

## Research

### Wood decomposition is more strongly controlled by temperature than by tree species and decomposer diversity in highly species rich subtropical forests

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While the number of studies on the role of biodiversity on ecosystem functioning is steadily increasing, a key component of biogeochemical cycling in forests, dead wood decay, has been largely neglected. It remains widely unknown whether and how dead wood decay is affected by diversity loss in forests. We studied the hierarchical effects of tree species diversity on wood decay rates in a subtropical forest landscape in south-east China via its influence on fungal OTU richness and invertebrate diversity using piecewise structural equation models. The experiment was conducted in natural forest plots that span a wide gradient of tree species diversity embedded in a heterogeneous topography. To account for interactions between macro-invertebrates and fungi, that potentially modify the influence of tree biodiversity and climate on dead wood decay, we compared a macro-invertebrate exclusion treatment with a control treatment that allowed access to all types of decomposers.

Diversity effects of trees on wood decay rates were mostly negative and mediated by the diversity of macro-invertebrates. However, the effects of tree species diversity or fungal OTU richness and macro-invertebrate diversity on wood decay rates were comparatively weak. Temperature affected decay rates positively and had the strongest influence in all treatments. While the exclusion of macro-invertebrates did not lead to a reduction of wood decay rates, our results suggest that they may however have a mediating role in the process. In the presence of invertebrates the predictability of wood decay rates was higher and we observed a tendency of a stronger temperature control.

Our results suggest that there is evidence for diversity effects on wood decomposition, but the temperature control is still more important. Thus, an increase in mean annual temperature will increase carbon and nutrient turnover through wood decomposition in subtropical forest irrespective of biotic composition.

Keywords: BEF-China, biodiversity, coarse woody debris, decay, fungal OTU richness, invertebrate diversity



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## Introduction

Dead wood decay is a key component of ecosystem functioning in forests (Harmon et al. 1986, Cornwell et al. 2009, Wirth et al. 2009), most importantly of carbon sequestration and release as well as nutrient cycling (Chambers et al. 2000, Wirth et al. 2009). Up to 20% of the world's carbon that is deposited in organic matter is stored in dead wood (Delaney et al. 1998). During the last decade, the ongoing loss of biodiversity has triggered numerous studies on the effects of biodiversity on ecosystem functioning in forests (Scherer-Lorenzen et al. 2007, Potvin and Gotelli 2008, Bruelheide et al. 2011, 2014, Baeten et al. 2013). A growing body of literature reports positive effects of forest biodiversity on various ecosystem functions (reviewed by Nadrowski et al. 2010, Duffy et al. 2017). Despite its importance, decomposition dynamics of dead wood have, so far, been widely neglected in forest biodiversity–ecosystem functioning (BEF) experiments. To our knowledge only two studies have recently tested effects of tree species and decomposer diversity on dead wood dynamics (Eichenberg et al. 2017, Kahl et al. 2017). Thus, it remains largely unknown whether and how dead wood decomposition is affected by changes in biodiversity beyond the well described effect of abiotic conditions. In this study, we considered different facets of diversity and their relationships as potential drivers of deadwood decomposition: tree species diversity and diversity within two main wood decomposer groups, fungi and invertebrates. In addition, we addressed decomposer functional diversity in an experiment excluding macro-invertebrates. We explored three modes of tree species diversity effects: via a modification of the microclimate for decomposition, via altering decomposer diversities, and via direct effects of unknown mechanism.

There is a general consensus that favourable climatic conditions (i.e. high temperatures and sufficient humidity) are conducive to high abundance and activity of decomposers, which consequently leads to high wood decay rates (Harmon et al. 1986, Weedon et al. 2009, Pietsch et al. 2014). The micro-climate at the forest-floor, where wood decomposition occurs, is partly controlled by tree species composition and diversity (Martius et al. 2004). Greater canopy complexity in mixed species forests, which is associated to increased tree species diversity, leads to more stable and favourable climatic conditions for the decomposer community (Prescott 2002, Martius et al. 2004). Thus, tree species diversity may indirectly influence dead wood decomposition via its link to stand microclimatic conditions.

There is increasing evidence that tree species diversity has positive bottom up effects on the diversity of decomposers. Community composition of trees translates into the diversity and quality of detritus substrate, which affects the diversity and abundance of detrital microbial populations (Moore et al. 2004). Consequently, small scale differences in community composition of trees alter the soil microbial community with distinctly different communities associated to certain tree species (Ushio et al. 2008, Urbanová et al.

2015, Pei et al. 2016). Similarly, tree species diversity promotes the diversity of macro-invertebrates (Balvanera et al. 2006), as different litter types support different subsets of fauna (Wardle et al. 2006). A link between decomposer diversity and wood decomposition rates has been shown in various ways. Increased fungal diversity can have positive effects on organic matter turnover, depending on the fungi involved (Cox et al. 2001, Hättenschwiler et al. 2005), and the colonization history (Fukami et al. 2010). Similarly, saproxylic invertebrate diversity may influence wood decay rates. Torres and Gonzáles (2005) reported higher wood decomposition rates at high levels of invertebrate species and functional group richness compared to low richness levels in two tropical forests. Additionally, a meta-analysis of 28 studies revealed that a reduction in invertebrate diversity results in a significant reduction of decomposition rates regardless of the experimental system (Srivastava et al. 2009). Such findings suggest that there may be an indirect link between tree species diversity and decomposition rates via the diversity of decomposers, but this has not been experimentally tested to date.

The strength and direction of the diversity effect of one decomposer group may depend on the activity and diversity of another one, reflecting effects of decomposer functional diversity. Wood decay is mainly accomplished by decomposers of two large functional groups, fungi and bacteria on the one hand and invertebrates on the other (Begon et al. 2005, Cornwell et al. 2009). In tropical and subtropical forests, termites are among the most effective invertebrate decomposers (Cornwell et al. 2009). There is evidence that invertebrates can account for 10–20% mass loss of annual dead wood input (Ulyshen 2016). But only a few studies have experimentally excluded invertebrates from wood decay (Eichenberg et al. 2017 and see review by Ulyshen and Wagner 2013) and the magnitude of the contribution of invertebrates and their diversity on wood decomposition remains inconclusive to date. In addition to studies reporting significantly lower decay rates when invertebrates are excluded (Müller et al. 2002, Eichenberg et al. 2017), there is evidence from tropical forests that invertebrate exclusion does not lead to reduced decay rates (Takamura and Kirton 1999, Takamura 2001). The latter case is especially interesting as termites were the most abundant invertebrate decomposers, suggesting that their exclusion should lead to significantly reduced decay rates. However, the effect of termites on wood decay may vary biogeographically, depending on the species involved (Ulyshen 2016). Interactions between termites and microorganisms have been shown to increase (Ulyshen et al. 2016) or inhibit (Rosengaus et al. 1998) microbial decay, which may potentially alter positive effects of termites on wood decay rates. Thus the effect of invertebrates on wood decay likely depends on the species involved and the biogeographic setting.

