Edelmann, P., Weisser, W.W., Ambarlı, D., Bässler, C., **Buscot, F.**, Hofrichter, M., Hoppe, B., Kellner, H., Minnich, C., **Moll, J.**, Persoh, D., Seibold, S., Seilwinder, C., Schulze, E.-D., Wöllauer, S., Borken, W. (2023):
Regional variation in deadwood decay of 13 tree species: Effects of climate, soil and forest structure
For. Ecol. Manage. **541** , art. 121094

https://doi.org/10.1016/j.foreco.2023.121094

Regional variation in deadwood decay of 13 tree species: effects of climate, soil and forest structure

Pascal Edelmann[1,2], Wolfgang W. Weisser[1], Didem Ambarlı[1,3], Claus Bässler[4,5], François Buscot[6,7], Martin Hofrichter[8], Björn Hoppe[9], Harald Kellner[8], Cynthia Minnich[10], Julia Moll[6], Derek Persoh[10], Sebastian Seibold[11,1], Claudia Seilwinder [1], Ernst-Detlef Schulze[12], Stephan Wöllauer[13], Werner Borken[10*]

Affiliations

[1]Terrestrial Ecology Research Group, Department of Ecology and Ecosystem Management, Center of School of Life and Food Sciences Weihenstephan, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising-Weihenstephan, Germany

[2]Ecosystem Dynamics and Forest Management Research Group, Department of Ecology and Ecosystem Management, Center of School of Life and Food Sciences, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

[3]Department of Biological Sciences, Middle East Technical University, Ankara, Turkey

[4]National Park Bavarian Forest, Freyunger Str. 2 94481 Grafenau, Germany

[5]Goethe University Frankfurt, Faculty of Biological Sciences, Institute for Ecology, Evolution and Diversity, Conservation Biology, 60438 Frankfurt am Main, Germany

[6]Helmholtz Centre for Environmental Research - UFZ, Department of Soil Ecology, Th.-Lieser- Str. 4, 06120 Halle (Saale), Germany

[7]German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany

[8]Environmental Biotechnology, International Institute Zittau, Technische Universität Dresden, Markt 23, 02763 Zittau, Germany

[9]Julius Kühn Institute (JKI) – Federal Research Centre for Cultivated Plants, Institute for National and International Plant Health, Messeweg 11/12, 38104 Braunschweig, Germany

[10]Soil Ecology, University of Bayreuth, Bayreuth Center of Ecology and Environmental Research (BayCEER), Dr.-Hans-Frisch-Str. 1-3, 95448 Bayreuth, Germany

[11]Forest Zoology, Technische Universität Dresden, Pienner Str. 7, 01737 Tharandt, Germany

[12]Max-Planck-Institute for Biogeochemistry, Hans-Knöll-Strasse 10, 07745 Jena, Germany

[13]Philipps-Universität Marburg, Fachbereich Geographie, Deutschhausstraße 12, 35032 Marburg, Germany (Stephan.woellauer@geo.uni-marburg.de)

Corresponding author: Werner Borken

Abstract

Deadwood provides important ecological and biogeochemical functions in forest ecosystems. These functions rely on tree species-specific decay dynamics, but only few studies investigated how exogenous parameters affected the decay of deadwood at the regional scale. Here, we explore the influence of climate, soil traits and forest structure on decay dynamics and mass loss of logs of 13 tree species in 29 plots across three regions in Germany. This long-term experiment (BELongDead) comprises 1,066 logs of 9 angiosperms and 4 gymnosperms and covers a decay time of almost 10 years. Mass loss of logs was relatively high for the temperate climate with partly different half-lives ranging from 6 to 13 years (mean 8.9 ± 2.2 years). Diffuse-porous angiosperms lost 70 ± 13 % of their initial mass, followed by gymnosperms (49 ± 16 %) and ring-porous angiosperms (46 ± 12 %) within the study period. We applied three different mathematical models to fit mass loss in time and found that a linear model is most appropriate for 10 tree species. A sigmoidal model best described the mass loss of *Fraxinus*, *Quercus* and *Pinus* logs. A multivariate analysis revealed a significant effect of soil, temperature and precipitation on mass loss at the plot level. Mass loss increased with decreasing soil nutrient content, possibly as a result of enhanced bidirectional element translocations between nutrient-poor soils and logs by fungal hyphae. Temperature had a positive effect on mass loss, whereas increasing precipitation and soil moisture were negatively related to mass loss. The region with warmer, moderately humid climate and unfavourable soil properties led to overall higher mass loss (66 ± 4 %) whereas the other two regions were indifferent (both 57 ± 3 %). Forest structure, including canopy cover, share of coniferous trees and the stock of deadwood in the vicinity of the logs explained only a small part of the variability in mass loss. High variability within individual tree species suggests that other factors such as organismic diversity and microbial activity have stronger impact on the decay process at the regional scale than exogenous factors.

Keywords

Coarse woody debris, deadwood, mass loss, tree species, climate, forest soil

Highlights

- Mass loss of logs of 13 tree species over 9.8 years is best described by a linear or a sigmoidal model
- Logs of diffuse-porous angiosperms decay faster than ring-porous angiosperms and gymnosperms
- Logs of the same tree species exhibit large variability in mass loss across 29 forest sites
- Mass loss is highest in the region with higher temperature, dry and nutrient-poor soils
- Forest structure including deadwood stock in the neighborhood had little influence on mass loss

Introduction

Deadwood is important for biodiversity (e.g., Chmura et al., 2016; Jonsson et al., 2005; Seibold et al., 2015; Stokland et al., 2012; Ulyshen, 2018) and carbon (C) storage (Cornwell et al., 2009; Pan et al., 2011; Seibold et al., 2021) in forest ecosystems. These functions rely on the residence time of deadwood influenced by size, exposition (lying or standing) and tree species-specific wood traits such as chemical composition and wood density (Christensen et al., 2005; Kulakowski et al., 2017). Dead lying trunks (logs) have contact to soil and are subjected to relatively rapid decay or mass loss as opposed to standing dead trees (snags) (Storaunet and Rolstad, 2002). Microbial decomposition, fragmentation into particles of different sizes, and leaching of dissolved compounds contribute to deadwood decay (Harmon et al., 1986). Microbial decomposition is the prevailing process, but the contribution of leaching and fragmentation can increase at later decay stages and vary among tree species and environmental conditions (Arthur et al., 1993; Lasota et al., 2018). Fungi are typically the key decomposers of deadwood in temperate and boreal regions (Bässler et al., 2010; Jonsson et al., 2005), but archaea, bacteria and micro- to macrofauna also use deadwood ingredients or its conversion products and fragments for energy gain and buildup of biomass (Ceja-Navarro et al., 2014; Moll et al., 2018; Seibold et al., 2021; Ulyshen, 2016). Structure and activity of the decomposer community are complex and adapt to the changed wood chemistry as decay progresses (van der Wal et al., 2013). There is evidence of a relationship between organismic diversity and decay rates (Kahl et al., 2017), however, it is still unclear how the diversity of deadwood-degrading organisms controls the log decay of individual tree species.

The decay of logs is also influenced by chemical wood traits, and the proportion of sapwood and heartwood (Kahl et al., 2017; Noll et al., 2016). High concentrations of phenolic extractives (e.g., quercitin) reduce the activity of extracellular enzymes and thus the biochemical breakdown of the major wood polymers lignin, cellulose and hemicelluloses (Valette et al., 2017). In addition, the content and composition of lignin may affect the microbial decomposition. Especially the lignin components of gymnosperms are more stable than those of angiosperms due to an increased level of guaiacyl subunits (Müller-Hagedorn et al., 2003). Low availability of macronutrients such as nitrogen and phosphorous may further limit the decomposition of deadwood (Cheng et al., 2011). Taken together, the chemical composition of deadwood is tree-species specific, and can thus lead to different microbial activity and decay of logs among tree species.

Exogenous factors such as climate, openness of canopies and other location-specific parameters also play a significant role in deadwood decay (Harmon et al., 2020; Seibold et al., 2021; Zanne et al., 2022). Temperature is known as a major driver of microbial activity, which increases with rising temperature, and thus, controls the residence time of deadwood in forests (Rinne-Garmston et al., 2019; Wang et al., 2002). Wood moisture, which depends on precipitation and evaporation, additionally influences microbial activity in deadwood (Green et al., 2022). However, the control of wood moisture is more complex than temperature (Seibold et al., 2021). Both, low water availability during dry periods as well as high water contents with correspondingly oxygen (O_2) depletion have been shown to limit the decomposition of litter in general (Paul and Clark, 1989). Gas diffusion is ~10,000 times smaller in water than in air, and thus high water contents limit the O_2 availability, especially inside the logs. Moreover, the potential of low O_2 availability is higher in later than in early decay stages because of increasing deadwood porosity and water-holding capacity (Covey et al., 2016). The canopy structure may have no direct effect on the decay process, but an indirect effect through its influence on temperature, water availability and radiation (Thom et al., 2020). While these exogenous factors have been shown to affect decomposition, they have been mostly investigated over large climate gradients. The importance of regional differences in exogenous factors and whether log decay of individual tree species responds differently to exogenous factors has rarely been investigated.

Another exogenous factor that could affect the decay of logs is the underlying soil. Low nutrient concentrations in deadwood promote the expansion of fungal hyphae in underlying soil to meet their nutritional requirements. Nutrient translocations from soils into deadwood have been described for N and P (Boddy and Watkinson, 1995; Philpott et al., 2014), but other limited nutrients could also be taken up by fungal hyphae from soils and redistributed into deadwood (e.g. metals that are required by lignin and cellulose oxidizing enzymes: Fe, Mn, Cu). Although the mechanism is known, it is still unclear whether log decay is controlled by nutrient levels in forest soils.

Simple decay models are commonly used to describe the temporal course of deadwood decay. Further aims of modeling are the estimation of the decay constant, the residence time or half-life of deadwood in a forest. Mass loss or density loss over time are frequently used to estimate decay parameters with linear, exponential, or sigmoidal models (Chambers et al., 2000; Freschet et al., 2012b; Müller-Using and Bartsch, 2009). A linear decay is given at constant mass loss or density loss during the entire decay time. One pool exponential decay assumes a first-order kinetic and declining decay activity per unit mass with decreasing mass or density. Sigmoidal models indicate either fast or slow decay during the initial decay stage and thereafter a decrease or increase in the decay dynamic, respectively. Estimated half-life or residence time of deadwood allow comparisons of these models. These parameters as well as decay dynamics can improve our understanding of the function of deadwood for inhabiting organisms and for C storage in forests. However, there is no universal decay model that can be applied to coarse woody debris of different tree species. Decay dynamics and best model type can even differ for logs of the same tree species (Fraver et al., 2013). Therefore, we applied different decay models to assess reliable estimates of decay constants or residence times for different tree species.

