Title

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

Authors

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43

44 **Abstract**

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

64 **Keywords:**

65 Wood decomposition, ecosystem function, saproxylic beetles, Biodiversity Exploratories,
66 deadwood experiment

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69 **Highlights**

- 70   • 1128 deadwood logs of 13 tree species are exposed in 30 plots in 3 regions
- 71   • enzyme activities and organismic diversity are strong drivers of decay rates
- 72   • tree species composition in forests has a long lasting effect on deadwood decay

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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; Valentin *et al.*, 2014; Kahl *et al.*, 2015) or negatively (Fukami *et al.*, 2010a) 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.*, 2010b), 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; Watanabe and Tokuda, 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 forests 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 700–1,000 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 (**B**iodiversity **E**xploratories **L**ong term **D**eadwood) 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*,

220 *Carpinus betulus*, *Fagus sylvatica*, *Fraxinus excelsior*, *Populus* spp. (*P. tremula* and hybrids),
221 *Prunus avium*, and *Quercus* spp. (*Q. robur*, *Q. petraea*), *Tilia* spp. (*T. cordata*, *T.*
222 *platyphyllos*) and four Gymnosperms: *Larix decidua*, *Picea abies*, *Pinus sylvestris*, and
223 *Pseudotsuga menziesii*). All logs are approximately 4 m long and have a mean diameter of 31
224 $\pm$ 5.9 cm (SD). All logs were cut in winter 2008/2009 in the federal state of Thuringia
225 (Germany) and then transported to each plot. Within a subplot, the 13 logs were placed in
226 random order beside each other with a distance of ca. 1 m between logs. We carefully
227 followed a protocol to minimize the potential bias by colonization of logs prior to
228 translocation to the experimental sites. Owing to limited supplies, *P. avium* logs are missing
229 on 27, *Acer* spp. on 2 and *Fagus sylvatica* on 1 of the 90 subplots (Kahl *et al.*, 2015). One
230 subplot with 12 logs in the exploratory Schorfheide was unlawfully removed in 2012,
231 reducing the total number of logs to 1128.

232

233 **2.3 Wood decay rate**

234 Deadwood decay rate was calculated based on density loss. Initial wood density was
235 determined using discs that were cut in 2009 immediately after exposure from all logs. The
236 discs were then dried at 65°C and stored in a warehouse. After removing the bark the discs
237 were drilled with a 1 cm diameter auger and a cordless power drill in radial direction to the
238 pith. The second sampling from the exposed logs took place in June 2015. Owing to the
239 advanced decay in 2015, logs were, after removing the bark, drilled with a 4 cm diameter
240 Forstner bit in 60cm distance from one end of the log. The Forstner bit allows drilling clean
241 cylindrical holes even in decayed wood material. In both 2009 and 2015, wood shavings were
242 carefully collected and dried at 65°C until no further decrease in weight was detected. Dry
243 wood density (g cm^{-3}) in 2009 and 2015 was calculated as ratio of dry wood weight (g) and
244 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=1cm auger vs. d=4cm 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 Figure 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.

270

271 **2.4. Predictors of decay rates**

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

278 *2.4.1. Wood properties*

279 *Anatomical, mechanical and physical wood properties*

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

284 *Chemical wood properties*

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

293   *Organic extractives, pH-value and lignin*

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

303

304   *2.4.2. Enzymatic activities*

305   In 2012, wood samples were taken using a cordless drill (Makita BDF 451) equipped with a
306   wood auger (20 mm x 450 mm). Activities of degradative enzyme were determined in 379
307   wood samples (1 subplot per plot) in 2012. In the aqueous extracts of the milled samples,
308   lignin-related oxidoreductases (*laccase* EC 1.10.3.2, manganese peroxidase EC 1.11.1.13 and
309   general peroxidase activity EC 1.11.1.7/14/16; Kellner *et al.*, 2014) were assayed
310   spectrophotometrically with ABTS (2,2'-azino-bis(3-ethylbenzothiazoline-6-sulfonic acid) as
311   substrate according to Arnstadt *et al.* (2016a; 2016b). The activities of manganese peroxidase
312   and general peroxidase were summed up to *total peroxidase* (POX) activity. Hydrolytic
313   enzyme activities related to polysaccharide disintegration, i.e. *endocellulase* (EC 3.2.1.4), and
314   (*endo*)*xylanase* (EC 3.2.1.8), were measured spectrophotometrically applying AZO-cellulose
315   and AZO-xylan as substrates, respectively, following the protocol of Megazymes (Bray,
316   Ireland) (Vetrovsky *et al.*, 2011).