There is growing evidence that decomposer organisms and multi-trophic interactions across different groups of decomposers (i.e. fungi and macro-invertebrates) may be crucial for the relationship between tree species diversity

and decomposition rates as well as between climate and decomposition rates (Zuo et al. 2014, Bradford et al. 2017, Keiser and Bradford 2017). Macro-invertebrates cause physical damage to wood, facilitating access for cord-forming fungi (Stokland et al. 2012), and they serve as vectors for fungi within or on their bodies (Swift and Boddy 1984). Grazing of invertebrates on wood decaying fungi has been shown to reduce fungal growth, but with often positive effects for decomposition due to higher enzyme activities of the remaining fungi (A'Bear et al. 2014). Moreover, macro-invertebrates alter microclimatic conditions inside the wood by tunnelling and fragmenting it, which leads to better ventilation and higher moisture contents (Stokland et al. 2012). Such ecological interactions between macro-invertebrates and fungi may be vital for the relationship between tree species diversity as well as climate and wood decay rates.

We studied the wood decay rates of two regionally common and often dominating tree species, the evergreen broad-leaved *Schima superba* and the conifer *Pinus massoniana*. We chose these representatives of angiosperms and gymnosperms, respectively, as these two clades are characterised by fundamentally different wood trait configurations (Weedon et al. 2009, Pietsch et al. 2014), which are also related to contrasting termite feeding preference (Bustamante and Martius 1998). Thus the two important species are likely to exhibit different interactions with decomposer diversity and abiotic conditions (Brovkin et al. 2012). While testing for trait identity effects of the decomposing wood was decidedly not the goal of this study, including the contrasting clades allows us to assess – as a first approximation – the sensitivity of the tested relationships to phylogeny and may help us to evaluate their generality. Our experiment was part of the BEF-China experiment (Bruelheide et al. 2011), which is situated in a highly diverse subtropical secondary forest in southeast China covering heterogeneous topography and microclimatic conditions. Twenty-seven permanent study plots were established to cover a diversity and successional gradient independent of topographic and climatic heterogeneity (Bruelheide et al. 2011). Wood decomposition was observed over a period of two years and associated to variation in diversity of tree species, wood decomposing fungi and macro-invertebrates. To study the influence of invertebrate exclusion on the relationship between biodiversity as well as climate and wood decomposition, we allowed all decomposers in a control treatment and excluded macro-invertebrates in an exclusion treatment.

Using this experimental setup we tested the following hypotheses: 1) tree species diversity increases wood decay rates indirectly by improving the microclimate for decomposition, 2) tree species diversity increases the diversity of fungi and macro-invertebrates which, in turn, increases wood decay rates, 3) the exclusion of macro-invertebrates decreases wood decomposition rates, and 4) the exclusion of macro-invertebrates weakens the effects of tree species diversity and climate on wood decay rates.

## Material and methods

### Study site and plot selection

We conducted this study in the Gutianshan National Nature Reserve (GNNR), Zhejiang Province, Southeast China (29°8'18"–29°17'29"N, 118°2'14"–118°11'12"E). The GNNR covers an area of ~81 km<sup>2</sup> of subtropical broad-leaved forest with a total of 1426 seed–plant species of which 258 are tree and shrub species (Lou and Jin 1999). The climate is typical for subtropical monsoon regions. Mean annual temperature is 15.1°C and mean annual precipitation is 1936.7 mm (Hu and Yu 2008). The bed rock materials in the GNNR are granite and saprolite and the soils are predominantly cambisols (Geißler et al. 2012). Within the scope of the Biodiversity Ecosystem Functioning experiment BEF-China (DFG-FOR 891) 27 permanent study plots of 30 × 30 m were established in the GNNR in 2008 at an elevational range between 250 and 900 m a.s.l. The plots were randomly selected within the GNNR to span a gradient of woody (tree and shrub) plant species richness (25–69 species per plot) and successional age (<20 to >80 years) (a detailed description of the study sites is given in Bruelheide et al. 2011; Fig. 1).

### Plot related variables

Plot elevation, tree species richness and abundance, and forest age were recorded during plot establishment in 2008 (Bruelheide et al. 2011). Temperature and relative humidity were constantly measured in each plot for the duration of the experiment with data loggers. The climate data were used to calculate mean values for the duration of the experiment. For further analyses we used Shannon's diversity index of the tree species based on relative species abundances. Abundance was given as basal area of trees and shrubs with a dbh of ≥3 cm. We included forest age in our analysis to control for potential effects of age on microclimatic variation. We additionally included plot elevation, as it is generally the main driver of temperature variation, which is the most important co-variate of wood decay in climates with ample moisture supply.

### Wood decomposition

We selected two tree species to monitor plot-specific variation in dead wood decomposition, the angiosperm *Schima superba* (Theaceaceae) and the gymnosperm *Pinus massoniana* (Pinaceae). These species are among the most dominant tree species of the GNNR (Bruelheide et al. 2011). Angiosperms and gymnosperms differ substantially in their chemical composition, physiological characteristics and decomposer communities. For example, termites prefer less dense wood of higher nutritional value (Bustamante and Martius 1998). These differences are also reflected by generally higher decay rates of angiosperms compared to gymnosperms (Weedon et al. 2009, Pietsch et al. 2014). But it was not our aim to study species-specific or trait-related differences

