Ecosystems (2021) 24: 955–967
https://doi.org/10.1007/s10021-020-00562-z

ECOSYSTEMS

Changes in Chemical and Microbial Soil Parameters Following 8 Years of Deadwood Decay: An Experiment with Logs of 13 Tree Species in 30 Forests

Cynthia Minnich,[1] Derek Peršoh,[2] Christian Poll,[3] and Werner Borken[1]*

[1]*Department of Soil Ecology, University of Bayreuth, Bayreuth, Germany;* [2]*Department of Geobotany, Ruhr-Universität Bochum, Bochum, Germany;* [3]*Soil Biology Department, Institute of Soil Science and Land Evaluation, University of Hohenheim, Stuttgart, Germany*

Abstract

Deadwood may alter the chemical and microbial properties of forest soils. However, it is unclear how downed deadwood (logs) of different tree species affect nutrients, microbial activity and biomass in different forest soils and regions. We investigated the effect of logs on underlying soils after 8 years of decomposition in an experiment consisting of 13 log tree species replicated at 30 forest sites across three German regions with distinct climate and geology. Soils beneath logs were compared to soils without recognizable influence of deadwood (control) 8 m away. Carbon, nitrogen, phosphorous and calcium concentrations increased by 5–18% in the soils under logs, whereas soil potassium, magnesium, iron, manganese and aluminum were not or slightly negatively affected by logs. Soils beneath logs exhibited 33%, 18% and 54% higher carbon mineralization, microbial biomass and ergosterol (component of fungal cell membranes) contents, respectively. Despite major differences in decay rates, the effect on soil properties hardly differed among the 13 log tree species. The effect of logs on microbial and chemical soil parameters increased with decreasing concentration of carbon, nitrogen, phosphorous and pH in the prevailing forest soils. Consequently, the strongest effects of logs on soil parameters occurred in plots with low soil nutrient contents and low soil pH. Our results suggest that logs of all tree species primarily increase the microbial activity and nutrient contents of acidic and nutrient-poor soils.

Key words: Deadwood; Coarse woody debris; Tree species; Soil nutrients; Microbial biomass; Biodiversity exploratories; Forest soil.

Received 27 August 2019; accepted 28 August 2020;
published online 21 September 2020

Electronic supplementary material: The online version of this article (https://doi.org/10.1007/s10021-020-00562-z) contains supplementary material, which is available to authorized users.

Author Contributions CM performed the research and analyzed the data; CP provided ergosterol data; CM and WB wrote the paper with contributions from all authors; WB and DP designed the study; all authors revised the paper critically and gave final approval for publication.

**Corresponding author; e-mail:* werner.borken@uni-bayreuth.de

Highlights

- Logs increased microbial activity and biomass in underlying forest soils.
- Effects of logs on soil traits was strongest in

nutrient-poor soils.
- Log (tree) species had little influence on chemical and microbial soil traits.

Introduction

Deadwood is an important habitat and substrate for many organisms (Harmon and others 1986). The ecological functions of deadwood are linked to its size, stock, chemical composition, decomposability and exposure in forest ecosystems (Stokland and others 2012). Downed deadwood (logs) has direct contact to the soil surface and therefore the potential to alter the traits of underlying soil during the decomposition process. The annual input of carbon (C) by a decomposing log is mostly several orders of magnitude greater per unit soil area than the annual C input by aboveground litterfall. As deadwood is a carbon-rich substrate, logs represent long-term hot spots for deadwood-decaying microorganisms (Benbow and others 2019). Soil microorganisms may also benefit from log decay. Microbial biomass and respiration increased in an organic layer under decomposing deadwood (Peršoh and Borken 2017). Plausible mechanisms for increasing microbial activity in soils are leaching of dissolved organic matter from logs (Bantle and others 2014a; Kahl and others 2012) and ingrowth of fungal hyphae from deadwood into soil (Philpott and others 2014). Otherwise, nutrient translocation by fungal hyphae from soils into logs or infiltration of throughfall can contribute to nutrient supply of deadwood-decaying microorganisms (Philpott and others 2014; Rinne and others 2017; Wells and Boddy 1995). At later decay stages, deadwood can be regarded as a nutrient source for underlying forest soils (Goldin and Hutchinson 2013).

Interactions between logs and forest soils and the respective implications on soil properties have hardly been investigated. The few existing studies revealed different effects on chemical and microbial soil properties. Deadwood may ameliorate underlying soils (Bade and others 2015; Gonzalez-Polo and others 2013; Stutz and others 2017), but it can also trigger decreasing gross nitrogen (N) mineralization, fine root biomass and soil pH by leaching of acidic extractives (Goldin and Hutchinson 2013; Spears and others 2003; Spears and Lajtha 2004; Zalamea and others 2016). Differences in log species, decay stage, climate and soil properties could be responsible for the different findings in these different studies.

The influence of deadwood on soil properties can vary among tree species (Błońska and others 2017; Peršoh and Borken 2017; Piaszczyk and others 2019). Coniferous, diffuse-porous and ring-porous deciduous tree species exhibit great differences in wood structure, ratio of heartwood to sapwood, nutrient concentration, tannin content, lignin structure and extractives. The decomposition process depends on deadwood-decaying fungal communities including key species which are selective for certain tree species or wood traits (Baber and others 2016; Baldrian and others 2016; Leonhardt and others 2019). Logs of conifers and ring-porous deciduous trees decay slower than those of diffuse-porous deciduous trees (Arnstadt and others 2016; Kahl and others 2017). The input of carbon and nutrients into underlying soils could differ among log species and decay stages, which would likely affect growth of soil fungi.

The effect of logs on underlying forest soils may differ among soil types or soil properties. Acidic forest soils increased in base saturation, microbial biomass and microbial activity in the presence of beech deadwood (Kappes and others (2007). Wambsganss and others (2017) reported that soil pH can control the influence of logs on soil properties in the early stage of decay. Soils with low pH and low nutrient availability seem to respond more strongly to logs than nutrient-rich soils with high pH. Recalcitrant deadwood such as Douglas fir (*Pseudotsuga menziesii*), however, decreased nutrient concentrations and pH of the underlying soil by input of fulvic acids (Klinka and others 1995).

In this study, we assessed the impact of logs on underlying soil in a long-term experiment, where logs of 13 temperate tree species were exposed in 30 forests at three regions in Germany with distinct climate, geology and soils. We aimed to evaluate how chemical and microbial soil parameters responded to logs after 8 years of decay. Microbial soil parameters were analyzed for three log species (*Fagus sylvatica*, *Quercus* sp., *Picea abies*) in three regions and for 13 log species in one region. We hypothesized that (1) logs would increase carbon mineralization, microbial biomass, organic C and nutrient concentrations, in underlying soils, (2) the relative effects of logs on microbial and chemical parameters would differ among log species and (3) the relative effect of logs on underlying soils would be stronger at plots or in regions with nutrient-poor and acidic soils.

