wood is predominantly decomposed by basidiomycete fungi divided into two functional groups—brown and white rot fungi. These groups of fungi differ in the way they colonise wood cells as well as in their capacity to degrade the recalcitrant lignin component of wood (Rayner and Boddy 1988). The cell walls of wood consist of several layers built up mainly from cellulose, hemicellulose and lignin. Brown rot fungi have the ability to degrade cellulose and hemicellulose by an oxidative process using H_2O_2. White rot fungi are, in addition to cellulose and hemicellulose, also able to fully degrade the lignin constituents of the wood. They utilise the enzyme laccase for the cleavage of aromatic rings in the lignin structure, and a range of other enzymes that generate or transfer oxidants, such as glucose oxidase, manganese peroxidase and ligninase for lignin degradation (Deacon 1997). Wood has a high carbon/nitrogen ratio and therefore metabolic efficiency in terms of nitrogen acquisition is of great importance for species establishment and function in the wood substrate (Cooke and Rayner 1984).

Here, microcosm systems containing wood chips were used to study artificially assembled communities of brown and white rot fungi, replicated under constant and fluctuating temperature regimes. The aims of the study were to investigate effects of species richness and temperature fluctuations on: (1) competition, by comparing the number and identities of the fungal species that were added to the microcosm with the species that were re-isolated at the end of the experiment, (2) the rate of spruce wood decomposition, and (3) the metabolic efficiency, estimated as the amount of the mycelial cell wall component chitin formed per amount of degraded wood.

Materials and methods

Fungal isolates

We used 16 species of basidiomycete wood-decay fungi, collected on *Picea abies* (L.) Karst. logs in Sweden and Finland: 8 species of brown rot fungi: *Amylocystis lapponica* (Romell) Singer, *Antrodia heteromorpha* (Fr.:Fr.) Donk, *Serpula himantioides* (Fr.) Karst., *Oligoporus placenta* (Fr.) MJ Larsen & Lombard (NT), *Fomitopsis pinicola* (Sw.:Fr) Karst. Ryvarden, *Gloeophyllum sepiarium* (Wulf.:Fr.) Karst., *Fomitopsis rosea* (Alb. & Schw.):Fr and *Pycnoporellus fulgens* (Fr.) Donk; and 8 species of white rot fungi: *Resinicium bicolor* (Alb. & Schw. Ex Fr.) Parm, *Junghunia collabens* (Fr.), *Phlebiopsis gigantea* (Fr.:Fr.), *Phellinus ferrugineofuscus* (Karst.) Bourdot, *Phellinus nigrolimitatus* (Romell) Burd. & Galz., *Laurilia sulcata* (Burt) Pouzar, *Stereum sanguinolentum* (Alb. & Schw.):Fr and *Phlebia centrifuga* Karst. One strain per species was used to avoid possible confusion of intra- and interspecific competiton in the microcosm communities.

Microcosms

Wood chips, approximately 1×5×5 mm, were manufactured from the bark and trunk of *P. abies* trees by the use of a chainsaw. The wood was dried in a heating cabinet for 3 days and autoclaved twice at 121°C for 1 h, with a 1-h incubation inbetween. Mycelium-covered agar plates were filled with wood chips and incubated until the wood was thoroughly colonised by all species. The microcosms used in this study consisted of two 150-ml PVC beakers connected by a sterile filter (sterifil-D, millipore). A nylon mesh cylinder (0.5–1 mm mesh) was filled with ca. 6.0 g (dry weight) of sieved >1 mm wood chips, autoclaved as described earlier, and placed in the centre of the upper beaker. Wood chips inoculated with fungi as described were placed on top of and beneath the mesh cylinder. In order to maintain relative humidity near 100% during the whole experiment, 10 ml of water was added to the bottom container. The microcosms were opened only for watering of the wood chips. The fungal communities were assembled and inoculated to the microcosms according to Appendix 1, with monocultures randomly assigned into the design. This experimental design was chosen to permit detection of "species effects" in diverse treatments (Huston 1997). In our design, we were able to follow both single species and the effects of certain species combinations in complex communities as opposed to a design randomised at all levels of species richness.