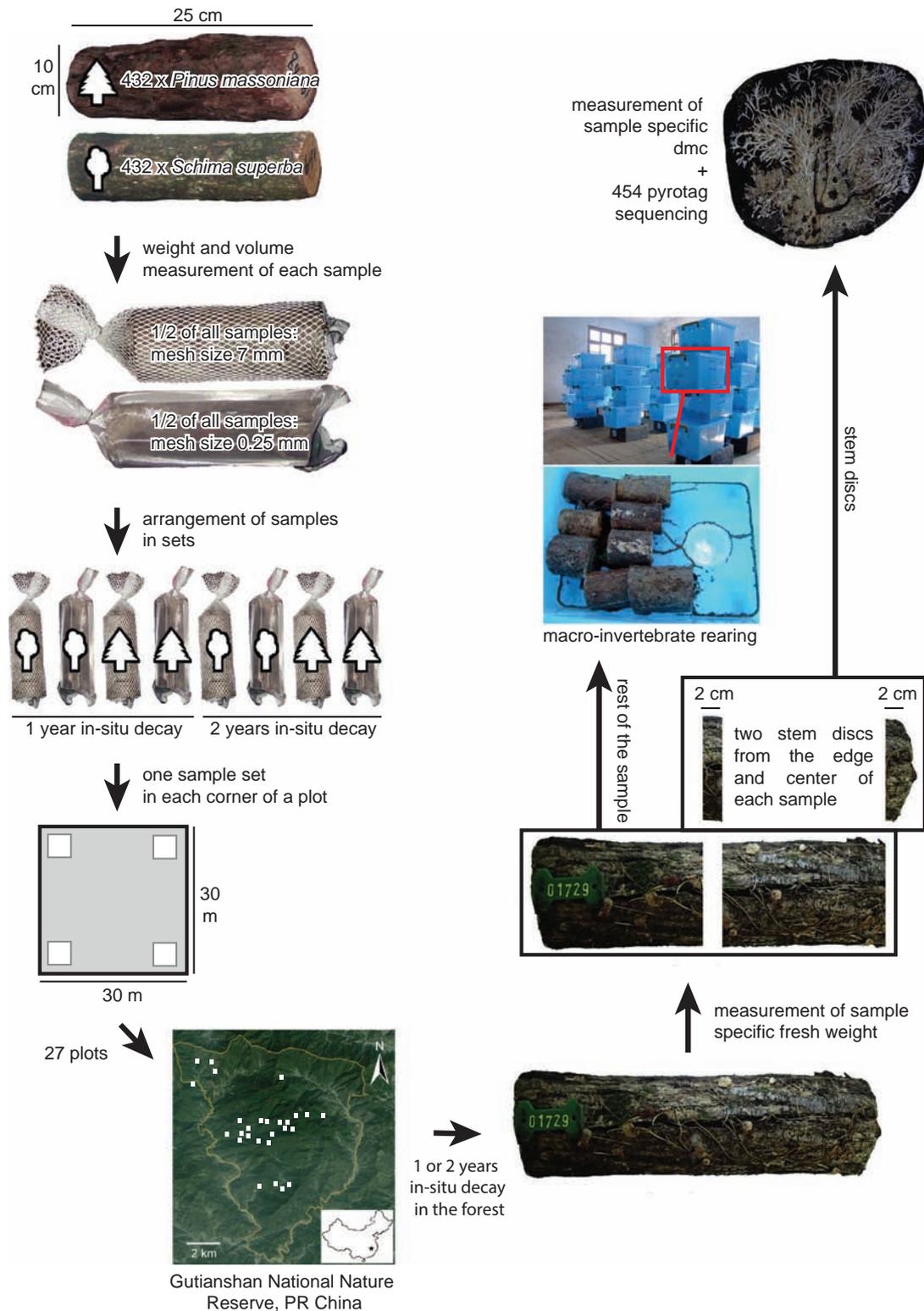


Figure 1. Workflow of experimental setup and analysis. A total of 864 wood samples from freshly cut stem wood of *Schima superba* and *Pinus massoniana* were deployed in 27 permanent study plots of different tree species diversity in the Gutianshan National Nature Reserve, Zhejiang Province, PR China. Half of the wood was deployed in mesh bags with 0.25 mm mesh size to exclude macro-invertebrates from wood decay, the other half was deployed in mesh bags with 7 mm mesh size as control treatment to allow access for all decomposers. After one and two years of in situ wood decay, respectively, we retrieved the samples to measure mass loss on a dry weight basis. We additionally reared macro-invertebrates from the decomposed samples and analysed fungal richness. Map of the Gutianshan National Nature Reserve adjusted from Staab et al. (2014).

in decay rates. Rather, the selection of an angiosperm and a gymnosperm can be seen as a minimum requirement to reflect potentially strong phylogenetic differences. If similar relationships of abiotic conditions and organismic diversity with wood decay rates emerge across the angiosperm and gymnosperm wood, this would point to a high generality of our results. We used freshly cut stem wood with bark, which was harvested in the vicinity of the study area. All wood originated from a single site to keep intraspecific trait variation due to environmental plasticity at a minimum as well as to preclude major differences in initial endophytic fungal composition. We selected trees with a diameter at breast height of  $10 \pm 2$  cm and free of visible fungal or invertebrate infection. We cut the samples to  $25 \pm 0.5$  cm length and recorded the initial weight and volume. From each harvested tree we took three stem discs at the stem's base, middle and crown base for initial measurements of individual specific dry matter content. Samples were not dried prior to deployment in the field, and we quantified their initial dry weight based on the dry matter content of the respective harvest tree as the mean dry matter content of the three stem discs per harvest tree.

The two tree species were each subjected to two treatments (Fig. 1). In the control treatment, we allowed all decomposers to access the wood, while in the exclusion treatment we excluded macro-invertebrates. We used a mesh bag approach with 7 mm mesh size for the control treatment and  $250 \mu\text{m}$  for the exclusion treatment. The size of the mesh bags was  $20 \times 40$  cm and they were closed with cable ties. Depositing the wood of the control treatment in mesh bags was necessary to retrieve all woody material after decomposition, including small fragments that were detached during the course of decomposition. This way we obtained more accurate estimates of the decomposition rates in both treatments. Additionally, the mesh bags facilitated fixing the samples in the sometimes very steep terrain of the study sites (slope  $20\text{--}50^\circ$ ).

In each of the 27 study plots we selected four decomposition sites close to the corners of the plot to reflect within-plot variation of wood decay and thus to obtain representative and precise mean decomposition rates at the plot scale (Fig. 1). Each of the four decomposition sites was equipped with eight samples, comprising two species with two treatments, replicated twice for two sequential harvests (32 samples per plot). The wood was deployed between July and August 2010 at the end of the rainy season where the activity of invertebrates and fungi is high. The first retrieval was conducted in October 2011, the second in September 2012. Fifty-nine out of 864 litterbags of the exclusion treatment were damaged and there the wood was colonized by termites. These samples were eliminated from the analysis.

After retrieval we immediately carefully removed all non-woody material such as soil or moss adhering to the samples and weighed the wood samples for mass loss determination in the lab. Two stem discs (2 cm) were cut from each sample, one from the edge and one from the middle. The visible inspection of the interior of each sample showed that there was no soil material transported into the samples by termites

or other invertebrates. The major proportion of each disc was dried to determine sample specific dry matter content and express mass loss on a dry weight basis. A fraction of each disc was immediately frozen at  $-20^\circ\text{C}$  for further analysis.

### Fungal community composition

To analyse the fungal community composition, we used 454 pyrotag sequencing on samples collected in 2012. This analysis was limited to the wood of one replicate decomposition site per plot due to the high costs of the analysis. We describe the analysis of the fungal community composition in the Supplementary material Appendix 1. We used fungal operational taxonomic unit (OTU) richness as diversity measure for the fungi. Next to richness data, it is possible to obtain absolute and relative abundance data for each fungal OTU from next generation sequencing. These data could be used to calculate a Shannon or Simpson index for fungal diversity. But the fungal abundance data can be highly variable with per sample sequence read coverage (Amend et al. 2010). Thus diversity indices are likely to introduce error sources compared to fungal OTU richness, which relies on the presence or absence of taxa or OTUs. In conclusion, fungal OTU richness is a simple and conservative measure compared to diversity indices, but it is probably the most reliable one. This especially applies when sequence related biases and errors for richness estimation are eliminated and when sample-based rarefaction curves are saturated or near to saturation as in our study (Supplementary material Appendix 1 Fig. A1). In the subsequent statistical analyses, we therefore used the fungal OTU richness for each species-by-treatment combination on a plot basis. The raw sequence datasets are available at the European Nucleotide Archive under the study number PRJEB8978 (<[www.ebi.ac.uk/ena/data/view/PRJEB8978](http://www.ebi.ac.uk/ena/data/view/PRJEB8978)>). Fungal biome OTU table, OTU representative sequences and the bioinformatics scripts are available at Dryad (<<http://datadryad.org/resource/doi:10.5061/dryad.54qr4>>).

### Macro-invertebrate community composition

To determine the xylobiont and saproxylic invertebrate community, we reared them from the remaining part of all retrieved samples with custom-made emergence chambers (Fig. 1; modified after Ferro and Carlton 2011). We pooled the wood by species and treatment per plot and installed 108 emergence chambers in total for each of the two time steps (27 study plots  $\times$  two species  $\times$  two treatments). We ran the emergence chambers for ten months following each harvest. After that time, we observed no further emergence of invertebrates from the wood samples. The wood from the invertebrate exclusion treatment was incubated as control to test if the treatment was successful. A detailed description of the invertebrate rearing is available in the Supplementary material Appendix 1. All individuals were identified to species level where possible and otherwise to genus or family level. When the species could not be determined we assigned

morpho-species based on morphological properties of the specimens. We counted the abundance of individuals per species and calculated Shannon's diversity index of macro-invertebrates for each species-by-treatment combination on a plot basis. A species list of the reared invertebrates is given in the Supplementary material Appendix 2.