Materials and Methods

Experimental Design and Sampling

This study was part of the ''Biodiversity Exploratories'' in which ecosystem processes and biodiversity were investigated to survey long-term effects on larger scales in three different regions in Germany (Kahl and others 2017): (1) the UNESCO Biosphere Reserve Schwäbische Alb (ALB), located in the low mountain ranges of southwest Germany; (2) the National Park Hainich-Dün (HAI) and its surrounding extents, situated in the hilly landscape of Central Germany and (3) the UNESCO Biosphere Reserve Schorfheide-Chorin (SCH), a young glacially formed lowland in northeast Germany (Fischer and others 2010) (Table 1). *Fagus sylvatica* and *Picea abies* were the dominating tree species in the forests at ALB and HAI, while SCH included *Fagus sylvatica* and *Pinus sylvestris* forests. The BELongDead (Biodiversity Exploratories Long term Deadwood) experiment was established at 30 forest plots of the Biodiversity Exploratories. Stems from 13 tree species, each at least 30 cm diameter and 4 m length, were harvested in the federal state of Thuringia (Germany) in the winter of 2008/2009. Logs of all 13 tree species were arranged in parallel in a random order on the forest floor at each of the 30 forest plots (390 logs in total) in the spring of 2009. Plots had an area of one hectare and were unevenly distributed within the exploratories with distances between 1 and 50 km. The inner spacing between individual logs was $\sim$ 1 m and the distance to living trees varied within and among the plots. Log species include four gymnosperms: *Larix decidua*, *Picea abies*, *Pinus sylvestris* and *Pseudotsuga menziesii*, seven angiosperms with a diffuse-porous wood structure: *Acer* sp. (*A. pseudoplatanus*, *A. platanoides*, *A. campestre*), *Betula pendula*, *Carpinus betulus*, *Fagus sylvatica*, *Populus* sp. (*P. tremula* and hybrids), *Prunus avium*, and *Tilia* sp. (*T. cordata*, *T. platyphyllos*) and two angiosperms with a ring-porous wood structure: *Fraxinus excelsior* and *Quercus* sp. (*Q. robur*, *Q. petraea*). Supplemental data on forest type, stand history, stand age and soil type of individual plots are given in Table S1. For further information about the BELongDead experiment, see Kahl and others (2017).

For the present study, soil samples were collected at two positions directly under each log using a sampler of 15 cm in length, 5 cm in width and 7 cm in depth in June 2017. Control soils without visible influence of deadwood were taken at three positions 8 m away from the edge of the log subplots. Two control positions were located laterally to the logs and one position at the front of the logs. The Oi and Oe horizons were removed before sampling of control soils as those were not available under logs. Soil samples were pooled to one sample per log of each tree species and to one control sample per plot. After removal of roots, stones and leaves, soil samples were mixed and then passed through a 2-mm sieve. For microbial analysis, subsamples were adjusted to 60% of the maximum water-holding capacity and stored at a temperature of 5 °C. Further subsamples were dried at 60 °C for chemical analysis.

Table 1. Environmental Characteristics and Soil Properties (0–10 cm) of the Three Study Regions

	Schwäbische Alb ALB	Hainich HAI	Schorfheide-Chorin SCH
Altitude a.s.l. (m)[a]	460–860	285–550	3–140
MAT (°C)[a]	6.0–7.0	6.5–8.0	8.0–8.5
MAP (mm)[a]	700–1000	500–800	500–600
Geology[a]	Calcareous bedrock (Jurassic)	Loess deposits on limestone	Young glacial deposits
Soil type (WRB)[a]	Cambisol, leptosol	Luvisol, stagnosol	Albeluvisol, cambisol
Sand (%)[b]	2.6–10.9 (6.1)	2.8–7.7 (4.4)	74.3–98.1 (89.1)
Silt (%)[b]	29.6 -66.8 (49.1)	50.9–79.0 (66.0)	1.8–23.7 (9.3)
Clay (%)[b]	31.8–67.0 (44.8)	16.4–45.7 (29.7)	0.1–2.5 (1.6)
Bulk density (g cm^{-3})	0.61–0.94 (0.75)	0.74–1.15 (0.92)	1.03–1.22 (1.15)
TOC (%)	2.9–10.6 (5.1)	1.7–11.7 (3.4)	1.4–12.1 (2.6)
N (%)	0.2–0.8 (0.4)	0.1–0.7 (0.2)	0.1–0.5 (0.1)
P (mg g^{-1})	0.7–2.6 (1.1)	0.3–1.3 (0.6)	0.1–0.7 (0.3)
Molar C:N ratio	14.0–16.9 (15.3)	14.2–20.0 (15.6)	18.0–25.5 (21.6)
Molar N:P ratio	5.7–10.2 (7.9)	7.2–17.0 (10.3)	5.4–27.4 (14.1)

Values represent minimum to maximum, means are given in parentheses.
[a]Fischer and others (2010); [b]Kaiser and others (2016).

Chemical Parameters

Soil pH was measured in the soil–water slurry (ratio of 1:2.5) after 1 h equilibration. For the statistical analysis, soil pH values were transformed to proton concentrations (mol H_3O^+ l^{-1}). Total organic carbon (TOC) and total nitrogen (N) were measured in milled samples with a CN analyzer (Vario Max CN, Elementar, Germany). If carbonates were present as indicated by pH (H_2O) > 6.3, the portions of inorganic carbon (TIC) were determined according to Horváth and others (2005). Briefly, 0.5 g of dry soil was filled in 12 ml glass vials, which were closed airtight with a septum. Carbonates were removed by injection of 1 ml 3.5 M HCl into the vials. Room temperature, air pressure and gas pressure in the vials were measured after 2 h. Proportions of TIC were calculated by the ideal gas law using the increase in gas pressure by CO_2 production in the vials, the gas volume of vials, the universal gas constant R and the room temperature.

Element concentrations of P, K, Ca, Mg, Fe, Mn and Al were determined by aqua regia (37% HCl and 65% HNO_3 in a volume ratio of 3:1) extraction in a microwave (Mars 5, CEM, Germany). For the digestion, 8 ml of aqua regia was added to 200 mg dry soil. Extracts were then transferred to 50-ml volumetric flasks, diluted with deionized water and filtered through nylon filters (0.45 µm). Element concentrations in the extracts were determined using ICP-OES (Optima 3200 xl, Perkin Elmer, Germany) and AAS (SpectraA 220 Z, Varian, USA).

Microbial Parameters

Carbon mineralization, microbial biomass and fungal biomass were measured of all samples from the HAI plots. From the ALB and SCH plots, microbial parameters were only assessed for soils under logs of *Fagus sylvatica*, *Picea abies* and *Quercus* sp. and control.

Carbon mineralization of soils was determined in 120 ml glass vials at 20 °C during 3-day incubations. One day before incubation, samples were filled in glass vials and acclimated at a temperature of 20 °C. Then, vials were closed with septa and subsequently flushed with synthetic air for 3 min. CO_2 concentrations in the vials were measured at the beginning and end of the incubations using a gas chromatograph (8610C, SRI instruments, USA). Carbon mineralization rates (µg C g^{-1} dry soil h^{-1}) were calculated as the slope of the CO_2 concentration during the incubation time and corrected for air temperature and pressure.

