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Article

Drivers of CO_2 Emission Rates from Dead Wood Logs of 13 Tree Species in the Initial Decomposition Phase

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Abstract: Large dead wood is an important structural component of forest ecosystems and a main component of forest carbon cycles. CO_2 emissions from dead wood can be used as a proxy for actual decomposition rates. The main drivers of CO_2 emission rates for dead wood of temperate European tree species are largely unknown. We applied a novel, closed chamber measurement technique to 360 dead wood logs of 13 important tree species in three regions in Germany. We found that tree species identity was with 71% independent contribution to the model (R^2 = 0.62) the most important driver of volume-based CO_2 emission rates, with angiosperms having on average higher rates than conifers. Wood temperature and fungal species richness had a positive effect on CO_2 emission rates, whereas wood density had a negative effect. This is the first time that positive fungal species

richness—wood decomposition relationship in temperate forests was shown. Certain fungal species were associated with high or low CO_2 emission rates. In addition, as indicated by separate models for each tree species, forest management intensity, study region, and the water content as well as C and N concentration of dead wood influenced CO_2 emission rates.

Keywords: wood-inhabiting fungi; temperate forests; Biodiversity Exploratories; forest management; infrared gas analyzer

1. Introduction

Large dead wood is an important structural component of forest ecosystems [1] and it influences a large number of ecosystem functions [2,3], of which the most relevant are carbon (C) storage [4,5], nutrient cycling [6], and provision of habitat for wood-dwelling organism and resource for xylophageous species [7]. In European forests, dead wood is of paramount importance for forest biodiversity [8,9] Dead wood provides a large and dynamic terrestrial C pool that is generally more resistant to decomposition than other plant litter [10,11]. The estimated global C stock in dead wood of 73 ± 6 Pg C makes up 8% of total C stocks in the world's forests [12]. However, decaying dead wood like any decaying matter is a transient C pool. Respirational C loss (referred to as CO_2 emissions) is the main process of dead wood decomposition [3], whereas fragmentation and leaching contribute typically only to a small extent to the loss of dead wood from ecosystems [13]. Wood decaying fungi are the main agents inducing respirational C loss [14–16] and are highly specialized in their foraging strategies [17]. The capacity of fungi to decay wood components varies from one taxonomic group to another, but as a fungal community, they are able to break down all components of wood such as structural (hemicellulose, cellulose and lignin) and non-structural compounds (e.g., sugars, lipids, and peptides) [18]. For wood decay, the fungal phyla *Ascomycota* and *Basidiomycota* have the highest importance. Both differ considerably in their enzymatic spectra and cause characteristic rot types, e.g., soft-rot typical for *Ascomycota*, brown and white-rot for the latter. Dead wood CO_2 emission rates depend on dead wood tree species identity [19] and on the fungal decomposer community [20]. In addition, they are controlled by environmental conditions that do affect the activity of fungal decomposers [21–23].

Fungal respiration rates double or triple with every 10 °C increase (Q10) between 13 °C and 30 °C [3,19]. Moreover, extremely low and extremely high moisture content in wood can limit the fungal decomposer activity. The range of moisture tolerance depends on the species and differs between *Basidiomycota* (30% to 160% dry weight basis) and *Ascomycota* (up to 240%) [3]. Variations in CO_2 emission rates are also caused by variations in physical, chemical and structural wood properties of different tree species [19]. Coniferous tree species for instance support a less diverse fungal community than angiosperm tree species do [24]. Whereas nearly all individual fungal species exhibit a clear preference for either coniferous or angiosperm wood [25], below this systematic level the majority of wood-inhabiting fungi are not closely associated with tree genera or species [24]. Yet, dead wood tree species identity strongly influences fungal species richness and diversity [21,26]. Experiments with

selected fungal species that analyzed the relationship between fungal diversity and decomposition rate of soil organic matter found a saturation of this process at rather low levels of fungal species diversity [27]. In another experiment with dead wood, it was shown that the fungal diversity-decomposition rate relationship depended on wood decay stages [19,28]. While a decrease of fungal diversity during the initial to intermediate stages of decay was associated with lower respiration rates, no effects were detected at later stages [28]. It is known that fungal species richness and community composition are also influenced by forest management [29,30]. But beside this indirect effect, forest management could also affect dead wood CO_2 emission rates by e.g., altering microclimate [31] or the litter layer.

According to Harmon *et al.* (1995) [32], the importance of dead wood tree species identity dominates over the influence of climatic variables in the decomposition of dead wood in dry tropical forests. A study by Bradford *et al.* (2014) [33] in eastern US temperate forests showed that the local factors (e.g., fungal colonization, temperature), and not climate, primarily control the microbial activity and consequently the carbon dynamics of decomposing wood at regional scales. Investigations based on a local-scale support findings that fungal colonization is a much better predictor of decomposition rates (based on mass loss) than temperature [33]. From this perspective, the conventional paradigm that climatic variables are the main drivers of decomposition (determined as CO_2 emission rates) [34] seems to be an artifact of using local-level mean values in previous studies [33]. Studies on dead wood decomposition rates are often performed on a limited number of tree species with a few cultured fungal species, as an *in vitro* experiment, or under controlled laboratory conditions. These results thus might be a poor reflection of the natural decomposition process, the fungal community and their relation to tree species and environmental conditions.

The abovementioned studies illustrate that we have some information on the factors that influence dead wood decomposition, but until now, knowledge about variations in CO_2 emission rates of dead wood as influenced by the combination of tree species identity, fungal decomposer diversity and environmental variables is insufficient to accurately consider dead wood decomposition in forest ecosystem carbon models. Therefore, it is critical to develop a better understanding of important drivers on dead wood decomposition in European temperate forest ecosystems.

