



Wood decay rates of 13 temperate tree species in relation to wood properties, enzyme activities and organismic diversities



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ABSTRACT

Deadwood decay is an important ecosystem process in forest ecosystems, but the relative contribution of specific wood properties of tree species, activities of wood-degrading enzymes, and decomposer communities such as fungi and insects is unclear. We ask whether wood properties, in particular differences between angiosperms and gymnosperms, and organismic diversity of colonizers contribute to wood decomposition. To test this, we exposed deadwood logs of 13 tree species, covering four gymnosperms and nine angiosperm species, in 30 plots under different forest management in three regions in Germany. After a decomposition time of 6.5 years *Carpinus betulus* and *Fagus sylvatica* showed the highest decay rates. We found a positive correlation of decay rate with enzyme activities, chemical wood properties (S, K concentration) and organismic diversity, while, heartwood character, lignin content, extractive concentration and phenol content were negatively correlated with decay rate across all 13 tree species. By applying a multi-model inference approach we found that the activity of the wood-degrading enzymes laccase and endocellulase, beetle diversity, heartwood presence, wood ray height and fungal diversity were the most important predictor variables for wood decay. Although we were not able to identify direct cause and effect relations by our approach, we conclude that enzyme activity and organismic diversity are the main drivers of wood decay rate, which greatly differed among tree species. Maintaining high tree species diversity will therefore result in high structural deadwood diversity in terms of decay rate and decay stage.

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1. Introduction

Deadwood is known to be an important structural component of forests (Bauhus et al., 2009) that influences a large number of ecosystem functions (Harmon et al., 1986; Cornwell et al., 2009)

and is a critical resource for wood-dwelling organisms (Lonsdale et al., 2008; Rondeux and Sanchez, 2010; Stokland et al., 2012).

The rate of deadwood decay, as a combination of biological respiration, leaching and fragmentation (Harmon et al., 1986), is mainly the result of organismic activity (e.g. fungi, insects), determined by intrinsic (e.g. tree species properties) and environmental factors (e.g. temperature, moisture). In the early phase of decay, biological respiration (i.e. mineralization of wood components to CO₂) is the main process, while leaching only accounts for about 1–2% of mass loss (Kahl, 2008; Bantle et al., 2014). Fragmentation can also cause a substantial mass loss of deadwood, e.g. 18–30% of decomposition rates over the first 18 years in some European tree species (Herrmann et al., 2015), and it may become even more important in the late phase of decomposition (up to 40%; Harmon et al., 1986).

Decay rates for common European tree species have been well documented for different climatic regions (Pietsch et al., 2014). First estimates were reported for *Quercus* spp., *Fraxinus excelsior*, *Betula* spp. and *Corylus avellana* (Swift et al., 1976; Christensen, 1977) already in the 1970s. However, decay rates for less abundant tree species such as *Carpinus betulus*, *Prunus avium* or *Tilia* spp. have not been quantified.

Estimates on decay rates are often based on a chronosequence approach, where *in-situ* deadwood is sampled of different times since death and compared. This approach has a sampling bias, due to the fact that deadwood with low decay rates is more likely to be sampled than deadwood with high decay rates, which may have already decayed completely at the time of observation (Kruys et al., 2002). This may result in an underestimation of deadwood decay rates. To quantify true decay rates, these should be measured during the entire time course of wood decay. An unbiased estimation of decay rates can either be achieved by resampling of sites that include all recently killed trees, or by experiments that place deadwood logs in forests. Such site-based multi-species studies on decay rates including angiosperms and gymnosperms are, however, still largely lacking (Weedon et al., 2009).

Decay rates of different tree species could be largely affected by functional group or species-specific wood traits. A meta-analysis of Weedon et al. (2009) showed that gymnosperms generally tend to have lower decay rates than angiosperms. In gymnosperms, solvent extractable organic compounds (extractives) comprise mainly terpenes and their derivatives, which slow down fungal growth and degradation activity (Dix and Webster, 1995; Pearce, 1996). In contrast, in angiosperms the chemical composition of extractives is more diverse, reaching from resin-like materials of carbohydrate gum in cherry (Pearce, 1996), which may not affect decay, to phenolic compounds (e.g. quercetin) and tannins in oak, which inhibit fungal growth (Hart and Hillis, 1972; Aloui et al., 2004). Furthermore, the lignin of gymnosperms is more difficult to oxidize compared to that of angiosperms, since it consists to more than 90% of guaiacyl moieties, compared to 0–33% in angiosperm lignin. The lignin of angiosperms contains a higher proportion of sinapyl moieties that degrades more easily (Brunow, 2001; Higuchi, 2006). Guaiacyl units make the lignin of gymnosperms particularly compact, which impedes enzymatic attack in general (Hatakka and Hammel, 2010).

Within angiosperms, wood traits such as phosphorus and nitrogen content, and low C:N ratio are positively correlated with decay rates (Weedon et al., 2009). It is also well known (EN350-2, 1994) that tree species with distinct heartwood (e.g. *Quercus* spp.) tend to have higher resistance against wood-decaying fungi. The content of extractives, such as tannins and terpenoids/resins, in heartwood is often higher than in sapwood and the extracts from heartwood are usually more toxic (Scheffer, 1966; Hillis, 1999; Gierlinger et al., 2004).

Furthermore differences in the presence of organisms and their activity might affect wood decay. A high diversity of saproxylic fungi and beetle species in logs of different tree species have been shown in previous studies (Baber et al., 2016; Gossner et al., 2016). In wood decomposition mediated by fungi, the main secreted enzymes are oxidoreductases modifying lignin via radical formation with the help of dioxygen (laccase) or hydrogen peroxide (several peroxidases), and diverse glycoside hydrolases, which hydrolytically cleave the major polysaccharides (cellulose, hemicelluloses) to sugars (Hatakka and Hammel, 2010; Kellner et al., 2014; Arnstadt et al., 2016a; Noll et al., 2016). While substantial lignin decomposition is exclusively mediated by white-rot basidiomycetes possessing high-redox potential peroxidases (i.e. class II manganese and lignin peroxidases, Floudas et al., 2012), cellulose and hemicelluloses can be disintegrated by all wood-decomposing fungi (white-, brown- and soft-rot fungi), as well as by specialized bacteria. The resulting sugars, e.g. cellobiose, glucose, xylose, mannose, and arabinose, serve as carbon and energy source (Riley et al., 2014). Against this background, the activities of laccase, manganese and general peroxidases can be used as proxy for lignin attack. The same is true for *endo*-1,4- β -glucanase and *endo*-1,4- β -xylanase, which mediate the first step in the breakdown of the polysaccharide backbone by forming oligo-, di- and monosaccharides (Kögel-Knabner, 2002) representing the enzymatic polysaccharide disintegration. Despite the importance of these enzymes for wood decomposition, their relation to decay rates of deadwood has never been studied. Only few publications have so far analyzed enzymes in deadwood (Valaskova et al., 2009; Větrovský et al., 2011; van der Wal et al., 2015; Arnstadt et al., 2016a; Baldrian et al., 2016; Noll et al., 2016; Purahong et al., 2016).

Differences in fungal species identity and fungal communities can cause distinct differences in decay rates (Boddy, 2001; Kahl et al., 2015). However, to date no consistent relationship between deadwood decomposition and fungal decomposer diversity has been demonstrated (van der Wal et al., 2013). It has been shown that decay rates can be either positively (Setälä and McLean, 2004; Tiunov and Scheu, 2005; Toljander et al., 2006; Valentín et al., 2014; Kahl et al., 2015) or negatively (Fukami et al., 2010) correlated with fungal species richness. Based on the quantification of fungal operational taxonomic units (OTU), Hoppe et al. (2015) found no correlation between total richness (using molecular NGS 454 data) and wood decomposition rate in both coniferous (*Picea abies*) and deciduous (*Fagus sylvatica*) deadwood. Admittedly, there is an undeniable relationship between fungal community composition and wood decomposition. The fungal assembly history (Fukami et al., 2010), the presence of species with extraordinary decomposition activities (Lindner et al., 2011; Kubartová et al., 2012) and the environmental conditions (Renvall, 1995; Høiland and Bendiksen, 1996) can determine the strength of this relationship. Van der Wal et al. (2015) showed that the most important factors explaining variation in wood decay rates can change over time and the strength of competitive interactions between fungi may level off with increased wood decay. This study furthermore showed that wood moisture content contributed especially to explain sapwood decay in early decay stages, whereas fungal community composition and species richness were the best predictors for mass loss in the later stages (van der Wal et al., 2015).