Microbial carbon (Cmic) and nitrogen (Nmic) were assessed by chloroform fumigation-extraction method (CFE) by Brookes and others (1985) and Vance and others (1987). Extraction for microbial phosphorus (Pmic) was performed according to Bray and Kurtz (1945). Fresh and sieved subsamples were fumigated at room temperature in a desiccator under a chloroform atmosphere for 24 h. Fumigated and non-fumigated subsamples were both extracted with 0.5 M K_2SO_4 and shaken overhead for 45 min at 100 rev. min^{-1} in a soil solution ratio of 1:10 for Cmic and Nmic. Carbon and nitrogen concentrations in the extracts were measured with a CN analyzer (multi N/C 2100, Analytik Jena, Germany). For Pmic, fumigated and non-fumigated subsamples were extracted in Bray-1 solution (0.03 M NH_4F + 0.025 M HCl) in a soil solution ratio of 1:5 (Bray and Kurtz 1945). PO_4 concentrations in the extracts were determined calorimetrically by the molybdenum-blue method by Murphy and Riley (1962). Before addition of the molybdenum-blue reagent, 0.1 M boric acid was added to prevent interactions with fluoride ions and to obtained color formation. After 20 min, PO_4 concentrations were measured with a microplate reader (M200 pro, Tecan, Switzerland). For calculations of microbial C, N, and P, differences between fumigated and non-fumigated were calculated and corrected by a factor of 0.45 (Cmic, Nmic) or 0.40 (Pmic) to account for non-extractable microbial C, N, and P (Jenkinson and others 2004).

Ergosterol content was estimated as a proxy for the fungal biomass by using the method of Djajakirana and others (1996) with modification of Enowashu and others (2009). One gram of fresh soil was extracted in 25 ml ethanol and shaken horizontally for 30 min at 200 rev. min^{-1} prior to centrifugation at 2888×*g* for 12 min. Subsequently, an aliquot of 20 ml was evaporated in a rotary evaporator at 47 °C under vacuum atmosphere. The dry extract was dissolved in 2 ml methanol (HPLC grade) in an ultrasonic bath and filtered through a syringe filter (cellulose-acetate, 0.45 µm) into brown glass vials. Quantitative analysis was performed by injection of 20 µl into a HPLC autosampler (Beckmann Coulter, System Gold 125 Solvent Module), settings were: main column 150 × 3 mm Spherisorb octadecyl silan ODS II, mobile phase 100% methanol, flow rate 0.5 ml h^{-1}, and detection with an UV detector (Beckmann Coulter, System Gold 166) at a wavelength of 282 nm. Ergosterol is a proxy for the fungal biomass; however, its abundance in the fungal membrane (Peacock and Goosey 1989)

varies among fungus species and their physiological condition (Ruzicka and others 2000; Baldrian and others 2013).

Statistical Analysis

The overall effect of logs on microbial and chemical parameters in underlying soils (hypothesis 1) was tested with linear mixed-effects models (lme) with treatment as fixed effect and plot as random effect using absolute values of soil parameters from controls and treatments. Response variables y were differently transformed ($y^{1/3}$, $y^{1/4}$, Tukey's Ladder of powers, or as last resort rank transformation) if required to fulfill normality of the model and homogeneity of variance across groups. Selection of the best transformation was done by using the Akaike information criterion (AIC). For lme we used R version 3.4.0 (R Core team 2015) in combination with the lme4 package (Bates and others 2015), the restricted maximum likelihood (REML) approach and the ''Nelder Mead'' optimizer followed by Tukey's post hoc test.

We performed redundancy analyses (RDA) using CANOCO 5 (ter Braak and Smilauer 2012) to explore the response ratios of soil chemical and microbial parameters (response variables) in dependency from log species (hypothesis 2), plots and region (nested explanatory variables). Response ratios of soil parameters were calculated as natural logarithm of the ratio of treatment to control. Since soil microbial parameters were not determined under all logs at ALB and SCH, we executed three RDAs: (1) 13 log species from HAI (9 plots) with all soil parameters, (2) three log species (*Fagus*, *Picea*, and *Quercus*) from ALB, HAI and SCH (30 plots) with all soil parameters and (3) 13 log species from ALB, HAI and SCH (30 plots) with chemical soil parameters. Response ratios were centered and significance was tested using a permutation test (499 permutations) for the canonical axes.

A matrix coding the dissimilarity among plots (hypothesis 3) was calculated using Primer7 version 7.0.11 (Clarke and Gorley 2015), based on average distance according to the parameters pH (H_2O), TOC, N and P content of the control soils (n = 30). The matrix was visualized via nMDS ordination. Pearson correlation of the underlying parameters (i.e., pH (H_2O), TOC, TN and P content of the control samples) with the MDS axis 1 (x-axis) and 2 (y-axis) were superimposed on the graph as well as correlations with response ratios of all soil parameters to treatment by log exposure. Correlations $< r = 0.3$ were excluded from graphical visualization.

Results

Total Effects of Logs on Soil Parameters

Logs altered 13 of 19 microbial or chemical soil parameters across the 30 plots (Table 2). Carbon mineralization, microbial biomass and ergosterol content increased by 13–54% in underlying soils. Ergosterol content exhibited the strongest increase of all parameters. The effect of logs was weaker when C mineralization and microbial biomass were related to TOC, N or P content of soils, indicating that the increases in microbial parameters were linked to some extent to higher contents of soil organic matter under logs. The rise in the ratios of C mineralization to TOC or microbial P to soil P indicates an increase in the microbial utilization of TOC and soil P resources, respectively.

Logs had different effects on individual soil chemical parameters (Table 2). Increases were found for TOC (18%), soil N (12%) and soil P (5%). The relatively small increase in soil P was accompanied by a strong increase in microbial P by 35%. An increase by 16% was found for soil Ca content, whereas K and Mg contents were not altered. Metal contents of Mn and Al did not vary with treatment, but Fe content was slightly lower under logs relative to controls (Table 2). Mean proton concentration slightly decreased from $10^{-4.36}$ to $10^{-4.42}$ mol l^{-1} indicating enhanced proton buffering or less dissociated organic acids in soils beneath logs.

Log Species

The first two axes of the redundancy analysis explained, respectively, 24.0% ($p < 0.002$) and 13.0% ($p < 0.002$) of the variation in the response ratios of microbial and chemical soil parameters by log species and plots at the HAI region (Figure 1). The RDA clustered 11 log species close to the center, indicating that these log species were relatively indifferent to the response ratios with particularly short distances among the four coniferous log species. Only logs of *Fraxinus* and *Carpinus* had greater distances to the center and tended to change soil Mn, Mg, K, Fe and Al contents (*Fraxinus*) or soil Ca content (*Carpinus*). However, plots scattered more strongly than log species and plots were occasionally associated with specific response ratios. Dissimilarities emerged in response ratios between the beech and spruce forests. The spruce forests (HEW 1–3, Table S1) were either positively

Table 2. Mean (± SE) Microbial and Chemical Soil Parameters of Controls and Treatments Grouped by Plot (n = 30)