317

318 *2.4.3. Fungal species richness based on fruit bodies*

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

331

332 *2.4.4. Fungal molecular operational taxonomic units*

333 In addition to the identification of macrofungi, we also used a molecular method to quantify
334 fungal richness. Fungal automated ribosomal intergenic spacer analysis (F-ARISA) was
335 performed as described in Purahong *et al.* (2014a; 2016). Briefly, DNA was extracted from
336 100 mg of each homogenized wood sample (see method for enzyme activities above) using
337 the ZR Soil Microbe DNA MiniPrep kit (Zymo Research, Irvine, CA, USA), according to the
338 manufacturer's instructions. Fungal ITS was amplified using FAM-labelled primer ITS1-F
339 (5'- CTTGGTCATTTAGAGGAAGTAA-3', Gardes and Bruns, 1993) and unlabelled ITS4
340 (5'-TCCTCCGCTTATTGATATGC-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. *Saproxylic Coleoptera*

Saproxylic Coleoptera emerging from the logs were sampled by closed emergence eclectors for three years, 2010 to 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 saproxylic according to Seibold *et al.* (2015). We calculated beetle species richness for each tree species by averaging over logs and year, rarefied to lowest sample size of all tree species (104 log-years).

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

366

367 2.5. Tree phylogeny

368 Because tree species may not be regarded as independent samples, we considered the
369 phylogenetic relatedness between tree species. Therefore we used a bioinformatics pipeline
370 implemented in the R package megaptera (Heibl, 2014), to derive a set of alignments on
371 which our phylogenetic hypothesis is based. We screened all protein-encoding and rRNA
372 genes of chloroplast and mitochondrion as well as the nuclear rRNA genes, the histone H3
373 gene and the phytochrome C gene. For each tree genus and genetic locus, we downloaded all
374 available accessions from GenBank and BOLDSYSTEMS. Under the assumption of
375 monophyletic genera, we created majority-rule consensus sequences of all congeneric
376 sequences that passed the quality checks. 11 loci provided the best taxonomic coverage and
377 were concatenated into a final supermatrix: *atp1*, *atp6*, *atp9*, *ndhF*, *rbcL*, *cox1*, *cox3*, *matR*,
378 *nd4L*, *nd6*, 16S rRNA. Tree topology and ultrametric branch lengths were modelled in a
379 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 percent or more and the tree topology is in accordance with current knowledge (Supplement Figure 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 analysing 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 & 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 und 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).

Figure 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.

3.2. Effect of predictor variables on decay rates

The strongest correlations with decay rate were found for presence of heartwood and organic extractives, 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, 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).

Figure 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.

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 ΔAIC of < 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 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).

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	
	Rank1	Rank1	Rank2
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

483

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

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 menziessii* (*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).

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 tylosis 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

561 fungal growth (Scheffer, 1966; Hillis, 1999; Gierlinger *et al.*, 2004). Lignin as a molecular
562 glue represents a barrier to wood decomposition (Dix and Webster, 1995; Stokland *et al.*,
563 2012) by hindering the penetration of enzyme molecules to the lignocellulose complex
564 (Hatakka and Hammel, 2010), and as such a higher amount will slow down the decay.
565 Freschet *et al.* (2012) demonstrated previously that the initial lignin content of trees is
566 negatively correlated with decay rate. Moreover, we found for pH a weak positive correlation
567 with decay rate, similar to Freschet *et al.* (2012), which might be attributed to non-structural
568 secondary metabolites of heartwood, like organic acids, which contribute to decay resistance
569 (Harmon *et al.*, 1986; Pearce, 1996).