In this study, we investigated deadwood decay of 13 tree species in the framework of the large scale field experiment 'BELongDead' (Biodiversity Exploratory Deadwood Experiment, Kahl et al., 2017). Logs of 13 tree species were placed in 29 forests in three regions in Germany. We asked the following questions:

1. Which model provides the best fit for the mass loss of logs of different tree species?
2. How does log decay of 13 tree species differ between regions with similar climatic conditions?
3. What is the influence of temperature, moisture, soil traits and forest structure on log decay?

2. Methods

2.1 Study areas

The BELongDead (**B**iodiversity **E**xploratories **Long-**term **Dead**wood) experiment is an interdisciplinary study on the diversity and function of deadwood-inhabiting organisms during the entire decay process of logs. It is part of the large-scale and long-term project 'Biodiversity Exploratories' to study the relationships between biodiversity, land-use intensity and ecosystem processes in three regions (exploratories) in Germany (Fischer et al., 2010). The exploratories are located in the UNESCO Biosphere Reserve Schorfheide-Chorin in northeast Germany (52°47'25"-53°13'26" N, 13°23'27"-14°08'53"E, 3-140 m a.s.l.), in 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 southwest 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, mean annual precipitation (MAP) is highest in the Swabian Alb, followed by Hainich-Dün (500–800 mm) and Schorfheide-Chorin (520–580 mm). Mean annual air temperature (MAT) 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). Soils developed on Jurassic limestone (Swabian Alb), Muschelkalk limestone, often covered by loess deposits (Hainich-Dün), and glacial till, often covered by glacio-fluvial or aeolian sand (Schorfheide-Chorin) (Fischer et al., 2010). The soil types and chemical-physical soil properties vary greatly within and between the exploratories (Minnich et al., 2021).

2.2 Experimental setup

The BELongDead experiment was established on a total of 30 plots (9 in Schorfheide-Chorin (SCH), 9 in Swabian Alb (ALB), 12 in Hainich-Dün (HAI)) in 2009. A storm event caused the loss of one experimental plot in Hainich. The plots included different forest types and management intensities, i.e., unmanaged forests dominated by European beech (n=9), managed even- and uneven-aged forests dominated by European beech (n=12), and intensively managed even-aged Norway spruce and Scots pine plantations (n=8). Logs of 13 tree species were exposed in each of the three subplots per plot (in total 1131 logs). Tree species included nine angiosperms: *Acer* spp. (*A. pseudoplatanus, A. platanoides*), *Betula pendula*, *Carpinus betulus*, *Fagus sylvatica*, *Fraxinus excelsior*, *Populus* spp. (*P. tremula* and hybrids), *Prunus avium*, *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 were 4 ± 0.1 m long and had a mean diameter of 31 ± 5.9 cm (SD). Living trees were felled in the winter of 2008/2009 in the Federal State of Thuringia (Germany) to obtain fresh logs of similar quality for the experiment. After transportation to each subplot, logs of the 13 tree species were placed in random order beside each other with a distance of ~1 m between logs in March to April 2009.

2.3 Density, mass and volume loss of logs

Initial wood densities of logs were first measured during the set-up of the experiment in 2009, but they were underestimated due to methodological inaccuracies and were thus, substituted by new measurements in 2020. For new measurements, three mature trees of each species of similar diameter as described above were harvested in the state forest of Thuringia in the winter of 2019/2020. Two ~10 cm thick wood discs were taken from each log's lower and upper section using a chainsaw. Two representative subsamples of 300-600 cm^3 of each wood disc were cut and dried at 60°C until constant mass. Wood density ($g\ cm^{-3}$) without bark of one subsample per wood disc was determined by water displacement method after applying a thin layer of paraffin to the wood surface. According to Archimedes' principle, water displacement of paraffin-treated wood samples was measured at room temperature in a water-filled beaker using a scale. Wood mass (60°C) was corrected for residual water content by drying a second subsample at 103°C until mass constancy. It was assumed that the mean wood density of each tree species from 2020 is representative for the initial wood density of logs in 2009.

Deadwood densities of each log were determined by different methods in 2012, 2015 and 2018. The sampling methods differed between the years due to ongoing experiments and the need to adapt the sampling method to progressive wood decay. In 2012 and 2015, after removing small pieces of bark, holes were drilled in radial direction to the log center using a Forstner drill bit (4 cm in diameter) and a cordless power drill at a 60 cm distance from one end of the log (see Kahl et al., 2017). The Forstner drill bit allowed the drilling of exact cylindrical holes in logs. Wood shavings from the drill holes were quantitatively collected and dried at 60°C until constant mass. Wood mass at 60°C was corrected to drying at 103°C assuming 2% residual water content for all tree species. Wood density (g cm^{-3}) was calculated as quotient of dry wood weight (g) and drill hole volume (cm^3). To calculate the log-specific mass or mass loss in 2012 and 2015, the decline in log volume since 2009 had to be taken into account (see below, equations 1 and 2).

In 2018, wood density of each log was determined from ~10 cm thick wood discs, and if existing, also wood fragments that could be assigned to a disc. The discs were taken with a chainsaw at a 20-30 cm distance from one end of the log. The exact distance to the end of the log as well as mean diameter and thickness of each disc were immediately measured in the field. All discs and fragments were placed in paper bags and dried at 60°C in ventilated ovens for 2-4 weeks. After weighing, a representative pie-shaped piece was cut from each disc, weighed and dried at 103°C to constant mass to determine the residual water content. Dry mass of an entire disc with the associated fragments was calculated using the residual water content (on average 2%). Deadwood density was assessed using the dry mass (disc and fragments) and the volume of the disc. The volume of deadwood fragments was ignored, since these were rarely found and the mass was small in relation to the disk (<5%).

To estimate the volume loss of logs, we made use of initial log diameters that were measured from each log at five positions at a distance of 1 m in 2009. Linear interpolation between two positions, assuming a conical log shape, allowed the estimate of the initial diameter for each section of the log. The exact position and thickness of the disc taken in 2018 was used to calculate the initial volume of the respective disc in 2009. Based on the initial (2009) and final volume (2018) of a disc and the decay time between 2009 and 2018 (9.83 yr), the volume loss factor (*VLF, dimensionless*) at time *t* was calculated for each log as follows:

$$VLF_t = 1 - \left(\frac{1 - Vr}{9.83} \times t\right) \quad (1)$$

where V_r (dimensionless) is the relative volume of a wood disc in 2018 (normalized to 1 in 2009), 9.83 (yr) is the decay time between 2009 and 2018, and t (yr) is the decay time since application of logs in 2009. This approach assumes a linear decrease in log volume over time. Deadwood mass (M_t) was calculated for different sampling times as follows:

$$M_t = D_t \, x \, V_{2009} \, x \, VLF_t \quad (2)$$

where D_t (g cm^{-3}) is the measured density of deadwood in year *t*, V_{2009} (cm^3) is the initial volume of the disc taken in 2018. Initial deadwood mass in 2009 was calculated using the mean wood density determined in 2020 (see above). Deadwood mass reported here refers to dry mass (103°C) and assumes representative estimates of D_t, V$_{2009}$ and VLF_t for each log.

2.4 Mass loss and decay models

Mass loss of each log was calculated as the relative difference (%) between the deadwood mass in 2009 and 2018 (9.83 years). For modeling log decay, initial log mass was normalized to 1 and the respective deadwood mass in 2012, 2015 and 2018 was related to 1.

The average relative decrease in log mass of each tree species across all subplots was estimated using three models:

Exponential: $$RM = b \, x \, e^{-kt} \quad (3)$$

Linear: $$RM = b - kt \quad (4)$$

Sigmoidal: $$RM = \frac{1}{1 + e\,(c(log\,(t) - log\,(d)))} \quad (5)$$

where *RM* represents the relative decrease in log mass as a function of time, *k* is the decay constant (yr^{-1}), *t* is the time (yr), *b* is the initial mass (normalized to 1), c and d are parameter estimates (dimensionless) of the sigmoidal model. Parameter estimates of the models were used to predict the average time for loss of 50% (L50, half life) and 95% (L95, residence time) of initial mass.

2.5 Environmental parameters

Various environmental parameters were compiled using the database BExIS of the Biodiversity Exploratories (https://www.biodiversity-exploratories.de/en/public-data-bexis/) to test their effect on log decay. Mean annual temperature (MAT) at 10 cm height above the forest floor, mean sum of annual precipitation (MAP) and soil water content (SWC) at 10 cm depth were continuously recorded in each forest site since 2008 in 10 minute intervals and averaged for the complete time series (2009 – 2018). Canopy cover (Canopy) was assessed via airborne LiDAR survey during leaf-on conditions as the proportion of first returns above 2 meters height in 2009 (BExIS ID 30925, not publicly available, Gossner et al., 2021). The conifer share (Conifer) is based on the basal area represented by conifers and was calculated based on forest inventories conducted between 2009 and 2011 (BExIS ID 18270, Schall and Ammer, 2014). Canopy and Conifer are described as fractions between 0 and 1. For aboveground deadwood stocks (CWD, coarse woody debris without logs of the BELongDead experiment), the volume of stumps, downed and standing deadwood > 25 cm in diameter were determined on an area of 100 m x 100 m during a deadwood inventory in 2012 (BExIS ID 24546, Schall et al., 2019). Chemical and microbial soil properties (Fe, Mn, P, ergosterol concentrations and pH) of the top mineral soil from 0-7 cm depth and at a distance of 8 m from the logs were determined in one subplot of each forest site (Minnich et al., 2021). Soil data were available in BExIS under ID 25726 and ID 25727.

2.6 Statistical Analysis

Prior to the analyses, we dropped all logs with incomplete time series (1066 logs remaining). To answer our first research question, we fitted linear, exponential, and negative sigmoidal models (see 2.4) to find the best-performing decay model for each tree species seperately. The best models were determined by comparing Bayesian Information Criteria (BIC, best model indicated by lowest BIC). Random slope effects were included on plot level for each tree species to account for the nested design. Additionally, we used the *offset* function within R to set the intercept to a fixed value of 1. For the mixed linear and exponential functions, we used the *lme4* package (Bates et al., 2015), and for the sigmoidal functions, we used the *medrc* package (Ritz et al., 2013). Using the coefficients of the best models, we estimated the model-specific decay times (years) for 50% and 95% mass loss of each tree species. To address our second research question, we performed an ANOVA to test for differences in relative mass loss after 9.83 years among tree species, regions and their interactions. For this analysis, mass loss was arcsine transformed to achieve normality of the residuals. Furthermore, for this analysis, we added the subplots nested within plots as a random effect to account for the experimental design. Differences between tree species were determined via Post-hoc tests (Tukey) using the *emmeans* (Lenth, 2022) and *multcomp* (Hothorn et al., 2008) packages in R.