When the inoculated wood chips were applied, the space below and above each cylinder was divided into eight sectors. Each sector was filled with approximately 0.5 ml of pre-inoculated wood. Two replica microcosms were made for each of the 16 monocultures. Sixteen communities were prepared, containing two species: four with brown rot fungi only, four with white rot fungi only, and eight with a mixture of fungi from the two functional groups. The two-species communities were inoculated so that four adjacent sectors above and four below the cylinder included the same species. Sixteen communities were assembled with four species: four with brown rot fungi, four with white rot fungi, and eight mixed communities. Inoculated wood chips of the same species were placed on two opposite sectors, both above and below the cylinder. Sixteen communities were assembled with eight species: four microcosms with brown rot fungi only, four with white rot fungi only, and eight mixed communities. Wood chips with the same fungal species were placed in one sector above and one sector below the cylinder. Eight microcosms were prepared that contained all 16 species (for the fluctuating temperature treatment five microcosms were made for the 16-species communities). The one sector occupied by each species in the 16-species communities was positioned so that the species occurred above the cylinder in

some microcosms and below in some, and so that both white and brown rot fungi were present in both positions at all times.

The duration of the experiment was 6 months. The communities described were subjected to two temperature treatments. Both treatments were incubated in the dark. After an initial incubation period at a constant temperature of 19°C for 1 month, one set of the microcosms were subjected to a fluctuating temperature regime (T-treatment), the systems were exposed to 11, 31, 23, 7, 27, 15 and 19°C, during 3 weeks, respectively, resulting in an average temperature of 19°C. Temperatures were chosen to represent a temperature range wood decomposing fungi encounter during the growth season in a boreal forest ecosystem. The other set of microcosm systems were kept at a constant temperature of 19°C, (C-treatment). The inoculated wood was irrigated with 2 ml of autoclaved deionised water when showing signs of drought, i.e. when no condensed water was visible on the walls of the container and the color of the wood suggested dryness (approximately every 3 weeks). In order to keep the level of moisture constant in the wood, water was added at need and not in equal amounts to all containers. Opening of the lid of the containers under sterile conditions every 3 weeks allowed for additional gas exchange.

Re-isolation of fungal species

All wood or fungal material surrounding the mesh cylinders was removed. Seven wood chips were sampled from each mesh bag from standardised locations. The samples were placed on Hagem agar medium and incubated for 1–2 weeks. The species identity of the basidiomycetes growing out from the wood chips was determined visually, by macroscopical as well as microscopical characteristics (Nobles 1965). In uncertain cases, isolates were paired with the original isolates to identify the isolate through the formation of intersterility patterns (Holmer and Stenlid 1997). A molecular approach to species persistence was not chosen due to the risk of false positives based on the amplification of dead mycelium.

Wood chip weight loss

The mesh cylinders were weighed after they had been dried for 24 h at 95°C, and the weight loss of the wood in the mesh bags was calculated. The chitin content of all wood samples was measured at the end of the experiment by means of HPLC analysis of glucosamine according to Ekblad and Näsholm (1996). Briefly, the wood was ground in a ball-mill, hydrolysed in 6 M HCl and the amount of glucosamine was measured in the hydrolysate. Since chitin is a fungal cell wall polysaccharide that is absent in non-colonised wood, the chitin content can be used to estimate the fungal fraction of a mixed substrate. It has been shown that chitin as well as ergosterol measurements give reliable relative interspecific measures of fungal biomass in microcosm systems (Ekblad et al. 1998). Our fungal biomass estimations were based on the chitin content of pure mycelium samples from *F. pinicola* and *S. himantioides* from this study, and on measured fungal biomass in beech wood (Swift 1973). The amount of glucosamine formed per amount of degraded wood was used as an index of metabolic efficiency.

Statistical analysis

Effects of temperature treatment, number of added species and decay strategies on species persistence, decomposition and metabolic efficiency as well as two-way interactions according to Table 1 were evaluated by 3-way ANOVA. Data on decomposition and metabolic efficiency were log-transformed before statistical analysis. Microcosms with no re-isolated fungi were excluded before the analysis. Numbers of replicates under the constant temperature regime were: 32 (17) for monocultures, $n = 16$ (15) for 2-, $n = 16$ (11) for 4-, $n = 16$ (10) for 8-, and $n = 8$ (8) for 16-species systems. Numbers of replicates under the fluctuating temperature regime were: 32 (25) for monocultures, $n = 16$ (16) for 2-, $n = 16$ (16) for 4-, $n = 16$ (15) for 8-, and $n = 5$ (5) for 16-species systems. Numbers in brackets represent the number of microcosms where living mycelium was re-isolated.

Fisher's least squares differences were used to evaluate statistical significance of differences between individual combinations of temperature treatment and number of added species.