Insects also play an important role in the wood decomposition process. Based on a meta-analysis, Ulyshen (2016) estimates the contributions of invertebrates to wood decomposition to account for 10–20%. He suggests four main underlying mechanisms: (1) enzymatic digestion by endogenous enzymes (Watanabe and Tokuda, 2001, 2010) as well as by enzymes produced by endo- (gut microbes; e.g. Suh et al., 2005) and ectosymbionts (e.g. fungi

cultivating ambrosia beetles; e.g. Hofstetter et al., 2015a), (2) substrate alteration by tunnelling and fragmentation and therefore building entrance ports for other species, e.g. fungi or later successional species, (3) biotic interactions with microbes (e.g. alteration of microbial communities) and other invertebrates (e.g. by predation, competitive exclusion) and (4) nitrogen fertilization which promotes nitrogen fixation by endosymbiotic and free-living bacteria. In Central Europe, where termites are absent, large wood-boring beetles are assumed to be most influential and their presence more important than species richness itself, but detailed studies on the importance of insect species richness for wood decomposition of different tree species are still lacking (Ulyshen, 2016).

While our knowledge on wood decay rates in relation to wood properties and organismic diversity has increased in the past decades, there are still large uncertainties how the different factors interact and differ between tree species. Unbiased estimates from field deadwood experiments are scarce. Here, we report on the results of a large-scale field experiment where logs of 13 tree species were placed into 30 forest stands in Germany. We studied decay rates, wood properties and organismic diversity.

We asked the following questions:

1. Do gymnosperms show consistently lower rates of decay than angiosperms under common environmental conditions?
2. Are anatomical, chemical or structural wood traits good predictors of decay rates?
3. Are biotic factors such as enzymatic activities of wood-degrading enzymes and species richness of fungi and insects good predictors of decay rates?

2. Methods

2.1. Study area

The study was conducted within the “Biodiversity Exploratories”, a large-scale and long-term project to investigate the relationship between land-use intensity, biodiversity and ecosystem processes in three different regions (exploratories) in Germany (for details, see Fischer et al., 2010); the UNESCO Biosphere Reserve Schorfheide-Chorin in North-Eastern Germany (52°47'25"–53°13'26"N/13°23'27"–14°08'53"E, 3–140 m a.s.l.), the National Park Hainich and surrounding Hainich-Dün area in Central Germany (50°56'14"–51°22'43"N/10°10'24"–10°46'45"E, 285–550 m a.s.l.), and the UNESCO Biosphere Reserve Swabian Alb in South-Western Germany (48°20'28"–48°32'02"N/9°10'49"–09°35'54"E, 460–860 m a.s.l.). With 700–1000 mm, annual precipitation is highest in the Swabian Alb, followed by Hainich-Dün (500–800 mm) and Schorfheide-Chorin (520–580 mm). The mean annual temperature increases from Swabian Alb (6.0–7.0 °C) to Hainich-Dün (6.5–8.0 °C) to Schorfheide-Chorin (8.0–8.5 °C) (Fischer et al., 2010).

2.2. BElongDead experiment

The BElongDead (Biodiversity Exploratories Long term Deadwood) Experiment was established on a total of 30 plots (9 in Schorfheide-Chorin and Swabian Alb, and 12 in Hainich-Dün) in 2009. The 30 plots cover a range of forest types and management intensities including extensively managed or unmanaged forests dominated by European beech (9), managed even- and uneven-aged forests dominated by European beech (12), and intensively managed even-aged coniferous (Norway spruce and Scots pine) plantations (9).

On each plot deadwood logs of 13 tree genera (henceforth tree species for simplicity) were exposed in three replicates (subplots)

($n = 1170$ logs). Tree species include nine Angiosperms: *Acer* spp. (*A. pseudoplatanus*, *A. platanoides*, *A. campestre*), *Betula pendula*, *Carpinus betulus*, *Fagus sylvatica*, *Fraxinus excelsior*, *Populus* spp. (*P. tremula* and hybrids), *Prunus avium*, and *Quercus* spp. (*Q. robur*, *Q. petraea*), *Tilia* spp. (*T. cordata*, *T. platyphyllos*) and four Gymnosperms: *Larix decidua*, *Picea abies*, *Pinus sylvestris*, and *Pseudotsuga menziesii*. All logs are approximately 4 m long and have a mean diameter of 31 ± 5.9 cm (SD). All logs were cut in winter 2008/2009 in the federal state of Thuringia (Germany) and then transported to each plot. Within a subplot, the 13 logs were placed in random order beside each other with a distance of ca. 1 m between logs. We carefully followed a protocol to minimize the potential bias by colonization of logs prior to translocation to the experimental sites. Owing to limited supplies, *P. avium* logs are missing on 27, *Acer* spp. on 2 and *Fagus sylvatica* on 1 of the 90 subplots (Kahl et al., 2015). One subplot with 12 logs in the exploratory Schorfheide was unlawfully removed in 2012, reducing the total number of logs to 1128.

2.3. Wood decay rate

Deadwood decay rate was calculated based on density loss. Initial wood density was determined using discs that were cut in 2009 immediately after exposure from all logs. The discs were then dried at 65 °C and stored in a warehouse. After removing the bark the discs were drilled with a 1 cm diameter auger and a cordless power drill in radial direction to the pith. The second sampling from the exposed logs took place in June 2015. Owing to the advanced decay in 2015, logs were, after removing the bark, drilled with a 4 cm diameter Forstner bit in 60 cm distance from one end of the log. The Forstner bit allows drilling clean cylindrical holes even in decayed wood material. In both 2009 and 2015, wood shavings were carefully collected and dried at 65 °C until no further decrease in weight was detected. Dry wood density (g cm^{-3}) in 2009 and 2015 was calculated as ratio of dry wood weight (g) and drill hole volume (cm^3). Decay rate constant (k) using density loss for each log was calculated based on an exponential decay function as proposed by Olson (1963). Decay time between 2009 and 2015 was set to 6.5 years. Negative decay rates occurred in individual logs of 12 out of 13 tree species (except *Carpinus betulus*; Supplement Table A3-1), which seems to be a specific problem of our applied methods. Since negative decay rates, which would mean an increase in density during decay, are rather unlikely, we believe that our methods for the determination of wood density were not as precise as they should be. The following reasons could lead to the observed discrepancies: First, initial wood density was based on discs cut from each log in 2009. These discs represent only about 2% of the log, while samples in 2015 were taken at least 50 cm away from where the discs were cut. We do not know how large the density variability is within each log. Second, the discs were dried in 2009 before sampling while the logs in 2015 were moist. The shrinkage of the wood after drying in 2009 should have caused an even higher density. The average volume shrinkage is about 0.42% per percent water content (Wagenführ, 2006). Third, differences in the used drilling devices ($d = 1$ cm auger vs. $d = 4$ cm forstner bit) in dry vs. moist wood. It could be that our method of volume determination was not precise enough. To this point we cannot say why we found these negative decay rates in some of the logs. Although this is a major concern in our study we believe that all tree species were affected in the same way and that the relative relationship in decay rates between tree species remained largely unaffected (Supplement Fig. A3-1 & A3-2). In cases where negative decay rates were measured for individual logs between inventory periods, these rates were set to 0. These results were only used for the illustration of decay rate distribution within and among tree species.

For correlations with predictors of wood decay we used decay rates based on single exponential models of wood density loss of all logs for each tree species. Average wood density of all logs per tree species in 2009 (undecayed) and in 2015 (after six years of decay) were used as input variables for the calculation of decay rates.

2.4. Predictors of decay rates

We measured a number of anatomical, mechanical, physical and chemical wood properties, enzyme activities, and organismic species richness for all 13 tree species, to analyze how these correlate with wood decay rates. Due to methodological and time limitations some of the traits were extracted from literature or assessed only on a subset of logs. Hence, the number of replicates for measured variables varies for each method (Table 1). We used mean values per tree species for the analysis (Supplement Table A3-2).

2.4.1. Wood properties

2.4.1.1. Anatomical, mechanical and physical wood properties. Species-specific bark proportion, occurrence of distinct heartwood, ratio of longitudinal parenchyma in wood to total wood volume, wood ray height and wood ray thickness were taken from the literature (Wagenführ, 2006). Wood density in 2009 was measured as described above.

2.4.1.2. Chemical wood properties. Initial chemical properties of sapwood were determined from discs of three logs per tree species ($n = 3$), taken immediately after exposure of logs on the forest floor, then dried and cut in wedge-like pieces, representing the proportion of all tree rings. Carbon and nitrogen concentrations of milled sapwood were analyzed using a CN analyzer. Following pressure digestion, phosphorous, sulphur, potassium, calcium, magnesium and manganese were determined by inductively coupled plasma with optical emission spectrometry (ICP-OES). Sapwood shavings were extracted with deionized water (1:15) for spectroscopic analysis of water soluble phenols (Box, 1983), calibrated with phenol as standards.