570 4.2.2. Biotic factors

571 Activities of all observed enzymes (laccase, total peroxidase, endocellulase, xylanase) were
572 positively correlated with decay rates, and were revealed to be the most important predictors
573 of wood decay in our multiple regression analysis. Enzyme activities can be seen as a proxy
574 for fungal activity in deadwood. Especially endocellulase activity, which can actually be a
575 conglomeration of genetically diverse enzymes from different organisms including fungi,
576 insects and their microbial symbionts (Baldrian and Valášková, 2008; Watanabe and Tokuda,
577 2010; Lombard *et al.*, 2014), is a major driver of microbial decay. Given the fact that
578 saprotrophic microorganisms have to gain their metabolic energy from sugars, and cellulose
579 (β -1,4-linked glucose homopolymer) that constitutes up to 50% of wood, it seems rather
580 logical to find this strong correlation and it as best model predictor. (Endo)xylanase, which
581 hydrolyzes the hemicellulose backbone (β -1,4-linked xylose heteropolymer) contributes also
582 substantially to the carbon (pentoses) and energy supply of microorganisms including fungi
583 (Polizeli *et al.*, 2005). Further enzymes, like laccase and peroxidases mediate the rather slow
584 process of lignin decomposition and also contribute to the detoxification of plant ingredients
585 (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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1   **Supplementary material**

2

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

5   Kahl T., Arnstadt T., Baber K., Bässler C., Bauhus J., Borken W., Buscot F., Floren, A., Heibl
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7   Matzner, E., Otto P., Purahong W., Seilwinder C., Schulze ED., Wende B., Weisser W.W.,
8   Gossner M.M.

9

10   **Content:**

11   Appendix A1: Correlations among variables and phylogenetic signal

12   Appendix A2: Details on variable selection by PCA

13   Appendix A3: Details on model selection

14

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20 **Figure A1-1:** Correlation between all variables used in this study. The colour code indicates

21 the Spearman's rank correlation coefficient for each single correlation by means of size and

22 intensity.

Figure A1-2: Phylogenetic tree topology for the 13 studied tree genera. Tree topology and ultrametric branch lengths were modelled in a maximum likelihood framework. Confidence in the topology of our phylogenetic hypothesis was assessed with non-parametric bootstrap. All branches received bootstrap support of 83 percent or more and the tree topology is in accordance with current knowledge. For details see Methods section of the main manuscript.

Table A1-1: Phylogenetic signal (Pagel's lambda and Blomberg's k) in dependent and independent variables used in present analyses. Significant ($p < 0.05$) and marginally non-significant ($p < 0.10$) phylogenetic signal is highlighted in bold and bold-italic, respectively.

	Pagel's lambda	p-value	Blomberg's K	p-value
Bark ratio	0.000	1.000	0.442	0.565
Heartwood	1.052	0.005	0.917	0.169
Parenchym ratio	1.052	0.002	1.061	0.029
Ray height	1.031	0.076	1.034	0.033
Ray thickness	1.042	0.061	1.005	0.029
Wood density	0.766	0.036	0.822	0.159
C	0.232	0.735	0.828	0.149
N	0.000	1.000	0.167	0.932
P	0.000	1.000	0.772	0.168
S	0.814	0.032	0.955	0.063
Ca	0.000	1.000	0.455	0.666
K	0.958	0.018	1.228	0.004
Mg	0.000	1.000	0.622	0.395
Mn	0.000	1.000	0.394	0.602
Phenol	0.000	1.000	0.431	0.606
Lignin	1.047	0.008	1.287	0.010
Extractives	0.000	1.000	0.670	0.288
pH	0.000	1.000	0.675	0.268
Laccase	0.019	0.956	0.145	0.881
Endocellulase	0.185	0.694	0.467	0.540
Xylanase	0.266	0.546	0.402	0.643
Peroxidase	0.990	0.202	0.927	0.064
Coleoptera richness(mean)	0.217	0.712	0.326	0.703
Coleoptera richness (rarefied)	0.000	1.000	0.243	0.855
Fungi fruit body richness (mean)	0.873	0.038	1.102	0.022
Fungi fruit body richness (rarefied)	0.468	0.219	0.410	0.623
Fungi_ARISA (mean)	0.000	1.000	0.296	0.801
Decay rate	0.594	0.115	0.561	0.452

Appendix A2: Details on variable selection by PCA

Figure A2-1: Biplots for uncorrected PCAs of physical wood traits (a), chemical wood traits (b) and enzyme activity and organismic diversity (c). For all three groups of variables, the first three axis explain more than 70% of the variance.