Here, we intended to investigate the combined influence of tree species identity of dead wood, richness and identity of wood decomposing fungal species, local factors (region, forest management intensity), wood properties (density, C and nitrogen (N) concentrations), and environmental conditions in wood (water content, temperature) on CO_2 emissions rates of dead wood in an experimental setting under natural conditions. The employed BELongDead experiment comprises dead wood logs of 13 different tree species that were placed adjacent to 30 forest plots in 2009, representing different forest management intensities in three regions in Germany. In contrast to autochthonous dead wood in the forest, this experiment offers the unique opportunity to study the effects of dead wood tree species identity, locality, and fungal species richness and identity. This experiment is largely independent of known drivers of decomposition such as size (diameter, length) [23,35,36], position (standing, hanging, downed) [37,38] and the previous and unknown succession of fungi in dead wood logs [39].

We measured short-term CO_2 emission rates, instead of wood mass loss, which represents medium- to long-term decomposition rates, to assess the current decomposition rates and its main drivers. The objectives of this study were to identify the relative importance of the main drivers of CO_2

emission rates from dead wood after three years of field exposure, referred to as the initial phase of decomposition. We hypothesized:

1. That the variation in CO_2 emission rates is predominantly explained by tree species identity and fungal species richness.
2. That increasing fungal species richness accelerates decomposition.
3. That the efficiency of fungal decomposers will depend on the presence of some key species.
4. That differences in CO_2 emission rates within dead wood tree species are influenced by environmental conditions in dead wood (e.g., temperature, water content) affecting the microbial activity.

2. Methods

2.1. Study Area

This study was conducted within the framework of the "Biodiversity Exploratories" (BE), which is an open research platform to investigate the relationship between land use intensity, biodiversity and ecosystem processes in three different regions (exploratories) in Germany (Table 1).

Table 1. Main characteristics of the three Biodiversity Exploratories [40].

Exploratory	Schorfheide-Chorin (S-C)	Hainich-Dün (H-D)	Swabian Alb (ALB)
Location	NE Germany	Central Germany	SW Germany
Geology	Young glacial landscape	Calcareous bedrock with loess layer	Calcareous bedrock with karst phenomena
Dominant soil type	Cambisol	Luvisol, Stagnosol	Cambisol, Leptosol
Altitude a.s.l.	3–140 m	285–550 m	460–860 m
Mean annual temperature	8–8.5 °C	6.5–8 °C	6–7 °C
Mean annual precipitation	500–600 mm	500–800 mm	700–1000 mm
Dominant tree species	*Fagus sylvatica* *Pinus sylvestris*	*Fagus sylvatica* *Picea abies*	*Fagus sylvatica* *Picea abies*

The BELongDead Experiment, in which this study was carried out, is located at 30 very intensively measured plots (VIPs) of the Biodiversity Exploratories (number of VIPs; 9 in Schorfheide-Chorin and Swabian Alb, and 12 in Hainich-Dün). The selection of the plots was originally based on forest type and soil depth; detailed information on the implementation and design of the Biodiversity Exploratories is provided by Fischer *et al.* 2010 [40]. The 30 VIPs cover a range of forest types and management intensities including extensively managed or unmanaged forests dominated by European beech, age class and selection cutting forests dominated by European beech, and intensively managed even-aged coniferous (Norway spruce and Scots pine) forests. The forest management intensity of the 30 VIPs has been expressed using the ForMI (Forest Management Intensity index) of Kahl and Bauhus 2014 [41]. This index is the sum of three components taking into account: the proportion of (1) harvested tree volume; (2) tree species that are not part of the natural forest community; and (3) dead wood

showing signs of saw cuts [41]. Each component ranges between 0 (no sign of management) and 1 (intensive management) [41].

2.2. BELongDead Experiment

The BELongDead (Biodiversity Exploratories Long term Dead wood) experiment, which was established in 2009, comprises dead wood logs of 13 tree species (4 genera and 9 species—referred to as "tree species") in three exploratories (n = 1140 logs). The dead wood logs of the 13 tree species (9 Angiosperms: *Acer* spp., *Betula pendula*, *Carpinus betulus*, *Fagus sylvatica*, *Fraxinus excelsior*, *Populus* spp., *Prunus avium*, and *Quercus* spp., *Tilia* spp. and 4 Conifers: *Larix decidua*, *Picea abies*, *Pinus sylvestris*, and *Pseudotsuga menziesii*) are approximately 4 m long and have a mean diameter of 31 ± 5.9 cm (SD). We refer to these 13 tree species as temperate European forest tree species although *Pseudotsuga menziesii* is not native to Europe. All logs were freshly cut in 2008 and 2009 in the state of Thuringia (Germany) and then transported to each VIP. At each of the 30 VIPs, 3 subplots were established with 13 logs (one of each tree species) each, adding up to approximately 39 logs per VIP. The logs were placed in random order beside each other with a distance of *ca.* 1 m between logs [42]. Owing to limited supplies, *P. avium* logs are missing on 27, *Acer* spp. on 2 and *Fagus sylvatica* on 1 of the 90 subplots. Our study focused on one of the three subplots per VIP (n = 30) and excluded one complete VIP in the exploratory Hainich-Dün. In addition, some logs that were inaccessible or difficult to handle with the used CO_2 emission measurement technique were excluded from the design. In total we investigated 360 logs, which resulted in 29 replicates per tree species, except for *Acer* spp. (28 logs), *Fraxinus excelsior* (28 logs), *Larix decidua* (27 logs), *Populus* spp. (28 logs), *Prunus avium* (18 logs) and *Tilia* spp. (28 logs) (Table S1).

2.3. Measurement of CO_2 Emission Rates

In autumn 2012, CO_2 emission rates were measured on these 360 logs. We used a closed chamber system that consisted of a custom-made chamber for the inclusion of a log segment and a device for the measurement of CO_2 concentrations inside the chamber. The CO_2 emission rate of each log was calculated based on the slope of the linear CO_2 concentration increase in the chamber. The chamber was built from a plastic barrel encasing a volume of 171 L with an inner diameter of 57 cm and a length of 70 cm. One side of the barrel closes airtight with a lid. The opposite side also closes airtight with a tube made of cellular rubber (2 mm thick) stretched over the barrel and tightly attached. This tube acts as the flexible air seal between the barrel and the log. To fit the barrel over one end of the log, the log was lifted with the aid of a logging cart at one end for about 30 cm and kept in this position during measurements (Figure 1). At 55 cm distance from the end of the log, a seal made of flexible cellular rubber (20 × 200 × 2000 mm) was wrapped around the log at least two times and strapped to the log with a tension belt. After fitting the barrel over the log, the barrel seal was tightly strapped using a tension belt onto the seal that was around the log to ensure an airtight, although flexible connection (Figure 1). This type of closed chamber technique is probably only suitable for logs without branches and roots in the initial phase of decomposition where the log can be lifted without breaking and a tight seal between chamber and log can be achieved.