2.4.1.3. Organic extractives, pH-value and lignin. Organic extractives (e.g. tannins and terpenoids/resins) were measured gravimetrically after extraction of the dried and milled wood samples (same samples as for chemical wood properties) with acetone in an accelerated solvent extraction device (Dionex ASE 200). Afterwards, the Klason lignin content of the extracted wood samples was determined gravimetrically after further grinding and sequential hydrolysis with sulphuric acid. The part of acid soluble lignin was measured spectrophotometrically in the hydrolysate and summed up with Klason lignin to the total lignin content (Arnstadt et al., 2016a). For pH measurement, the milled wood samples were extracted with deionized water and the pH detected with an electrode in the aqueous supernatant (Arnstadt et al., 2016a).

2.4.2. Enzymatic activities

In 2012, wood samples were taken using a cordless drill (Makita BDF 451) equipped with a wood auger (20 mm × 450 mm). Activities of degradative enzyme were determined in 379 wood samples (1 subplot per plot) in 2012. In the aqueous extracts of the milled samples, lignin-related oxidoreductases (laccase EC 1.10.3.2, manganese peroxidase EC 1.11.1.13 and general peroxidase activity EC 1.11.1.7/14/16; Kellner et al., 2014) were assayed spectrophotometrically with ABTS (2,2'-azino-bis(3-ethylbenzothiazoline-6-sulfonic acid) as substrate according to Arnstadt et al. (2016a, 2016b). The activities of manganese peroxidase and general peroxidase

were summed up to total peroxidase (POX) activity. Hydrolytic enzyme activities related to polysaccharide disintegration, i.e. endocellulase (EC 3.2.1.4), and (endo)xylanase (EC 3.2.1.8), were measured spectrophotometrically applying AZO-cellulose and AZO-xylan as substrates, respectively, following the protocol of Megazymes (Bray, Ireland) (Vetrovsky et al., 2011).

2.4.3. Fungal species richness based on fruit bodies

Fungal fruit body data were gathered on 379 out of 1128 logs (1 subplot per plot) in autumn (September to October) 2012 during the peak fruiting season (Halme and Kotiaho, 2012) parallel to the wood sampling for molecular, wood chemical and enzyme activity analysis. We collected macrofungi with a fruit body, fruit body aggregation or stroma size of at least 5 mm diameter. The fungal inventory covered Basidiomycota (mainly corticioid and poroid fungi) and macrofungal groups from the phylum Ascomycota (especially Pyrenomycetes and Discosmycetes). We investigated exclusively the visible part of the log and did not remove moss or bark. The fungal species were identified in situ or, if necessary collected for later microscopical identification. Collected specimens were dried and deposited at the Herbarium Universitatis Lipsiensis LZ (University Leipzig, Germany). We used species richness for each tree species averaged per log as well as rarefied to lowest sample size (20 logs) as predictor variables in our models.

2.4.4. Fungal molecular operational taxonomic units

In addition to the identification of macrofungi, we also used a molecular method to quantify fungal richness. Fungal automated ribosomal intergenic spacer analysis (F-ARISA) was performed as described in Purahong et al. (2014a, 2016). Briefly, DNA was extracted from 100 mg of each homogenized wood sample (see method for enzyme activities above) using the ZR Soil Microbe DNA MiniPrep kit (Zymo Research, Irvine, CA, USA), according to the manufacturer's instructions. Fungal ITS was amplified using FAM-labelled primer ITS1-F (5'-CTTGGTCATTAGAGGAAGTAA-3', Gardes and Bruns, 1993) and unlabelled ITS4 (5'-TCCTCCGCTTATT GATATGC-3', White et al., 1990). The amplified PCR fragments were discriminated by capillary electrophoresis and raw profiles were analyzed using the Gene Mapper Software 4.0 (Applied Biosystems). All peaks of the fragments between 390 and 1000 bp that appeared in two technical PCR replicates were used for further analyses. Operational taxonomic unit (OTU) binning was carried out using an interactive custom binning script (Ramette, 2009) in R version 2.14.1 (R Core Team, 2011). Fungal OTUs were defined as described previously by Green et al. (2004) for the F-ARISA approach and may differ from those OTU definitions relying on sequences (Purahong et al., 2014b). They could, alternatively, be called ribotypes (Gleeson et al., 2005). We used fungal OTU richness for each tree species averaged per log as well as total OTU richness of 27 logs (equal number of replicates per tree species) as predictor variables in our models.

2.4.5. Saproxyl Coleoptera

Saproxyl Coleoptera emerging from the logs were sampled by closed emergence collectors for three years, 2010–2012 (for details, see Müller et al., 2015; Gossner et al., 2016). These traps sample insects emerging from the logs over a full season. Traps were installed in March 2010 (first subplot) and March 2011 (second subplot). Sampling vials were emptied monthly until the end of October and samples were stored in 70% ethanol. In autumn, traps were dismantled for the winter. The traps were moved 35 cm down the log every year. Specimens were sorted to order by student helpers and all Coleoptera were identified to species level by taxonomic specialists. Species were classified as saproxyl according to Seibold et al. (2015). We calculated beetle species

Table 1

Number of replicates (logs) per tree species and years of sampling for decay rate and each predictor category.

Tree species	Decay rate 2009–2015	Wood density 2009	Wood chemistry 2009	Enzymes 2012	Fungi fruit body 2012	Fungi OTU 2012	Coleoptera 2010–2012
Angiosperms							
<i>Acer</i>	85	85	3	29	29	27	59
<i>Betula</i>	87	87	3	30	30	27	60
<i>Carpinus</i>	88	88	3	30	30	27	60
<i>Fagus</i>	85	85	3	30	30	27	59
<i>Fraxinus</i>	87	87	3	30	30	27	60
<i>Populus</i>	86	86	3	30	30	27	60
<i>Prunus</i>	62	62	3	20	20	27	46
<i>Quercus</i>	87	87	3	30	30	27	60
<i>Tilia</i>	88	89	3	30	30	27	60
Gymnosperms							
<i>Larix</i>	89	89	3	29	29	27	60
<i>Picea</i>	87	88	3	30	30	27	60
<i>Pinus</i>	85	86	3	30	30	27	60
<i>Pseudotsuga</i>	87	87	3	31	31	27	60

richness for each tree species by averaging over logs and year, rarefied to lowest sample size of all tree species (104 log-years).

2.5. Tree phylogeny

Because tree species may not be regarded as independent samples, we considered the phylogenetic relatedness between tree species. Therefore we used a bioinformatics pipeline implemented in the R package megaptera (Heibl, 2014), to derive a set of alignments on which our phylogenetic hypothesis is based. We screened all protein-encoding and rRNA genes of chloroplast and mitochondrion as well as the nuclear rRNA genes, the histone H3 gene and the phytochrome C gene. For each tree genus and genetic locus, we downloaded all available accessions from GenBank and BOLDSYSTEMS. Under the assumption of monophyletic genera, we created majority-rule consensus sequences of all congeneric sequences that passed the quality checks. 11 loci provided the best taxonomic coverage and were concatenated into a final supermatrix: *atp1*, *atp6*, *atp9*, *ndhF*, *rbcL*, *cox1*, *cox3*, *matR*, *nd4L*, *nd6*, 16S rRNA. Tree topology and ultrametric branch lengths were modelled in a maximum likelihood framework using RAXML version 8.2.4 (Stamatakis, 2014) and the function *chronos* in the R package *ape* (Paradis et al., 2004). Confidence in the topology of our phylogenetic hypothesis was assessed with non-parametric bootstrap using stopping criteria described in Pattengale et al. (2010). All branches received bootstrap support of 83% or more and the tree topology is in accordance with current knowledge (Supplement Fig. A1–2).

2.6. Statistical analysis

All analyses were conducted in R version 3.2.2 (RCoreTeam, 2015). We calculated Spearman's rank correlation coefficients to show the correlations between the dependent variable decay rate and all independent variables.