Figure A2-2: Biplots for phylogenetically corrected PCAs of physical wood traits (a), chemical wood traits (b) and enzyme activity and organismic diversity (c). For all three groups of variables, the first three axis explain more than 70% of the variance.

Table A2-1: Loadings of variables on PCA axis in the uncorrected PCAs of physical wood traits, chemical wood traits and enzyme activity and organismic diversity. Variables with the highest loadings on the first three PCA axes are bold. For explanation of variables see Fig. A2-1.

Physical wood traits						
	PC1	PC2	PC3	PC4	PC5	PC6
Barkprop	-0.05	0.57	-0.07	0.77	0.12	-0.25
Heart	0.17	0.53	-0.60	-0.31	-0.46	0.16
Paren	0.51	-0.13	-0.45	0.06	0.67	0.25
Rhei	0.56	0.07	0.48	0.25	-0.32	0.54
Rthi	-0.42	-0.42	-0.39	0.44	-0.25	0.49
Pd09	0.47	-0.45	-0.22	0.22	-0.41	-0.56
Cum. variance explained	0.38	0.67	0.80	0.92	1.00	1.00

Chemical wood traits												
	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12
BC	0.37	-0.23	0.18	-0.14	0.15	-0.30	0.41	-0.16	0.17	0.04	-0.45	0.45
BN	-0.28	0.19	-0.34	0.32	-0.01	-0.52	0.08	0.27	-0.24	0.39	0.00	0.31
BP	-0.41	-0.12	-0.02	0.15	0.16	0.18	0.36	-0.25	-0.56	-0.25	-0.37	-0.16
BS	-0.36	0.13	0.19	-0.27	-0.23	-0.24	0.37	-0.45	0.24	0.34	0.22	-0.27
BCa	-0.26	-0.24	-0.39	0.36	0.22	0.11	0.08	-0.29	0.52	-0.24	0.23	0.24
BK	-0.36	0.08	0.31	-0.36	0.01	-0.14	0.04	0.22	-0.11	-0.50	0.33	0.45
BMg	-0.32	-0.38	0.14	-0.08	0.31	-0.20	-0.01	0.53	0.32	0.03	-0.23	-0.40
BMn	0.20	-0.32	0.16	0.42	-0.44	-0.47	0.03	-0.05	-0.09	-0.37	0.17	-0.24
BPh	0.09	0.53	-0.43	-0.19	-0.10	-0.20	0.18	0.09	0.23	-0.46	-0.28	-0.24
Lignin	0.14	-0.38	-0.42	-0.28	-0.29	0.25	0.49	0.32	-0.12	0.09	0.26	-0.01
Organic extractives	0.33	0.10	-0.03	-0.03	0.68	-0.23	0.20	-0.07	-0.20	-0.03	0.47	-0.25
pH	0.06	0.36	0.39	0.47	-0.03	0.32	0.49	0.33	0.19	0.02	0.06	0.01
Cum. variance explained	0.40	0.56	0.71	0.82	0.89	0.95	0.97	0.99	1.00	1.00	1.00	1.00

Enzyme activity and organismic diversity									
	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Lac	0.21	0.23	-0.76	-0.36	0.26	-0.08	0.01	-0.31	0.15
Pox	0.35	0.44	-0.04	0.09	0.07	-0.04	-0.58	0.40	-0.40
Ec	0.39	0.26	0.13	0.31	-0.07	-0.58	0.25	0.12	0.49
X	0.36	0.30	0.15	0.38	0.14	0.66	0.18	-0.35	0.05
Col_MW	0.36	-0.40	0.09	0.13	0.39	-0.34	0.20	-0.26	-0.56
Col_Rar	0.31	-0.46	0.18	-0.17	0.43	0.17	-0.39	0.17	0.48
FungiFK_MW	0.41	-0.21	-0.20	-0.22	-0.27	0.28	0.48	0.56	-0.12
FungiFK_rar	0.38	-0.24	0.00	-0.08	-0.70	-0.04	-0.34	-0.42	0.01
FungiOTU	0.13	0.34	0.55	-0.72	0.05	-0.05	0.14	-0.14	-0.06
Cum. variance explained	0.51	0.73	0.83	0.92	0.96	0.98	0.99	1.00	1.00