Species persistence, expressed as the fraction of added species that survived through the experiment, was analysed using a generalised linear model under a binomial distribution.

Results

Species persistence

Although up to 16 species of wood decaying fungi were added to each microcosm system, the number of species persisting after 6 months was generally low in all systems, leading to a significant ($P < 0.0001$) negative relationship between the number of added species and species survival.A maximum of four species were re-isolated from a single microcosm, in microcosms subjected to temperatures fluctuating between 7 and 31°C, the number of persisting species was significantly higher ($P < 0.0001$) than in microcosms subjected to a constant temperature of 19°C (Fig. 1a, Table 1).

Decomposition

Weight loss of wood was affected by temperature fluctuations ($P < 0.04$) and the initial species richness

Table 1 Type III analysis of a generalised linear model under binomial distribution with species persistence (re-isolated species/added species) in wood-chip microcosms containing artificially assembled communities of wood rotting fungi as the dependent variable

Source	*df*	χ^2	Pr > χ^2
Temperature	1	16.9	< 0.0001
No. added species	4	94.36	< 0.0001
Decay strategy	2	0.30	0.8606
Temperature × no. added species	4	3.82	0.4304

($P < 0.001$) as well as by the interaction between these parameters ($P < 0.005$) (Fig. 1b, Table 2). Under the fluctuating temperature regime, we found increased decomposition rates in four-species communities compared to the other diversity treatments ($P < 0.003$). Under the constant temperature regime, however, there was a negative relationship between the number of added species and wood weight loss, with significantly lower ($P < 0.03$) decomposition rates in four-, eight- and sixteen-species communities than in monocultures and two-species communities. In the four- and eight-species communities, the average decomposition rates were higher ($P < 0.0001$ and $P < 0.05$, respectively) under the fluctuating temperature regime than under constant temperature, but no significant differences could be detected at the highest level of species richness. Decay rates were significantly affected by decay type ($P < 0.02$) as well as the interaction temperature treatment and decay type ($P < 0.05$). Microcosms with brown rot fungi had higher decomposition rates than microcosms with white rot fungi under the fluctuating temperature ($P < 0.01$). This relationship was reversed under the constant temperature where microcosms with white rot fungi had higher decomposition rates than microcosms with brown rot fungi ($P < 0.01$). Mixed microcosms were intermediate in their decomposition.

All calculations with regard to decomposition were based on the total weight loss of the inoculated wood chips. Analyses were also performed with the fungal biomass subtracted from the total weight loss as described in the Materials and methods section. The results from these calculations did not differ from the data presented above and are therefore not shown.