## Statistical analysis

Mass loss proceeded faster during the first year of decomposition compared to the second year, indicating an exponential wood decay without a significant lag-phase. We thus calculated an exponential decay rate  $k$  ( $\text{year}^{-1}$ ) for each sample (Olson 1963). We found that decay rates were strongly related to even slight variations in sample specific volume. To account for this source of variation we specified a linear mixed effects model for  $k$  with volume, tree species and treatment as fixed effects and plot as random effect. Using this model we then predicted  $k$  values for the overall mean volume and added the residuals obtained from the model (Supplementary material Appendix 3 Fig. A2 for the relationship of predicted versus observed data). All subsequent analyses were conducted with the volume-corrected  $k$  values. To obtain robust estimates of plot-specific decay rates for each species-by-treatment combination, we calculated the average value of the respective decomposition rates from all four decomposition sites per plot and both harvests. Thus each decay rate that enters the subsequent analyses is an average value of eight individual values (four decomposition sites  $\times$  two harvests), reducing within-stand variability substantially.

To analyse the community composition of macro-invertebrates and fungi and to test whether the communities in the different species and treatments were different from each other we used permutational MANOVA and non-metric multidimensional scaling (NMDS) based on a Bray–Curtis distance matrix. Analyses were performed in the 'vegan' package of R (Oksanen et al. 2015).

We used piecewise structural equation modelling (pSEM, Lefcheck 2016) to test direct and indirect effects of forest age, tree species diversity, elevation, mean temperature, invertebrate diversity and fungal OTU richness on  $k$  values, and to further construct a network of multivariate interactions between the variables. Mean temperature is an important driver of variation in decomposition rates and as such used widely in global vegetation models to predict carbon and nutrient dynamics from decomposition processes. In previous versions of the analysis we also included relative humidity, but it had no effect on decay rates and we thus eliminated it from the final analysis (Supplementary material Appendix 3 Table A2). The major advantage of pSEM over traditional variance–covariance based SEM is that it can accommodate small sample sizes because it fits multiple individual linear models for the incorporated variables together to a causal network. All variables used in the pSEMs were standardized using z-scores to obtain standardized coefficients. To aid model specification and the interpretation of results, we first analysed bivariate relationships between the incorporated

variables (Grace et al. 2012). We then constructed pSEMs based on the schematic diagram in Fig. 2 and specified the component models for the individual variables as linear models. Variable selection for the component models was based on the Akaike information criterion (AIC) in a stepwise model selection process (Venables and Ripley 2002). With the AIC model selection criterion all variables, the significant as well as the non-significant ones, in the model contain valuable information for the explanation of the observed variation. We thus interpreted all significant as well as non-significant paths of the models. Where necessary, we square-root-, log- or square-transformed variables to meet criteria of normal distribution. To evaluate the overall fit of the pSEMs we used Fisher's C statistic and Shipley's test of d-separation to check for missing paths in the models (Shipley 2009).

We specified four individual models for each species-by-treatment combination (*S. superba* control treatment, *S. superba* exclusion treatment, *P. massoniana* control treatment and *P. massoniana* exclusion treatment) to reveal potential differences of causal relationships across the plot-specific variables (forest age, elevation, tree species diversity and temperature), the variables that are unique for each species-by-treatment combination (invertebrate diversity and fungal OTU richness) and their respective decay rates.

All statistical analyses were performed in R 3.2.3 (<[www.r-project.org](http://www.r-project.org)>). The pSEMs were fitted with the 'sem.fit' function and standardized path coefficients were obtained with the 'sem.coefs' function of the 'piecewiseSEM' package (Lefcheck 2016).

## Data deposition

Data available from the BEF China Data Portal <<http://china.befdata.biow.uni-leipzig.de/>> (Pietsch et al. 2018).

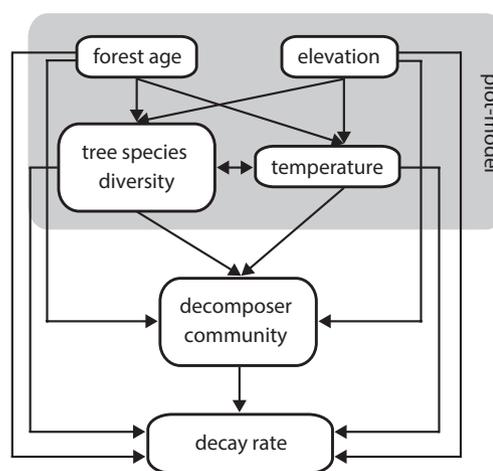


Figure 2. Conceptual realization of the pSEM structure. Decomposer community is represented by fungal OTU richness and in the control treatment additionally by macro-invertebrate diversity. The plot-model part was kept constant for the models of all species-by-treatment combinations.

## Results

### Environmental and structural heterogeneity

Mean decay rates in the different plots ranged from 0.10 to 0.33 year<sup>-1</sup> for *Schima superba* and from 0.11 to 0.39 year<sup>-1</sup> for *Pinus massoniana*. Variation in mean temperature was exclusively driven by elevation and not by plot age or tree species diversity at the plot-level (Fig. 3). Thus tree species diversity did not have a positive effect on wood decay rates which was driven by the microclimate. Tree species diversity increased with forest age and decreased with elevation despite the fact that the plot selection was initially intended

to decouple these variables (Bruehlheide et al. 2011). Plots at higher elevations had lower mean temperatures.

### Tree species and decomposer diversity effects on decay

We expected to find a positive effect of stand-level tree species diversity on the decomposer diversities in our wood samples, which would in turn have a positive effect on their decomposition rates. We only found a positive indirect effect of tree species diversity on wood decay in the *S. superba* exclusion treatment (Fig. 3b, 4). This indirect effect was composed of a negative effect of tree species diversity on fungal OTU richness and a negative effect of fungal OTU richness on wood