For analyzing the importance of different predictor variables for wood decay, we used two approaches; in one we considered the phylogenetic relatedness between tree species, in the other not. To reduce the number of explanatory variables, we first classified them in three groups: (i) anatomical, mechanical and physical wood traits, (ii) chemical wood traits and (iii) enzymes and organismic diversity. We then used either uncorrected (function *prcomp*) or phylogenetically corrected PCAs (function *phyl.pca* in the R package *phytools*; Revell, 2012) based on correlation matrices. Variables were log or square root transformed when necessary to meet assumptions of normality. For each PCA, the first three PCA

axes explaining at least 70% of the variance were selected. We selected the variable that showed the strongest correlation with the corresponding PCA axis. The correlations among selected variables was Pearson's $r < 0.70$ in all cases. According to Tabachnick and Fidell (1996) the independent variables with a bivariate correlation stronger than 0.70 should not be included in multiple regression analysis. The selected set of variables were standardized (scaled to zero mean and unit variance) and then used in either linear (function *lm*) or phylogenetic linear multiple regression models (*phylolm* function in the R package *phylolm*; Ho and Ane, 2014) with decay rate as dependent variable. For model selection, we applied the multimodel inference approach as proposed by Grueber et al. (2011). We first formulated a global model including all predictor variables and conducted automated model selection with subsets of the global model by the dredge function based on AICc (small-sample-size corrected version of AIC) in the R package *MuMIn* (Bartoń, 2016). We subsequently selected the best models based on $\Delta AIC < 2$ (substantial support) and $AIC < 7$ (some support) as suggested by Burnham et al. (2011) using the *get.models* function. The relative importance of each independent variable was assessed by calculating the cumulative Akaike weights of models containing a particular predictor.

We calculated the phylogenetic signal (Pagel's λ and Blomberg's k) for each variable by using the *phylosig* function in the R package *phytools* (Revell, 2012).

3. Results

3.1. Decay rates of different tree species

Average decay rates (k ; incl. negative values) of gymnosperms ($0.014 \pm 0.016 \text{ y}^{-1}$, $N = 4$) were significantly lower than those of angiosperms ($0.046 \pm 0.021 \text{ y}^{-1}$, $N = 9$; LM: $t = 3.178$, $p = 0.009$, $R^2_{\text{adj}} = 0.431$). Highest decay rates in angiosperms were found for *Carpinus betulus* and *Fagus sylvatica*, while lowest were found for *Fraxinus excelsior* and *Quercus* spp. The overall lowest decay rates were recorded for *Larix decidua* and *Pseudotsuga menziesii* (Fig. 1).

3.2. Effect of predictor variables on decay rates

The strongest correlations with decay rate were found for presence of heartwood and organic extractions, both of which were negative (Fig. 2 & Supplement Fig. A1–1). All enzymatic activities, fungal species richness and S and K concentrations showed strong positive correlations (correlation coefficient > 0.70 ; Fig. 2 & Supplement Fig. A1–1). Among independent variables, parenchyma ratio,

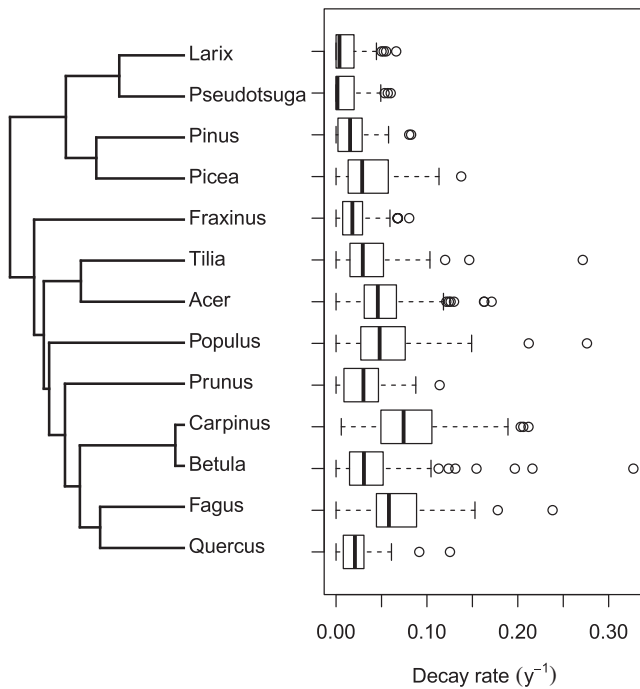


Fig. 1. Decay rates of 13 tree species using density loss between 2009 and 2015 based on exponential decay. Proposed phylogeny of tree genera is shown for illustrative purpose only. A tree including bootstrap values is provided in the supplement (Fig. A1-2). Median values, 25%/75% percentiles (Box) and Min-Max values (Whiskers) excluding outliers are shown.

K, Lignin and mean fungi fruit body richness showed a strong phylogenetic signal (Pagel's lambda and Blomberg's $k < 0.05$; Supplement Table A1-1).

3.3. Correlations among predictive variables

In uncorrected PCA, ray height, proportion of bark and the occurrence of distinct heartwood were selected among physical wood traits (Supplement Fig. A2-1a). For chemical wood traits (Supplement Fig. A2-1b), the concentrations of phosphorus, phenols and lignin were chosen. For enzyme activities and organismic diversity, laccase activity, rarefied coleopteran species richness and mean fungal fruit body species richness were selected (Supplement Fig. A2-1c). The phylogenetically corrected PCA resulted in the same variables except for laccase which was replaced by endocellulase (Supplement Fig. A2-2). For details see Tables A2-1 & A2-2 in the Supplement.

3.4. Relative importance of predictive variables

Model selection revealed that the variables best predicting wood decay were laccase activity, rarefied Coleoptera species richness, the occurrence of distinct heartwood and wood ray height (within the best models; $\Delta AIC < 7$). When a phylogenetic correction was performed, the variables were the same except for laccase activity, which was replaced by endocellulase activity. In the uncorrected model additionally mean fungal fruit body species richness was selected. When using a $\Delta AIC < 2$, only the models with rarefied Coleoptera species richness and laccase activity was selected as best model based on the uncorrected approach and the models with rarefied Coleoptera species richness and endocellulase activity and either with or without heartwood were selected

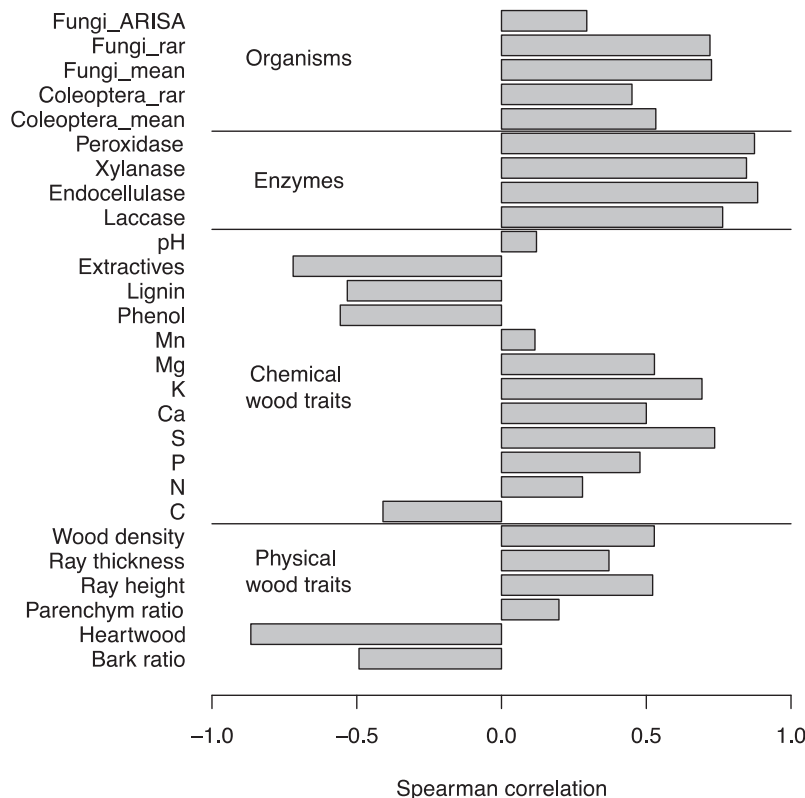


Fig. 2. Correlation between the dependent variable decay rate and the independent variables for all tree species. The Spearman's rank correlation coefficient for each variable is given. For phylogenetic signal in traits, see Supplement Table A1-1.

Table 2

Best models ($\Delta AICc < 2$) for linear multiple regression models with decay rate as dependent variable. Model selection was conducted based on AICc (small-sample-size corrected version of AIC). Please note that in the uncorrected model laccase and in the phylogenetically corrected model endocellulase was used as predictor variable. NA: This predictor is not included in a particular model.