Soil parameter	Control	Treatment	Log effect	z-value	Transformation	p value
C mineralization (μg C g^{-1} soil h^{-1})	0.64 (0.09)	0.85 (0.07)	0.09 (0.02)	4.71	y1/3	< **0.001**
Microbial C (mg kg^{-1})	742 (104)	876 (94)	21.8 (6.9)	3.18	Rank	**0.001**
Microbial N (mg kg^{-1})	149 (23)	168 (21)	0.12 (0.05)	2.32	y1/4	**0.020**
Microbial P (mg kg^{-1})	31.5 (4.4)	42.5 (3.6)	0.14 (0.03)	4.25	Tukey	< **0.001**
Ergosterol (μg g^{1})	11.8 (2.8)	18.2 (2.3)	0.05 (0.01)	4.90	Tukey	< **0.001**
C mineralization:TOC	2.35 (0.17)	2.83 (0.12)	34.8 (9.0)	3.88	Rank	< **0.001**
Microbial C:TOC	0.019 (0.001)	0.020 (0.001)	5.5 (9.1)	0.61	Rank	0.543
Microbial N:N	0.052 (0.004)	0.053 (0.003)	− 0.4 (7.8)	− 0.05	Rank	0.961
Microbial P:P	0.062 (0.009)	0.080 (0.008)	0.04 (0.01)	4.06	y1/4	< **0.001**
TOC (%)	3.66 (0.33)	4.31 (0.28)	52.5 (11.9)	4.42	Rank	< **0.001**
N (%)	0.26 (0.02)	0.29 (0.02)	39.9 (9.5)	4.21	Rank	< **0.001**
P (%)	0.064 (0.008)	0.067 (0.008)	10.8 (5.1)	2.10	Rank	**0.036**
K (mg g^{-1})	2.83 (0.42)	2.90 (0.41)	7.4 (5.6)	1.31	Rank	0.190
Ca (mg g^{-1})	3.87 (0.95)	4.47 (0.91)	25.2 (6.9)	3.63	Rank	< **0.001**
Mg (mg g^{-1})	3.63 (0.45)	3.45 (0.43)	− 2.1 (5.4)	− 0.39	Rank	0.695
Fe (mg g^{-1})	22.8 (2.5)	22.3 (2.5)	− 7.2 (3.4)	− 2.13	Rank	**0.033**
Mn (mg g^{-1})	0.95 (0.11)	0.94 (0.11)	− 3.9 (7.3)	− 0.53	Rank	0.598
Al (mg g^{-1})	26.0 (3.4)	25.8 (3.4)	− 5.4 (3.7)	− 1.46	Rank	0.144
a (H^+)	$10^{-4.36}$ ($10^{-5.0}$)	$10^{-4.42}$ ($10^{-5.1}$)	− 18.8 (9.2)	− 2.05	Rank	**0.041**

Estimates of fixed effects (log effect ± SE), z and p values resulted from linear effects models using transformed data of controls and treatments. Significant effects are shown in bold font.

associated with increasing proton concentration (HEW 3) or were hardly associated with response ratios of microbial parameters, Ca, TOC, N and P contents. In contrast, most beech forests showed either stronger response ratios of Mn, Mg, K, Fe and Al contents or of microbial parameters, Ca, TOC, N and P contents.

A similar pattern arose from the RDA with the log species *Fagus*, *Quercus*, *Picea* and respective response ratios from all 30 plots (Figure 2). Log species and region clustered close to the center whereas plots of specific regions did not cluster. The first two RDA axes together explained 45.8% (27.8% ($p < 0.002$) in axis1 and 18.0% ($p < 0.002$) in axis2) of the variance in response ratios. Microbial phosphorous (Pmic), TOC, ergosterol and N responded relatively strong and uniform to the three log species. Response ratios of Cmic, Nmic, Cmin were less strong and only weakly correlated with Pmic. The RDA also found that microbial parameters, TOC N, P and Ca responded differently to logs than proton concentration, Fe, Mn, Mg, Al, and K.

The RDA with 13 log species and 30 plots explained 38.4% (28.5% ($p < 0.002$) in axis1 and 9.9% ($p < 0.002$) in axis2) of the relative changes in soil chemical parameters (Figure 3). Response ratios of soil N, P and TOC were strongest in three pine (SEW 2, 3, 4) and two beech forests (SEW 7, 9) at SCH. Response ratios of Ca and K also were associated with three plots at SCH (SEW 2, 3, 9). Log species clustered close to the center and did not explain the variability of soil chemical response ratios. Response ratio of proton concentration, ordinated at axis1, had the strongest explanatory power and was not correlated with other soil parameters.

Soil Chemical Gradients

The nMDS analysis revealed clear differences among the plots at ALB and SCH according to soil pH and nutrient contents (TOC, N, P) in control soils and great variation for the plots at HAI (Figure 4). Soil nutrient contents (TOC, N, P) were strongly associated, whereas the link between soil nutrient contents and soil pH was weaker. Response ratios of all soil microbial parameters and some soil nutrients (TOC, N, P, Ca) were negatively correlated with soil nutrients/pH, indicating that the effect of logs on soils increased along a soil chemical gradient with decreasing nutrient contents (TOC, N, P) and pH. This resulted in increasing response ratios from ALB to HAI to SCH. The

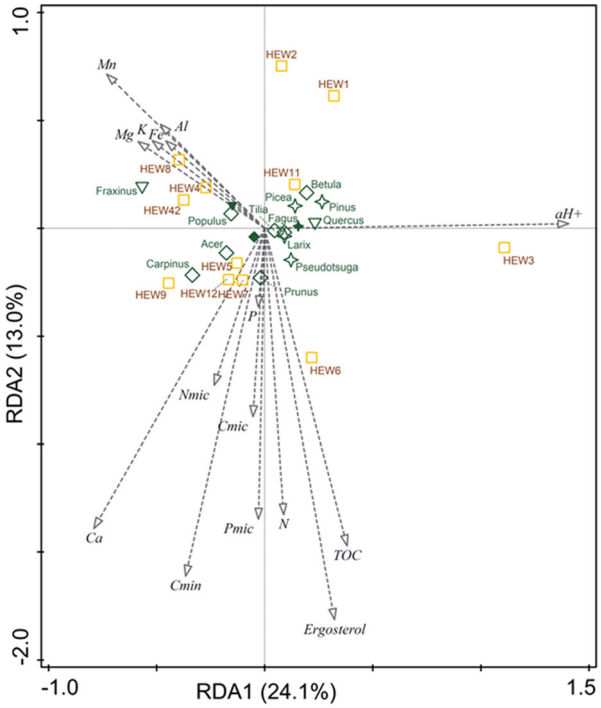

Figure 1. Redundancy analysis showing the dissimilarity of 13 log species and 12 plots at HAI and their influence on response ratios (dashed lines) of soil chemical and microbial parameters. Phyllogenetic assignment or wood structure of individual log species is indicated by different symbols: deciduous ring porous (triangle), deciduous diffuse porous (rhombus), coniferous (star).

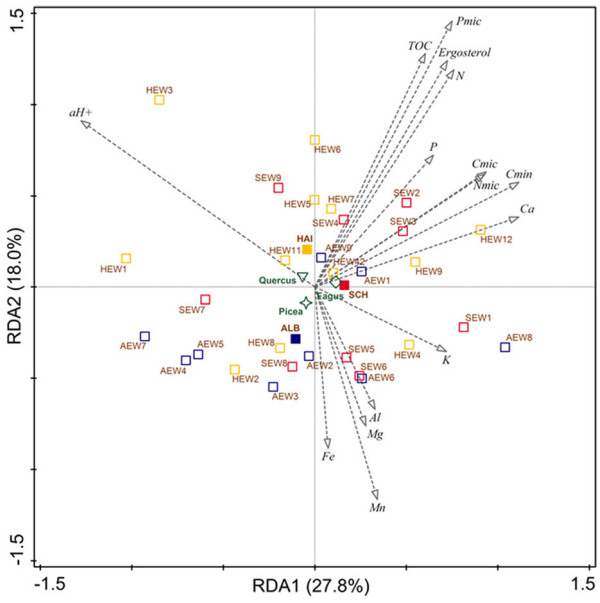

Figure 2. Redundancy analysis showing the dissimilarity of three log species (*Fagus, Picea, Quercus*), and 30 plots at ALB, HAI and SCH, and their influence on response ratios (dashed lines) of soil chemical and microbial parameters.