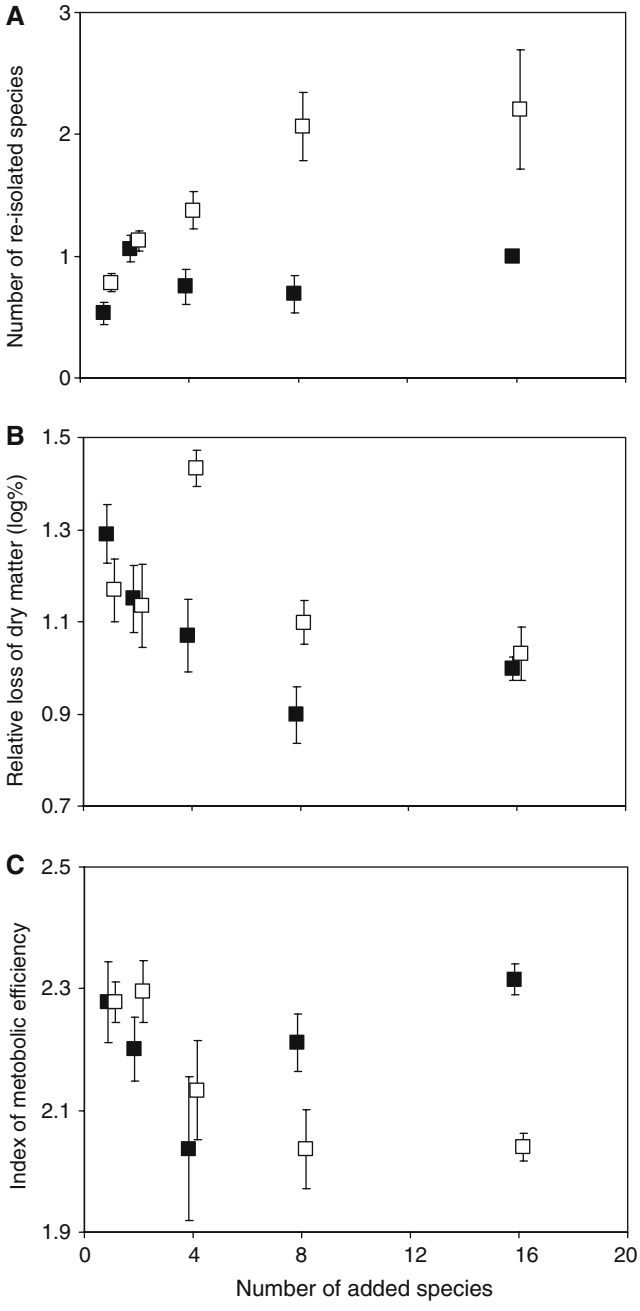

Fig. 1 Species persistence, decomposition rate and metabolic efficiency of wood-degrading fungi in relation to the number of species added to microcosm communities. *Open symbols* represent microcosms exposed to a fluctuating temperature regime, whereas *closed symbols* represent microcosms exposed to constant temperature (*Error bars* 1 SE). **a** Average number of species re-isolated 6 months after inoculation. **b** Weight loss of wood during 6 months of incubation expressed as the log-transformed % weight loss. **c** Metabolic efficiency estimated as the log-transformed amount of glucosamine in wood hydrolysate (μg/g of degraded wood). Figures of decomposition and metabolic efficiency are based on results from microcosms with surviving fungi only

Metabolic efficiency

Metabolic efficiency was significantly affected by the interaction between temperature treatment and the number of added species ($P < 0.02$) with a negative relationship between the metabolic efficiency and the number of added species under the fluctuating temperature regime, where metabolic efficiency was significantly lower in the 4-, 8-, and 16-species microcosms than in mono- and two-species microcosms ($P < 0.05$) (Fig. 1c, Table 2). In microcosms with the highest diversity level metabolic efficiency was significantly lower under the fluctuating temperature regime than under the constant temperature regime ($P < 0.04$). Furthermore, white rot

Table 2 ANOVA of log-transformed decomposition rates (*Dec*) and metabolic efficiency (*ME*) in wood-chip microcosms containing artificially assembled communities of wood rotting fungi

Source	*df*	Type III SS		Mean square		*F*-value		Pr > *F*	
		Dec	ME	Dec	ME	Dec	ME	Dec	ME
Temperature	1	0.28	0.16	0.28	0.16	4.46	3.06	0.04	0.08
No. added species	4	1.30	0.68	0.32	0.17	5.16	3.26	0.001	0.01
Decay strategy	2	0.53	0.68	0.27	0.34	4.23	6.55	0.02	0.00
Temp. × no. added species	4	1.11	0.68	0.28	0.17	4.42	3.21	0.002	0.02
Temp. × decay strategy	2	0.39	0.25	0.19	0.12	3.091	2.40	0.05	0.09
Error	159	12.05	10.10						

Analysis was based on results from microcosms with surviving fungi only

fungi had significantly ($P < 0.005$) higher metabolic efficiency than brown rot fungi.

Discussion

The overall low species persistence under the constant temperature regime, regardless of the initial species richness, agrees well with the view that intense competition is considered the most important interaction among wood decaying basidiomycetes (Boddy 2000). Pair-wise interactions among these fungi regularly result in combative physical exclusion of one of the competitors (Holmer and Stenlid 1993). In contrast, the significantly higher species persistence under the fluctuating temperature suggests that the high competition is relaxed in the fluctuating environment. The idea that a fluctuating environment permits co-existence of competing species in simple environments was first proposed as a mechanism to explain planktonic algal diversity (Hutchinson 1961), but there are few examples of experimental evidence for this suggestion. In aquatic environments, Naeem and Li (1997) and Petchey et al. (1999) showed decreased extinction rates in fluctuating environments as compared with stable environments. Our study provides experimental evidence for a similar effect in terrestrial environments.

In the control treatment, *R. bicolor* overtook most of the communities where it was introduced, resulting in a low number of re-isolated species. *R. bicolor* is known from previous experimental studies to be a strong competitor (Holmer and Stenlid 1997). The low survival rates found under the constant temperature regime may be explained by the absence of external nitrogen and phosphorus sources, such as soil or foliage litter. Laboratory microcosms also lack the continuous input of spores and vegetative mycelia experienced under field conditions. Under fluctuating temperature, however, the number of persisting species in the microcosms correspond well to the actual number of species found in natural communities, when substrates of similar size as our microcosms are considered, for example, in Norway spruce logs (Gustafsson 2002) or beech stumps (Coates 1983).