	Uncorrected	Corrected	
	Rank 1	Rank 1	Rank 2
AICc	−41.928	−43.113	−41.307
$\Delta AICc$	0.000	0.000	1.806
Weight	0.238	0.448	0.182
Adj. R ²	0.769	NA	NA
df	4	5	6
Intercept	−0.172	0.169	0.187
Bark ratio	NA	NA	NA
Phenol	NA	NA	NA
P	NA	NA	NA
Rarefied beetle richness	0.002	0.019	0.021
Laccase/Endocellulase	0.022	0.041	0.033
Heartwood	NA	NA	−0.033
Lignin	NA	NA	NA
Mean fungal fruit body richness	NA	NA	NA
Wood ray height	NA	NA	NA

as best models based on the phylogenetically corrected approach (Table 2, Supplement Table A3-1 & A3-2). This shows that laccase and endocellulase activity, rarefied Coleoptera species richness and the occurrence of distinct heartwood were of the selected ones the most important predictors of wood decay of the 13 studied tree species (Fig. 3). Mean fungal species richness and lignin content had a relatively higher importance when using uncorrected models compared to phylogenetically corrected models, which can be explained by the strong phylogenetic signal in these variables (see Supplement Table A1-1).

4. Discussion

4.1. Decay rate

This is the first study that presents decay rates of 13 tree species in a deadwood experiment in temperate European forests, including tree species for which decay rates were so far unknown, i.e. *Carpinus betulus*, *Prunus avium* and *Tilia* spp. Interestingly, the respective data for decay rates of *Carpinus betulus* were found to be the highest compared to all other tree species in this study (Fig. 1). The decay rates of 10 tree species studied in common with Pietsch et al. (2014) correlated well between both studies ($r^2 = 0.49$, $p = 0.02$). This is additionally supported by a strong linear correlation ($r^2 = 0.59$, $p = 0.002$) of our data with CO₂ emission rates in 2012 (Kahl et al., 2015), which can be seen as a proxy for actual decay rates. The observed lower decay rates for gymnosperms than angiosperms has already been described by Weedon et al. (2009) and answers question one.

The presented decay rates are based on 6 years of observation in an experimental setup. This time frame is rather short in terms of deadwood decay in temperate European forests where the residence time ($t_{0.95}$) of *Fagus sylvatica* is estimated to be between 30 (Müller-Using and Bartsch, 2009) and 50 years (Kahl et al., 2012). Using our decay rates, we would estimate the residence time ($t_{0.95} = 3/k$) to range between 39 years for *Carpinus betulus* and a rather unrealistic 1901 years for *Pseudotsuga menziesii* (*Fagus sylvatica*: 46 years). It is thus likely that decay rates will change in the coming years. For some tree species the decomposition process is probably still in an initial stage, or in the stage of a lag phase, as proposed by Harmon et al. (1986) and Freschet et al. (2012), in particular in *Pseudotsuga menziesii*. Probably some key players of the initial phase such as bark beetles are less successful in this non-native tree species (Roques et al., 2006).

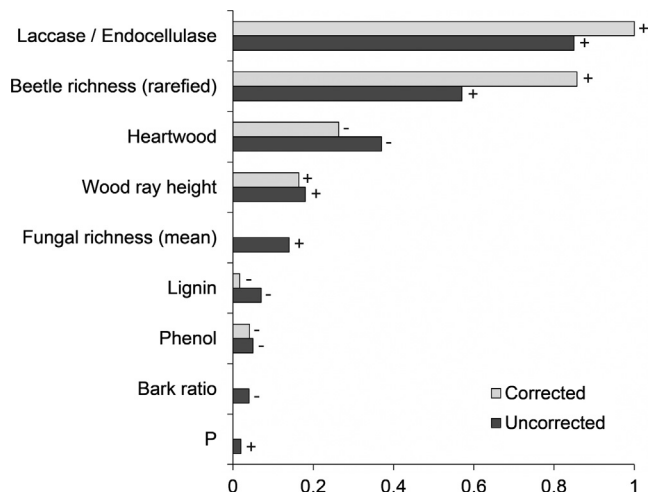


Fig. 3. Importance values (assessed by the cumulative Akaike weights of models containing a particular predictor) of predictor variables in explaining decay rates of the 13 different tree species based on model averaging with $\Delta AIC < 7$. Values for uncorrected and phylogenetically corrected models are shown. Signs indicate whether the effect on wood decay is positive or negative. For details see Tables S1 and S2 in the Supplement.

The available data on wood density in 2009 and 2015 do not allow us to say whether the exponential decay is the best way to model decay rates for each of the 13 tree species. Nevertheless, we hypothesize that the relative differences between tree species will stay largely constant. The experimental design did allow us to study the decay rate and its influencing factors independently of the autochthonous tree species, of the cause of tree death and of climatic and edaphic conditions. Since all logs were cut in the same area, we assume that all logs have a similar history of initial properties such as colonization with endophytic fungi and insects. Whether or not this reduced the variability of the observed decay rates cannot be deduced from our data.

4.2. Effect of wood properties and diversity on wood decay rate

4.2.1. Physical, anatomical and chemical wood properties

With respect to physical and anatomical wood properties, we found negative correlations for bark ratio and presence of distinct heartwood with decay rate. The latter was an important predictor in our multiple regression analysis. Thicker bark with its high amount of hydrophobic suberin can decrease the decay rate by protecting wood from the colonization by fungi and insects (Freschet et al., 2012; Graça, 2015). Heartwood is known to contain higher amounts of secondary metabolites (phenols, tannins, stilbenes) than sapwood. These metabolites hamper the growth of fungi resulting in lower decay rates (Dix and Webster, 1995). Wood ray width, height and parenchyma ratio were all positively correlated with decay rate. All of these wood properties are expressions of parenchyma cells in wood. These cells, on the one hand, allow for radial transport of small molecules including crucial dioxygen (O₂), low molecular compounds and nutrients in wood and could therefore be responsible for increased concentrations of these compounds inside a tree, which in turn could increase decay rate. On the other hand, they are essential for the process of thylolysis that is important for heartwood formation and may finally decrease decay rates. Furthermore, a high ratio of ray cells will facilitate the colonization of wood by hyphae and improve their radial distribution within the xylem (Schwarze, 2007). Wood density was positively correlated with decay rates in our experiment, for all tree species (Fig. 2), but also for the angiosperms only. The opposite was shown for 26 neotropical species in Amazonia

(Hérault et al., 2010). A positive correlation of wood density with decay rate in all 13 tree species could be explained by higher resin content and increased proportion of recalcitrant guaiacyl units in lignin in gymnosperms resulting in lower decay rates. The reasons for the positive relation in angiosperms remain unclear.

With respect to chemical wood properties, all element concentrations were positively correlated with the decay rate, except for the C content (though the interspecific variation in the C concentration was rather small). Surprisingly, sulphur showed the strongest effect on decay rate. It has been shown that sulphur addition increases fungal growth in wood (Schmalenberger et al., 2011). Besides N and P (Sinsabaugh et al., 1993), S, which is essential for two amino acids and various biochemical cofactors, seems to be one of the limiting macronutrients for fungal growth and hence for wood decay. We attribute the negative correlation between C content and wood decay to the higher relative carbon content of lignin as compared to cellulose or hemicelluloses. This is due to the high degree of lignin methoxylation and the fact that carbon in the aromatic rings of lignin binds less hydrogen atoms or functional groups than carbon in the pyranose rings of polysaccharides. In other words, the variation in the carbon content coincides in part with the variation in lignin concentration.

The concentrations of phenols, lignin and extractives were all negatively correlated with decay rate. Phenols and organic extractives such as resins are known to generally inhibit fungal growth (Scheffer, 1966; Hillis, 1999; Gierlinger et al., 2004). Lignin as a molecular glue represents a barrier to wood decomposition (Dix and Webster, 1995; Stokland et al., 2012) by hindering the penetration of enzyme molecules to the lignocellulose complex (Hatakka and Hammel, 2010), and as such a higher amount will slow down the decay. Freschet et al. (2012) demonstrated previously that the initial lignin content of trees is negatively correlated with decay rate. Moreover, we found for pH a weak positive correlation with decay rate, similar to Freschet et al. (2012), which might be attributed to non-structural secondary metabolites of heartwood, like organic acids, which contribute to decay resistance (Harmon et al., 1986; Pearce, 1996).