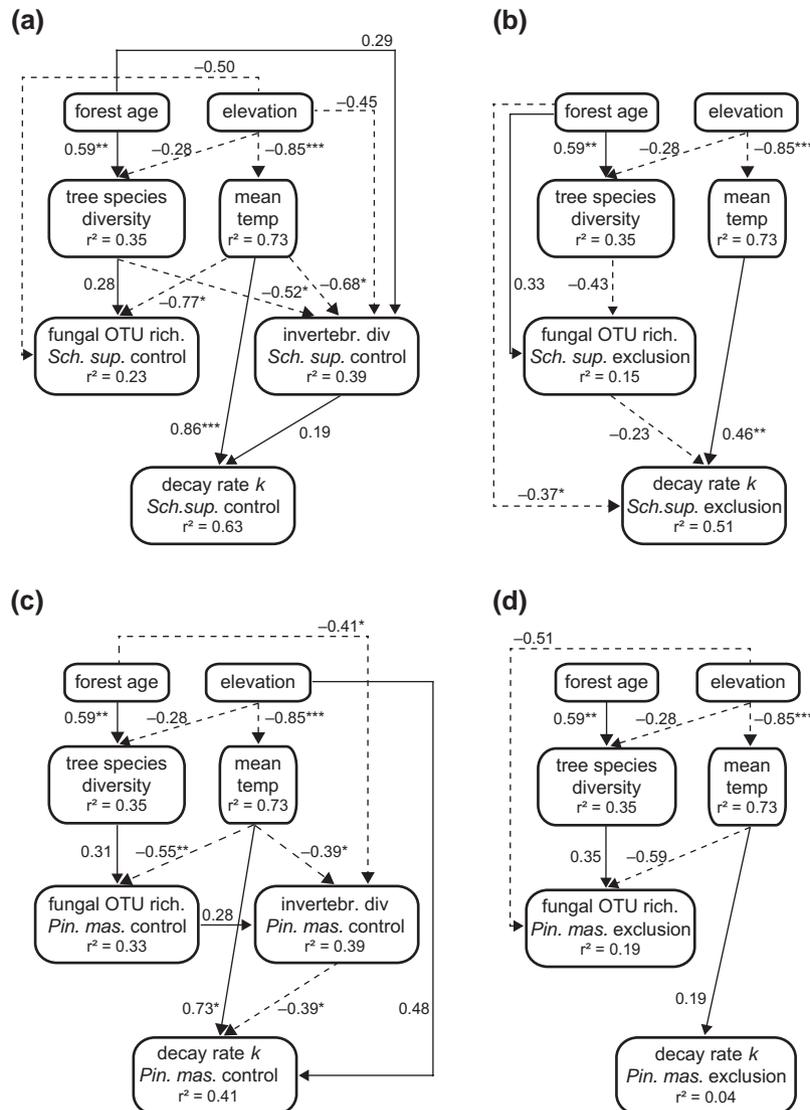


Figure 3. Structural equation models for both species and treatments. (a) *S. superba* control treatment, Fisher's  $C = 8.33$ ,  $p = 0.99$ ; (b) *S. superba* exclusion treatment, Fisher's  $C = 11.86$ ,  $p = 0.75$ ; (c) *P. massoniana* control treatment, Fisher's  $C = 13.06$ ,  $p = 0.79$ ; (d) *P. massoniana* exclusion treatment, Fisher's  $C = 9.91$ ,  $p = 0.97$ . Solid lines represent positive relationships, dotted lines negative. Standardized path coefficients and significance levels are shown for each pair of connected variables; \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.5$ . temp = temperature, fungal OTU rich. = fungal OTU richness, invertebr. div = macro-invertebrate diversity, *Sch. Sup.* = *Schima superba*, *Pin. mas.* = *Pinus massoniana*. Detailed model results are given in the Supplementary material Appendix 3 Table A1.

decay. In the control treatment of both species, the indirect effect of tree species diversity on wood decay was negative (Fig. 4). In *S. superba*, tree species diversity negatively affected macro-invertebrate diversity and macro-invertebrate diversity positively affected wood decay (Fig. 3a). In *P. massoniana*, tree species diversity affected fungal OTU richness positively, which in turn affected macro-invertebrate diversity positively, but the latter one had a negative effect on wood decay rates (Fig. 3c). In the exclusion treatment of *P. massoniana* we found no indirect effect of tree species diversity on wood decay rates (Fig. 3d). We found no evidence for a direct effect of tree species diversity on wood decay rates in any species or treatment.

### No effect of macro-invertebrate exclusion

While *P. massoniana* wood decomposed significantly faster than *S. superba* wood, we found no difference in decay rates between the macro-invertebrate exclusion and control treatments in both species (Fig. 5).

The macro-invertebrate as well as the fungal communities differed between *P. massoniana* and *S. superba* wood, but the fungal communities did not vary between the control and exclusion treatment within species (Table 2).

### Biotic and abiotic control on wood decay is modified by the presence of macro-invertebrates

Despite the fact that decomposition rates as well as fungal community composition did not vary between the control and exclusion treatment within species, our pSEM analyses revealed that biotic and abiotic controls of decay rates varied

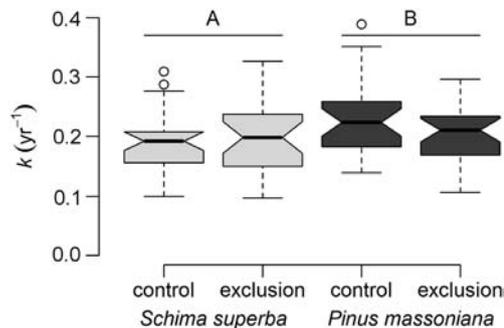


Figure 5. Variation of decay rate  $k$  between species and treatments across all 27 study plots. Grey = *Schima superba*, black = *Pinus massoniana*. Letters represent significant differences between the two species (F-value = 4.38,  $p = 0.04$ ). We detected no treatment effect in either of the species.

considerably between the two species as well as between the two treatments (Fig. 3, 4). In the presence of macro-invertebrates (control treatment), our models showed a higher predictability of decay rates than in the exclusion treatment (by 12% and 37% higher explained variance compared to the exclusion treatments in *S. superba* and *P. massoniana*, respectively). Additionally, the models for *S. superba* explained a substantially higher proportion of variance in wood decay than the models for *P. massoniana* (Fig. 3).

The effect of temperature on wood decay was always positive and it was the strongest among all considered variables. Fungal OTU richness as well as invertebrate diversity both decreased with increasing temperature. Furthermore, we observed a trend in both species that the temperature control on wood decay tended to be stronger in the control

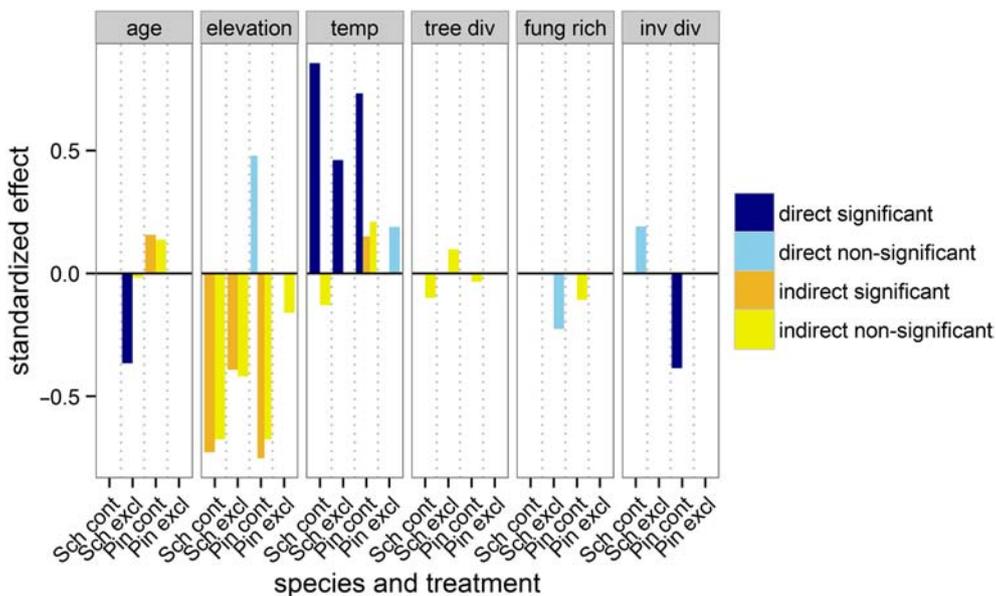


Figure 4. Effect sizes of direct (blue) and indirect (yellow) effects of biotic and abiotic factors on the decay rate  $k$ . Significant relationships are shown in dark colour, non-significant relationships in light colour. temp = temperature, tree div = tree species diversity, fun rich = fungal OTU richness, inv div = macro-invertebrate diversity, Sch cont = *S. superba* control treatment, Sch excl = *S. superba* invertebrate exclusion treatment, Pin cont = *P. massoniana* control treatment, Pin excl = *P. massoniana* invertebrate exclusion treatment.

treatment compared to the exclusion treatment. However, the differences of the temperature effect on wood decay were not significant across species and treatment combinations (Supplementary material Appendix 3 Fig. A3). We found direct as well as indirect temperature effects on wood decay in the control treatments (Fig. 4), where the latter were mediated via a negative effect of temperature on macro-invertebrate diversity (Fig. 3). In the exclusion treatments, the effect of temperature was always direct. Besides the positive effect of temperature, we found no significant effect of any other co-variable on the decay rates of *P. massoniana* in the exclusion treatment.