Figure 1. Closed chamber system used for CO_2 emission measurements under field conditions.

A temperature and air humidity sensor (HMP-110, Vaisala, Helsinki, Finland) were mounted inside the barrel lid as well as a fan to ensure thorough mixing inside the chamber. The lid was connected with 4 mm PTFE tubes to a pump (NMP-015 B, KNF Neuberger GmbH, Freiburg im Breisgau, Germany) that circulated the air through a flow-through non-dispersive infrared CO_2 sensor (CARBOCAP GMP343, Vaisala, Helsinki, Finland). The signals from the measurement devices were transmitted to and recorded by a data logger (Delta-T Logger DL2e, Umweltanalytische Produkte GmbH, Ibbenbüren, Germany) every five seconds. Each dead wood log was measured once for five minutes or shorter in case the CO_2 concentration in the chamber exceeded the limit of the CO_2 sensor (1000 ppm). Additionally, we recorded the length and the diameter of the enclosed log section. Dead wood log temperature was measured at 10 cm depth inside holes drilled during a prior wood sampling campaign. We found a weak but significant linear correlation between wood temperature and mean temperature inside the chamber during measurement ($T_{wood} = 0.63 \times T_{chamber} + 2.37$, $p < 0.001$, $R^2 = 0.50$). CO_2 emission rates were calculated from the slope of a linear model that was fitted to the increase in CO_2 concentration after closing the chamber. Corrections included the calculations of CO_2 concentrations in dry air and finally for the volume of the enclosed log section. The CO_2 emission rate was calculated as the quantity of carbon emitted per cubic meter of wood per day (g $C \cdot m^{-3} \cdot day^{-1}$). We chose volume as reference for CO_2 emission rates for two reasons: (1) volume was the best explanatory variable for CO_2 emission rates compared with surface area and weight; and (2) we wanted to have dead wood density as an independent variable in our analysis. The main reason for that was that dead wood density changes over the course of decomposition while volume stays constant until fragmentation starts in later stages of decomposition.

For the purpose of this study, we assumed that CO_2 emission rates from dead wood are mainly caused and driven by fungal decomposition of wood. This is not entirely true since also bacteria, algae, mosses, and invertebrates as parts of the xylobiotic community also contribute to a small extent to CO_2 emission rates [23,43,44].

2.4. Wood Properties

In autumn 2012, one wood sample per log was taken without bark at 0.5 m distance from one end of the log by drilling in an angle of 45° through the middle of the log with a 1 cm auger and a cordless power drill. To estimate wood density and water content, the wood shavings were dried at 65 °C to constant weight. A subsample of the wood shavings was ground into a fine powder using a ball mill (MM301, Retsch, Haan, Germany). Wood C and N concentrations were determined through total

combustion using a Truspec elemental analyzer (Leco, St. Joseph, MI, USA). Note for later interpretation, that wood traits of decayed wood were measured and used for the analysis.

2.5. Fungal Inventory

For the fungal survey, we applied an inventory design based on fruit body identification. The inventory was limited to macrofungi with a fruit body, fruit body aggregation or stroma size of at least 5 mm diameter. This criterion ensured a reliable detectability of fungal species under field conditions (visible to the naked eye). As a consequence of this criterion, the fungal inventory covered mainly *Basidiomycota* (first of all corticioid and poroid fungi), but also macrofungal groups from the phylum *Ascomycota* (*pyrenomycetes* and *discomycetes*). All fungal fruit body data were gathered by one survey per log in autumn (September to October) 2012 during the peak fruiting season [45] parallel to the CO_2 emission rate measurements. The species were identified *in situ* or, when the identification was unreliable in the field, collected for later microscopical identification. Dried specimens were deposited at the Herbarium Universitatis Lipsiensis LZ (University Leipzig, Germany). In the course of the inventory, we investigated exclusively the visible part of the log and did not remove moss, bark or other material covering the logs. Data analyses of this study only include fungal species occurring on the 1 m long section of the log (including the cut surface) where CO_2 emission measurements were carried out.

2.6. Statistical Analysis

In order to calculate wood inhabiting fungal species richness among the dead wood logs, we used presence-absence data of the fungal species inventory. Continuous variables were checked for normal distribution and log transformed if necessary (CO_2 emission rates, water content and wood temperature). We compared linear models to assess the effects of dead wood tree species identity as a categorical variable, wood density ($g \cdot cm^{-3}$), water content (water percent dry matter), C and N concentration (%), wood temperature (°C), forest management intensity (ForMI) and region (three exploratories) on the response variable CO_2 emission rate in a best-fit global model. Additionally, separate linear models were tested for each tree species individually including all mentioned variables. Best model selection was conducted in the software R [46] in both cases via "glmulti" [47] automated full information criteria based model selection approach evaluated on the basis of Bayesian information criteria (BIC). Owing to limitations in the data (one measurement per log) we excluded interactions between the variables and tested only for additive effects in the linear models. The function "glmulti" cannot handle missing data, so we had to remove 5 logs from our analysis resulting in a total of 355 logs. We used the function "hier.part" from the R-package "hier.part" [48] to calculate the independent contribution of each variable from the best-fit global model.