4.2.2. Biotic factors

Activities of all observed enzymes (laccase, total peroxidase, endocellulase, xylanase) were positively correlated with decay rates, and were revealed to be the most important predictors of wood decay in our multiple regression analysis. Enzyme activities can be seen as a proxy for fungal activity in deadwood. Especially endocellulase activity, which can actually be a conglomeration of genetically diverse enzymes from different organisms including fungi, insects and their microbial symbionts (Baldrian and Valášková, 2008; Watanabe and Tokuda, 2010; Lombard et al., 2014), is a major driver of microbial decay. Given the fact that saprotrophic microorganisms have to gain their metabolic energy from sugars, and cellulose (β -1,4-linked glucose homopolymer) that constitutes up to 50% of wood, it seems rather logical to find this strong correlation and it as best model predictor. (Endo)xylanase, which hydrolyzes the hemicellulose backbone (β -1,4-linked xylose heteropolymer) contributes also substantially to the carbon (pentoses) and energy supply of microorganisms including fungi (Polizeli et al., 2005). Further enzymes, like laccase and peroxidases mediate the rather slow process of lignin decomposition and also contribute to the detoxification of plant ingredients (e.g. aromatics); lignin degradation is mainly mediated by basidiomycetous fungi causing white-rot (Baldrian, 2006; Hatakka and Hammel, 2010). However, in particular the activities of lignin-modifying enzymes were shown to be highly variable in larger wood sampling campaigns (Arnstadt et al., 2016a; Baldrian et al., 2016; Noll et al., 2016), and thus it is remarkable to see here these strong and also meaningful correlations.

Organisms such as fungi and Coleoptera are key agents of wood decay. Fungal and coleopteran diversity (alpha diversity, i.e. mean species richness per log and gamma diversity, i.e. rarified species richness across all logs) were both positively correlated with decay rates. Both were selected as important variables in a multiple regression analysis. Saproxylic fungi and beetles have evolved many mutualistic commensal relationships (e.g. Hofstetter et al., 2015b), and thus their unidirectional effects are not surprising. CO₂ emission rates of these logs also support a positive correlation with fungal species richness across tree species, and also independent of tree species (Kahl et al., 2015). Easily degradable wood might be inhabited by a large or a small number of species, but still may have comparable fungal and/or beetle biomass, which could result in similar decay rates. But obviously this is not the case, and easily degradable wood tends to be inhabited rather by a larger number of species than by a few species. Our results are therefore in line with studies demonstrating a positive relationship between species richness and decay rate which supports the view of synergistic or facilitative interactions among species (Tiunov and Scheu, 2005).

Looking at the whole residence time of logs, the positive correlation between diversity and decay rate could also be an observation bias due to organismic succession. Comparing two tree species, one with a low and one with a high decay rate, the species having a low decay rate will always have a longer residence time in the forest providing substrate for organisms. At the same point in time, the two tree species will be in different successional phases. In a finite substrate such as deadwood, three successional phases occur: initial, optimal, final with low, high and low species diversity, respectively (Stokland et al., 2012). Comparing a tree species such as *Carpinus betulus*, which is after 6 years in the optimal phase of succession, with *Fraxinus excelsior*, which is in the initial phase, seems incorrect. A correct solution would be a comparison after the logs are fully decomposed or by comparing them at the same point of relative mass loss (Arnstadt et al., 2016b). By continuing our experiment over the next decade we will be able to better estimate this potential bias.

4.3. Management implications

Our results indicate that fungi, beetles and enzymes play an important role for wood decomposition. The detailed pathways of the relationships could not be identified by the present study and needs further investigation. Nevertheless, our results suggest that not only particular key species, but also overall organismic diversity is important for wood decay. An expected negative influence of intensified forest management on saproxylic species diversity therefore most likely also negatively affects the process of wood decomposition. Due to different successional pathways of different tree species, showing great differences in decay rates and therefore residence times, a mix of different tree species in deadwood enrichment strategies might be most effective for promoting species diversity.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.02.012>.