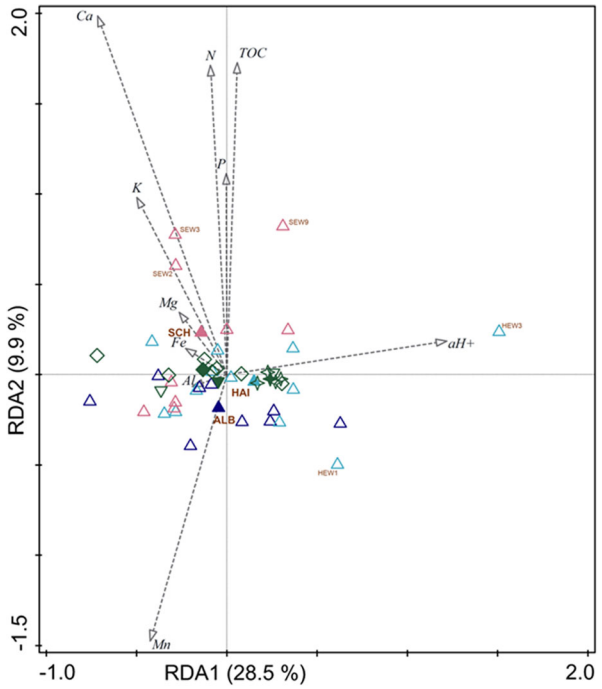

Figure 3. Redundancy analysis showing the dissimilarity of 13 log species and 30 plots at ALB, HAI and SCH, and their influence on response ratios (dashed lines) of soil chemical parameters. Phyllogenetic assignment or wood structure of individual log species is indicated by different symbols: deciduous ring porous (triangle), deciduous diffuse porous (rhombus), coniferous (star).

strongest correlation (indicated by length of arrow) with nMDS-1 was found for C mineralization (Pearson $r = -0.67$) followed by TOC ($r = -0.61$), N ($r = -0.58$), Ca ($r = -0.54$), ergosterol ($r = -0.45$) and microbial biomass C, N, P ($r = -0.37$ to -0.44). Response ratios of proton concentration ($r = -0.40$) and K ($r = -0.32$) were rather controlled by pH (that is, separated along axis NMDS-2). Both parameters decreased with increasing pH in control soils.

Discussion

Our results confirm the effect of logs on microbial and chemical parameters in underlying soils following 8 years of decomposition. We had further expected logs of 13 tree species to differ in the magnitude of their effect on soil parameters, based on differences in chemical composition and decomposability of deadwood. The overall effect of logs species on soil parameters was relatively consistent although highly variable for individual log species. Responses of soil parameters to logs partly differed among forest sites with predominantly stronger responses in nutrient-poor and acidic soils.

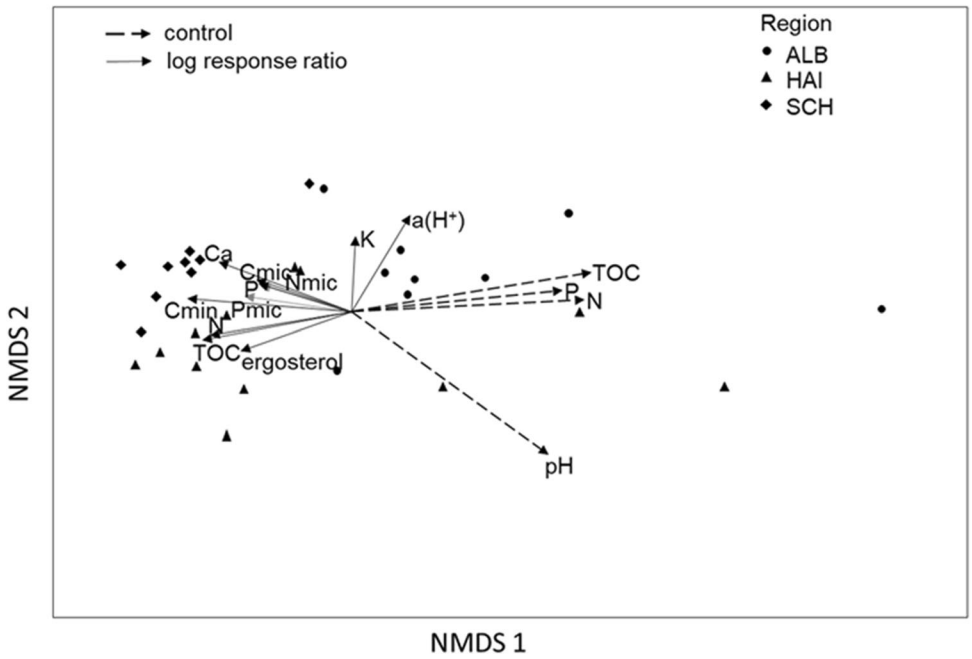

Figure 4. Dissimilarity among plots (n = 30) of three regions (ALB, HAI, SCH) based on average pH (H_2O), TOC, TN and P content of the control soils. Pearson correlation (indicated by length of solid lines) of soil pH (H_2O), TOC, TN and P content of the control samples with Response ratios of soil parameters (TOC, N, P, Ca, K, C mineralization, microbial biomass C, N, P and ergosterol) beneath logs.

Here, we explore possible explanations for the increase in microbial and chemical soil parameters, discuss the lack of log species effects and evaluate site-specific differences that could have led to different responses of soils to log exposure.

Absolute Log Effects

The results support our hypothesis that C mineralization, microbial biomass and TOC would be higher in soils under decaying logs than in soils where decaying wood was absent. The most striking change was the increase in ergosterol indicating that logs fostered, in particular, fungal growth in the underlying forest soils. We assume a taxonomically heterogeneous and site-specific shift of a subset of the soil fungal community under logs as no specific or new fungal taxa were identified (Peršoh, unpublished data).

Several mechanisms could explain why soil microbial parameters responded positively to decomposing logs. First, C mineralization and biomass were stimulated or primed by inputs of dissolved organic matter (DOM). Even small amounts of easily available compounds can activate soil microorganisms (Blagodatskaya and Kuzyakov 2008) and enhance the mineralization of soil organic matter, known as positive priming effect (Fontaine and others 2007). Logs release considerable amounts of DOM into soil by leaching (Bantle and others 2014a; Bantle and others 2014b; Hafner and others 2005; Kuehne and others 2008; Lajtha and others 2005), controlled by the amount of precipitation and the leachable DOM pool (Fravolini and others 2016; Shorohova and Kapitsa 2014). Soluble metabolites from the enzymatic decay of cellulose and hemicellulose represent an easily available and important fraction of the DOM pool (Lombardi and others 2013; Noll and others 2016). Second, incorporation of particulate wood fragments into soil can additionally increase the organic matter content (Harmon and others 1986). This mechanism becomes more relevant at advanced stages of log decay. Saproxylic invertebrates could enhance both leaching of DOM and input of deadwood fragments into soil by drilling holes and disposal of frass (Parisi and others 2018). A third mechanism is the ingrowth of fungal hyphae from logs into soil. Some deadwood-decaying species like *Armillaria* sp. form large mycelial cords to exploit new resources and to take up nutrients from soils (Lamour and others 2007; Oliveira Longa and others 2018). All three mechanisms could have contributed to the increases in microbial parameters and TOC content in log covered soils. Elevated TOC concentrations, enzymatic activities, microbial growth and respiration in soils under logs have

been reported by other studies (Gonzalez-Polo and others 2013; Spears and others 2003; Piaszczyk and others 2019). The effect of logs on soil microbial parameters seems to be related to the decay stage of logs. Błońska and others (2017) found higher β-glucosidase and dehydrogenase activities in soils at advanced decay stages than at early decay stages of logs. *In-situ* enzyme activities, C mineralization and microbial biomass in soils can differ from laboratory assays under controlled temperature and moisture conditions. Hence, our laboratory assays provide standardized ex situ differences in microbial parameters between controls and treatments.