To show the relationship with CO_2 emission rates, we plotted observed data from all 355 logs separately for each significant explanatory variable. Additionally, these plots include the effect size, calculated using the function "allEffects" in the R-package "effects" [49], of each variable corrected for the influence of the other significant variables in the best-fit global linear model. In case of the dead wood tree species, the effect size is shown as the mean and confidence interval (95%) for each tree species corrected for the variables wood temperature, fungal species richness and wood density. For the

continuous variables wood temperature, fungal species richness and wood density, the effect size is displayed in the form of regression lines. The significance level for all analyses was set at $p = 0.05$.

Finally, we show associations between fungal species identity and CO_2 emission rates for each dead wood tree species. These associations are purely descriptive and do not represent significant correlations between CO_2 emission rates and fungal species identity. We selected fungal species that occurred on more than 5 of the 355 logs and show their association to high or low CO_2 emission rates. We used the mean of the linear model residuals for each tree species to classify whether the mean CO_2 emission rate associated with the occurrence of each fungal species was high or low.

3. Results

3.1. Drivers of CO_2 Emission Rates

The best-fit global model of CO_2 emission rates included dead wood tree species, wood temperature, wood density and fungal species richness as the main drivers of CO_2 emission rates in dead wood (Table 2). The best-fit global model explained 62% of variance in CO_2 emission rates. Whereas the significant effects of wood temperature and fungal species richness on CO_2 emission rates were positive ($p < 0.05$), the effect of wood density was negative (Table 2; Figures 2–5). Variance partitioning showed that the independent contribution of dead wood tree species was by far the most important (71%), whereas wood temperature (14%), fungal species richness (12%) and wood density (3%) contributed only a smaller proportion.

Table 2. Model estimates, standardized coefficients and standard error obtained from the best-fit global linear model with CO_2 emission rates (log transformed) as dependent variable ($n = 355$ logs).

Variable	Estimate	Standardized Coefficient	Std. Error	*t* value	*P* [(1)]
***Acer* (Intercept)**	2.8888	0.0000	0.2908	9.933	**0.0000** ***
Betula	0.4857	0.2048	0.1122	4.328	**0.0000** ***
Carpinus	0.7314	0.3084	0.1186	6.168	**0.0000** ***
Fagus	0.5555	0.2342	0.1143	4.858	**0.0000** ***
Fraxinus	0.1306	0.0542	0.1160	1.126	0.2611
Larix	−0.6026	−0.2459	0.1129	−5.338	**0.0000** ***
Picea	−0.1923	−0.0798	0.1215	−1.583	0.1144
Pinus	−0.7312	−0.3034	0.1145	−6.386	**0.0000** ***
Populus	−0.2200	−0.0898	0.1175	−1.872	0.0621
Prunus	0.3303	0.1116	0.1256	2.629	**0.0090** **
Pseudotsuga	−0.6641	−0.2800	0.1102	−6.025	**0.0000** ***
Quercus	−0.2623	−0.1106	0.1099	−2.387	**0.0175** *
Tilia	0.1195	0.0496	0.1154	1.035	0.3012
Log (wood temperature)	0.7575	0.2684	0.0941	8.049	**0.0000** ***
Wood density	−1.8525	−0.2559	0.3602	−5.144	**0.0000** ***
Fungal species richness	0.0385	0.1214	0.0132	2.926	**0.0037** **

[(1)] Significance codes: *** (0), ** (≥ 0.001), * (≥ 0.01).

Dead wood CO_2 emission rates varied strongly among the 13 tree species (Figure 2). The emission rates were on average higher for the angiosperms (78.3 ± 2.84 (S.E.) g $C \cdot m^{-3} \cdot day^{-1}$) than for the conifers (40.8 ± 2.56 (S.E.) g $C \cdot m^{-3} \cdot day^{-1}$). Especially *Carpinus*, *Betula* and *Fagus* wood exhibited high CO_2 emission rates. The majority of the conifers show low CO_2 emission rates except for *Picea*. In most cases, the effect size for each dead wood tree species was comparable to the median CO_2 emission rate (Figure 2). The relationship between wood temperature and CO_2 emission rates was almost similar to the effect size of wood temperature in the model (Table 2; Figure 3). In contrast, for fungal species richness the effect size was lower than the original relationship between species richness and CO_2 emission rates (Table 2; Figure 4) but still contributed significantly to the best-fit global model. In the case of wood density, a significant negative correlation was observed with the best-fit global model (Table 2), but no significance was found when analyzing linear trends of CO_2 emission rates (Figure 5).