References

- Aloui, F., Ayadi, N., Charrier, F., Charrier, B., 2004. Durability of European oak (*Quercus petraea* and *Quercus robur*) against white rot fungi (*Coriolus versicolor*): relations with phenol extractives. *Holz als Roh- und Werkstoff* 62, 286–290.
- Arnstadt, T., Hoppe, B., Kahl, T., Kellner, H., Krüger, D., Bässler, C., Bauhus, J., Hofrichter, M., 2016a. Patterns of laccase and peroxidases in coarse woody debris of *Fagus sylvatica*, *Picea abies* and *Pinus sylvestris* and their relation to different wood parameters. *Eur. J. For. Res.* 135, 109–124.
- Arnstadt, T., Hoppe, B., Kahl, T., Kellner, H., Krüger, D., Bauhus, J., Hofrichter, M., 2016b. Dynamics of fungal community composition, decomposition and resulting deadwood properties in logs of *Fagus sylvatica*, *Picea abies* and *Pinus sylvestris*. *For. Ecol. Manage.* 382, 129–142.
- Baber, K., Otto, P., Kahl, T., Gossner, M.M., Wirth, C., Gminder, A., Bässler, C., 2016. Disentangling the effects of forest-stand type and dead-wood origin of the early successional stage on the diversity of wood-inhabiting fungi. *For. Ecol. Manage.* 377, 161–169.
- Baldrian, P., 2006. Fungal laccases-occurrence and properties. *FEMS Microbiol. Rev.* 30, 215–242.
- Baldrian, P., Valášková, V., 2008. Degradation of cellulose by basidiomycetous fungi. *FEMS Microbiol. Rev.* 32, 501–521.
- Baldrian, P., Zrůstová, P., Tláškal, V., Davidová, A., Merhautová, V., Vřška, T., 2016. Fungi associated with decomposing deadwood in a natural beech-dominated forest. *Fungal Ecol.* 23, 109–122.
- Bantle, A., Borken, W., Ellerbrock, R.H., Schulze, E.D., Weisser, W.W., Matzner, E., 2014. Quantity and quality of dissolved organic carbon released from coarse woody debris of different tree species in the early phase of decomposition. *For. Ecol. Manage.* 329, 287–294.
- Bartoň, K., 2016. Package ‘MuMIn’: Multi-Model Inference. R-Package 1.15.6 <<https://CRAN.R-project.org/package=MuMIn>>.
- Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. *For. Ecol. Manage.* 258, 525–537.
- Boddy, L., 2001. Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. *Ecol. Bull.*, 43–56.
- Box, J.D., 1983. Investigation of the Folin-Ciocalteu phenol reagent for the determination of polyphenolic substances in natural waters. *Water Res.* 17, 511–525.
- Brunow, G., 2001. Methods to reveal the structure of lignin. Lignin, humic substances and coal. In: Hofrichter, M., Steinbüchel, A. (Eds.), *Biopolymers, Lignin, Humic Substances and Coal*, vol. 1. Wiley-VCH Verlag GmbH & Co., Weinheim, pp. 89–99.
- Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* 65, 23–35.
- Christensen, O., 1977. Estimation of standing crop and turnover of dead wood in a Danish oak forest. *Oikos* 28, 177–186.
- Cornwell, W.K., Cornelissen, J.H.C., Allison, S.D., Bauhus, J., Eggleton, P., Preston, C. M., Scarff, F., Weedon, J.T., Wirth, C., Zanne, A.E., 2009. Plant traits and wood fates across the globe: rotted, burned, or consumed? *Glob. Change Biol.* 15, 2431–2449.
- Dix, N.J., Webster, J., 1995. *Fungal Ecology*. Springer, Wallington, Surrey.
- EN350-2, 1994. Durability of Wood and Wood-based Products – Natural Durability of Solid Wood. Guide to Natural Durability and Treatability of Selected Wood Species of Importance in Europe.
- Fischer, M., Bossdorf, O., Gockel, S., Hansel, F., Hemp, A., Hessenmoller, D., Korte, G., Nieschulze, J., Pfeiffer, S., Prati, D., Renner, S., Schöning, I., Schumacher, U., Wells, K., Buscot, F., Kalko, E.K.V., Linsenmair, K.E., Schulze, E.D., Weisser, W.W., 2010. Implementing large-scale and long-term functional biodiversity research: the Biodiversity Exploratories. *Basic Appl. Ecol.* 11, 473–485.
- Floudas, D., Binder, M., Riley, R., Barry, K., Blanchette, R.A., Henrissat, B., Martínez, A. T., Otilar, R., Spatafora, J.W., Yadav, J.S., Aerts, A., Benoit, I., Boyd, A., Carlson, A., Copeland, A., Coutinho, P.M., de Vries, R.P., Ferreira, P., Findley, K., Foster, B., Gaskell, J., Glotzer, D., Görecki, P., Heitman, J., Hesse, C., Hori, C., Igarashi, K., Jurgens, J.A., Kallen, N., Kersten, P., Kohler, A., Kues, U., Kumar, T.K.A., Kuo, A., LaButti, K., Larrondo, L.F., Lindquist, E., Ling, A., Lombard, V., Lucas, S., Lundell, T., Martin, R., McLaughlin, D.J., Morgenstern, I., Morin, E., Murat, C., Nagy, L.G., Nolan, M., Ohm, R.A., Patyshakuliyeva, A., Rokas, A., Ruiz-Dueñas, F.J., Sabat, G., Salamov, A., Samejima, M., Schmutz, J., Slot, J.C., St John, F., Stenlid, J., Sun, H., Sun, S., Syed, K., Tsang, A., Wiebenga, A., Young, D., Pisabarro, A., Eastwood, D.C., Martin, F., Cullen, D., Grigoriev, I.V., Hibbett, D.S., 2012. The Paleozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal genomes. *Science* 336, 1715–1719.
- Freschet, G.T., Weedon, J.T., Aerts, R., van Hal, J.R., Cornelissen, J.H.C., 2012. Interspecific differences in wood decay rates: insights from a new short-term method to study long-term wood decomposition. *J. Ecol.* 100, 161–170.
- Fukami, T., Dickie, I.A., Paula Wilkie, J., Paulus, B.C., Park, D., Roberts, A., Buchanan, P. K., Allen, R.B., 2010. Assembly history dictates ecosystem functioning: evidence from wood decomposer communities. *Ecol. Lett.* 13, 675–684.
- Gardes, M., Bruns, T.D., 1993. ITS primers with enhanced specificity for basidiomycetes – application to the identification of mycorrhizae and rusts. *Mol. Ecol.* 2, 113–118.
- Gierlinger, N., Jacques, D., Schwanninger, M., Wimmer, R., Pâques, L.E., 2004. Heartwood extractives and lignin content of different larch species (*Larix* sp.) and relationships to brown-rot decay-resistance. *Trees* 18, 230–236.
- Gleeson, D.B., Clipson, N., Melville, K., Gadd, G.M., McDermott, F.P., 2005. Characterization of fungal community structure on a weathered pegmatitic granite. *Microb. Ecol.* 50, 360–368.
- Gossner, M.M., Wende, B., Levick, S., Schall, P., Floren, A., Linsenmair, K.E., Steffan-Dewenter, I., Schulze, E.-D., Weisser, W.W., 2016. Deadwood enrichment in European forests – which tree species should be used to promote saproxylic beetle diversity? *Biol. Conserv.* 201, 92–102.
- Graça, J., 2015. Suberin: the biopolyester at the frontier of plants. *Front. Chem.* 3.
- Green, J.L., Holmes, A.J., Westoby, M., Oliver, I., Briscoe, D., Dangerfield, M., Gillings, M., Beattie, A.J., 2004. Spatial scaling of microbial eukaryote diversity. *Nature* 432, 747–750.
- Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* 24, 699–711.
- Halme, P., Kotiaho, J.S., 2012. The importance of timing and number of surveys in fungal biodiversity research. *Biodivers. Conserv.* 21, 205–219.
- Harmon, M., Franklin, J., Swanson, F., Sollins, P., Gregory, V., Lattin, J., Anderson, N., Cline, S., Aumen, N., Lienkaemper, G., Cromack, K., Cummins, K., 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15, 133–302.
- Hart, J.H., Hillis, W.E., 1972. Inhibition of wood-rotting fungi by Ellagitannins in the heartwood of *Quercus alba*. *Phytopathology* 62, 620–626.
- Hatakka, A., Hammel, K.E., 2010. Fungal biodegradation of lignocelluloses. In: Osiewacz, H.D. (Ed.), *The Mycota: A Comprehensive Treatise on Fungi as Experimental Systems for Basic and Applied Research*. Springer, pp. 319–340.
- Heibl, C., 2014. megaptera: MEGAPhylogeny Techniques in R. R Package Version 1.0-0. <<https://CRAN.R-project.org/package=megaptera>>.
- Hérault, B., Beauchêne, J., Muller, F., Wagner, F., Baraloto, C., Blanc, L., Martin, J.-M., 2010. Modeling decay rates of dead wood in a neotropical forest. *Oecologia* 164, 243–251.
- Herrmann, S., Kahl, T., Bauhus, J., 2015. Decomposition dynamics of coarse woody debris of three important central European tree species. *For. Ecosyst.* 2, 1–14.
- Higuchi, T., 2006. Look back over the studies of lignin biochemistry. *J. Wood Sci.* 52, 2–8.
- Hillis, W.E., 1999. The formation of heartwood and its extractives. In: Romeo, J.T. (Ed.), *Phytochemicals in Human Health Protection, Nutrition, and Plant Defense*. Springer, Boston, MA, US, pp. 215–253.
- Ho, L.S.T., Ane, C., 2014. A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Syst. Biol.* 63, 397–408.
- Hofstetter, R.W., Dinkins-Bookwalter, J., Davies, T.S., Klepzig, K.D., 2015a. Symbiotic associations of bark beetles. In: Vega, F.E., Hofstetter, R.W. (Eds.), *Bark Beetles*. Academic Press, San Diego, pp. 209–245 (Chapter 6).
- Hofstetter, R.W., Dinkins-Bookwalter, J., Davis, T.S., Klepzig, K.D., 2015b. Symbiotic associations of bark beetles. In: Vega, F.E., Hofstetter, R.W. (Eds.), *Bark Beetles*. Academic Press, San Diego, pp. 209–245 (Chapter 6).
- Høiland, K., Bendiksen, E., 1996. Biodiversity of wood-inhabiting fungi in a boreal coniferous forest in Ser-Trendelag County, Central Norway. *Nord. J. Bot.* 16, 643–659.
- Hoppe, B., Purahong, W., Wubet, T., Kahl, T., Bauhus, J., Arnstadt, T., Hofrichter, M., Buscot, F., Krüger, D., 2015. Linking molecular deadwood-inhabiting fungal diversity and community dynamics to ecosystem functions and processes in Central European forests. *Fungal Divers.*, 1–13.
- Kahl, T., 2008. Kohlenstofftransport aus dem Totholz in den Boden. In: Fakultät für Forst- und Umweltwissenschaften. Albert-Ludwigs-Universität Freiburg im Breisgau, Freiburg im Breisgau, p. 108.
- Kahl, T., Baber, K., Otto, P., Wirth, C., Bauhus, J., 2015. Drivers of CO₂ emission rates from dead wood logs of 13 tree species in the initial decomposition phase. *Forests* 6, 2484.
- Kahl, T., Mund, M., Bauhus, J., Schulze, E., 2012. Dissolved organic carbon from European beech logs: patterns of input to and retention by surface soil. *Ecoscience* 19, 1–10.