We further hypothesized increasing nutrient concentrations, but only N, P and Ca concentrations were higher in soils under logs. Although nutrient concentrations are small in logs, the input of solutes, wood fragments and fungal hyphae by the three mechanisms (see above) can explain at least partially those nutrient increases. Initial N concentrations of all logs species were small varying between 0.3 and 1.9 g kg^{-1} (Bantle and others 2014b). However, despite small N concentrations, logs acted as net N source mainly by leaching of dissolved organic N (Bantle and others 2014b). Biological fixation of dinitrogen by diazotrophic archaea or bacteria seems to be a widespread process to overcome N deficiency in deadwood (Mäkipää and others 2018; Rinne and others 2017). Elevated N inputs by atmospheric deposition of reactive N across German forests (Borken and Matzner 2004) likely facilitated the net release of N from logs.

Logs comprise relatively small amounts of P and Ca even though the concentrations in bark are several times greater than in sapwood or heartwood (Schowalter and others 1998). Therefore, bark could be a source of nutrients transferred into soil by percolating rainwater or by incorporation of bark fragments. Incorporation of sapwood or heartwood fragments, however, would diminish the P and Ca concentrations. Another explanation for increasing soil P and Ca concentrations under logs could be redistribution from deeper soil layers or surrounding soil by fungal hyphae. In particular, microbial P increased under logs by 35% whereas the increase in total soil P content was small. Transfer of P by hyphae of wood decaying fungi from soil toward deadwood was proved by application of P isotopes (Boddy and Watkinson 1995; Hughes and Boddy 1994; Wells and Boddy 1995). Fungal transfer would also explain accumulation of Ca beneath logs even though experimental evidence is required to support this assumption.

Logs did not affect total soil contents of K, Mg, Mn and Al because of relatively high background values in untreated soils. We attribute the small and ecological irrelevant change in Fe to the dilution by the input of organic matter. The average increase in TOC was 0.65% (Table 2) which is equivalent to an increase in organic matter of about 1.3%. We assume that the former forest floor was incorporated in the mineral soils and that this input affected the element concentration in soils beneath logs compared to controls. However, this phenomenon is apparently restricted to coniferous forests with relatively thick forest floors. In the beech forests, the influence of logs on soil traits was possibly underestimated because forest floors consisted mainly of thin Oi and Oe horizons. While soils of control plots received regular litter input, this source was excluded in soils under logs.

Log Species

Contrary to our hypothesis, the species identity of decaying logs had little effect on underlying soil properties. We expected differences among individual log species because of differences in nutrient content, wood chemistry and decay rate. Initial amounts of nutrients such as N, P, Ca, K and Mg differed by up to 8–10 times among the 13 log species (Kahl and others 2017). The changes in soil chemical parameters, however, were similar beneath the 13 log species and highly variable for individual log species after 8 years of decay. We can only speculate that the effect of log species on soil parameters will increase with progressive decay of logs. At the final stage of wood decay, a large portion of wood nutrients could potentially accumulate in underlying soils. For example, the total possible average increase in soil Ca concentration would be about 140% for *Acer* logs and 14% for *Pseudotsuga* logs, considering the mean Ca concentration of control soils (Table 2) and the initial Ca concentrations of respective log species (Kahl and others 2017). The observed mean increase in soil Ca concentration by 16% under all log species (Table 2) suggests that a great portion of Ca and other nutrients remain in the logs for a long time. Immobilization of nutrients in fungal hyphae and biomass of other log inhabiting organisms would slow down the release of nutrients from logs to soils. However, log species with low nutrient contents and slow decay rates have little potential to increase nutrient concentration especially of nutrient-rich soils.

In contrast to nutrients, logs of all tree species represent large C pools. Similar increases in soil

TOC suggest that remarkable C input by DOC leaching, incorporation of deadwood fragments or fungal translocation takes place under logs of distinct tree species. Homogenized soil and uniform temperature and moisture conditions perhaps are needed to identify different effects of various log species on soil parameters. Indeed, in a laboratory incubation study, microbial activity and biomass of a homogenized organic horizon increased more strongly in the presence of fast-decaying than of slow-decaying deadwood (Peršoh and Borken 2017).

Soil Chemical Gradients

Our results showed that the relative effect of logs on underlying soils increased along a soil chemical gradient from nutrient-rich to nutrient-poor, acidic soils. The increase in microbial and chemical soil parameter was most noticeable in soils at SCH with relatively low clay, TOC, N, P contents and low pH (Table 1 and S1). Additionally, high soil C/N and N/P ratios indicate low quality and decomposability of soil organic matter at SCH. Similar responses were observed for few plots at ALB and HAI with low nutrient concentrations, suggesting that the relevance of logs for the soil status is greater in forests with nutrient-poor soils. This agrees with the study of Stutz and others (2017) reporting a similar effect on soil pH and soil organic matter by logs of *Abies alba*. This finding, however, was not confirmed for logs of *Fagus sylvatica*. An inconsistent pattern was also found in the study by Wambsganss and others (2017), where the free light fraction of soil organic matter increased by 57% through deadwood in silicate soils with low pH, but decreased by 23% in calcareous soils with high pH. Our study does not support a negative effect of logs on TOC in calcareous soils, although the effect was smaller in the few soils with pH above 6 (Table S1). Kappes and others (2007) stated that logs ameliorate acidic forest soils, verified through higher pH, Ca^{2+}, Mg^{2+} and microbial biomass under decomposing logs. Our results suggest that the soil ameliorating effect of logs is limited to microbial parameters, TOC, N, P, Ca and pH. As discussed above, differences among the plots could grow toward the final decay stage when log residues are increasingly incorporated into soils.

Other Potential Factors and Ecosystem Relevance

A large part of the variability in response ratios of soil parameters was not explained by log species and soil chemical gradients or plots. Particularly, the similarity of the responses under different log species raises the question if other factors have more explanatory power. We did not study the changes in bulk density under logs, but it can be assumed that soils were compacted by logs. Undisturbed top soils at the study sites had bulk densities of 0.61–1.22 g cm^{-3} (Table 1) and were prone to compaction by logs. Associated changes in water availability and oxygen regime could have altered C mineralization, microbial biomass and soil chemical parameters. These indirect effects by soil compaction could have offset the influence of different log traits on soil parameters. Soil temperature and moisture records in controls and treatments would show how logs affect the microclimatic conditions and thereby microbial process rates in underlying soils.

The direct implications of soil microbial and chemical changes by logs for functioning of forest ecosystems are small considering the covered soil surface by logs. However, interactions between soils and logs could be crucial for log decomposition and for the community of organisms that live in logs. As discussed above, fungal hyphae can take up nutrients from soils and reduce nutrient deficiencies in wood (for example, Boddy and Watkinson 1995). More research is required to also explore the transfer of specific micronutrients from soils to logs. The interface between decomposing logs and underlying soils represents a continuum of limited to extreme gradient in nutrients and C availability. The resulting interactions would be compromised by removal of logs in addition to the already well-known reduction in structural diversity of forest ecosystems (Storch and others 2018).