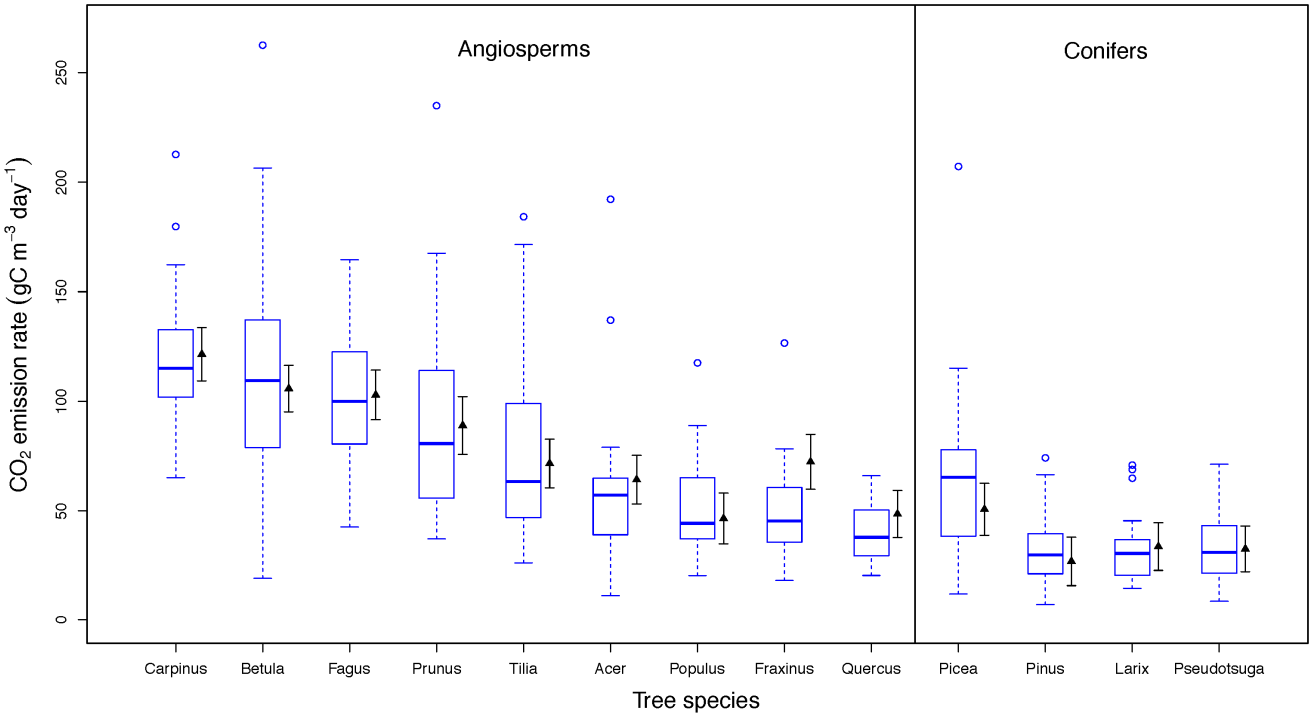

Figure 2. Relationship between CO_2 emission rates and the significant explanatory variable dead wood tree species for the best-fit global model. Triangles with lines represent the mean effect size and 95% confidence interval for each tree species corrected for the influence of the other variables in the best-fit global model. The blue boxplots represent field observations from 355 logs.

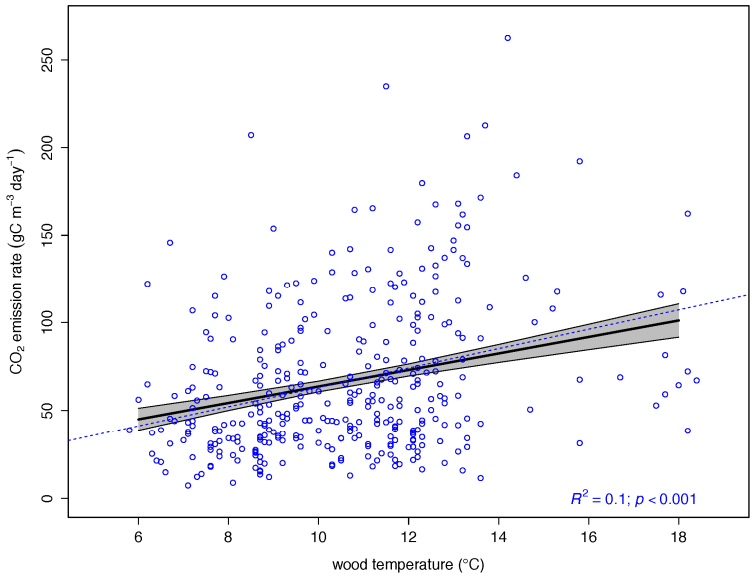

Figure 3. Relationship between CO_2 emission rates and the significant explanatory variable wood temperature for the best-fit global model. Solid regression line and the surrounding grey 95% confidence interval shows the significant main effect and is corrected for the influence of the other variables in the best-fit global model. The blue data points represent field observations from 355 logs. The blue dashed regression line represents the linear correlation based on the field observation data.

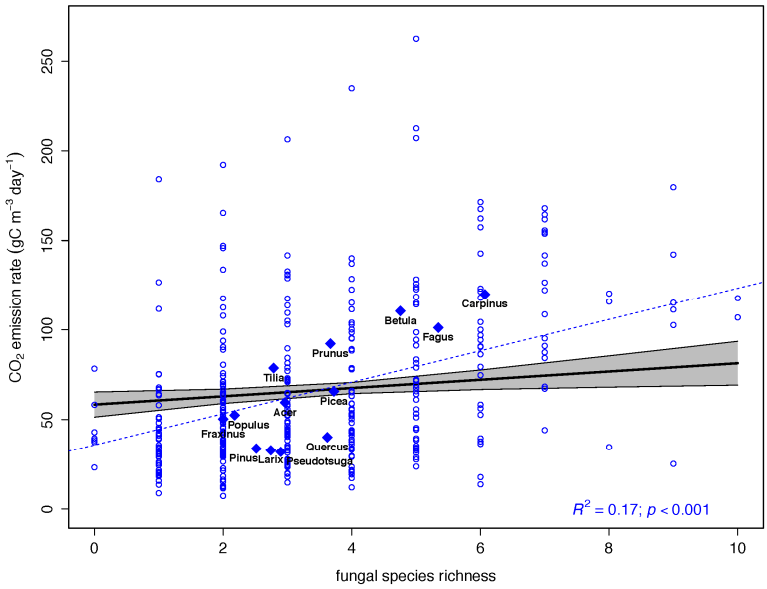

Figure 4. Relationship between CO_2 emission rates and the significant explanatory variable fungal species richness for the best-fit global model. Solid regression line and the surrounding grey 95% confidence interval shows the significant main effect and is corrected for the influence of the other variables in the best-fit global model. The blue data points represent field observations from 355 logs. The blue dashed regression line represents the linear correlation based on the field observation data. Blue diamonds represent mean field observation values by tree species.