## Discussion

There is growing evidence for a positive effect of biodiversity on various ecosystem functions in forests (Nadrowski et al. 2010, Duffy et al. 2017). We asked whether biodiversity affects wood decay rates, which are linked to carbon retention and nutrient cycling of deadwood. We tested if this relationship is controlled by indirect effects of tree species diversity on variations in microclimate and/or by effects on the decomposer diversity. We found only weak effects of tree species diversity on wood decay rates, which were exclusively driven by the decomposer community but not by an effect of tree species diversity on microclimatic variations. Wood decay rates were most strongly controlled by mean plot temperature, regardless of the species or treatment, despite the fact that plot temperatures varied much less than the diversities of trees and decomposers (plot temperatures, tree species and decomposer diversities varied by a factor of 1.2, 2 and 6–21, respectively).

### No effects of tree species diversity on wood decay rates via modification of microclimate

According to our first hypothesis we expected that tree species diversity increases wood decay rates indirectly by improving the microclimatic conditions for decomposition. This hypothesis was not confirmed as we could not detect an effect of tree species diversity on plot temperatures. This result was surprising, since other studies in our plot network found that tree diversity increased basal area (Barrufol et al. 2013) and the efficiency of space exploitation by trees (Lang et al. 2012). Both effects produce a denser canopy and thus tend to produce a moister and more buffered understory microclimate, which is conducive to decomposition. This may be especially true for humidity. Yet, humidity was not affected by tree species diversity in our system and also had no effect itself on decomposition (Supplementary material Appendix 3 Table A2). Tree species diversity effects on microclimate may not just act on the overall annual averages, but by buffering variation. Indeed we found that temperature amplitudes were lower in more diverse forest plots (Supplementary material Appendix 3 Fig. A4), indicating that diversity can buffer extreme temperature events. But in contrast to annual mean

plot temperatures, temperature amplitudes had no effect on wood decay rates in either species-by-treatment combination.

One may argue that tree species functional composition rather than diversity controls the microclimate, most prominently via differences in canopy transparency and leaf habitus (deciduous versus evergreen). Our framework only allows an indirect test of tree composition effects via the variable forest age. Successional age is one of the strongest intrinsic biotic filters modifying the functional composition of our plots from pioneer dominated young stands with a high proportion of deciduous species to mature stands with a higher proportion of evergreen angiosperms (Bruehlheide et al. 2011). Since forest age had no effect on plot mean temperatures in any treatment, we conclude that diversity effects are likely not overruled by compositional effects.

### Effects of tree species diversity on wood decay rates via modification of decomposer diversity

In our second hypothesis we stated that wood decomposition rates would be indirectly influenced by tree species diversity via positive effects on the decomposer diversities that in turn increase wood decay rates. To support this hypothesis, we expected to find positive pathways connecting tree diversity and decomposer diversity and the latter to decomposition rates. Our results do not support this hypothesis for each of the possible composite paths (Fig. 3). We found an indirect negative effect of tree species diversity on wood decay rates in the control treatment of both species, which was driven by the diversity of macro-invertebrates. Additionally, we found a positive effect of tree species diversity on fungal OTU richness in three treatments (in the exclusion treatment of *Schima superba* the effect was negative), which also did not translate into a positive effect on decomposition rates.

In the past, various studies showed a strong influence of tree species diversity on decomposer diversities (Moore et al. 2004, Balvanera et al. 2006, Ushio et al. 2008), as well as of decomposer diversities on decomposition rates (Cox et al. 2001, Hättenschwiler et al. 2005, Torres and González 2005, Srivastava et al. 2009). One might argue that the statistical power of 27 study plots in our experiment was not sufficient to exhaustively reflect the factors influencing wood decomposition. The limitation of 27 study plots might especially be critical for traditional SEM analyses, which is usually applied to large sample sizes (Grace 2006). We accounted for this by applying piecewise SEMs (pSEMs), where the degrees of freedom for modelling individual variables as well as for the overall model are increased compared to variance-covariance based SEMs (Lefcheck 2016). As an indication that the method is reliable in our framework, our pSEM analyses revealed the well-established temperature dependency of wood decay (Fig. 3, 4; Meentemeyer 1978, Harmon et al. 1986, Chambers et al. 2000). The temperature effect was even detected despite the fact that plot temperatures varied only by a factor of 1.2, while the variation in tree species diversity (2-fold) as well as in the decomposer diversities (6- to 21-fold) were both considerably larger (Table 1).

Table 1. Range and standard deviation (SD) of plot specific decay rates ( $k$ ) and predictors. OTUs = operational taxonomic units,  $H$  = Shannon's diversity index.

Variable	Unit	Min	Max	SD
Age	years	22	116	26
Elevation	m a.s.l.	251	903	168
Mean temperature	°C	14.79	17.90	0.87
Mean relative humidity	%	84.00	93.28	2.45
Tree diversity	$H$	1.80	3.41	0.42
Fungal richness <i>S. superba</i> control	no. of OTUs	7	79	18.96
Fungal richness <i>S. superba</i> exclusion	no. of OTUs	7	72	17.90
Fungal richness <i>P. massoniana</i> control	no. of OTUs	13	103	23.73
Fungal richness <i>P. massoniana</i> exclusion	no. of OTUs	16	95	21.62
Macro-invertebrate diversity <i>S. superba</i> control	$H$	0	2.14	0.64
Macro-invertebrate diversity <i>P. massoniana</i> control	$H$	0.16	2.25	0.59
$k$ <i>S. superba</i> control	year <sup>-1</sup>	0.10	0.31	0.05
$k$ <i>S. superba</i> exclusion	year <sup>-1</sup>	0.10	0.33	0.06
$k$ <i>P. massoniana</i> control	year <sup>-1</sup>	0.14	0.39	0.06
$k$ <i>P. massoniana</i> exclusion	year <sup>-1</sup>	0.11	0.30	0.05

For the first part of the second hypothesis, we expected that decomposer diversities within our samples would increase with tree species diversity of the surrounding stand. This trend would especially apply to generalist decomposers that would benefit from higher resource heterogeneity and the availability of more diverse habitats (Lodge et al. 1995, Gessner et al. 2010, Stokland et al. 2012). For specialist decomposers, higher tree species diversity rather leads to decreased abundances of the respective focal tree species and consequently higher tree species diversity may lead to a lower diversity of decomposers (Wardle 2002). This was observed for the relationship between tree species diversity and macro-invertebrate diversity of *S. superba* (Fig. 3). There is evidence that specialist decomposers are more abundant in well defended tree species, while generalists favor less well defended ones (Stokland et al. 2012). *Schima superba* is protected by high wood density (0.7 g cm<sup>-3</sup>) and low wood nitrogen concentration (0.05%), two wood traits that are known to negatively affect wood decomposition rates and thus decomposer activity (Cornwell et al. 2009, Weedon et al. 2009, Pietsch et al. 2014).