To address our third research question, environmental parameters (see 2.5) were used to analyze differences in mass loss of logs among the exploratories, forest types, and forest stand characteristics at the plot level and identify the most relevant abiotic drivers of deadwood decay. We used a principal component analysis (PCA, built-in *prcomp* function in R) to overview the relationships of 12 environmental variables and mass loss (Table S1, Supplement). To determine the effects of environmental variables, we checked the contribution and correlation of each variable to the most important principal components. If necessary, environmental parameters were transformed for the PCA to achieve normality of the residuals. We used box-cox-transformation, except for the conifer share in forest stands, for which an arcsine transformation was applied (Table S1). As *Acer* logs on plot HEW42 were missing, we filled relative mass loss for this plot using the mean value for *Acer* in HAI (64%). All variables (dependent and independent) were standardized (*decostand* function of the *vegan* package, Oksanen et al., 2020) before the multivariate analyses. Additionally, we calculated linear models of the relative mass loss of all tree species for each of the environmental parameters in interaction with region. All model calculations were conducted in R version 4.0.3 (R Core Team, 2020).

Results

Decay models, half-life and residence time of logs

According to the BIC values, the exponential model revealed the weakest fits to the mass loss of all tree species (Table 1). In contrast, BIC values of the linear and sigmoidal models were relatively close for most tree species. Mass loss of *Acer*, *Betula*, *Carpinus*, *Fagus*, *Populus*, *Prunus*, *Tilia, Larix, Picea,* and *Pseudotsuga* were best explained by the linear model. Mass loss of all other tree species was best fitted by a sigmoidal model, although the shape of the sigmoidal fit differed among the tree species (Fig. 1). *Pinus* and *Quercus* showed higher mass loss during the initial decay phase and slowed down as decay progressed. In contrast, mass loss of *Fraxinus* was relatively low in the initial phase and accelerated in the following years. Estimated half-lives (L50) of logs were mostly similar for the same tree species using the model parameters of the linear, exponential and sigmoidal model (Table 1). However, the time differences between the models sharply increased when estimating the 95% mass loss (L95) for the 13 tree species. The linear model predicted the shortest (11 to 24 years) and the sigmoidal model (28 to 623 years) the longest decay times for 95% mass loss. Larger deviations between the two models were found primarily for tree species with low mass loss. The exponential model yielded consistently lower decay constants (k) and longer residence times (L95) than the linear model.

Wood density and mass loss of tree species in different regions

Mean initial wood densities varied between 0.44 and 0.70 g cm^{-3} among the nine angiosperms and between 0.45 and 0.50 g cm^{-3} among the four gymnosperms (Table 2). In 2018, after 9.83 years of decay, angiosperms had mean wood densities of 0.17 - 0.46 g cm^{-3} and gymnosperms of 0.21 and 0.35 g cm^{-3}. Of all tree species, *Carpinus* had the lowest (0.17 g cm^{-3}) and *Quercus* the highest wood density (0.46 g cm^{-3}). Accordingly, tree species-specific mass loss ranged between 42 and 80%, with *Larix* as the slowest and *Carpinus* as the fastest decaying tree species. Overall, mass loss significantly differed among tree species ($p<0.001$). Mass loss of *Picea* was not different to *Acer*, *Populus* and *Prunus,* but higher than of *Fraxinus, Quercus* and the three other gymnosperms. Mean mass loss of diffuse-porous angiosperms was >60%, whereas ring-porous angiosperms and gymnosperms exhibited mass losses of <50%, except *Picea* (62%).

Mass loss of logs from the same tree species strongly differed within and across the three regions, as indicated by large standard deviations (Table 2, Fig. 2). The ANOVA revealed a significant effect ($p<0.001$) of region on mass loss for all tree species (Fig. 2, Table S2). The highest mass loss occurred at SCH, whereas the differences for individual tree species between ALB and HAI were mostly small and not significant. It is noticeable that *Acer* was the only tree species with lower mean mass loss in SCH than in HAI and ALB, although the differences were not significant. Mass loss of *Populus* and *Quercus* were also very similar and not significantly different among the three regions. The significant interaction ($p<0.001$) between region and tree species indicated inconsistent patterns in mass loss for the 13 tree species between HAI and ALB (Table S2).

Effects of exogenous factors on mass loss

The PCA showed the scattering of the 29 plots in the three regions, indicating large differences in their characteristics both within and across the regions (Fig. 3). Particularly large differences emerged between SCH and HAI or ALB, while few plots from ALB and HAI clustered. The first two PCA axes explained 69.4 % of the variation in climate, soil parameters and forest stand characteristics across all tree species and regions. The first PCA axis explained 50.7% of the variability of exogenous parameters and was significantly correlated with mass loss ($R^2 = 0.52$, $p<0.001$), where the exploratory power decreased in the order soil Fe, Mn, SWC, P, pH, C:N, MAT, MAP and ergosterol (Table S3 & Table S4). Thus, soil parameters had a stronger effect on mass loss than MAT and MAP. PCA axis 2 explained 18.7% of the exogenous parameter variation and was mainly driven by conifer share and canopy cover. Mass loss also correlated significantly with PCA axis 2 ($R^2 = 0.13$, p=0.04). The plot-specific volume of CWD in the neighborhood of logs had no discernible influence on mass loss (Table S3). As the interaction between axes 1 and 2 was not significant, plot-specific mass loss responded similarly to the exogenous factors (Table S4). Individual PCA analyses and linear models indicated that mass loss of only nine tree species (*Betula*, *Carpinus*, *Fagus*, *Fraxinus*, *Prunus*, *Tilia*, *Picea*, *Pinus*, *Pseudotsuga*) was correlated with axis 1 (Table S5). Moreover, axis 2 was only correlated with mass loss of three tree species (*Fagus*, *Fraxinus*, *Larix*).

We further tested the effect of all exogenous factors shown in Fig. 3 on the mean plot-specific mass loss separately for each region. Region-specific Pearson correlations between mean mass loss of all tree species and site parameters revealed no significant relationships, except for soil Mn concentration in SCH (Fig. 4). The concentrations of soil Mn were smaller at SCH (0.24 mg g^{-1}) as compared to ALB (1.35 mg g^{-1}) and HAI (1.17 mg g^{-1}) and positively correlated (r=0.72, p=0.03) with mass loss in SCH.

Discussion

After almost ten years, logs of diffuse-porous angiosperms showed the highest mass loss, whereas smaller mass loss was observed for the ring-porous angiosperms *Fraxinus* and *Quercus*, and the four gymnosperms. Average half-lives of 6-13 years of the 13 tree species indicate relatively rapid mass loss for the climatic conditions in the study regions. We further explored how plot-specific or regional environmental factors impact the mass loss of logs. Average higher mass loss occurred in the relatively warm-dry and nutrient-poor SCH region (66%) as compared to HAI (57%) and ALB (57%). Soil properties, MAT and MAP had relatively strong effects on plot-specific mass loss, whereas the effect of forest structure was small. The high variability in mass loss for individual tree species suggests that other factors, such as differences between the decomposer communities and microclimatic conditions in the logs, create large variability in mass loss within and among plots.

Limiations of decay models and half-lives of logs

Mass loss was best described by either the linear or the sigmoidal model for the 9.8-year decay phase. The exponential model yielded poorer fits to the mass loss, which could be related, at least for some tree species, to the fact that the decay process was yet not completed and that only four sampling dates were available for modeling. Changes in the resource quality through preferential degradation of sapwood and retention of heartwood, or the stronger fragmentation with improved accessibility for deadwood decomposers could have caused a turning point in the decay dynamics. Therefore, we cannot rule out that the exponential, sigmoidal or another model is more suitable to describe the entire decay process than the linear model. While the sigmoidal model best describes the mass loss of *Pinus*, *Fraxinus* and *Quercus*, estimates of residence times (L95 > 100 years) are unlikely for temperate regions. The sigmoidal model requires thus more advanced decay for the prediction of the residence time of logs in our experiment.

Overall, the linear model has the lowest uncertainty for the future decay process, especially for tree species that had lost more than two-thirds of their mass. In agreement with our study, the decay of *Fagus* and *Picea* logs in unmanaged forests also showed linear dynamics although those logs had a history as standing deadwood (snags) before falling to the forest floor (Krüger et al., 2014). In contrast, mass loss of *Betula*, *Picea* and *Pinus* logs with snag-history followed sigmoidal decay dynamics in boreal forests (Mäkinen et al., 2006). A comparison with other studies (Aakala, 2010; Freschet et al., 2012a; Müller-Using and Bartsch, 2009; Petrillo et al., 2016) shows that decay patterns and models can differ for the same tree species. A combination of several factors such as climate, local conditions, log size, cause of tree death and eventual history as snag may influence the decay dynamics and the half-lives.

Taken together, half-lives of 6-13 years across all tree species are relatively short compared to other studies under similar climatic conditions. For instance, Müller-Using and Bartsch (2009) reported half-lives for *Fagus* logs of 10 years. Herrmann et al. (2015) estimated half-lives of 13 years for *Fagus*, 21 years for *Picea* and 22 years for *Pinus* logs. Likewise, Freschet et al. (2012b) also calculated longer half-lives for *Betula*, *Pinus* and *Populus* logs. Tree species specific mass loss has been described as a function of log diameter (Herrmann et al., 2015), temperature (Russell et al., 2015), decomposer community (Kahl et al., 2017; Rajala et al., 2012; Seibold et al., 2021), cause and conditions since tree death (Mäkinen et al., 2006). We assume that the short half-lives in our study are related to the use of freshly cut trunks and the almost complete contact of logs with the forest floor. The open cut surfaces on logs could have accelerated the colonization and establishment of decomposer communities in the initial decay phase. Moreover, soil contact creates favorable microclimatic conditions for microorganisms and allows the uptake of nutrients via fungal hyphae and rhizomorphs from soil (see below). These experimental boundary conditions have possibly contributed to the rapid mass loss of logs in our study.

Tree species-specific effects on mass loss

Mass loss significantly differed for some tree species, which is probably related to different wood traits as previously reported by Kahl et al. (2017) for our logs. At a higher phylogenetic level, the differences were more pronounced with higher mass loss for diffuse-porous angiosperms than for ring-porous angiosperms or gymnosperms. There was one exception - logs of the gymnosperm *Picea* decayed relatively fast and were not different to logs of *Acer*, *Populus* and *Prunus*. The rapid decay of *Picea* logs could be due to a brown-rot fungus, *Fomitopsis pinicola*, which is common and adapted to the degradation of *Picea* deadwood (Leonhardt et al., 2019). The linear course of mass loss does yet not indicate a decrease in decay of *Picea* logs. In contrast, *Quercus* and *Pinus* logs showed an accelerated mass loss in the first years of the experiment, which can be attributed to the rapid decay of sapwood. As the sapwood of these tree species disappears, the sigmoidal decay dynamics may reflect a slowdown of mass loss of recalcitrant heartwood in subsequent years. An exception is *Fraxinus* as it is the only tree species that exhibits delayed mass loss during the first 2-3 years and thereafter an increase in mass loss. To the best of our knowledge, a delayed decay of *Fraxinus* logs has not yet been reported from other studies. Similar to mass loss, leaching of dissolved organic carbon (DOC) from *Fraxinus* logs was also very low during the first years in our experiment (Bantle et al., 2014). Leaching could be an important process in the initial decay phase as it removes potentially inhibitory compounds such as soluble phenolics and aldehydes (Sanz et al., 2012). Phenolics and aldehydes can affect enzymatic activities by inhibition and competitive reactions (Aloui et al., 2004), and thereby the growth and spreading of wood-degrading microorganisms in logs. Of the angiosperms, *Fraxinus, Prunus,* and *Quercus* had the highest initial levels of phenolics (Kahl et al., 2017) as well as the smallest mass loss, but only *Quercus* and *Prunus* logs showed high DOC leaching losses (Bantle et al., 2014). Hence, the level of phenolics and their removal by leaching are possible drivers for the differences in mass loss among the 13 tree species.