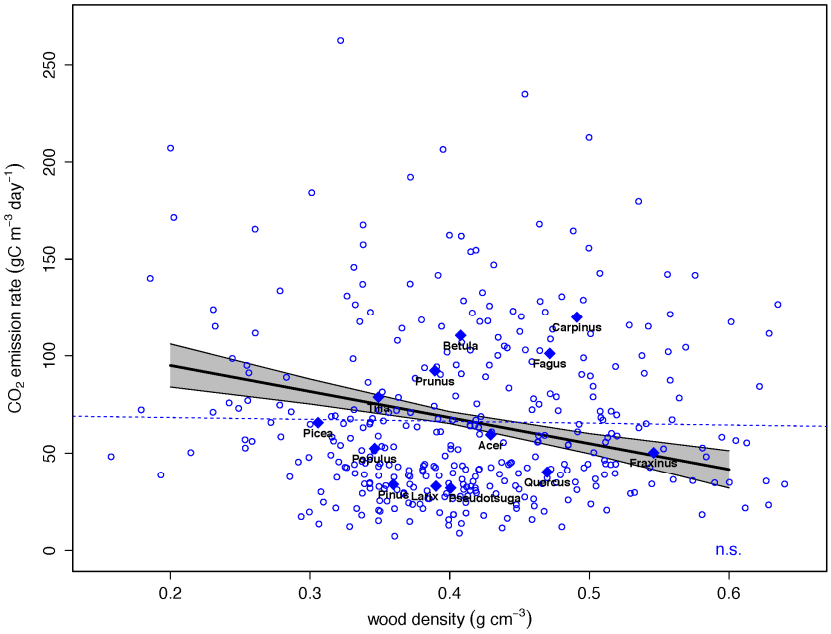

Figure 5. Relationship between CO_2 emission rates and the significant explanatory variable wood density for the best-fit global model. Solid regression line and the surrounding grey 95% confidence interval shows the significant main effect and is corrected for the influence of the other variables in the best-fit global model. The blue data points represent field observations from 355 logs. The blue dashed regression line represents the linear correlation based on the field observation data. Blue diamonds represent mean field observation values by tree species.

3.2. Drivers of CO_2 Emission Rates in Dead Wood Tree Species

As the best-fit global model showed, dead wood tree species identity was by far the most dominant driver of CO_2 emission rates. We calculated separate models to identify the main drivers of CO_2 emission rates within each tree species. We applied the same set of explanatory variables as for the previous model. Among these tree species models, we found strong differences in the relative importance of explanatory variables for CO_2 emission rates (Table S2). In *Acer*, *Fagus* and *Fraxinus*, none of the chosen explanatory variables could explain the variation in CO_2 emission rates. In all other tree species, wood temperature had a positive influence on CO_2 emission rates (Table S2). Increasing forest management intensity had a positive effect on CO_2 emission rates in *Betula*, *Larix* and *Pseudotsuga* dead wood, whereas a negative effect was found in *Tilia*. A weak regional influence was detected for dead wood of *Betula*, *Carpinus* and *Pseudotsuga*. As shown in the best-fit global model, wood density has a negative impact on CO_2 emission rates, but this pattern was reflected in three tree species only: *Carpinus* (−0.3194; Table S2), *Picea* (−0.5156; Table S2) and *Tilia* (−0.4831, Table S2). Dead wood water content was negatively related to CO_2 emission rates for *Pseudotsuga* and *Picea*. For *Betula*, a negative correlation for C-concentration and for *Populus* a positive correlation with N-concentration in dead wood was found. The positive correlation of CO_2 emission rates with fungal species richness in the best-fit global model was at the level of individual tree species only confirmed for *Prunus*.

3.3. Fungal Species Identity and CO_2 Emission Rates

The fungal inventory resulted in a total of 136 fungal species of which 101 species belonged to the phylum *Basidiomycota*, and 35 species to the phylum *Ascomycota* (Table S3). Out of those, the 41 most abundant species (minimum occurrence on five logs) were chosen for further analysis (Figure 6). The occurrence of *Basidiomycota* showed no clear distinction between angiosperm and coniferous tree species, while *Ascomycota* clearly preferred angiosperm tree species (Figure 6). To illustrate substrate specificity on high systematic level two examples are given, *Trichaptum abietinum* occurred only on conifers and *Lasiosphaeria ovina* occurred only on angiosperms. The strongest associations of *Basidiomycota* with high CO_2 emission rates were found, for *Bjerkandera adusta* and *Fomitopsis pinicola* on *Larix* and for *Skeletocutis amorpha* on *Picea*. The strongest associations of *Ascomycota* with high CO_2 emission rates were found for *Eutypa lata* on *Populus* and *Lasiosphaeria ovina* on *Acer*. In contrast, the strongest associations of *Basidiomycota* with low CO_2 emission rates were found for *Botryobasidium pruinatum* on *Prunus*, and for *Ascomycota* for *Lasiosphaeria ovina* also on *Prunus.*

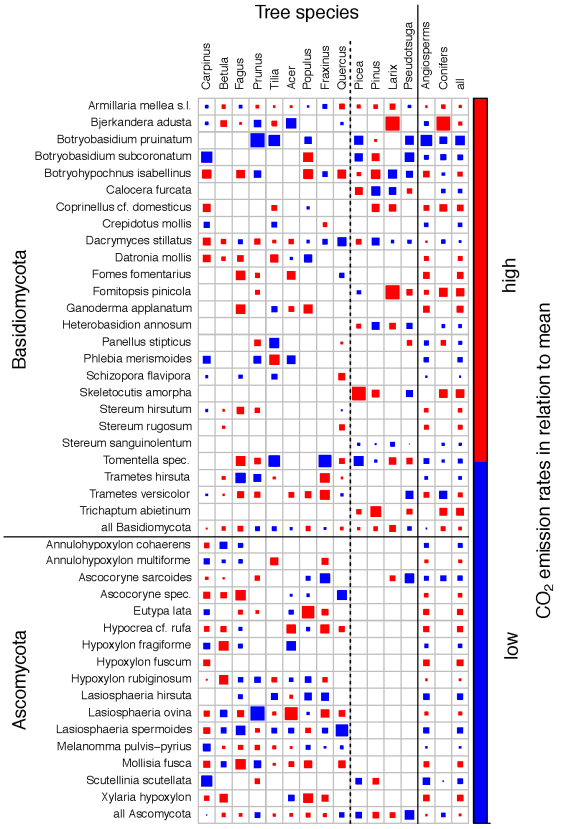

Figure 6. Associations between CO_2 emission rates and occurrence of fungal species (Table S3) for each dead wood tree species. Fungal species are sorted by phylum. Dead wood tree species are sorted as in Figure 2. We used the mean of the linear model residuals for each tree species to classify whether the mean CO_2 emission rate for each fungal species is high (red) or low (blue). The size of the squares gives the strength of the association. For example: a large red square means that there is a strong association with high CO_2 emission rates.