With respect to the fungal and invertebrate communities we discovered in our samples, it is important to keep in mind that the diversity of decomposers must always be seen as a picture at a given point in time of the whole decomposition process. The composition and diversity of saproxylic

fungi and invertebrates is influenced by the time of arrival of individual species (Fukami et al. 2010, Penttilä et al. 2013, Stoklosa et al. 2016). Consequently, the colonization of dead wood is a successive process and the composition and diversity of saproxylic fungi and invertebrates varies with ongoing decay (Penttilä et al. 2013, Zuo et al. 2014).

For the second part of hypothesis two, we expected that macro-invertebrate diversity and fungal OTU richness would increase wood decomposition rates. We found a positive effect of macro-invertebrate diversity on decomposition rates for *S. superba* and a negative effect of macro-invertebrate diversity for *Pinus massoniana* as well as of fungal OTU richness for *S. superba* (exclusion treatment). That the effect of macro-invertebrates on wood decay was negative in *P. massoniana* and positive in *S. superba* may indicate that certain macro-invertebrates were repressed in the gymnosperm at high diversities. We found that the communities of fungi as well as macro-invertebrates differed significantly between the two species (Table 2). The most abundant macro-invertebrates in the gymnosperm wood were termites that were on average 3.5 times more numerous per sample than all other macro-invertebrates combined. In the angiosperm wood, on the other hand, the abundance of termites was almost equal to the abundance of all other macro-invertebrates combined. Termites favour *Pinus* over *Schima* wood due to nutritional value and wood density

Table 2. PERMANOVA results on the influence of species (*S. superba* and *P. massoniana*) and treatment (control and macro-invertebrate exclusion, only for fungi) on macro-invertebrate and fungal communities. For a graphical representation of the results see Supplementary material Appendix 3 Fig. A7.

Model variable	df	Sum of sqs	Mean sqs	F	r <sup>2</sup>	p
Macro-invertebrate communities						
Species	1	0.65	0.65	2.61	0.06	0.001
Residuals	45	11.17	0.25		0.95	
Fungal communities						
Species	2	2.62	1.31	3.18	0.05	0.001
Treatment	1	0.32	0.32	0.77	0.01	0.741
Residuals	111	45.61	0.41		0.94	

(Bustamante and Martius 1998, Bignell and Eggleton 2000). A regression of macro-invertebrate diversity against termite abundance indeed showed a reduction of termites at high macro-invertebrate diversities, which was stronger in the gymnosperm compared to the angiosperm (Supplementary material Appendix 3 Fig. A5). Additionally, higher macro-invertebrate diversity may be associated to a higher diversity and/or abundance of ants preying upon termites, thus potentially decreasing decomposition efficiency (Warren and Bradford 2012). In consequence, decomposition rates of *Pinus* wood were not accelerated with increasing macro-invertebrate diversity due to competition between termites and other macro-invertebrates.

The absence of an effect of fungal OTU richness on wood decay rates in three out of four cases may indicate that community composition of fungi is more important for the variation in wood decomposition rates than richness alone. Purahong et al. (2017) explored the relationship between fungal OTU richness and community composition with wood decay rates from the same samples as our study and found weak negative effects of richness on decay when both species and treatments were pooled ( $\rho = -0.22$ ). This weak negative relationship reflects the respective relationship we recovered in the exclusion treatment of *S. superba* ( $\rho = -0.23$ ). Furthermore, Purahong et al. (2017) found significant effects of fungal community composition for wood decay rates in both species. A study on two tree species from a temperate forest showed that wood decomposition rates were controlled by the succession of fungal communities over the course of decomposition as well as by competition scenarios among fungal taxa rather than by fungal OTU richness (Hoppe et al. 2016).

We estimated the wood-inhabiting fungal richness using a high resolution culture independent technique (454 pyrotag sequencing, Next Generation Sequencing). We thereby obtained a more in-depth picture of the wood-inhabiting fungal community in deadwood compared to studies using sporocarp surveys or culturing techniques (Purahong et al. 2017). The sample-based rarefaction curves (Supplementary material Appendix 1 Fig. A1) showed a saturation of fungal richness at the analysed sequencing depth for most samples, indicating that the observed OTU richness is a suitable measure for total fungal diversity.

As with all molecular techniques, it has to be kept in mind however that potential biases are inherent to the method, especially the sampling effect (Amend et al. 2010, Purahong et al. 2017). Specifically, when using universal primers the relative sequence read abundance of individual OTUs is always affected by other OTUs in the pool in response to the PCR reaction components (such as PCR primers or DNA capture beads). In general, OTUs with a high template abundance or PCR affinity will diminish the read abundance of other OTUs (Amend et al. 2010). In our study, we minimized such biases by using a sufficient amount of sequence reads per sample (3077) to ensure the ability of sequencing most of the fungal taxa in each wood sample. When sufficient amounts of

sequence reads per sample are attained, the low fungal richness that we observed in some deadwood samples is likely due to the fact that fungal richness was actually low. This can be explained by fungal–fungal interactions of the highly detected fungal OTUs (Hoppe et al. 2016), especially between *Xylaria* sp. and *Phanerochaete* sp. (Purahong et al. 2017).

Taken together, we found only weak effects of tree species diversity, fungal OTU richness and macro-invertebrate diversity on wood decay rates despite the fact that they varied considerably (Table 1). While being quite large, the diversity gradient in our study did not include monocultures. We found a minimum of 25 tree species, seven fungal OTUs and three macro-invertebrate species in our plots. However, the biodiversity ecosystem functioning curve saturates at high species richness (Cardinale et al. 2012). It is therefore likely that our system is already in the saturation stage for the relationship between diversity and wood decomposition, whereby species (trees or decomposers) are functionally redundant. Additionally the presence of key-stone taxa, for example termites that were present in almost all plots, may be more important than species diversity per se (Hättenschwiler et al. 2005). Finally, we did not manipulate fungal OTU richness and invertebrate diversity. This could be a reason why effects of the decomposer diversity in our study were comparatively weak in relation to other studies that controlled or manipulated decomposer diversities (Cox et al. 2001, Hättenschwiler et al. 2005).

### **No effect of macro-invertebrate exclusion on wood mass loss rates**

Our results showed no significant reduction of the decay rates in the macro-invertebrate exclusion treatment, which rejects our third hypothesis. In the past, there has been a debate about potential effects of mesh bags on micro-climatic conditions inside the bags towards higher moisture conditions (Kampichler and Bruckner 2009, Stoklosa et al. 2016). Higher moisture levels may induce differences in fungal species community composition and/or higher fungal activity in the fine mesh bags and consequently compensate for the effect of macro-invertebrate exclusion which may lead to an underestimation of the effect of macro-invertebrates in the control treatment (Stoklosa et al. 2016). Yet, our PERMANOVA analysis showed no differences of fungal community composition between the treatments (Table 2) and the moisture contents of the samples did not differ between treatments in a given species (Supplementary material Appendix 3 Fig. A6). We thus conclude that the mesh size had no effect on micro-climatic conditions inside the fine mesh bags that could lead to alterations of fungal community composition or fungal activity.