Carpinus is the tree species with the highest initial wood density and the highest mass loss. Some logs of this tree species were almost completely decomposed within 9.8 years. Mass loss of all other diffuse-porous angiosperms ranged between 61 and 74% and were partly statistically different, but we cannot explain the differences among these tree species by initial wood-chemical traits. It is often assumed that deadwood of angiosperms decays faster than that of gymnosperms (Weedon et al., 2009). However, ring-porous angiosperms (*Fraxinus*, *Quercus*) show similar or even lower mass losses than certain gymnosperms in our study. Further ring-porous angiosperms like *Robinia* are also known as slow-decaying tree species (Vek et al., 2020). The slower decay of ring-porous angiosperms could be related to the high concentration of antimicrobial substances and phenolic antioxidants (Sanz et al., 2012).

Effect of exogenous factors and region on mass loss

The correlation between PCA axis 1 and plot-specific mass loss highlights the importance of soil parameters and climate for the decay of logs. Soil parameters are closely related and collectively suggest that nutrient-poor soils strengthen the decay of logs. This is particularly true for soils at SCH, which are characterized by low pH, high C:N ratios and low nutrient levels (Minnich et al., 2021). We attribute the higher decay potential of logs on nutrient-poor soils to increasing expansion and activity of wood-inhabiting fungi in the underlying soil. As deadwood is extremely nutrient-poor, uptake of nutrients from soil by fungal hyphae is a pathway to overcome nutrient deficiency in logs (Philpott et al., 2014; Wells and Boddy, 1995). The supply with readily available carbohydrates in logs allows deadwood-degrading fungi to spread their mycelium in organic horizons of the forest floor or even in mineral soil horizons. Soils beneath logs in the BELongDead experiment exhibited higher ergosterol (biomarker for fungal biomass) concentrations (Minnich et al., 2021) and a shift in the fungal diversity towards more saprotrophic and less mycorrhizal fungi (D. Persoh, pers. comm.). These changes were stronger at SCH than at ALB and HAI because low soil fertility at SCH requires greater effort to acquire the same amount of nutrients. On the other hand, if the level of a specific nutrient is too small in the soil, mass loss may decrease. This seems to be an exception in the log-soil continuum, but the relationship between soil Mn concentration and mass loss at SCH suggests a limitation of fungal deadwood decomposition on extremely Mn-poor soils. A high Mn availability is essential for the induction and function of the key lignin-degrading enzyme, i.e. Mn-oxidizing peroxidase (Hofrichter, 2002). Biotic interactions between logs and soils have been demonstrated, but further studies are needed to assess the impact of soil traits on mass loss of logs.

Relatively high MAT and low MAP (Table S1) also contributed to higher mass loss at SCH while climatic differences between ALB and HAI did not affect mass loss. The influence of temperature on deadwood decay is expressed by a Q_{10} value of 2.4 (Chambers et al., 2000), indicating an increase in mass loss by 14% by a temperature rise of 1°C. Consequently, the higher mass loss at SCH can be explained, in part, by the temperature differences of 0.85°C and 0.51°C to ALB and HAI, respectively. The temperature difference of 0.34°C between HAI and ALB was apparently too small for a significant regional effect. For logs of *Fagus sylvatica*, highest mass loss was found in regions with warm-dry climate followed by warm-humid and cold-humid regions (Přívětivý et al., 2016). Thus, temperature in interaction with humidity is an important regional factor for mass loss.

It is noteworthy that mass loss was negatively affected by increased precipitation or soil moisture across all regions since litter decomposition is typically positively associated with water availability in well-drained forests (Borken and Matzner, 2009). This inverse pattern is possibly related to the high water holding capacity of logs, especially with low wood densities in later decay stages. Maximum water holding capacities varied between 230 and 750% in logs from the BELongDead experiment after ~12 years and were substantially higher in diffuse-porous angiosperms than in ring-porous angiosperms and gymnosperms (Groß et al., 2022). High water contents can severely limit the oxygen supply and lead to anoxic conditions and low microbial decomposition in logs. In fact, recent work showed the release of methane from logs, which can only be formed by methanogenesis under anoxic conditions (Covey et al., 2016). Hence, low precipitation associated with favorable oxygen availability in logs could have promoted the activity of wood-degrading organisms and mass loss more strongly at SCH than in the other regions. This effect on mass loss may have been enhanced by the sandy texture and low field capacity of soils at SCH. (Bond-Lamberty et al., 2002) also reported higher deadwood respiration on dry sites with well-drained soils compared to sites with poorly drained soils. On the other hand, it can be assumed that deadwood decomposition is temporally limited under very dry conditions due to insufficient water availability for microorganisms. As MAP and SWC are only proxies for water contents in logs, monitoring log moisture could help unravel the differences in log decay across individual tree species. We assume that canopy cover and conifer share are interrelated with MAT and MAP and see no direct link to the decay of logs.

Limitations of the study

In this experiment, we used non-local logs with potentially different properties and nutrient contents than logs from the study sites. It remains open to what extent the mass loss of these logs would differ from local logs. To study this effect, logs of local origin would have had to be applied in parallel. However, a study showed very similar nutrient levels in stem wood of the same tree species from forest sites in three countries (Hagen-Thorn et al., 2004). We assume that nutrient uptake from external sources (e.g., soil, throughfall, N_2 via biological nitrogen fixation) is thus more important for the decay process than small differences in the initial nutrient content of logs.

Tracking the mass loss of a single log over many years is based on some assumptions and requires the use of different methods. When calculating the mass loss, it was assumed that the density and decay state of the deadwood sample is representative of a total log although the decay state of the logs was mostly inhomogeneous. Thus, the large variability for the mass loss of a specific tree species across the three regions is partly due to the sometimes non-representative deadwood sample of a log. However, the uniform sampling procedure and the large number of replicates per tree species (Table 2) should result in a robust estimate of the mean mass loss. With the inclusion of volume loss of logs, which amounted to 12-29% after almost 10 years, the calculation of mass loss became more accurate. We recommend a higher resolution of the initial log diameters to achieve a more accurate estimate of volume loss. Progressing decomposition and fragmentation of logs will require further adjustments of the sampling method in the future.

Conclusions

Decay of logs was relatively fast with half-lives of 6 – 13 years for the 13 tree species estimated by linear or sigmoidal models, indicating that logs under similar environmental conditions can rapidly lose part of their function as habitat and carbon storage. The almost complete contact of logs with soils seems to accelerate the decay process in our study. Mass loss is highly variable, primarily determined by tree species and to lesser extent by regional factors. In temperate regions, high temperatures, low-moderate precipitation, well-drained and nutrient-poor soils could amplify the decay of logs. However, the function of soils, in particular the availability of soil nutrients, for the decay process remains unclear. Other factors as the diversity and activity of wood-degrading organisms could also contribute to the variability in mass loss at the local to regional scale. Assessment of tree species-specific mass loss is crucial for the management of deadwood in forests. Rapid mass loss requires more frequent replacements to maintain the deadwood stock and related ecological functions.

Acknowledgments

We thank Uwe Hell, Gerhard Müller, Constanze Stark, Sabrina Leonhardt, Beatrix Schnabel and many student helpers for technical assistance in the field and the laboratory. We also would like to thank Christian Ammer, Martin Gossner and Peter Schall for providing data for our analysis.

We thank the managers of the three Exploratories, Swen Renner and Kirsten Reichel-Jung (Alb), Sonja Gockel, Kerstin Wiesner, Katrin Lorenzen and Juliane Vogt (Hainich) as well as Andreas Hemp, Martin Gorke, Miriam Teuscher (Schorfheide) and all former managers for their work in maintaining the plot and project infrastructure; Simone Pfeiffer, Maren Gleisberg, Christiane Fischer, Jule Mangels and Victoria Grießmeier for giving support through the central office, Andreas Ostrowski for managing the central data base, and Markus Fischer, Eduard Linsenmair, Dominik Hessenmöller, Daniel Prati, Ingo Schöning, François Buscot, Ernst-Detlef Schulze, Wolfgang W. Weisser and the late Elisabeth Kalko for their role in setting up the Biodiversity Exploratories project. We thank the administration of the Hainich national park, the UNESCO Biosphere Reserve Swabian Alb and the UNESCO Biosphere Reserve Schorfheide-Chorin as well as all land owners for the excellent collaboration. The work has been (partly) funded by the DFG Priority Program 1374 "BiodiversityExploratories" (WE3081/21-4, BO1741/11-1). Field work permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg.

References

Aakala, T., 2010. Coarse woody debris in late-successional Picea abies forests in northern Europe: Variability in quantities and models of decay class dynamics. For Ecol Manage 260, 770–779. https://doi.org/10.1016/j.foreco.2010.05.035

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. https://doi.org/10.1007/s00107-004-0489-7

Arthur, M.A., Tritton, L.M., Fahey, T.J., 1993. Dead bole mass and nutrients remaining 23 years after clear-felling of a northern hardwood forest. Canadian Journal of Forest Research 23, 1298–1305. https://doi.org/10.1139/x93-166

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. https://doi.org/10.1016/j.foreco.2014.06.035

Bässler, C., Müller, J., Dziock, F., Brandl, R., 2010. Effects of resource availability and climate on the diversity of wood-decaying fungi. Journal of Ecology 98, 822–832. https://doi.org/10.1111/j.1365-2745.2010.01669.x

Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. J Stat Softw 67. https://doi.org/10.18637/jss.v067.i01

Boddy, L., Watkinson, S.C., 1995. Wood decomposition, higher fungi, and their role in nutrient redistribution. Canadian Journal of Botany 73. https://doi.org/10.1139/b95-400

Bond-Lamberty, B., Wang, C., Gower, S.T., 2002. Annual carbon flux from woody debris for a boreal black spruce fire chronosequence. Journal of Geophysical Research: Atmospheres 107, WFX 1-1. https://doi.org/10.1029/2001JD000839

Borken, W., Matzner, E., 2009. Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. Glob Chang Biol 15, 808–824. https://doi.org/10.1111/j.1365-2486.2008.01681.x

Ceja-Navarro, J.A., Nguyen, N.H., Karaoz, U., Gross, S.R., Herman, D.J., Andersen, G.L., Bruns, T.D., Pett-Ridge, J., Blackwell, M., Brodie, E.L., 2014. Compartmentalized microbial composition, oxygen gradients and nitrogen fixation in the gut of Odontotaenius disjunctus. ISME Journal 8, 6–18. https://doi.org/10.1038/ismej.2013.134