4. Discussion

4.1. Main Drivers of CO_2 Emission Rates

We identified dead wood tree species, wood temperature, fungal species richness and wood density as the main drivers of CO_2 emission rates in the initial phase of dead wood decomposition. Additional variables such as region, forest management intensity, and wood properties (water content, and C and N concentrations) had no significant influences on CO_2 emission rates in the best-fit global model.

To our knowledge, this is the first study where CO_2 emission rates of such a large number of temperate European tree species were analyzed at the same time and in a coherent design. Tree species identity was by far the most important variable in the best-fit global model. The effect size for tree species within the best-fit global model was largely similar to their original value of CO_2 emission rates. This indicates that wood temperature; wood density and fungal species richness had comparable effects on each tree species. Also, for decomposition rates of freshly logged and natural dead wood in neotropical forests, tree species identity was found to be the most prominent driver [32,50]. It has been proposed previously that wood trait variations are responsible for the dominating influence of tree species identity on decomposition rates [35,50]. Wood traits such as N-concentration, phosphorus-concentration, C:N ratio were found to correlate with decomposition rates of angiosperms, whereas gymnosperm wood generally decomposes slower than angiosperm wood [11,35]. Our study corroborates the statement on gymnosperms with *Picea* being the only exception. The wood traits (density, and C and N concentrations) determined in our study were measured three years after the onset of the decomposition process and therefore not comparable with original wood traits as discussed in Weedon *et al.* (2009) [35]. Up to now, dead wood CO_2 emission and decomposition rates have been estimated only for the most abundant temperate European tree species. Those findings are quite similar to our study results. Higher respirational C loss of beech compared to spruce and pine has been shown by Herrmann and Bauhus (2012) [19]. An order of decomposition rates with beech > spruce = pine > oak has been suggested by Rock *et al.* (2008) [51], which does not totally coincide with our results that yield an order of CO_2 emission rates with beech > spruce > oak > pine. In contrast to Rock *et al.* (2008) who looked at decomposition rates over the whole course of decomposition, our study shows CO_2 emission rates in the initial phase of decomposition. Possibly caused by interspecific differences in the initial lag phase [36], CO_2 emission rates show a slightly different picture than decomposition rates.

As expected, CO_2 emission rates increased with wood temperature. The effect size for wood temperature was similar to the original correlation between wood temperature and CO_2 emission rates, meaning that the effect of wood temperature is largely independent of tree species identity, wood density and fungal species richness. The increase of CO_2 emission rates by 2–3 times for every 10 °C wood temperature increase (Q10) has been shown in several laboratory and field based studies [3,19,52]. It is a remarkable finding of our study, that the independent contribution of wood temperature explained only 14% of our total best-fit global model variation. This could be caused by measurements at rather low temperatures (5.8 °C to 18.4 °C), although Chen *et al.* (2000) [52] showed that temperature sensitivity (Q10) was highest between 5 °C and 10 °C. And it could also be caused by the rather low gradient in temperature of 12.6 K. A larger gradient could possibly increase the independent contribution of temperature on CO_2 emission rates. Furthermore, we strongly believe that

the seasonal variation in temperature would affect wood temperature and thus CO_2 emission rates. But the sampling design (one measurement per log in autumn 2012) limited the observed temperature range.

Within the best-fit global model CO_2 emission rates decreased with increasing wood density. This is noteworthy since originally (Figure 5) no significant linear correlation between wood density and CO_2 emission rates was found. With our approach to base CO_2 emission rates on volume we could even expect a positive relationship between CO_2 emission rates and wood density. But the opposite is true. We assume that the CO_2 emission rate–wood density relationship changes during progressive wood decomposition. In the lag and initial phase of decomposition, a negative relationship between CO_2 emission rates and wood density exists, because wood with higher density is in an earlier successional stage and exhibits a lower activity of fungal decomposers while wood with lower density is in a later successional stage, already partially decayed and exhibits higher activity of fungal decomposers [16]. In the final stage of decomposition, a positive relationship between CO_2 emission rates and wood density can be expected since fungal decomposer activity should decrease after a certain mass loss in substrate.

As hypothesized, CO_2 emission rates were positively affected by fungal species richness. To our knowledge, this is the first field study that shows a positive fungal species richness–CO_2 emission rate relationship for dead wood. This result agrees with a lab study that proved a positive biodiversity–ecosystem process relationship for fungi and dead wood decomposition [28]. The effect size of fungal species richness was much lower than to be expected from the correlation between the raw data (Figure 4). This was caused by the hidden correlation between fungal species richness and tree species. Fungal species richness is known to be a function of dead wood tree species identity [21,53] and successional stage [54,55]. In our study, tree species with high fungal species richness also tended to have higher CO_2 emission rates (Figure 4). In the initial and early phase of decomposition, as a result of progressing colonization and fungal succession species richness, fungal growth and activity (CO_2 emission rates) are increasing. Tree species identity seems to determine the speed of initial fungal succession and therefore initial CO_2 emission rates. Although a large part of the correlation between fungal species richness and CO_2 emission rates was obviously explained by tree species identity, the independent contribution of fungal species richness to the best-fit global model was still 12%. This is almost as high as the independent contribution of temperature (14%) and underlines the importance of fungal species richness in our study. The observed importance of fungal species richness was not mirrored in the separate models for each tree species. Only for *Prunus avium* a significant positive effect was found.

4.2. Drivers of CO_2 Emission Rates in Dead Wood Tree Species

Wood temperature was the predominant driver of CO_2 emission rates in tree species-specific models, except for *Acer*, *Fagus* and *Fraxinus* where none of the explanatory variables explained any variance in CO_2 emission rates. This reflects the results of the best-fit global model, where temperature was the second most important driver of CO_2 emission rates after tree species.