Conclusions

Logs increase the concentration of many nutrients, pH, C mineralization and microbial biomass in underlying forest soils. The average increase in TOC from 3.66 to 4.31% within 8 years is many times higher than the typical increase in TOC by non-deadwood litter in temperate forest soils. Whether the increase in TOC and other nutrients is transient or consistent over many decades, is unclear. Surprisingly, the identity of log tree species had almost no effect on soil parameters, but the presence of any log species did influence soil parameters. With progressing decay of logs, the effect of log tree species on soils could emerge, as decay rates and composition of wood constituents differ among log species. The relative effect of logs on microbial and chemical soil parameters relies on the prevailing

soil traits. Acidic, nutrient-poor soils respond more strongly to logs than nutrient-rich forest soils. Integration of logs into forest management would increase the microbial, chemical and structural diversity of forest soils.

ACKNOWLEDGEMENTS

We thank Uwe Hell, Christopher Sadlowski and Karin Söllner for technical assistance and the Central Analytical Department of BayCEER for supporting chemical analyses. We thank the managers of the three Exploratories, Kirsten Reichel-Jung, Iris Steitz, Sandra Weithmann, Katrin Lorenzen, Juliane Vogt, Miriam Teuscher, and all former managers for their work in maintaining the plot and project infrastructure; Christiane Fischer 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. The work has been funded by the DFG Priority Program 1374 ''Infrastructure-Biodiversity-Exploratories'' (BO1741/11-1). Field work permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg.

DATA ACCESSIBILITY

The data will become publicly available at https://www.bexis.uni-jena.de/PublicData/PublicData.aspx under ID 25726 (soil chemical parameters) and ID 25727 (soil microbial parameters) according to the Rules of Procedure of the German Science Foundation (DFG) funded Biodiversity Exploratories.

Compliance with Ethical Standard

Conflict of interest The authors declare that they have no conflict of interest.

REFERENCES

Arnstadt T, Hoppe B, Kahl T, Kellner H, Krüger D, Bauhus J, Hofrichter M. 2016. Dynamics of fungal community composition, decomposition and resulting deadwood properties in logs of *Fagus sylvatica*, *Picea abies* and *Pinus sylvestris*. For Ecol Manag 382:129–42.

Baber K, Otto P, Kahl T, Gossner MM, Wirth C, Gminder A, Bässler C. 2016. Disentangling the effects of forest-stand type and dead-wood origin of the early successional stage on the diversity of wood-inhabiting fungi. For Ecol Manag 377:161–9.

Bade C, Jacob M, Leuschner C, Hauck M. 2015. Chemical properties of decaying wood in an old-growth spruce forest and effects on soil chemistry. Biogeochemistry 122:1–13.

Baldrian P, Větrovský T, Cajthaml T, Dobiášová P, Petránková M, Šnajdr J, Eichlerová I. 2013. Estimation of fungal biomass in forest litter and soil. Fungal Ecol 6:1–11.

Baldrian P, Zrůstová P, Tláskal V, Davidová A, Merhautová V, Vrška T. 2016. Fungi associated with decomposing deadwood in a natural beech-dominated forest. Fungal Ecol 23:109–22.

Bantle A, Borken W, Ellerbrock RH, Schulze ED, Weisser WW, Matzner E. 2014a. Quantity and quality of dissolved organic carbon released from coarse woody debris of different tree species in the early phase of decomposition. For Ecol Manag 329:287–94.

Bantle A, Borken W, Matzner E. 2014b. Dissolved nitrogen release from coarse woody debris of different tree species in the early phase of decomposition. For Ecol Manag 334:277–83.

Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48. https://doi.org/10.18637/jss.v067.i01.

Benbow ME, Barton PS, Ulyshen MD, Beasley JC, DeVault TL, Strickland MS, Tomberlin JK, Jordan HR, Pechal JL. 2019. Necrobiome framework for bridging decomposition ecology of autotrophically and heterotrophically derived organic matter. Ecol Monogr 89:e01331.

Blagodatskaya E, Kuzyakov Y. 2008. Mechanisms of real and apparent priming effects and their dependence on soil microbial biomass and community structure: critical review. Biol Fert Soils 45:115–31.

Błońska E, Kacprzyk M, Spólnik A. 2017. Effect of deadwood of different tree species in various stages of decomposition on biochemical soil properties and carbon storage. Ecol Res 32:193–203.

Boddy L, Watkinson SC. 1995. Wood decomposition, higher fungi, and their role in nutrient redistribution. Can J Bot 73:1377–83.

Borken W, Matzner E. 2004. Nitrate leaching in forest soils: an analysis of long-term monitoring sites in Germany. J Plant Nutr Soil Sci 167:277–83.

Bray RH, Kurtz LT. 1945. Determination of total, organic, and available forms of phosphorus in soils. Soil Sci 59:39–46.

Brookes PC, Landman A, Pruden G, Jenkinson DS. 1985. Chloroform fumigation and the release of soil nitrogen. A rapid direct extraction method to measure microbial biomass nitrogen in soil. Soil Biol Biochem 17:837–42.

Clarke KR, Gorley RN. 2015. Getting started with PRIMER v7. PRIMER-E. Plymouth: Plymouth Marine Laboratory.

Djajakirana G, Joergensen RG, Meyer B. 1996. Ergosterol and microbial biomass relationship in soil. Biol Fert Soils 22:299–304.

Enowashu E, Poll C, Lamersdorf N, Kandeler E. 2009. Microbial biomass and enzyme activities under reduced nitrogen deposition in a spruce forest soil. Appl Soil Ecol 43:11–21.

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 EKV, Linsenmair KE, Schulze E-D, Weisser WW. 2010. Implementing large-scale and long-term functional biodiversity research. The biodiversity exploratories. Basic Appl Ecol 11:473–85.

Fontaine S, Barot S, Barré P, Bdioui N, Mary B, Rumpel C. 2007. Stability of organic carbon in deep soil layers controlled by fresh carbon supply. Nature 450:277–80.

Fravolini G, Egli M, Derungs C, Cherubini P, Ascher-Jenull J, Gómez-Brandón M, Bardelli T, Tognetti R, Lombardi F, Marchetti M. 2016. Soil attributes and microclimate are important drivers of initial deadwood decay in sub-alpine Norway spruce forests. Sci Total Environ 569–570:1064–76.

Goldin SR, Hutchinson MF. 2013. Coarse woody debris modifies surface soils of degraded temperate eucalypt woodlands. Plant Soil 370:461–9.

Gonzalez-Polo M, Fernández-Souto A, Austin AT. 2013. Coarse woody debris stimulates soil enzymatic activity and litter decomposition in an old-growth temperate forest of Patagonia, Argentina. Ecosystems 16:1025–38.

Hafner SD, Groffman PM, Mitchell MJ. 2005. Leaching of dissolved organic carbon, dissolved organic nitrogen, and other solutes from coarse woody debris and litter in a mixed forest in New York State. Biogeochemistry 74:257–82.

Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR. 1986. Ecology of coarse woody debris in temperate ecosystems. In: MacFadyen A, Ford ED, Eds. Advances in ecological research, Vol. 15. Orlando: Academic Press. p 133–302.