Table A2-2: Loadings of variables on PCA axis in the phylogenetically corrected PCAs of physical wood traits, chemical wood traits and enzyme activity and organismic diversity. Variables with the highest loadings on the first three PCA axes are bold. For explanation of variables see Fig. A2-2.

Physical wood traits						
	PC1	PC2	PC3	PC4	PC5	PC6
Barkprop	-0.07	0.87	0.17	-0.36	-0.28	0.06
Heart	-0.53	0.40	0.61	0.42	0.13	-0.03
Paren	-0.66	-0.32	0.26	-0.57	0.24	-0.04
Rhei	-0.85	0.17	-0.35	0.05	-0.32	-0.09
Rthi	0.82	-0.22	0.41	-0.11	-0.32	-0.09
Pd09	-0.55	-0.71	0.23	0.10	-0.35	0.08
Cum. variance explained	0.40	0.67	0.81	0.91	1.00	1.00

Chemical wood traits												
	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12
BC	0.82	-0.32	0.24	-0.17	-0.14	-0.24	-0.23	-0.07	0.06	0.00	0.02	0.01
BN	-0.61	0.27	-0.46	0.37	0.01	-0.42	-0.04	0.12	-0.09	0.03	0.00	0.00
BP	-0.89	-0.16	-0.03	0.17	-0.15	0.14	-0.20	-0.11	-0.21	-0.02	0.02	0.00
BS	-0.80	0.17	0.26	-0.31	0.22	-0.19	-0.20	-0.20	0.09	0.03	-0.01	0.00
BCa	-0.58	-0.33	-0.52	0.42	-0.21	0.09	-0.04	-0.13	0.20	-0.02	-0.01	0.00
BK	-0.79	0.10	0.42	-0.41	0.00	-0.12	-0.02	0.10	-0.04	-0.04	-0.02	0.01
BMg	-0.71	-0.52	0.18	-0.09	-0.29	-0.16	0.00	0.23	0.12	0.00	0.01	-0.01
BMn	0.45	-0.45	0.22	0.49	0.41	-0.38	-0.01	-0.02	-0.03	-0.03	-0.01	0.00
BPh	0.19	0.72	-0.58	-0.22	0.09	-0.16	-0.10	0.04	0.09	-0.04	0.02	0.00
Lignin	0.31	-0.53	-0.56	-0.33	0.27	0.20	-0.27	0.14	-0.05	0.01	-0.01	0.00
Organic extractives	0.72	0.13	-0.04	-0.03	-0.64	-0.18	-0.11	-0.03	-0.08	0.00	-0.03	0.00
pH	0.13	0.49	0.53	0.55	0.03	0.26	-0.27	0.15	0.07	0.00	0.00	0.00
Cum. variance explained	0.40	0.56	0.71	0.82	0.89	0.95	0.97	0.99	1.00	1.00	1.00	1.00

Enzyme activity and organismic diversity									
	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Lac	-0.46	-0.32	0.75	-0.31	-0.16	0.03	0.01	-0.07	-0.01
Pox	-0.74	-0.62	0.04	0.08	-0.04	0.02	-0.22	0.09	0.02
Ec	-0.84	-0.37	-0.13	0.27	0.04	0.24	0.09	0.03	-0.03
X	-0.77	-0.43	-0.14	0.33	-0.09	-0.27	0.07	-0.08	0.00
Col_MW	-0.76	0.56	-0.09	0.11	-0.24	0.14	0.07	-0.06	0.03
Col_Rar	-0.65	0.65	-0.17	-0.15	-0.27	-0.07	-0.15	0.04	-0.03
FungiFK_MW	-0.87	0.29	0.20	-0.19	0.17	-0.11	0.18	0.12	0.01
FungiFK_rar	-0.81	0.34	0.00	-0.07	0.44	0.02	-0.13	-0.09	0.00
FungiOTU	-0.28	-0.48	-0.54	-0.63	-0.03	0.02	0.05	-0.03	0.00
Cum. variance explained	0.51	0.73	0.83	0.92	0.96	0.98	0.99	1.00	1.00

Figure A3-1: Logs with decay rates smaller than 0 in relation to decay rate for the 13 studied tree genera.

