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RESEARCH ARTICLE

Methodology matters for comparing coarse wood and bark decay rates across tree species

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Abstract

1. The importance of wood decay for global carbon and nutrient cycles is widely recognized. However, relatively little is known about bark decay dynamics, even though bark represents up to 25% of stem dry mass. Moreover, bark presence versus absence can significantly alter wood decay rates. Therefore, it really matters for the fate of carbon whether variation in bark and wood decay rates is coordinated across tree species.
2. Answering this question requires advances in methodology to measure both bark and wood mass loss accurately. Decay rates of large logs in the field are often quantified as loss in tissue density, in which case volume depletions of bark and wood can yield large underestimations.
3. To quantify the real decay rates, we assessed bark mass loss per stem surface area and wood mass loss based on volume-corrected density loss. We further defined the range of actual bark mass loss by considering bark cover loss. Then, we tested the correlation between bark and wood mass loss across 20 temperate tree species during 4 years of decomposition.
4. The area-based method generally showed more than 3-fold higher bark mass loss than the density-based method (even higher if considering bark cover loss), and volume-corrected wood mass losses were 1.08–1.12 times higher than density-based mass loss. The deviation of bark mass loss between the two methods was higher for tree species with thicker inner bark. Bark generally decomposed twice as fast as wood across species, and faster decaying bark came with faster decaying wood (R^2 = 0.26, p = 0.006).

5. We strongly suggest using corrected volume when assessing wood mass loss especially for the species with faster decomposable sapwood and all the wood at advanced decay stages. Further studies of coarse stem decomposition should consider trait 'afterlife' effects of inner bark and estimate fraction of stem bark cover to obtain more accurate decay rates.
6. Our new method should benefit our understanding of the in situ dynamics of woody debris decay and monitoring research in different forest ecosystems worldwide, and should aid meta-analyses across diverse studies.

KEYWORDS

asynchronous, dead wood, decomposition, ecological methodology, fragment loss, inner bark thickness, interspecific variation, volume loss

1 | INTRODUCTION

Dead trees are ecologically significant components of forest ecosystems (Harmon et al., 1986) and also account for a substantial fraction (73 ± 6 Pg) of the world's forest carbon stock (Pan et al., 2011). Their decay rates not only influence the mass of dead wood stored in forests and the global carbon cycle, but also play a profound role in forest ecosystem responses to global change, as dead wood decomposition is sensitive to increased temperature (Chambers, Higuchi, Schimel, Ferreira, & Melack, 2000). Decay rates vary consistently among tree species, even in a given forest environment, because of the legacy of variation in the traits of living trees (Weedon et al., 2009). Most previous studies have estimated stem decay rates by considering tree logs or branches as a single unit, without distinguishing explicitly between bark and wood, or their interactions (Hérault et al., 2010; Kahl et al., 2017). This has important limitations for understanding the process of decomposition and for understanding the consequences of decomposition for carbon cycling. First, bark and wood are very different in terms of chemical composition and anatomical structure, which can have an afterlife influence on microbial respiration rates, as well as on fragmentation induced by biotic agents (Shorohova & Kapitsa, 2014). Second, wood decomposition process can be altered by the bark cover around it, e.g. by forming a barrier to decomposing organisms and by modifying the microclimate under which wood can decay (Dossa et al., 2018; Franceschi, Krokene, Christiansen, & Krekling, 2005; Zuo et al., 2016). But whether wood decay is coordinated with bark decay has been less studied and the present methodological approaches of measuring bark and wood mass loss are fraught with challenge and lack of accuracy.

Bark is important for understanding and accurately quantifying woody debris decay rates, as it represents 10%–25% of the stem dry biomass and up to 25% of the stem volume (Franceschi et al., 2005). After a tree falls down, bark usually enters the decomposition process while still attached to wood, or as fragments fall on the forest floor. How long the bark remains attached depends on tree species, decay time and environmental conditions (Shorohova & Kapitsa, 2014), which suggests that bark and wood decay may be independent. To date, only one study has explicitly evaluated the relationship between bark and wood decay across species (Dossa et al., 2018). This study showed that the effect of bark presence on the decay of twigs is (a) species-specific, (b) usually negative and (c) stronger at early decay stage than later on, when much bark has fallen off. However, bark usually has a longer residence time on coarse logs than on twigs, which greatly extends the potential time for bark to affect wood decomposition, an issue that has had little attention. Whether bark decay rate can predict wood decay rate, and whether fast (vs. slow) decaying bark is usually coupled with fast (vs. slow) decaying wood remains unexplored. Yet, this is an important issue, as coupling of wood and bark decay across species would make it more straightforward to position woody debris of different species along an axis from slow to fast decay in a given environment. A specific aspect of such coupling is how, for different tree species, bark traits, decay rates and fates (attached or shed) directly influence wood decay. Therefore, whether the decay rate of bark naturally occurring on logs is coupled with wood decay, at least during early and mid-stage decay, is an important question in need of in-depth study.