Chambers, J.Q., Higuchi, N., Schimel, J.P., Ferreira, L. v., Melack, J.M., 2000. Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. Oecologia 122, 380–388. https://doi.org/10.1007/s004420050044

Cheng, S.S., Lin, C.Y., Gu, H.J., Chang, S.T., 2011. Antifungal activities and chemical composition of wood and leaf essential oils from cunninghamia konishii. Journal of Wood Chemistry and Technology 31, 204–217. https://doi.org/10.1080/02773813.2010.515049

Chmura, D., Żarnowiec, J., Staniaszek-Kik, M., 2016. Interactions between plant traits and environmental factors within and among montane forest belts: A study of vascular species colonising decaying logs. For Ecol Manage 379, 216–225. https://doi.org/10.1016/j.foreco.2016.08.024

Christensen, M., Hahn, K., Mountford, E.P., Ódor, P., Standovár, T., Rozenbergar, D., Diaci, J., Wijdeven, S., Meyer, P., Winter, S., Vrska, T., 2005. Dead wood in European beech (Fagus sylvatica) forest reserves. For Ecol Manage 210, 267–282. https://doi.org/10.1016/j.foreco.2005.02.032

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 Chang Biol 15, 2431–2449. https://doi.org/10.1111/j.1365-2486.2009.01916.x

Covey, K.R., de Mesquita, C.P.B., Oberle, B., Maynard, D.S., Bettigole, C., Crowther, T.W., Duguid, M.C., Steven, B., Zanne, A.E., Lapin, M., Ashton, M.S., Oliver, C.D., Lee, X., Bradford, M.A., 2016. Greenhouse trace gases in deadwood. Biogeochemistry 130, 215–226. https://doi.org/10.1007/s10533-016-0253-1

Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, 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. https://doi.org/10.1016/j.baae.2010.07.009

Fraver, S., Milo, A.M., Bradford, J.B., D'Amato, A.W., Kenefic, L., Palik, B.J., Woodall, C.W., Brissette, J., 2013. Woody Debris Volume Depletion Through Decay: Implications for Biomass and Carbon Accounting. Ecosystems 16, 1262–1272. https://doi.org/10.1007/s10021-013-9682-z

Freschet, G.T., Aerts, R., Cornelissen, J.H.C., 2012a. A plant economics spectrum of litter decomposability. Funct Ecol 26, 56–65. https://doi.org/10.1111/j.1365-2435.2011.01913.x

Freschet, G.T., Weedon, J.T., Aerts, R., van Hal, J.R., Cornelissen, J.H.C., 2012b. Interspecific differences in wood decay rates: Insights from a new short-term method to study long-term wood decomposition. Journal of Ecology 100, 161–170. https://doi.org/10.1111/j.1365-2745.2011.01896.x

Gossner, M.M., Levick, S., Schall, P., 2021. LIDAR-based canopy cover above BELongDead subplots 2008-2009, Version 2 [WWW Document]. Biodiversity Exploratories Information System. URL https://www.bexis.uni-jena.de/

Green, M.B., Fraver, S., Lutz, D.A., Woodall, C.W., D'Amato, A.W., Evans, D.M., 2022. Does deadwood moisture vary jointly with surface soil water content? Soil Science Society of America Journal 1–9. https://doi.org/10.1002/saj2.20413

Groß, C., Hossen, S., Hartmann, H., Noll, M., Borken, W., 2022. Biological nitrogen fixation and nifH gene abundance in deadwood of 13 different tree species. https://doi.org/10.21203/rs.3.rs-1645513/v1

Hagen-Thorn, A., Armolaitis, K., Callesen, I., Stjernquist, I., 2004. Macronutrients in tree stems and foliage: A comparative study of six temperate forest species planted at the same sites. Ann For Sci 61, 489–498. https://doi.org/10.1051/forest:2004043

Harmon, M.E., Fasth, B.G., Yatskov, M., Kastendick, D., Rock, J., Woodall, C.W., 2020. Release of coarse woody detritus-related carbon: A synthesis across forest biomes. Carbon Balance Manag. https://doi.org/10.1186/s13021-019-0136-6

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Cummins, K.W., 1986. Ecology of Coarse Woody Debris in Temperate Ecosystems, in: Advances in Ecological Research. pp. 133–302. https://doi.org/10.1016/S0065-2504(03)34002-4

Herrmann, S., Kahl, T., Bauhus, J., 2015. Decomposition dynamics of coarse woody debris of three important central European tree species. For Ecosyst 2. https://doi.org/10.1186/s40663-015-0052-5

Hofrichter, M., 2002. Review: lignin conversion by manganese peroxidase (MnP). Enzyme Microb Technol 30, 454–466. https://doi.org/10.1016/S0141-0229(01)00528-2

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biometrical Journal 50, 346–363. https://doi.org/10.1002/BIMJ.200810425

Jonsson, B.G., Kruys, N., Jonsson, T.R., Kruys, B.G., Ranius, N.&, 2005. Ecology of Species Living on Dead Wood-Lessons for Dead Wood Management. Silva Fennica 39.

Kahl, T., Arnstadt, T., Baber, K., Bässler, C., Bauhus, J., Borken, W., Buscot, F., Floren, A., Heibl, C., Hessenmöller, D., Hofrichter, M., Hoppe, B., Kellner, H., Krüger, D., Linsenmair, K.E., Matzner, E., Otto, P., Purahong, W., Seilwinder, C., Schulze, E.D., Wende, B., Weisser, W.W., Gossner, M.M., 2017. Wood decay rates of 13 temperate tree species in relation to wood properties, enzyme activities and organismic diversities. For Ecol Manage 391, 86–95. https://doi.org/10.1016/j.foreco.2017.02.012

Krüger, I., Muhr, J., Hartl-Meier, C., Schulz, C., Borken, W., 2014. Age determination of coarse woody debris with radiocarbon analysis and dendrochronological cross-dating. Eur J For Res 133, 931–939. https://doi.org/10.1007/s10342-014-0810-x

Kulakowski, D., Seidl, R., Holeksa, J., Kuuluvainen, T., Nagel, T.A., Panayotov, M., Svoboda, M., Thorn, S., Vacchiano, G., Whitlock, C., Wohlgemuth, T., Bebi, P., 2017. A walk on the wild side: Disturbance dynamics and the conservation and management of European mountain forest ecosystems. For Ecol Manage 388, 120–131. https://doi.org/10.1016/j.foreco.2016.07.037

Lasota, J., Błońska, E., Piaszczyk, W., Wiecheć, M., 2018. How the deadwood of different tree species in various stages of decomposition affected nutrient dynamics? J Soils Sediments 18, 2759–2769. https://doi.org/10.1007/s11368-017-1858-2

Lenth, R. v., 2022. emmeans: Estimated Marginal Means, aka Least-Squares Means. [WWW Document]. https://doi.org/10.1080/00031305.1980.10483031

Leonhardt, S., Hoppe, B., Stengel, E., Noll, L., Moll, J., Bässler, C., Dahl, A., Buscot, F., Hofrichter, M., Kellner, H., 2019. Molecular fungal community and its decomposition activity in sapwood and heartwood of 13 temperate European tree species. PLoS One 14, 1–21. https://doi.org/10.1371/journal.pone.0212120

Mäkinen, H., Hynynen, J., Siitonen, J., Sievänen, R., 2006. Predicting the decomposition of scots pine, norway spruce, and birch stems in Finland. Ecological Applications 16, 1865–1879. https://doi.org/10.1890/1051-0761(2006)016[1865:PTDOSP]2.0.CO;2

Minnich, C., Peršoh, D., Poll, C., Borken, W., 2021. Changes in Chemical and Microbial Soil Parameters Following 8 Years of Deadwood Decay: An Experiment with Logs of 13 Tree Species in 30 Forests. Ecosystems 24, 955–967. https://doi.org/10.1007/s10021-020-00562-z

Moll, J., Kellner, H., Leonhardt, S., Stengel, E., Dahl, A., Bässler, C., Buscot, F., Hofrichter, M., Hoppe, B., 2018. Bacteria inhabiting deadwood of 13 tree species are heterogeneously distributed between sapwood and heartwood. Environ Microbiol 20, 3744–3756. https://doi.org/10.1111/1462-2920.14376

Müller-Hagedorn, M., Bockhorn, H., Krebs, L., Müller, U., 2003. A comparative kinetic study on the pyrolysis of three different wood species. J Anal Appl Pyrolysis 68–69, 231–249. https://doi.org/10.1016/S0165-2370(03)00065-2

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. https://doi.org/10.1007/s10342-009-0264-8

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. https://doi.org/10.1016/J.FORECO.2016.07.035

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2020. vegan: Community Ecology Package. R package version 2.5-7. [WWW Document]. URL https://cran.r-project.org/package=vegan

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. Science (1979) 333, 988–993. https://doi.org/10.1126/science.1201609

Paul, E.A., Clark, F.E., 1989. Soil Microbiology and Biochemistry. Academic Press, San Diego.

Petrillo, M., Cherubini, P., Fravolini, G., Marchetti, M., Ascher-Jenull, J., Schärer, M., Synal, H.-A., Bertoldi, D., Camin, F., Larcher, R., Egli, M., 2016. Time since death and decay rate constants of Norway spruce and European larch deadwood in subalpine forests determined using dendrochronology and radiocarbon dating. Biogeosciences 13, 1537–1552. https://doi.org/10.5194/bg-13-1537-2016

Philpott, T.J., Prescott, C.E., Chapman, W.K., Grayston, S.J., 2014. Nitrogen translocation and accumulation by a cord-forming fungus (Hypholoma fasciculare) into simulated woody debris. For Ecol Manage 315, 121–128. https://doi.org/10.1016/j.foreco.2013.12.034

Přívětivý, T., Janík, D., Unar, P., Adam, D., Král, K., Vrška, T., 2016. How do environmental conditions affect the deadwood decomposition of European beech (Fagus sylvatica L.)? For Ecol Manage 381, 177–187. https://doi.org/10.1016/j.foreco.2016.09.033

R Core Team, 2020. R: A Language and Environment for Statistical Computing.