Figure A3-2: Frequency distribution of decay rates in logs of the 13 studied tree genera.

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74 **Table A3-1:** Details on wood density measures in 2009 and 2015, decay rates and number of logs analysed for the 13 tree genera

Tree genus	Average wood density 2009 (gcm ⁻³)	Average wood density 2015 (gcm ⁻³)	Average decay rate 2009-2015 (based on column 1 and 2)	Average decay rate 2009-2015 (based on single logs)	Median decay rate 2009-2015 (based on single logs)	SD decay rate 2009-2015 (based on single logs)	Average decay rate 2009-2015 (based on positive single log values)	Total number of logs	Total number of logs with decay rate <0	Total number of logs with decay rate >0
Acer	0.522	0.377	0.050	0.053	0.046	0.037	0.054	85	1	84
Betula	0.515	0.406	0.037	0.042	0.031	0.052	0.050	87	12	75
Carpinus	0.642	0.388	0.077	0.083	0.074	0.047	0.083	88	0	88
Fagus	0.604	0.396	0.065	0.069	0.058	0.043	0.071	85	1	84
Fraxinus	0.608	0.536	0.019	0.019	0.018	0.021	0.025	87	13	74
Populus	0.438	0.315	0.051	0.055	0.048	0.045	0.059	86	5	81
Prunus	0.493	0.404	0.031	0.031	0.030	0.031	0.038	62	7	55
Quercus	0.585	0.510	0.021	0.021	0.021	0.021	0.023	87	6	81
Tilia	0.445	0.355	0.035	0.038	0.029	0.041	0.043	88	7	81
Larix	0.434	0.423	0.004	0.003	0.004	0.027	0.021	89	37	52
Picea	0.362	0.289	0.035	0.035	0.029	0.034	0.043	87	12	75
Pinus	0.411	0.372	0.016	0.015	0.015	0.023	0.024	86	21	65
Pseudotsuga	0.406	0.402	0.002	0.002	0.001	0.027	0.021	87	40	47

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80 **Table A3-2: Wood traits for 13 tree species**