There is evidence that termites and ants inhibit microbial growth and activity by secreting antimicrobial compounds (Rosengaus et al. 1998, Bulmer et al. 2012, Warren and Bradford 2012). If microbial activity was suppressed by invertebrate activity, enhanced microbial activity in the

exclusion treatment would have compensated for the decay related to invertebrate feeding in the control treatment, irrespective of moisture regimes in the samples. Our data do not support interactions of termites with the fungal community, since the community composition of fungi in the decomposed samples did not differ with treatment (Table 2). Thus the effect of termites on wood decay rates likely depends on species specific interactions between the involved termites, microorganisms and the decomposing tree species.

Our results show that macro-invertebrates have little effect on wood decay, while microbial decomposers are the main agents of decay during the observed period. This finding contradicts recent studies from subtropical forests that found significantly lower decay rates of wood and bamboo in subtropical forests when termites were excluded (Liu et al. 2015, Eichenberg et al. 2017). However, both studies were conducted in forest communities with far lower leaf area index and a more open canopy structure than our system. Such differences reflect the fact that decomposers differ widely in their decomposition efficiency under differing environmental conditions. Accordingly, a global litter decomposition experiment provided evidence that the influence of invertebrates on decay rates depends on the climate (Wall et al. 2008). Fungi are especially effective in closed moist forests and suffer in open and dryer conditions, while termites are especially effective in dry tropical and subtropical environments (Stokland et al. 2012). Our results suggest that macro-invertebrate exclusion does not lead to reduced decay rates in ecosystems where environmental conditions are favourable for fungi, as opposed to open and dry ecosystems where environmental conditions are predominantly favourable for termites. This assertion is supported by the results of studies from a tropical forest in Malaysia (Takamura and Kirton 1999, Takamura 2001) and south-eastern US (Ulyshen et al. 2014) where termite exclusion did not necessarily affect wood decay rates negatively. The high potential for fungal decay at favourable environmental conditions may help to resolve the paradox of subtropical forests in Southeast Asia, in which termites are relatively less abundant and less diverse than in equivalent systems in Africa and South America (Eggleton et al. 1999), but where decomposition processes are not significantly less effective (Berge et al. 2008).

### **Tree species diversity effects on wood decay depend on the presence of macro-invertebrates**

In our fourth hypothesis we postulated that the exclusion of macro-invertebrates weakens the relationship between tree species diversity and wood decay rates. We did not find strong support for this hypothesis, but the effects of tree species diversity on wood decay still differed between the control and exclusion treatments in both species. The negative tree species diversity effect in the control treatments of both species was predominantly controlled by macro-invertebrate diversity (Fig. 3) and this pathway was disconnected in the exclusion treatments. Yet, the temperature control was always

stronger than the diversity control, despite the large diversity gradient of our system.

Our results show that the temperature control tended to be stronger in the presence of macro-invertebrates, but the difference between treatments was not significant. It has to be noted, however, that we found this trend in both species and the lack of significance may be due to the limited sample size of our study. Additionally, it fits in the line of evidence for similar interactions between decomposer organisms and the climate control of decay rates. Recent studies have for example shown that environmental factors regulate decomposer communities which consequently affects wood decay rates (Zuo et al. 2014), that the colonization by different decomposers can have stronger effects on wood decay rates than climate alone (Bradford et al. 2014), or that differences in decomposer functional ability can modify direct effects of climate on litter decomposition rates (Keiser and Bradford 2017). This suggests that the effects of tree species diversity as well as temperature, as one of the most well studied variables for wood decomposition rates, may be mediated through mutual interactions between and the presence of different decomposer groups. Future research in this direction will help to elucidate the role of decomposer organisms for the prediction of carbon and nutrient turnover through decomposition under changing climatic conditions.

### **Implications for long term decomposition**

Our experiment reveals causal effects of diversity (of tree species, fungi and macro-invertebrates) and temperature on wood decomposition rates during the initial stage of decay. Yet also late stage decay processes have critical implications for carbon and nutrient cycling through wood decay and controls may vary during later stages. Wood decay rates decrease with time, impeding the extrapolation of initial stage decay dynamics to long term dynamics (Berg and McClaugherty 2003, Pietsch et al. 2014). Still our results allow inferring on effects of biodiversity and temperature during later stages of decomposition. During the observed period of our experiment the exclusion of macro-invertebrates showed no effect on wood decay rates, indicating that fungi were the predominant agents of decay. We further found no evidence for an effect of invertebrate activity on fungal dead wood colonization in our study. With ongoing decay, however, invertebrate species assemblages change and there are generally more species in wood of advanced decay stages (Penttilä et al. 2013). There is furthermore evidence that wood which has been previously colonized by fungi is of higher nutritional value to invertebrates. Fungi reduce wood density by digesting and braking down structural components which makes it more attractive to invertebrate decomposers (Swift and Boddy 1984, Jonsell et al. 2005). Fungal enzymes can help cellulose digestion in xylophagous beetles (Martin 1987) and increasingly growing networks of fungal hyphae are a valuable nutrient source for invertebrates (Boddy and Watkinson 1995). Finally, fungal degradation can detoxify wood from repellent or toxic allelochemicals which makes

it subsequently accessible for invertebrates (Swift and Boddy 1984). The above mentioned positive effects of fungi for invertebrates indicate that invertebrates may become more important as wood decomposition progresses. Since indirect effects of tree species diversity on wood decay were driven by the presence and diversity of macro-invertebrates, tree species diversity effects may become more pronounced during later stages of wood decay.

## Conclusions

We provide evidence for weak tree species diversity and decomposer diversity effects on wood decay rates. However, results from a single substrate should not be extrapolated to the community level as the strength and direction of these effects differed between the two studied tree species. In all species and treatment combinations temperature had the strongest effect on wood decay rates, indicating that an increase in mean annual temperature as consequence to climate change might lead to higher carbon and nutrient turnover in subtropical forest landscapes. The fact that we only found weak effects of tree species and decomposer diversity on wood decomposition dynamics may indicate that the species in our experiment were largely functionally redundant and that certain keystone taxa for decomposition were always abundant. Whether and at which level a loss of tree and decomposer species is substantially impairing decomposition remains to be tested in dedicated experiments manipulating especially gradients in macro-invertebrate and fungal OTU species diversity and composition. This will only be possible in a more controlled setting (e.g. in the laboratory or mesocosm). The question should also be pursued using observational experiments like ours. To detect the more subtle biotic control factors and their interactions underlying CWD decomposition a higher number of plots may be needed.

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*Author's contributions* – KAP, JB, FB and CW conceived the ideas and designed the methodology; KAP, WP and BW collected the data; FB, WP and TW analysed fungal community composition; MY provided substantial help for the fieldwork in China; KAP analysed the data with help of KN and DE; KAP drafted the manuscript and all authors contributed critically to the draft and gave final approval for publication.

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Supplementary material (available online as Appendix oik-04879 at <[www.oikosjournal.org/appendix/oik-04879](http://www.oikosjournal.org/appendix/oik-04879)>). Appendix 1–3.