Rajala, T., Peltoniemi, M., Pennanen, T., Mäkipää, R., 2012. Fungal community dynamics in relation to substrate quality of decaying Norway spruce (Picea abies [L.] Karst.) logs in boreal forests. FEMS Microbiol Ecol 81, 494–505. https://doi.org/10.1111/j.1574-6941.2012.01376.x

Rinne-Garmston, K.T., Peltoniemi, K., Chen, J., Peltoniemi, M., Fritze, H., Mäkipää, R., 2019. Carbon flux from decomposing wood and its dependency on temperature, wood N 2 fixation rate, moisture and fungal composition in a Norway spruce forest. Glob Chang Biol 25, 1852–1867. https://doi.org/10.1111/gcb.14594

Ritz, C., Gerhard, D., Hothorn, L.A., 2013. A Unified Framework for Benchmark Dose Estimation Applied to Mixed Models and Model Averaging. http://dx.doi.org/10.1080/19466315.2012.757559 5, 79–90. https://doi.org/10.1080/19466315.2012.757559

Russell, M.B., Fraver, S., Aakala, T., Gove, J.H., Woodall, C.W., D'Amato, A.W., Ducey, M.J., 2015. Quantifying carbon stores and decomposition in dead wood: A review. For Ecol Manage. https://doi.org/10.1016/j.foreco.2015.04.033

Sanz, M., de Simón, B.F., Cadahía, E., Esteruelas, E., Muñoz, A.M., Hernández, T., Estrella, I., Pinto, E., 2012. LC-DAD/ESI-MS/MS study of phenolic compounds in ash (Fraxinus excelsior L. and F. americana L.) heartwood. Effect of toasting intensity at cooperage. J Mass Spectrom 47, 905–918. https://doi.org/10.1002/JMS.3040

Schall, P., Ammer, C., 2014. Stand composition, basal area on all forest EPs, 2008 - 2014 [WWW Document]. Biodiversity Exploratories Information System. URL https://www.bexis.uni-jena.de/ddm/data/Showdata/18270

Schall, P., Ammer, C., Bauhus, J., 2019. 1st Dead Wood Inventory of 148 forest EPs, item volumes, 2012 [WWW Document]. Biodiversity Exploratories Information System. URL https://www.bexis.uni-jena.de/ddm/data/Showdata/24546

Seibold, S., Bässler, C., Brandl, R., Gossner, M.M., Thorn, S., Ulyshen, M.D., Müller, J., 2015. Experimental studies of dead-wood biodiversity - A review identifying global gaps in knowledge. Biol Conserv 191, 139–149. https://doi.org/10.1016/j.biocon.2015.06.006

Seibold, S., Rammer, W., Hothorn, T., Seidl, R., Ulyshen, M.D., Lorz, J., Cadotte, M.W., Lindenmayer, D.B., Adhikari, Y.P., Aragón, R., Bae, S., Baldrian, P., Barimani Varandi, H., Barlow, J., Bässler, C., Beauchêne, J., Berenguer, E., Bergamin, R.S., Birkemoe, T., Boros, G., Brandl, R., Brustel, H., Burton, P.J., Cakpo-Tossou, Y.T., Castro, J., Cateau, E., Cobb, T.P., Farwig, N., Fernández, R.D., Firn, J., Gan, K.S., González, G., Gossner, M.M., Habel, J.C., Hébert, C., Heibl, C., Heikkala, O., Hemp, A., Hemp, C., Hjältén, J., Hotes, S., Kouki, J., Lachat, T., Liu, J., Liu, Y., Luo, Y.H., Macandog, D.M., Martina, P.E., Mukul, S.A., Nachin, B., Nisbet, K., O'Halloran, J., Oxbrough, A., Pandey, J.N., Pavlíček, T., Pawson, S.M., Rakotondranary, J.S., Ramanamanjato, J.B., Rossi, L., Schmidl, J., Schulze, M., Seaton, S., Stone, M.J., Stork, N.E., Suran, B., Sverdrup-Thygeson, A., Thorn, S., Thyagarajan, G., Wardlaw, T.J., Weisser, W.W., Yoon, S., Zhang, N., Müller, J., 2021. The contribution of insects to global forest deadwood decomposition. Nature 597, 77–81. https://doi.org/10.1038/s41586-021-03740-8

Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in dead wood, Biodiversity in Dead Wood. Cambridge University Press. https://doi.org/10.1017/CBO9781139025843

Storaunet, K.O., Rolstad, J., 2002. Time since death and fall of Norway spruce logs in old-growth and selectively cut boreal forest. Canadian Journal of Forest Research 32, 1801–1812. https://doi.org/10.1139/x02-105

Thom, D., Sommerfeld, A., Sebald, J., Hagge, J., Müller, J., Seidl, R., 2020. Effects of disturbance patterns and deadwood on the microclimate in European beech forests. Agric For Meteorol 291, 108066. https://doi.org/10.1016/j.agrformet.2020.108066

Ulyshen, M.D., 2018. Saproxylic Insects, Zoological Monographs. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-319-75937-1

Ulyshen, M.D., 2016. Wood decomposition as influenced by invertebrates. Biological Reviews 91, 70–85. https://doi.org/10.1111/brv.12158

Valette, N., Perrot, T., Sormani, R., Gelhaye, E., Morel-Rouhier, M., 2017. Antifungal activities of wood extractives. Fungal Biol Rev. https://doi.org/10.1016/j.fbr.2017.01.002

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. https://doi.org/10.1111/1574-6976.12001

Vek, V., Balzano, A., Poljanšek, I., Humar, M., Oven, P., 2020. Improving Fungal Decay Resistance of Less Durable Sapwood by Impregnation with Scots Pine Knotwood and Black Locust Heartwood Hydrophilic Extractives with Antifungal or Antioxidant Properties. Forests 11, 1024. https://doi.org/10.3390/f11091024

Wang, C., Bond-Lamberty, B., Gower, S.T., 2002. Environmental controls on carbon dioxide flux from black spruce coarse woody debris. Oecologia 132, 374–381. https://doi.org/10.1007/s00442-002-0987-4

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. https://doi.org/10.1111/j.1461-0248.2008.01259.x

Wells, J.M., Boddy, L., 1995. Effect of temperature on wood decay and translocation of soil-derived phosphorus in mycelial cord systems. New Phytologist 129, 289–297. https://doi.org/10.1111/j.1469-8137.1995.tb04299.x

Zanne, A.E., Flores-Moreno, H., Powell, J.R., Cornwell, W.K., Dalling, J.W., Austin, A.T., Classen, A.T., Eggleton, P., Okada, K., Parr, C.L., Adair, E.C., Adu-Bredu, S., Alam, M.A., Alvarez-Garzón, C., Apgaua, D., Aragón, R., Ardon, M., Arndt, S.K., Ashton, L.A., Barber, N.A., Beauchêne, J., Berg, M.P., Beringer, J., Boer, M.M., Bonet, J.A., Bunney, K., Burkhardt, T.J., Carvalho, D., Castillo-Figueroa, D., Cernusak, L.A., Cheesman, A.W., Cirne-Silva, T.M., Cleverly, J.R., Cornelissen, J.H.C., Curran, T.J., D'Angioli, A.M., Dallstream, C., Eisenhauer, N., Evouna Ondo, F., Fajardo, A., Fernandez, R.D., Ferrer, A., Fontes, M.A.L., Galatowitsch, M.L., González, G., Gottschall, F., Grace, P.R., Granda, E., Griffiths, H.M., Guerra Lara, M., Hasegawa, M., Hefting, M.M., Hinko-Najera, N., Hutley, L.B., Jones, J., Kahl, A., Karan, M., Keuskamp, J.A., Lardner, T., Liddell, M., Macfarlane, C., Macinnis-Ng, C., Mariano, R.F., Méndez, M.S., Meyer, W.S., Mori, A.S., Moura, A.S., Northwood, M., Ogaya, R., Oliveira, R.S., Orgiazzi, A., Pardo, J., Peguero, G., Penuelas, J., Perez, L.I., Posada, J.M., Prada, C.M., Přívětivý, T., Prober, S.M., Prunier, J., Quansah, G.W., Resco de Dios, V., Richter, R., Robertson, M.P., Rocha, L.F., Rúa, M.A., Sarmiento, C., Silberstein, R.P., Silva, M.C., Siqueira, F.F., Stillwagon, M.G., Stol, J., Taylor, M.K., Teste, F.P., Tng, D.Y.P., Tucker, D., Türke, M., Ulyshen, M.D., Valverde-Barrantes, O.J., van den Berg, E., van Logtestijn, R.S.P., Veen, G.F. (Ciska), Vogel, J.G., Wardlaw, T.J., Wiehl, G., Wirth, C., Woods, M.J., Zalamea, P.-C., 2022.

Termite sensitivity to temperature affects global wood decay rates. Science (1979) 377, 1440–1444. https://doi.org/10.1126/science.abo3856

Table 1. Parameter estimates and BIC from linear, exponential and sigmoidal models of log decay of 13 tree species after 9.8 years, and predicted time (years) for mass loss of 50% (L50) and 95% (L95) by each model. Bold values indicate lowest BIC.

	Linear				Exponential				Sigmoidal				
Tree species	k (yr^{-1})	BIC	L50 (yr)	L95 (yr)	k (yr^{-1})	BIC	L50 (yr)	L95 (yr)	c	d	BIC	L50 (yr)	L95 (yr)
Acer	-0.070	**-581.3**	7.2	13.7	-0.108	-81.3	6.4	27.7	1.32	6.62	-578.7	6.6	61.3
Betula	-0.076	**-491.5**	6.6	12.5	-0.132	152.7	5.3	22.7	1.33	5.76	-451.4	5.8	52.5
Carpinus	-0.083	**-655.3**	6.0	11.5	-0.162	291.6	4.3	18.6	1.94	5.40	-543.4	5.4	24.7
Fagus	-0.076	**-681.7**	6.6	12.6	-0.132	119.8	5.3	22.8	1.93	6.14	-631.9	6.1	28.3
Fraxinus	-0.039	-615.5	12.9	24.5	-0.052	-226.6	13.4	58.1	1.91	12.55	**-625.9**	12.6	58.6
Populus	-0.065	**-557.2**	7.7	14.6	-0.102	33.3	6.8	29.4	1.86	7.52	-501.0	7.5	36.8
Prunus	-0.061	**-364.0**	8.2	15.6	-0.092	-15.1	7.5	32.4	1.32	8.14	-303.5	8.1	75.7
Quercus	-0.055	-639.5	9.2	17.4	-0.073	-388.1	9.5	41.0	0.72	10.44	**-767.2**	10.4	623.1
Tilia	-0.069	**-530.5**	7.3	13.9	-0.114	144.3	6.1	26.4	1.45	7.14	-487.5	7.1	54.6
Larix	-0.043	**-604.6**	11.6	22.0	-0.058	-236.7	12.1	52.1	1.00	14.42	-597.6	14.4	274.0
Picea	-0.067	**-470.9**	7.5	14.3	-0.102	-61.8	6.8	29.3	0.69	8.46	-429.2	8.5	589.1
Pinus	-0.054	-564.6	9.3	17.6	-0.075	-198.9	9.2	39.9	0.84	12.24	**-628.5**	12.2	402.5
Pseudotsuga	-0.043	**-643.6**	11.6	22.0	-0.056	-350.3	12.4	53.5	1.24	12.74	-623.5	12.7	136.7

Table 2: Means (±SD) of wood density (WD) of 13 tree species in 2009 and 2018, volume loss factor in 2018 (VLF), number of logs, mass loss in 2018, and significant differences in mass loss among tree species based on ANOVA results. Different letters indicate significant differences at α=0.05.