Tree genus	Bark ratio (%)	Heart wood (y/n)	Paren chym ratio (%)	Ray height (μm)	Ray thick ness (μm)	Wood density (g/cm ³)	C (%)	N (%)	P (μg/g)	S (μg/g)	Ca (μg/g)	K (μg/g)	Mg (μg/g)	Mn (μg/g)	Phen ol (%)	Lignin (%)	Extrac tives (%)	pH	Laccase (mU/g)	Endoce llulase (mU/g)	Peroxi dase (mU/g)	Xylanase (mU/g)	Coleo ptera_ mean	Coleo ptera_ rar	Fungi_ mean	Fungi_ rar	Fungi_ ARISA
Acer	9.7	no	0	460	9	0.522	46	0.14	202.5	172	2307.6	1569	357	30.8	0.05	28.4	0.8	4.9	37.28	57.17	74.34	42.10	10.2	163.4	5.0	33.7	11.3
Betula	12.6	no	2	240	17	0.515	45.6	0.06	125.7	120	1288.4	1034	111	11.1	0.04	23.4	1.2	5.6	195.93	31.83	74.63	11.50	9.5	167.7	7.8	37.7	12.7
Carpinus	7.6	no	2	330	16	0.642	45.4	0.19	133.9	160	1850.3	1350	190	68.2	0.1	23.5	0.8	5.8	38.10	64.47	190.53	33.43	13.0	202.6	8.9	50.2	23.0
Fagus	7.4	no	5.2	2250	3	0.604	45.8	0.12	93.6	125	1017.3	1416	291	96.3	0.03	26.9	0.5	4.4	30.10	52.63	43.50	24.97	10.0	172.4	8.4	47.4	13.7
Fraxinus	14	yes	10.6	290	7	0.608	46	0.12	85.5	129	726.1	1836	206	4.9	0.17	26.6	1.8	4.2	9.70	17.60	13.73	9.57	5.8	146.2	3.2	25.3	15.0
Populus	25	no	0	340	11	0.438	45.7	0.08	116.6	126	1697.6	2213	511	6.7	0.03	25.5	0.9	5.3	41.80	64.23	152.47	17.87	9.0	155.8	4.4	36.6	16.0
Prunus	13	yes	0	400	8	0.493	46	0.13	67.2	69	820.7	871	151	12.2	0.12	24.0	3.3	5.6	14.20	34.25	1.70	4.20	11.2	177.0	6.5	46.0	4.0
Quercus	19.3	yes	4.9	38000	1	0.585	46.1	0.13	23	109	866.5	592	44	19.1	0.49	26.6	1.6	5.0	0.33	5.17	0.03	3.07	10.2	180.5	5.4	37.2	4.0
Tilia	14	no	2.5	480	7	0.445	46.8	0.13	68.2	74	949.6	686	206	131.8	0.04	23.1	2.8	5.8	45.23	20.30	40.77	10.37	8.6	172.3	4.7	39.8	17.0
Larix	20	yes	0.9	190	8	0.434	45.1	0.19	145.9	47	4411.3	343	202	26.6	0.1	28.4	1.4	4.6	0.48	10.45	0.72	4.21	7.8	164.6	4.4	33.4	10.5
Picea	12	no	1.4	150	5	0.362	46.6	0.07	37.3	61	1316.6	436	134	138.1	0.05	27.6	0.9	5.0	2.60	22.23	1.00	4.43	11.0	187.8	5.1	31.5	18.7
Pinus	12	yes	0	200	5	0.411	48.3	0.03	25.5	43	916.5	330	141	94.9	0.05	28.7	7.2	4.7	3.37	16.57	0.90	5.50	9.2	162.5	4.1	26.6	6.0
Pseudotsuga	14	yes	0	80	7	0.406	46.6	0.05	37.4	49	282.7	435	27	65.9	0.1	28.8	1.7	6.0	0.00	12.23	0.19	2.00	6.7	144.4	4.0	31.2	21.3

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83 Appendix A4: Details on model selection

84 **Table A4-1:** Best models ($\Delta\text{AICc} < 7$) for linear multiple regression models with decay rate as dependent variable. Model selection was conducted
85 based on AICc (small-sample-size corrected version of AIC). Please note that in the uncorrected model laccase and in the phylogenetically corrected
86 model (Table S2) endocellulase was used as predictor variable. NA: This predictor is not included in a particular model.