- Kellner, H., Luis, P., Pecyna, M.J., Barbi, F., Kapturska, D., Krüger, D., Zak, D.R., Marmesse, R., Vandenbol, M., Hofrichter, M., 2014. Widespread occurrence of expressed fungal secretory peroxidases in forest soils. *PLoS ONE* 9, e95557.
- Kögel-Knabner, I., 2002. The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. *Soil Biol. Biochem.* 34, 139–162.
- Kruys, N., Jonnsson, B., Stahl, G., 2002. A stage-based matrix model for decay-class dynamics of woody debris. *Ecol. Appl.* 12, 773–781.
- Kubartová, A., Ottosson, E., Dahlberg, A., Stenlid, J., 2012. Patterns of fungal communities among and within decaying logs, revealed by 454 sequencing. *Mol. Ecol.* 21, 4514–4532.
- Lindner, D.L., Vasaitis, R., Kubartová, A., Allmér, J., Johannesson, H., Banik, M.T., Stenlid, J., 2011. Initial fungal colonizer affects mass loss and fungal community development in *Picea abies* logs 6 yr after inoculation. *Fungal Ecol.* 4, 449–460.
- Lombard, V., Golaconda, R.H., Drula, E., Coutinho, P.M., Henrissat, B., 2014. The carbohydrate-active enzymes database (CAZY) in 2013. *Nucleic Acids Res.* 42, D490–D495.
- Lonsdale, D., Pautasso, M., Holdenrieder, O., 2008. Wood-decaying fungi in the forest: conservation needs and management options. *Eur. J. For. Res.* 127, 1–22.
- Müller-Using, S., Bartsch, N., 2009. Decay dynamic of coarse and fine woody debris of a beech (*Fagus sylvatica* L.) forest in Central Germany. *Eur. J. For. Res.* 128, 287–296.
- Müller, J., Wende, B., Strobl, C., Eugster, M., Gallenberger, I., Floren, A., Steffan-Dewenter, I., Linsenmair, K.E., Weisser, W.W., Gossner, M.M., 2015. Forest management and regional tree composition drive the host preference of saproxylic beetle communities. *J. Appl. Ecol.* 52, 753–762.
- Noll, L., Leonhardt, S., Arnstadt, T., Hoppe, B., Poll, C., Matzner, E., Hofrichter, M., Kellner, H., 2016. Fungal biomass and extracellular enzyme activities in coarse woody debris of 13 tree species in the early phase of decomposition. *For. Ecol. Manage.* 378, 181–192.
- Olson, J., 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44, 322–331.
- Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20, 289–290.
- Pattengale, N.D., Alipour, M., Bininda-Emonds, O.R.P., Moret, B.M.E., Stamatakis, A., 2010. How many bootstrap replicates are necessary? *J. Comput. Biol.* 17, 337–354.
- Pearce, R.B., 1996. Antimicrobial defences in the wood of living trees. *New Phytol.* 132, 203–233.
- Pietsch, K.A., Ogle, K., Cornelissen, J.H.C., Cornwell, W.K., Bönisch, G., Craine, J.M., Jackson, B.G., Kattge, J., Peltzer, D.A., Penuelas, J., Reich, P.B., Wardle, D.A., Weedon, J.T., Wright, I.J., Zanne, A.E., Wirth, C., 2014. Global relationship of wood and leaf litter decomposability: the role of functional traits within and across plant organs. *Glob. Ecol. Biogeogr.* 23, 1046–1057.
- Polizeli, M.L.T.M., Rizzatti, A.C.S., Monti, R., Terenzi, H.F., Jorge, J.A., Amorim, D.S., 2005. Xylanases from fungi: properties and industrial applications. *Appl. Microbiol. Biotechnol.* 67, 577–591.
- Purahong, W., Arnstadt, T., Kahl, T., Bauhus, J., Kellner, H., Hofrichter, M., Krüger, D., Buscot, F., Hoppe, B., 2016. Are correlations between deadwood fungal community structure, wood physico-chemical properties and lignin-modifying enzymes stable across different geographical regions? *Fungal Ecol.* 22, 98–105.
- Purahong, W., Hoppe, B., Kahl, T., Schlöter, M., Schulze, E.-D., Bauhus, J., Buscot, F., Krüger, D., 2014a. Changes within a single land-use category alter microbial diversity and community structure: molecular evidence from wood-inhabiting fungi in forest ecosystems. *J. Environ. Manage.* 139, 109–119.
- Purahong, W., Kahl, T., Schlöter, M., Bauhus, J., Buscot, F., Krüger, D., 2014b. Comparing fungal richness and community composition in coarse woody debris in Central European beech forests under three types of management. *Mycol. Prog.* 1–6.
- R Core Team, 2011. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ramette, A., 2009. Quantitative community fingerprinting methods for estimating the abundance of operational taxonomic units in natural microbial communities. *Appl. Environ. Microbiol.* 75, 2495–2505.
- RCoreTeam, 2015. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Renvall, P., 1995. Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. *Karstenia* 35, 1–51.
- Revell, L.J., 2012. Phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* 3, 217–223.
- Riley, R., Salamov, A.A., Brown, D.W., Nagy, L.G., Floudas, D., Held, B.W., Levasseur, A., Lombard, V., Morin, E., Otillar, R., Lindquist, E.A., Sun, H., LaButti, K.M., Schmutz, J., Jabbour, D., Luo, H., Baker, S.E., Pisabarro, A.G., Walton, J.D., Blanchette, H., Henrissat, B., Martin, F., Cullen, D., Hobbitt, D.S., Grigoriev, I.V., 2014. Extensive sampling of basidiomycete genomes demonstrates inadequacy of the white-rot/brown-rot paradigm for wood decay fungi. *Proc. Natl. Acad. Sci.* 111, 9923–9928.
- Rondeux, J., Sanchez, C., 2010. Review of indicators and field methods for monitoring biodiversity within national forest inventories. Core variable: Deadwood. *Environ. Monit. Assess.* 164, 617–630.
- Roques, A., Auger-Rozenberg, M.-A., Boivin, S., 2006. A lack of native congeners may limit colonization of introduced conifers by indigenous insects in Europe. *Can. J. For. Res.* 36, 299–313.
- Scheffer, T.C., 1966. Natural resistance of wood to microbial deterioration. *Annu. Rev. Phytopathol.* 4, 147–168.
- Schmalenberger, A., Pritzkow, W., Ojeda, J.J., Noll, M., 2011. Characterization of main sulfur source of wood-degrading basidiomycetes by S K-edge X-ray absorption near edge spectroscopy (XANES). *Int. Biodeterior. Biodegrad.* 65, 1215–1223.
- Schwarze, F.W.M.R., 2007. Wood decay under the microscope. *Fungal Biol. Rev.* 21, 133–170.
- Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S., Müller, J., 2015. Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conserv. Biol.* 29, 382–390.
- Setälä, H., McLean, M.A., 2004. Decomposition rate of organic substrates in relation to the species diversity of soil saprophytic fungi. *Oecologia* 139, 98–107.
- Sinsabaugh, R.L., Antibus, R.K., Linkins, A.E., McLaugherty, C.A., Rayburn, L., Repert, D., Weiland, T., 1993. Wood decomposition: nitrogen and phosphorus dynamics in relation to extracellular enzyme activity. *Ecology* 74, 1586–1593.
- Stamatakis, A., 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30, 1312–1313.
- Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. *Biodiversity in Dead Wood*. Cambridge University Press, Cambridge.
- Suh, S.-O., McHugh, J.V., Pollock, D.D., Blackwell, M., 2005. The beetle gut: a hyperdiverse source of novel yeasts. *Mycol. Res.* 109, 261–265.
- Swift, M.J., Healey, I.N., Hibberd, J.K., Sykes, J.M., Bampoe, V., Nesbitt, M.E., 1976. Decomposition of branch-wood in canopy and floor of a mixed deciduous woodland. *Oecologia* 26, 139–149.
- Tabachnick, B.G., Fidell, L.S., 1996. *Using Multivariate Statistics*. Harper Collins, New York.
- Tiunov, A.V., Scheu, S., 2005. Facilitative interactions rather than resource partitioning drive diversity-functioning relationships in laboratory fungal communities. *Ecol. Lett.* 8, 618–625.
- Toljander, J.F., Eberhardt, U., Toljander, Y.K., Paul, L.R., Taylor, A.F.S., 2006. Species composition of an ectomycorrhizal fungal community along a local nutrient gradient in a boreal forest. *New Phytol.* 170, 873–884.
- Ulyshen, M.D., 2016. Wood decomposition as influenced by invertebrates. *Biol. Rev.* 91, 70–85.
- Valaskova, V., de Boer, W., Klein Gunnewiek, P.J.A., Pospisek, M., Baldrian, P., 2009. Phylogenetic composition and properties of bacteria coexisting with the fungus *Hypholoma fasciculare* in decaying wood. *ISME J.* 3, 1218–1221.
- Valentín, L., Rajala, T., Peltoniemi, M., Heinonsalo, J., Pennanen, T., Mäkipää, R., 2014. Loss of diversity in wood-inhabiting fungal communities affects decomposition activity in Norway spruce wood. *Front. Microbiol.* 5, 1–11.
- van der Wal, A., Geydan, T.D., Kuyper, T.W., de Boer, W., 2013. A thready affair: linking fungal diversity and community dynamics to terrestrial decomposition processes. *FEMS Microbiol. Rev.* 37, 477–494.
- van der Wal, A., Ottosson, E., de Boer, W., 2015. Neglected role of fungal community composition in explaining variation in wood decay rates. *Ecology* 96, 124–133.
- Vetrovsky, T., Voriskova, J., Snajdr, J., Gabriel, J., Baldrian, P., 2011. Ecology of coarse wood decomposition by the saprotrophic fungus *Fomes fomentarius*. *Biodegradation* 22, 709–718.
- Větrovský, T., Voříšková, J., Snajdr, J., Gabriel, J., Baldrian, P., 2011. Ecology of coarse wood decomposition by the saprotrophic fungus *Fomes fomentarius*. *Biodegradation* 22, 709–718.
- Wagenführ, R., 2006. *Holzatlas*. Fachbuchverlag Leipzig im Carl Hanser Verlag, Leipzig.
- Watanabe, H., Tokuda, G., 2001. Animal cellulases. *Cell. Mol. Life Sci.* CMLS 58, 1167–1178.
- Watanabe, H., Tokuda, G., 2010. Cellulolytic systems in insects. *Annu. Rev. Entomol.* 55, 609–632.
- Weedon, J.T., Cornwell, W.K., Cornelissen, J.H.C., Zanne, A.E., Wirth, C., Coomes, D.A., 2009. Global meta-analysis of wood decomposition rates: a role for trait variation among tree species? *Ecol. Lett.* 12, 45–56.
- White, T.J., Bruns, T.D., Lee, S., Taylor, J., 1990. Amplification and direct sequencing of fungal ribosomal DNA genes for phylogenies. In: Innis, M.A., Gelfand, D.H., Sninsky, J.J., White, T.J. (Eds.), *PCR Protocols: A Guide to Methods and Applications*. Academic Press, San Diego, pp. 315–322.