The negative relationship between decomposition and initial diversity in fungal communities under constant temperature is at odds with the finding that increasing species richness promoted microbial activity in communities of bacteria (Wohl et al. 2004) and soil fungi (Setälä and McLean 2004; Tiunov and Scheu 2005). Single cell organisms such as bacteria may be less efficient in terms of interspecific competition compared to mycelia of wood-decaying basidiomycetes, which are able to translocate resources within the mycelium and compete with other adjacent species using the mycelium as a resource base (Boddy 2000). Niche complementarity was shown by Tiunov and Scheu (2005) to occur when sugar fungi and cellulolytic fungal species were mixed on a cellulose substrate. The discrepancy with the results of Tiunov and Scheu (2005) may be due to the different communities used in our two different studies, since 'sugar' and cellulolytic litter fungi may be more functionally different than brown and white rot fungi. Setälä and McLean (2004) use a general soil fungal community with a potential to cover many different decomposer niches.

The insurance hypothesis (Yachi and Loreau 1999) predicts a performance enhancing effect in diverse ecosystems where a fluctuating environment permits co-existence of strongly competing species. Indeed, we find such a performance enhancing effect in our systems, as indicated by the enhanced decomposition in systems with intermediate initial species richness under the fluctuating temperature. The observation that decomposition decreases with increasing number of inoculated species under constant temperature may be due to a decreasing inoculum potential of dominants together with a delayed colonisation of the substrate due to interactions. It has previously been shown that competitive interactions among wood decay fungi could involve a substantial metabolic cost (Wells and Boddy 2002). The cost of interactions may explain the negative relationship between metabolic efficiency, estimated as the efficiency in transforming wood to chitin, and initial species richness observed under the fluctuating temperature regime in this study. In the microcosms with the highest numbers of inoculated species, this metabolic cost may have counteracted the effects of niche complementarity, leading to a decline in decomposition in these communities (Fig. 1b). Under the constant temperature regime, on the other hand, no negative

effect of species richness on efficiency was found and the reason for this might be that the potential for interactions is low in constant environments where dominant species like *R. bicolor* rapidly dominate the substrate.

Experiments involving artificially assembled communities have been controversial, since claimed diversity effects may be due to the increasing probability of including high-performance species with increasing species richness (Huston 1997). In order to avoid this problem, all species in this study were equally represented at all levels of species richness, and duplicated monocultures of each species were included. The fact that highly competitive fungi progressively increase their dominance of communities to which they are added means that the analysis will be sensitive to the performance of these particular species. *R. bicolor*, the potential dominant under constant temperature, decomposed wood rapidly when growing in monoculture, but more slowly when overtaking complex communities. *Pycnoporellus fulgens*, in contrast, performed poorly in monoculture, but was re-isolated from the majority of the microcosms with high decomposition rates under fluctuating temperature. In the combined microcosms, *P. fulgens* was inoculated together with *F. rosea*, the most effective decomposer in the monocultures of this study. Although the latter did not always survive to the end of the experiment, the eight-fold increase of decomposition in these combinations compared to monocultures of *P. fulgens* suggests synergy among these two fungi. Interestingly, species of these two genera often co-occur in natural habitats (Niemelä et al. 1995). The high decomposition in microcosms with intermediate initial species richness cannot be explained by the complementarity of these two fungi alone, since this pattern is evident also in communities where these two species are absent. Overall, these observations suggest that the costs of antagonistic interactions as well as complementarity effects of wood-decaying fungi are more important in determining decomposition rates than the performance of single species.

Our dataset was designed to detect resource partitioning between the functional groups brown and white rot fungi, but this turned out be of little importance. Decay strategy was a significant factor to explain differences in metabolic efficiency and decomposition rate, yet no synergistic effects were seen in the mixed microcosms. This was at odds with the facilitative complementarity that was observed between cellulolytic and 'sugar' fungi by Tiunov and Scheu (2005). Stabilising mechanisms are essential for species co-existence and can be fluctuation-independent, such as resource partitioning, or dependent on fluctuations due to differential responses to the environment (Chesson 2000). In our experiment, mechanisms that depend on temperature fluctuations rather than resource partitioning have significant effects, which appear to be independent of functional groups.

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