In wood decomposition studies percentage density loss is usually assessed to represent decay rate, also for deriving the mass loss curve over time (Hérault et al., 2010; Kahl et al., 2017). However, this leads to an underestimation of wood decay rate, as volume depletion is not taken into account (Figure 1b). Measuring the real decay rate of coarse logs is challenging because the turnover time is long, up to decades or even centuries. Also, for big logs direct determination of dry mass at different time steps is usually impossible for logistic reasons or unreliable because of the field variability content. Most researchers tend to use chronosequence methods and decomposition-vector methods (Freschet, Weedon, Aerts, Hal, & Cornelissen, 2012; Harmon, Krankina, & Sexton, 1999) as alternatives, for which the challenge is to assess the original mass of dead trees. Consequently, determination of the original volume is the key step based on the cross-sectional area (A), which may be estimated from the mean radius (r) as ($A = \pi r^2$). One main approach is to estimate the original radius from less decomposed parts of the log (Harmon, Woodall, Fasth, & Sexton, 2008), whereas

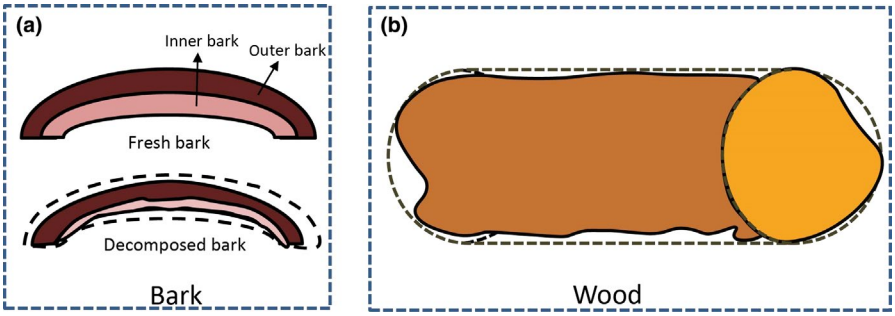

FIGURE 1 Conceptual framework of bark and wood volume depletion during decomposition. Panel (a) shows that volume loss was more rapid for the nutritional and thick inner bark than for the outer bark. Thus, mainly the hard-outer bark left after periods of decomposition, forming the new bark frame (bold line at decomposed bark). Panel (b) shows the wood frame collapse as decay advanced. The bold line is the new frame after years of decomposition while the dashed line is the original frame. The mass between the dashed and bold lines is underestimated when using density loss to calculate mass loss

another approach suggested to measure the cross-section width (horizontal diameter), which tends to remain relatively stable even through the most advanced decay stages (Fraver et al., 2013). However, both methods could introduce biases as log shapes are often irregular. The harmonization of standards in estimating original mass is poor, precluding meta-analyses on dead tree decay at large scales and among ecosystems. Thus, a standard approach with a high accuracy to reconstruct the original log volume is much needed.

The methods mentioned above mainly dealt with wood (i.e. xylem). Yet, how to accurately measure bark decay rate is one of the important unknowns (Rosell, Gleason, Mendez-Alonzo, Chang, & Westoby, 2014). Primarily, percentage density loss was previously used to represent bark decay rate but this approach was later criticized as it does not account for volume (thickness) loss and peeling loss (Shorohova et al., 2016) is composed of two contrasting layers, i.e. inner bark, which is mostly made up of living cells and related with translocation of photosynthates, and outer bark, which contains mostly dead cells and has a protective function (Rosell, 2016). This functional difference between bark layers can result in a relatively decomposable inner bark and more decay-resistant outer bark upon tree death, leading to relatively early and fast volume depletion of the inner bark (Figure 1a). To advocate an alternative and likely more accurate method, we employ an area-based bark mass loss methodology. This approach was previously applied to four tree species in a chronosequence study (Shorohova et al., 2016) but without quantitative comparison with the density-based method. Here, we are the first to explicitly compare bark mass loss based on tissue density with mass per area across multiple species. We hypothesize (i) that there is a strong asynchrony of decay between inner and outer bark. The mass loss of the inner bark dominates the whole-bark mass loss at early and mid-decay stage, while the outer bark dominates the whole-bark mass loss at mid- and late-decay stage. Using an area-based method will greatly increase both the accuracy of whole-bark mass loss and yield higher bark mass loss values.