	Rank1	Rank2	Rank3	Rank4	Rank5	Rank6	Rank7	Rank8	Rank9	Rank10	Rank11	Rank12	Rank13	Rank14	Rank15	Rank16	Rank17	Rank18	Rank19	Rank20	Rank21	Rank22	Rank23	Rank24	Rank25
AICc	-41.9	-39.1	-38.9	-38.5	-38.5	-38.4	-38.4	-38.4	-37.9	-37.8	-37.7	-37.1	-37.0	-36.8	-36.6	-36.6	-36.5	-36.4	-36.4	-35.7	-35.5	-35.4	-35.3	-35.2	-35.0
ΔAICc	0.000	2.857	2.999	3.382	3.429	3.509	3.554	3.559	4.064	4.164	4.248	4.849	4.950	5.161	5.286	5.296	5.477	5.494	5.554	6.226	6.456	6.512	6.651	6.699	6.969
weight	0.238	0.057	0.053	0.044	0.043	0.041	0.040	0.040	0.031	0.030	0.028	0.021	0.020	0.018	0.017	0.017	0.015	0.015	0.015	0.011	0.009	0.009	0.009	0.008	0.007
adj. R ²	0.769	0.792	0.790	0.701	0.619	0.781	0.780	0.697	0.600	0.682	0.680	0.757	0.662	0.657	0.749	0.749	0.745	0.745	0.744	0.627	0.826	0.619	0.721	0.614	0.606
df	4	5	5	4	3	5	5	4	3	4	4	5	4	4	5	5	5	5	5	4	6	4	5	4	4
Intercept	-0.172	-0.092	-0.979	0.053	0.120	-0.179	0.087	0.168	0.221	0.131	0.040	0.263	0.142	-0.012	-0.147	-0.125	0.105	-0.187	-0.178	0.206	-0.087	0.877	0.008	0.301	0.298
Bark ratio	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	-0.008	NA	NA	NA	-0.022	NA	NA	NA	NA	-0.022
Phenol	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.000	NA	NA	NA	NA	NA	NA
P	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.033	NA	NA	NA	NA	NA	-0.004	NA	NA	NA	NA	NA	0.026	NA
Rarefied beetle richness	0.002	0.001	0.002	NA	NA	0.002	NA	NA	NA	NA	NA	NA	NA	0.001	0.001	0.002	NA	0.002	0.002	NA	0.001	NA	NA	NA	NA
Laccase	0.022	0.016	0.027	0.020	0.025	0.023	0.015	0.015	NA	NA	0.026	0.017	NA	NA	0.021	0.022	0.013	0.021	0.022	0.023	0.016	NA	0.021	NA	NA
Heartwood	NA	-0.039	NA	NA	NA	NA	-0.061	-0.060	-0.106	-0.082	NA	-0.089	-0.109	-0.090	NA	NA	-0.048	NA	NA	NA	-0.045	-0.093	NA	-0.134	-0.097
Lignin	NA	NA	0.226	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	-0.203	NA	NA	NA
Mean fungal fruit body richness	NA	NA	NA	0.014	NA	NA	NA	NA	NA	0.014	NA	NA	NA	NA	0.004	NA	0.011	NA	NA	NA	NA	NA	0.011	NA	NA
Wood ray height	NA	NA	NA	NA	NA	0.008	0.013	NA	NA	NA	0.013	NA	0.013	NA	NA	NA	NA	NA	NA	NA	0.010	NA	0.010	NA	NA

88 **Table A4-2:** Best models ($\Delta\text{AICc} < 7$) for phylogenetic linear multiple regression models with decay rate as dependent variable. Model selection was
89 conducted based on AICc (small-sample-size corrected version of AIC). Please note that in the uncorrected model (Table S1) laccase and in the
90 phylogenetically corrected model endocellulase was used as predictor variable. NA: This predictor is not included in a particular model.

	Rank1	Rank2	Rank3	Rank4	Rank5	Rank6	Rank7	Rank8	Rank9
AICc	-43.113	-41.307	-39.086	-38.184	-38.107	-38.027	-37.301	-36.874	-36.198
ΔAICc	0.000	1.806	4.027	4.929	5.006	5.085	5.812	6.238	6.915
weight	0.448	0.182	0.060	0.038	0.037	0.035	0.025	0.020	0.014
adj. R^2	NA	NA	NA	NA	NA	NA	NA	NA	NA
df	5	6	5	4	6	6	6	7	6
Intercept	0.169	0.187	0.171	0.167	0.171	0.170	0.195	0.190	0.170
Bark ratio	NA	NA	NA	NA	NA	NA	NA	NA	NA
Phenol	NA	NA	NA	NA	NA	-0.010	NA	NA	NA
P	NA	NA	NA	NA	NA	NA	NA	NA	NA
Rarefied beetle richness	0.019	0.021	NA	NA	0.014	0.026	NA	0.025	0.018
Endocellulase	0.041	0.033	0.062	0.052	0.047	0.035	0.043	0.025	0.042
Heartwood	NA	-0.033	NA	NA	NA	NA	-0.049	-0.037	NA
Lignin	NA	NA	NA	NA	NA	NA	NA	NA	-0.006
Mean fungal fruit body richness	NA	NA	NA	NA	NA	NA	NA	NA	NA
Wood ray height	NA	NA	0.026	NA	0.013	NA	0.025	0.016	NA

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