Previous forest management intensity might influence dead wood decomposition through a different forest microclimate [56] or through different stocks of coarse woody debris that act as a reservoir for

wood-decaying fungi. In our study, forest management intensity had a negative effect on decomposition only for *Tilia*, meaning that in forests with lower management intensity a higher CO_2 emission rate was found. On the other hand, *Betula*, *Larix* and *Pseudotsuga* had higher CO_2 emission rates in more intensively managed forests. Taking into account that CO_2 emission rates in nine out 13 tree species were independent of forest management intensity, it appears that overall management does not have a considerable effect. As for the forest management intensity, the regional aspect plays an almost negligible role. Only *Betula*, *Carpinus* and *Pseudotsuga* show significant regional differences with a tendency to higher CO_2 emission rates in the exploratory Hainich Dün.

In the best-fit global model, wood density had a negative effect on CO_2 emission rates, but at the species-level this effect appeared only in *Carpinus*, *Picea* and *Tilia*. It seems that for these tree species a range of logs in different successional stages exist. In reference to the fungal succession we assume, that most of the tree species are in an initial phase of decomposition (*Hypoxylon fragiforme* and *Armiallaria mellea s.l.* rhizomorph), whereas some transition into the optimal phase (*Bjerkandera adusta*, *Stereum hirsutum*, and *Trametes* spp.). This would result in logs with high density and low activity in contrast to logs with lower density and higher activity. The results for a negative correlation with water content in *Picea* and *Pseudotsuga* are difficult to interpret since water content is in both cases within the tolerance range of 30% to 160% (dry weight based) for *Basidiomycota*, which means that they should have optimal growth conditions. The negative correlation of CO_2 emission rates with C-concentration for *Betula* and the positive correlation with N-concentration for *Populus* cannot be explained.

As mentioned before, except for *Prunus*, fungal species richness did not have an impact on CO_2 emission rates in 12 out of 13 tree species. This could either mean that no positive effect exists for other tree species or that this effect is only detectable in later stages of decomposition. In addition, decomposition of dead wood may be carried out by an unknown number of fungal species that were not detectable as fruit bodies during the duration of this study. The overall importance of fungal species richness in the best-fit global model is not invalidated by this result. It just means that the significant effect of fungal species richness is only detectable with a larger number of tree species.

4.3. Fungal Identity and CO_2 Emission Rates

Not tree species identity or any of the other variables are the main agents of decomposition, but the fungi whose wood decaying activity is driven by these variables. However, it is difficult to disentangle and quantify the direct effects of fungal decomposition and indirect effects of abiotic variables on CO_2 emission rates. Moreover, not only the fungal identity but also the fungal community composition and abundance affect the decay process. It is therefore important to remember that the method used here only shows associations between high or low CO_2 emission rates and the occurrence of certain fungal species (Figure 6). This approach was purely descriptive and cannot claim to identify causal relationships.

The decision to capture fungal data on the basis of fruit body production is reasonable because this fungal trait indicates high physiological activity and wood decomposition processes, respectively. But, on the other hand, high physiological activity does not necessarily induce fruit body production. Therefore there is no guarantee that all active fungal species were gathered with the applied method.

An additional fungal-specific characteristic is the hidden dimension of the mycelia within the substrate. Considering this, only presence-absence data were used. Because of the small-scale inventory (detailed study of 1 m of the log) this kind of data could be regarded as acceptable and meaningful.

Despite the mentioned constraints the results present strong evidence for the different wood decaying capacities of many macrofungi under field conditions (Figure 6). For instance, observed fungal species such as *Fomitopsis pinicola* and *Bjerkandera adusta*, which were associated with high CO_2 emission rates, are known as important dead wood decomposers [39,57]. The degree of CO_2 emission rates is not only determined by fungal identity and size of mycelia, but also by fungal community composition. For example, it is known for the observed genera *Hypocrea* (anamorph: *Trichoderma*) [58] and *Ascocoryne* [22] that they are able to produce antibiotics that obstruct the colonization with wood decaying fungi and therefore slow down wood decomposition. In our study, only for *Ascocoryne* an association with low CO_2 emission rates was found in *Fraxinus*, *Quercus* and *Pseudotsuga* (Figure 6).

Owing to random processes in fungal colonization of dead wood and later facilitative or competitive processes between fungal species, the fungal community is practically unique for each log [59]. In addition, wood-inhabiting fungi show a wide variety of strategies to gain and hold territories in wood, defined not least by their mode of dispersal and establishment, and by individual adaptation to the various disturbance and stress factors influencing life in decaying wood [60]. Nevertheless, the shown associations between fungal species and CO_2 emission rates can be used to search for species that inhibit or accelerate dead wood decomposition.

5. Conclusions

Tree species identity, wood temperature and fungal species richness are the main drivers of CO_2 emission rates in the initial decomposition of dead wood in important central European tree species. These variables should be considered in models of forest C storage and cycling. For fungal species richness this is the first time that a positive biodiversity–ecosystem process relationship was found for dead wood decomposition. Other variables such as wood density, water content, forest management intensity, region, and C- and N-concentration seem to be negligible for dead wood CO_2 emission rates in the initial phase of decomposition. Considering the true agents of wood decomposition, the wood-decaying fungi, we need to further improve our understanding of the decomposition process. However, to account for the effects of their species identity, abundance, and community composition on dead wood decomposition would require a much more complex approach than could be carried out in this study.

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Author Contributions

Tiemo Kahl, Jürgen Bauhus, Peter Otto and Kristin Baber conceived and designed the experiments; Tiemo Kahl, Kristin Baber and Peter Otto performed the analytical work; Tiemo Kahl and Kristin Baber analyzed the data; and Tiemo Kahl, Kristin Baber, Jürgen Bauhus, Christian Wirth and Peter Otto wrote the paper.

Conflicts of Interest

The authors declare no conflict of interest. The funding sponsors had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, and in the decision to publish the results.

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