A method combining manual drawing of the object outline and image analysis was first applied in our study, with the pre-knowledge that image analysis software performed with a high degree of accuracy in calculating cross-section area of natural logs (Ulyshen & Wagner, 2013). In our study, we further developed the method in estimating the original volume of decomposed log wood and bark mass loss, and quantifed the contribution of inner bark thickness and bark cover loss to the accuracy of bark mass loss in a standardized experimental setup. We hypothesize (ii) that both the inner bark thickness and bark cover loss are positively correlated with deviation of density-based bark mass loss from actual bark mass loss. Then we test our (null) hypothesis (iii): there is no consistent relationship between bark and wood decay rates across multiple temperate tree species.

2 | MATERIALS AND METHODS

2.1 | Study area

Two incubation sites were selected in the central area of the Netherlands, representing two extremes of the major acidity/texture/fertility axis of forest soils in NW Europe: site Flevoland (F, 52.46°N, 5.42°E) and site Schovenhorst (S, 52.25°N, 5.63°E). The soil in site F is calcareous, moist, fertile and close to neutral in pH while the soil in site S is well drained, acidic, podzolic and infertile. The dominant species in the canopy layer are *Populus* × *canadensis* in Flevoland, and *Larix kaempferi* in Schovenhorst. More details are given in Cornelissen et al. (2012).

2.2 | Experimental design

Ten temperate tree species (named 2012 cohort, see species list in Table 1), of which six angiosperms and four gymnosperms, were both incubated in the two sites in Feburary 2012. Eight species with a stem diameter of 25 ± 3 cm were collected from trees growing at one of the study areas, but trees of *Quercus robur* L. (QRO) and *Picea abies* L. (PAB) were collected from both sites and incubated in both sites, i.e. they were exchanged reciprocally between the sites. As these QRO and PAB trees differed in age and hence presumably in wood and bark

TABLE 1 Tree species collected from two environmentally contrasting collection sites (S, Schovenhorst; F, Flevoland) selected in the decomposition study. All species from the 2012 cohort were incubated in both sites, and the species from the 2013 cohort only incubated in site Flevoland. Tree species are arranged in alphabetical order within each cohort

Cohort	Code	Site	Tree species	Family	Type
2012	AGR	S	*Abies grandis* (Douglas ex D. Don) Lindley	Pinaceae	Gymnosperm
2012	BET	F	*Betula pendula* Roth	Betulaceae	Angiosperm
2012	FEX	F	*Fraxinus excelsior* L.	Oleaceae	Angiosperm
2012	FSY	F	*Fagus sylvatica* L.	Fagaceae	Angiosperm
2012	LKA	S	*Larix kaempferi* (Lamb.) Carr.	Pinaceae	Gymnosperm
2012	PAB	S + F	*Picea abies* L.	Pinaceae	Gymnosperm
2012	PME	S	*Pseudotsuga menziesii* (Mirb.) Franco	Pinaceae	Gymnosperm
2012	POP	F	*Populus* × *canadensis* Moench	Salicaceae	Angiosperm
2012	PTR	S	*Populus tremula* L.	Salicaceae	Angiosperm
2012	QRO	S + F	*Quercus robur* L.	Fagaceae	Angiosperm
2013	2FEX	F	*Fraxinus excelsior*	Oleaceae	Angiosperm
2013	ACE	F	*Acer pseudoplatanus*	Sapindaceae	Angiosperm
2013	AGL	F	*Alnus glutinosa*	Betulaceae	Angiosperm
2013	CBE	F	*Carpinus betulus*	Betulaceae	Angiosperm
2013	CSA	F	*Castanea sativa*	Fagaceae	Angiosperm
2013	PNI	F	*Pinus nigra*	Pinaceae	Angiosperm
2013	PRA	F	*Prunus avium*	Rosaceae	Angiosperm
2013	RPS	F	*Robinia pseudoacacia*	Fabaceae	Angiosperm
2013	SAL	F	*Salix alba*	Salicaceae	Angiosperm
2013	TIL	F	*Tilia cordata*	Malvaceae	Angiosperm
2013	ULM	F	*Ulmus* × *hollandica*	Ulmaceae	Angiosperm

quality (cf. Zuo et al., 2018 for branches), we treated these conspecific populations as different species here. Thus, six tree species, each represented by 10 individual trees, were extracted from each site. Each individual tree trunk was cut into five of 100 cm in length. Parts of trunks with major branches, damage or irregularities were left unsampled. Two 2-cm-thick discs were collected adjacent to log A (stem base) and log E (stem top) for initial density measurements and additional trait measurements including the inner and outer bark thickness. For details about the bark thickness measurement see Zuo et al. (2016). The five logs cut from the same tree were laid in the same incubation plot adjacent to each other labelling from A to E. There were five plots (statistical blocks) per site. Thus, in total 600 logs were incubated in February 2012: 2 sites × 12 tree species × 5 plots × 5 logs. For further details of the experimental design see Cornelissen et al. (2012).