Tree species	WD 2009 (g cm^{-3})	WD 2018 (g cm^{-3})	VLF 2018 (cm^{3} cm^{-3})	Logs (n)	Mass loss (%)	Significance
Acer	0.63 (0.01)	0.26 (0.08)	0.85 (0.10)	82	64.7 (10.5)	cd
Betula	0.65 (0.04)	0.20 (0.09)	0.85 (0.10)	84	73.5 (11.5)	b
Carpinus	0.70 (0.04)	0.17 (0.08)	0.78 (0.11)	85	80.4 (9.8)	a
Fagus	0.68 (0.08)	0.20 (0.07)	0.87 (0.09)	83	73.8 (9.2)	b
Fraxinus	0.61 (0.03)	0.40 (0.10)	0.88 (0.08)	85	42.6 (14.5)	f
Populus	0.44 (0.02)	0.20 (0.07)	0.77 (0.12)	81	65.7 (10.7)	cd
Prunus	0.53 (0.03)	0.21 (0.07)	0.82 (0.10)	60	61.4 (13.7)	d
Quercus	0.64 (0.03)	0.46 (0.07)	0.71 (0.11)	84	49.2 (7.6)	e
Tilia	0.50 (0.04)	0.21 (0.08)	0.77 (0.10)	83	67.6 (13.8)	bc
Larix	0.48 (0.05)	0.35 (0.08)	0.80 (0.10)	85	42.4 (14.0)	f
Picea	0.45 (0.03)	0.21 (0.06)	0.82 (0.10)	84	61.5 (13.0)	d
Pinus	0.50 (0.02)	0.30 (0.08)	0.84 (0.11)	85	50.0 (15.4)	e
Pseudotsuga	0.49 (0.03)	0.32 (0.07)	0.87 (0.08)	85	42.7 (12.3)	f

Figure captions

Figure 1. Relative decrease in log mass of 13 tree species between 2009 and 2018, sorted by gymnosperms, diffuse-porous and ring-porous angiosperms. The linear or sigmoidal model was applied according to the lowest BIC (see Table 2).

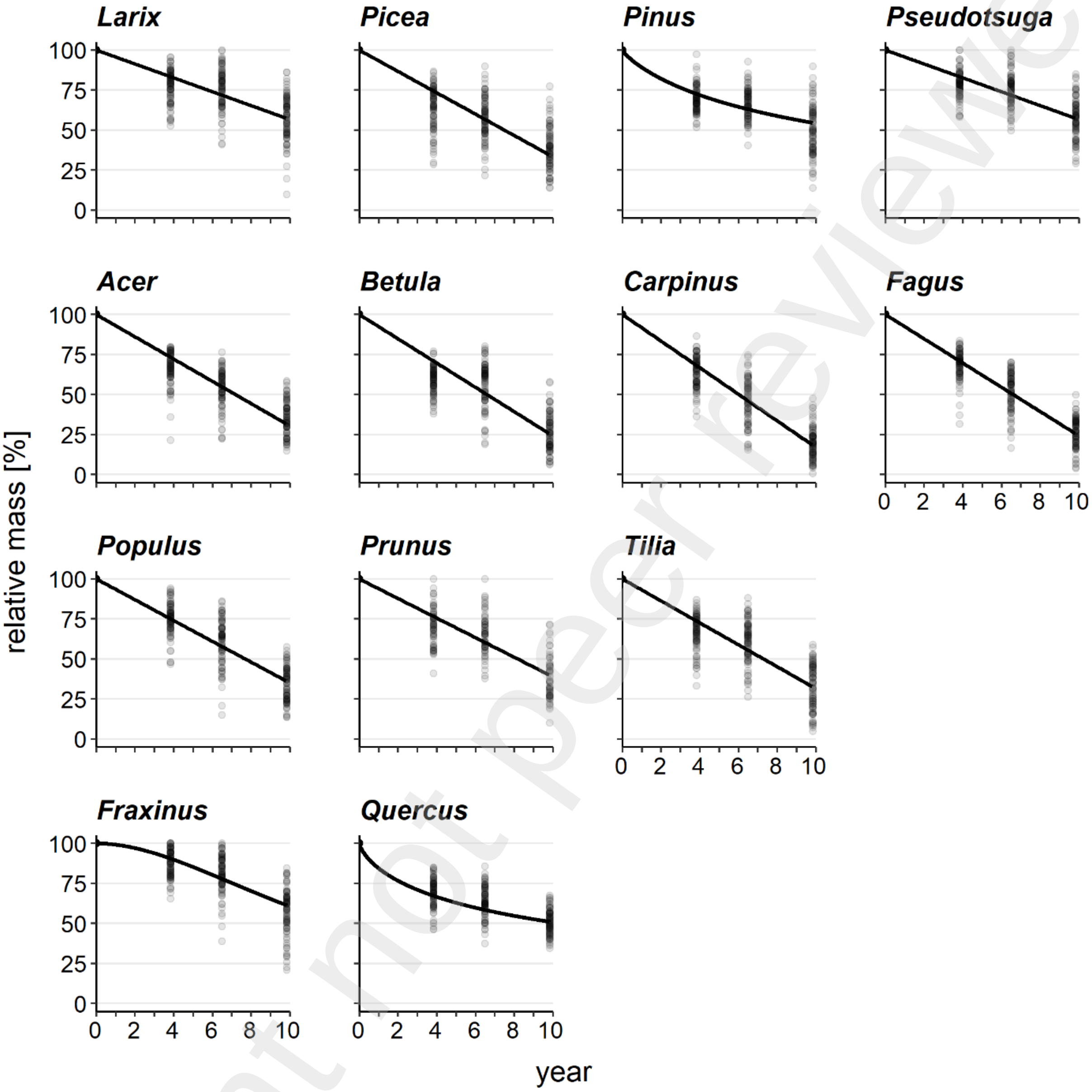
Figure 2. Boxplot (median with 25-75 percentile) with relative mass loss of 13 tree species in three regions after 9.8 years.

Figure 3. Principle Component Analysis of mean mass loss of logs from 13 tree species, climate parameters, soil properties, and forest stand characteristics across 29 sites in three regions.

Figure 4. Relationship between mean mass loss of 13 tree species and soil Mn concentration in the three regions ALB, HAI and SCH.