Horváth B, Opara-Nadi O, Beese F. 2005. A simple method for measuring the carbonate content of soils. Soil Sci Soc Am J 69:1066–8.

Hughes CL, Boddy L. 1994. Translocation of 32P between wood resources recently colonised by mycelial cord systems of *Phanerochaete velutina*. FEMS Microbiol Ecol 14:201–12.

Jenkinson DS, Brookes PC, Powlson DS. 2004. Measuring soil microbial biomass. Soil Biol Biochem 36:5–7.

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 KE, Matzner E, Otto P, Purahong W, Seilwinder C, Schulze E-D, Wende B, Weisser WW, Gossner MM. 2017. Wood decay rates of 13 temperate tree species in relation to wood properties, enzyme activities and organismic diversities. For Ecol Manag 391:86–95.

Kahl T, Mund M, Bauhus J, Schulze E-D. 2012. Dissolved organic carbon from European beech logs. Patterns of input to and retention by surface soil. Écoscience 19:364–73.

Kaiser K, Wemheuer B, Korolkow V, Wemheuer F, Nacke H, Schöning I, Schrumpf M, Daniel R. 2016. Driving forces of soil bacterial community structure, diversity, and function in temperate grasslands and forests. Sci Rep 6:33696. https://doi.org/10.1038/srep33696.

Kappes H, Catalano C, Topp W. 2007. Coarse woody debris ameliorates chemical and biotic soil parameters of acidified broad-leaved forests. Appl Soil Ecol 36:190–8.

Klinka K, Lavkulich LM, Wang Q, Feller MC. 1995. Influence of decaying wood on chemical properties of forest floors and surface mineral soils: a pilot study. Ann For Sci 52:523–33.

Kuehne C, Donath C, Müller-Using SI, Bartsch N. 2008. Nutrient fluxes via leaching from coarse woody debris in a *Fagus sylvatica* forest in the Solling Mountains, Germany. Can J For Res 38:2405–13.

Lajtha K, Crow SE, Yano Y, Kaushal SS, Sulzman E, Sollins P, Spears JDH. 2005. Detrital controls on soil solution N and dissolved organic matter in soils. A field experiment. Biogeochemistry 76:261–81.

Lamour A, Termorshuizen AJ, Volker D, Jeger MJ. 2007. Network formation by rhizomorphs of *Armillaria lutea* in natural soil. Their description and ecological significance. FEMS Microbiol Ecol 62:222–32.

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:e0212120.

Lombardi F, Cherubini P, Tognetti R, Cocozza C, Lasserre B, Marchetti M. 2013. Investigating biochemical processes to assess deadwood decay of beech and silver fir in Mediterranean mountain forests. Ann For Sci 70:101–11.

Mäkipää R, Leppänen SM, Sanz Munoz S, Smolander A, Tiirola M, Tuomivirta T, Fritze H. 2018. Methanotrophs are core members of the diazotroph community in decaying Norway spruce logs. Soil Biol Biochem 120:230–2.

Murphy J, Riley JP. 1962. A modified single solution method for the determination of phosphate in natural waters. Anal Chim Acta 27:31–6.

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 Manag 378:181–92.

Oliveira Longa CM, Francioli D, Gómez-Brandón M, Ascher-Jenull J, Bardelli T, Pietramellara G, Egli M, Sartori G, Insam H. 2018. Culturable fungi associated with wood decay of *Picea abies* in subalpine forest soils: a field-mesocosm case study. Forest 11:781–5.

Parisi F, Pioli S, Lombardi F, Fravolini G, Marchetti M, Tognetti R. 2018. Linking deadwood traits with saproxylic invertebrates and fungi in European forests—a review. Iforest 11:423–36.

Peacock GA, Goosey MW. 1989. Separation of fungal sterols by normal-phase high-performance liquid chromatography. Application to the evaluation of ergosterol biosynthesis inhibitors. J Chromatogr A 469:293–304.

Peršoh D, Borken W. 2017. Impact of woody debris of different tree species on the microbial activity and community of an underlying organic horizon. Soil Biol Biochem 115:516–25.

Philpott TJ, Prescott CE, Chapman WK, Grayston SJ. 2014. Nitrogen translocation and accumulation by a cord-forming fungus (*Hypholoma fasciculare*) into simulated woody debris. For Ecol Manag 315:121–8.

Piaszczyk W, Błońska E, Lasota J. 2019. Soil biochemical properties and stabilization of soil organic matter in relation to deadwood of different species. FEMS Microbiol Ecol . https://doi.org/10.1093/femsec/fiz011.

R Core Team. 2015. R: A language and environment for statistical computing. https://www.r-project.org/.

Rinne KT, Rajala T, Peltoniemi K, Chen J, Smolander A, Mäkipää R, Treseder K. 2017. Accumulation rates and sources of external nitrogen in decaying wood in a Norway spruce dominated forest. Funct Ecol 31:530–41.

Ruzicka S, Edgerton D, Norman M, Hill T. 2000. The utility of ergosterol as a bioindicator of fungi in temperate soils. Soil Biol Biochem 32:989–1005.

Schowalter TD, Zhang YL, Sabin TE. 1998. Decomposition and nutrient dynamics of oak Quercus spp. logs after five years of decomposition. Ecography 21:3–10.

Shorohova E, Kapitsa E. 2014. Influence of the substrate and ecosystem attributes on the decomposition rates of coarse woody debris in European boreal forests. For Ecol Manag 315:173–84.

Spears JDH, Holub SM, Harmon ME, Lajtha K. 2003. The influence of decomposing logs on soil biology and nutrient cycling in an old-growth mixed coniferous forest in Oregon, U.S.A. Can J For Res 33:2193–201.

Spears JDH, Lajtha K. 2004. The imprint of coarse woody debris on soil chemistry in the western Oregon Cascades. Biogeochemistry 71:163–75.

Stokland JN, Siitonen J, Jonsson BG. 2012. Biodiversity in dead wood. Cambridge: Cambridge University Press.

Storch F, Dormann CF, Bauhus J. 2018. Quantifying forest structural diversity based on large-scale inventory data: a new approach to support biodiversity monitoring. Forest Ecosystems 5:1–14. https://doi.org/10.1186/s40663-018-0151-1.

Stutz KP, Dann D, Wambsganss J, Scherer-Lorenzen M, Lang F. 2017. Phenolic matter from deadwood can impact forest soil properties. Geoderma 288:204–12.

ter Braak CJF, Smilauer P. 2012. Canoco reference manual and user's guide: software for ordination, version 5.0. https://research.wur.nl/en/publications/canoco-reference-manual-and-users-guide-software-for-ordination-v.

Vance ED, Brookes PC, Jenkinson DS. 1987. An extraction method for measuring soil microbial biomass C. Soil Biol Biochem 19:703–7.

Wambsganss J, Stutz KP, Lang F. 2017. European beech deadwood can increase soil organic carbon sequestration in forest topsoils. For Ecol Manag 405:200–9.

Wells JM, Boddy L. 1995. Phosphorus translocation by saprotrophic basidiomycete mycelial cord systems on the floor of a mixed deciduous woodland. Mycol Res 99:977–80.

Zalamea M, González G, Lodge D. 2016. Physical, chemical, and biological properties of soil under decaying wood in a tropical wet forest in Puerto Rico. Forests . https://doi.org/10.3390/f7080168.