864

Figure 1

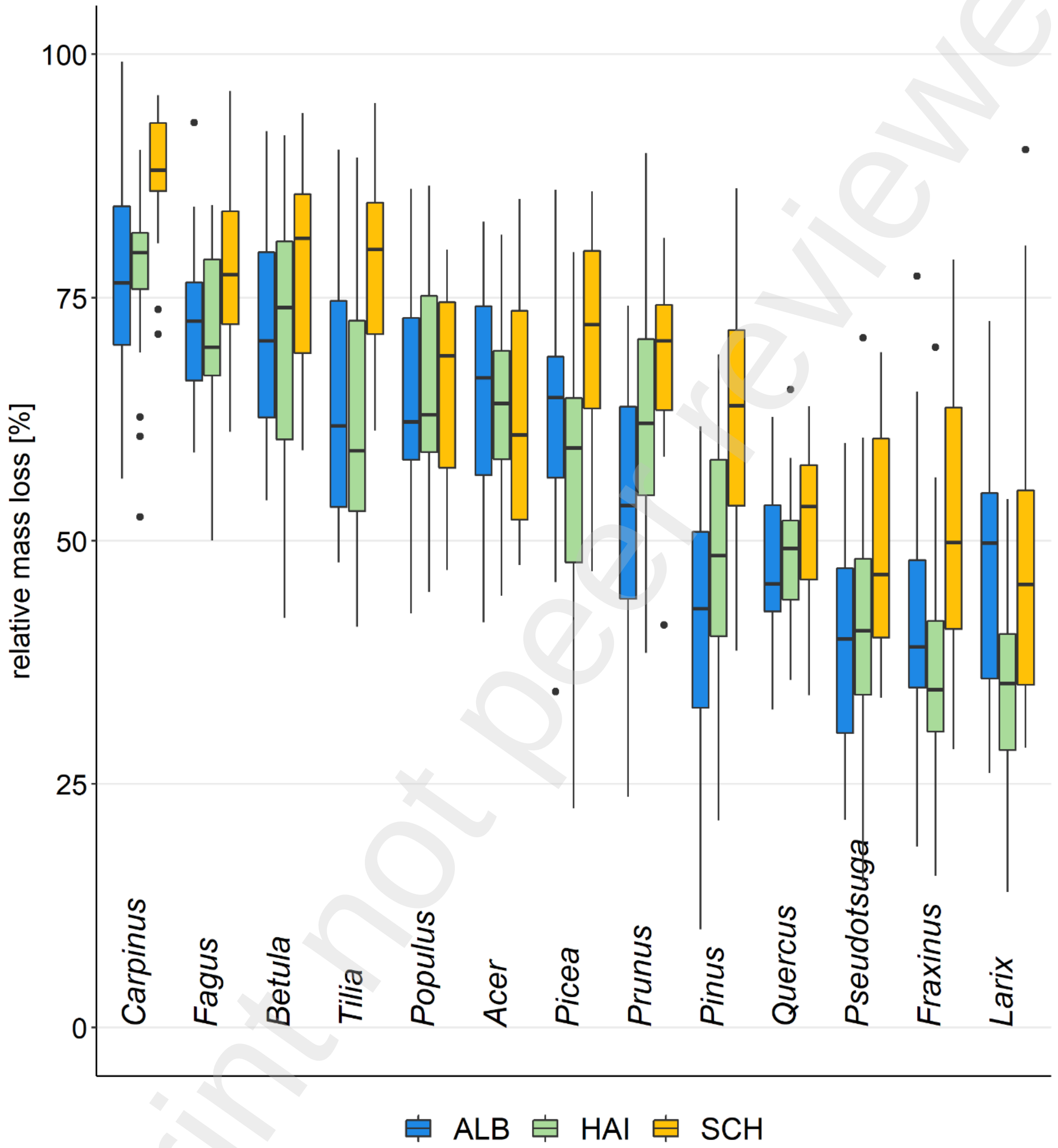


865

866

867

Figure 2

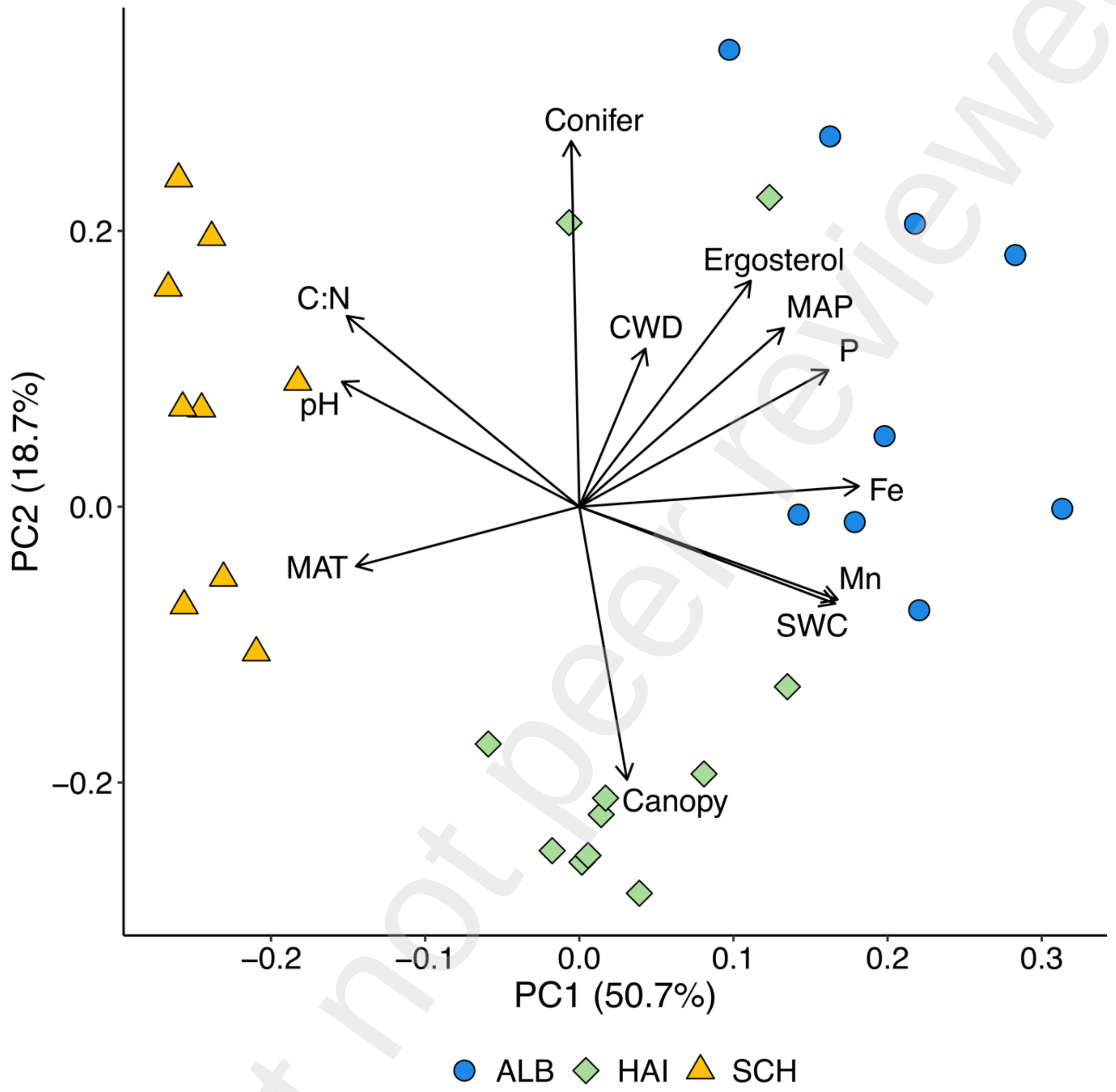


868

869

870

Figure 3

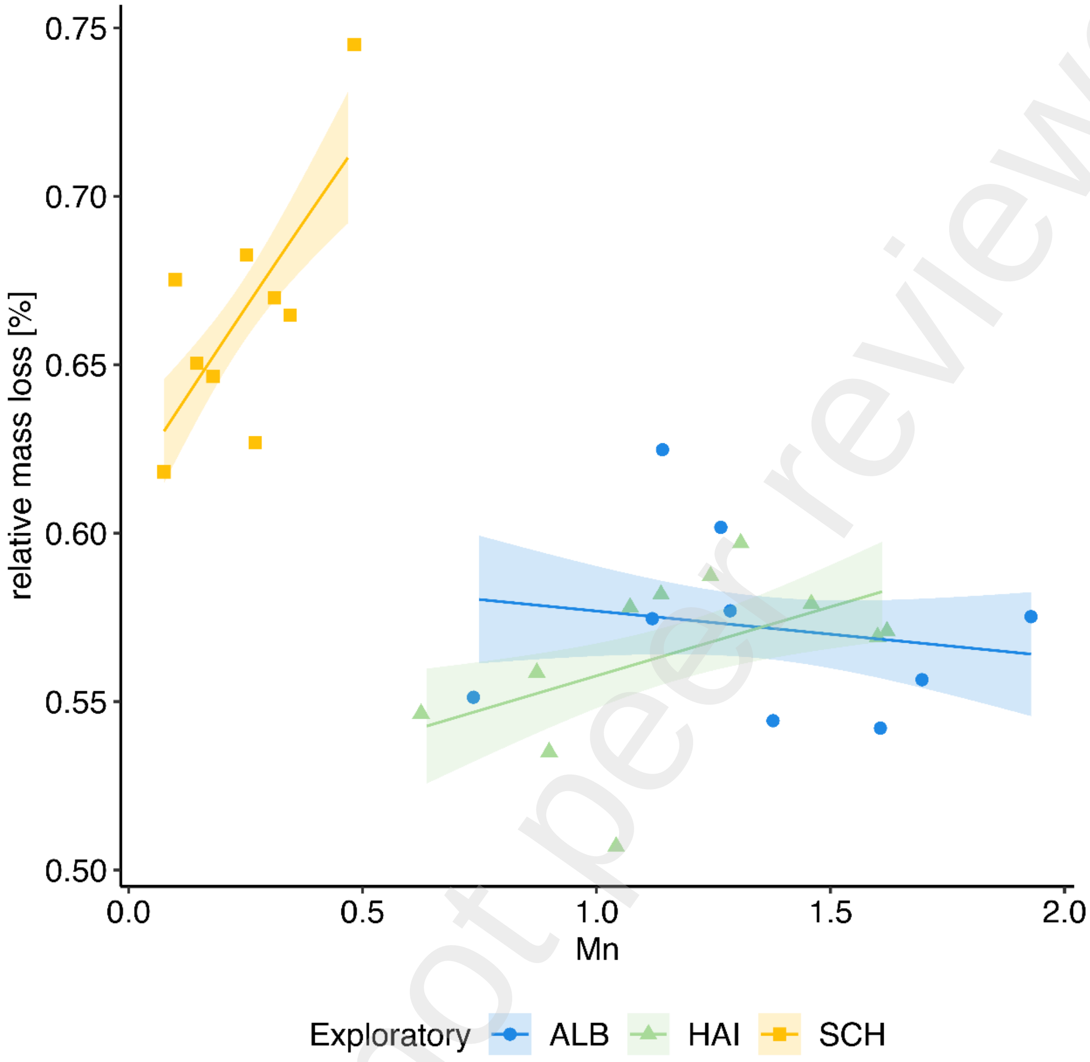


871

872

873

Figure 4



874

875

Supplement

Table S1: Exogenous factors (mean ± s.d.) for the three regions ALB, HAI and SCH used in the PCA. CWD (coarse woody debris) represents the deadwood stock without experimental logs. Transformation indicates that data were transformed to achieve normality of residuals.

Parameter	Description	ALB	HAI	SCH	Transformation	PCA
MAT	Mean annual air temperature at 10 cm [°C]	8.27 (0.32)	8.61 (0.41)	9.12 (0.29)	-	X
MAP	Mean annual precipitation [mm y^{-1}]	942 (34)	590 (18)	601 (44)	-	X
SWC	Volumetric soil water content at 10 cm depth [%]	34.6 (4.2)	29.7 (5.6)	13.9 (2.6)	-	X
Canopy	LiDAR-based canopy cover [%]	90.3 (6.3)	90.8 (8.7)	86.1 (13.2)	Box-Cox Lambda: 1.99	X
Conifer	Share of conifers in plots [%]	42.7 (42.2)	16.1 (36.1)	39.5 (47.4)	Arcus-sinus	X
CWD	CWD stock [m^3 ha^{-1}]	31.0 (17.2)	20.4 (11.9)	23.1 (10.3)	-	X
C:N	Ratio of soil organic C to total soil N	15.3 (1.0)	15.2 (1.0)	21.6 (2.6)	Box-Cox Lambda: -0.99	X
Ergosterol	Soil ergosterol concentration [µg g^{-1}]	19.8 (10.9)	8.5 (8.4)	6.3 (1.7)	Box-Cox Lambda: -0.14	X
P	Soil P concentration [mg g^{-1}]	0.11 (0.05)	0.05 (0.02)	0.03 (0.01)	Box-Cox Lambda: 0.05	X
Fe	Soil Fe concentration [mg g^{-1}]	37.0 (6.5)	24.8 (6.2)	5.4 (1.7)	Box-Cox Lambda: 0.64	X
Mn	Soil Mn concentration [mg g^{-1}]	1.35 (0.35)	1.17 (0.31)	0.24 (0.13)	-	X
pH	Soil H^+ concentration [mol l^{-1}]	2×10^{-5} (4×10^{-5})	10^{-5} (10^{-5})	10^{-4} (5×10^{-5})	Box-Cox Lambda: 0.18	X

Table S2: ANOVA results of mass loss by tree species and region.

Term	Sumsq	meansq	NumDF	Statistic	p
Tree species	19.65	1.64	12	121.69	<0.001
Region	0.96	0.48	2	35.55	<0.001
Interaction					
Tree species x Region	1.41	0.06	24	4.36	<0.001

Table S3: Correlation and contribution of exogenous factors with first two axes of the PCA.

Variable	Correlation		Contribution (%)	
	Dim. 1	Dim. 2	Dim. 1	Dim. 2
MAT	-0.77	-0.14	9.77	0.87
MAP	0.71	0.42	8.20	7.81
SWC	0.88	-0.23	12.82	2.30
Canopy	0.16	-0.64	0.45	18.23
Conifer	-0.03	0.86	0.01	32.70
Fe	0.96	0.05	15.30	0.10
Mn	0.89	-0.22	13.07	2.11
pH	-0.82	0.29	11.04	3.82
CWD	0.23	0.37	0.86	6.11
C:N	-0.80	0.45	10.58	8.90
P	0.86	0.32	12.14	4.56
Ergosterol	0.59	0.53	5.76	12.49

Table S4: Statistic results of mass loss by principal components 1 and 2.

Term	Coefficient	SE	NumDF	t value	p
PC 1	-0.016	0.003	1	-5.525	<0.001
PC 2	0.009	0.005	1	2.081	0.047

Table S5: p values of linear models of arcsine transformed mass loss of 13 tree species and principal components 1 and 2.

Tree species	PC 1	PC 2
Acer	0.82	0.47
Betula	**0.03**	0.12
Carpinus	**<0.001**	0.35
Fagus	**0.03**	**0.02**
Fraxinus	**0.03**	**0.03**
Populus	0.61	0.38
Prunus	**0.001**	0.07
Quercus	0.08	0.35
Tilia	**<0.001**	0.80
Larix	0.52	**0.002**
Picea	**<0.001**	0.22
Pinus	**<0.001**	0.80
Pseudotsuga	**<0.001**	0.07