In February 2016, one log per tree species was randomly collected in each subplot. After recording the fraction of the log covered by bark, all the logs were sawn into two 50-cm-long subsamples. From one subsample a vertical plank was extracted from the centre (from air exposed to soil exposed). From the remaining two semi-cylinders, one semi-cylinder was used for the mass loss measurements. The other subsample was carefully laid back in its original position (for animal extraction, see Andringa et al., 2019).

2.3 | Density loss measurement

Bark and wood density loss were measured separately. Densities were calculated as dry mass divided by the fresh sample volume, which was measured using the water replacement method. Bark and wood dry mass were measured after oven drying at 60°C until equilibrium mass. Bark and wood density before decomposition (T_0) were measured using the discs cut adjacent to log A and log E. To increase the accuracy of measurement, logs were divided into three groups based on the labels, i.e. A, BCD and E. The initial and final samples were paired as closely as possible, i.e. for the logs labelled with A (or E), we used the density of adjacent disc A (or E) separately as T_0. For the rest, we used the average density of disc A and E. Bark and wood density after 4 years decomposition (T_4) was measured based on the semi-cylinders. The density-based mass loss (ML_1) was calculated as (Equation 1):

$$ML_1 = \frac{\rho_0 - M_4/V_4}{\rho_0}, \quad (1)$$

ρ_0: bark/wood density at T_0 (g/cm^3); M_4: bark/wood dry mass at T_4 (g); V_4: bark/wood water replacement volume at T_4 (cm^3); BML_1 and WML_1 were used as bark and wood density loss specifically in the figures in Results.

2.4 | Area-based bark mass loss

We quantified mass per unit stem surface area at T_0 and T_4 respectively to calculate percentage bark mass loss (area-based method, $\Delta g/cm^2$). Area-based mass at T_0 was measured using the disc samples collected at the time of incubation, and four approximately 2 cm × 5 cm bark pieces were collected for measurement. To measure area-based bark mass loss at T_4, four approximately 2 cm × 5 cm bark pieces (two pieces from top and two pieces from bottom of log) that together seemed representative of the bark decay status of each log were extracted. After collecting the bark samples, we flattened the bark slightly by hand, with minimum damage to the bark, then drew the outline on white paper and scanned the image on a flat-bed scanner (Ricoh MP C4502) to calculate the area (cm^2) (Image J; https://imagej.nih.gov/ij/download.html). Then, we collected all the bark including fallen-off during handling into a paper bag, together oven drying at 60℃. Bark dry mass was measured after 7 × 24 hr. The area-based bark mass equals dry mass divided by area. The percentage of bark mass loss equals the proportional difference of the area-based mass between T_0 and T_4 (Equation 2), which we name minimum bark mass loss (BML_2):

$$BML_2 = \frac{S_0 - S_4}{S_0}, \quad (2)$$

S_0, S_4: area-based dry mass of bark at T_0, T_4 (g/cm^2).

With the above approach, bark coverage loss at T_4 was ignored. This leads to an underestimation when part of the bark falls off during decay. While the detached fragments may represent bark mass loss from the perspective of the log, the extent to which they represent bark mass loss depends on their subsequent decomposition rates, which may differ from those of attached bark. Thus, we contrast BML_2, i.e. assuming bark coverage was 100% at T_4, with maximum bark mass loss (Equation 3, BML_3) considering losses of bark fragments and assuming all the fragments decomposed immediately. To calculate the percentage of bark that fell off, we estimated the fraction of bark cover of each log at T_4 visually, as bark cover at T_0 was always 100% in our study.

$$BML_3 = \frac{S_0 - (S_4 \times C_{B\%})}{S_0}, \quad (3)$$

$C_{B\%}$: the fraction of bark cover at T_4 (%).

The actual bark mass loss should always lie within the range between BML_2 and BML_3.

2.5 | Volume-corrected wood mass loss

To obtain wood mass loss, it is important that density at T_0 and T_4 is expressed on the basis of the original (T_0) volume of the log. In this study, the water replacement method was immediately used for the remaining logs after transporting to the laboratory, while the volume reconstruction work was done afterwards. To estimate the T_0 stem volume (V_r) for the log that has decomposed for years, it is important to avoid biases related to material fragmentation. To reconstruct the initial volume, we drew the outlines of the top and bottom cross-section for each log on paper. For the missing parts, based on visual observation, we reconstructed the original outline on the paper based on the intact or less decomposed part of the log (Figure S3). Then we scanned the reconstruction of the outline and measured the area inside the outline from the scan by image J (see above). Moreover, because the logs were already air dried, volumetric shrinkage due to water loss should be considered. To correct the shrinkage, a volumetric shrinkage value was applied (derived from a literature review see Rijsdijk & Laming, 1994). We obtained the log volume as averaged cross-sectional areas (i.e. top and bottom cross-section of each log) times length of the log based on Newton's method (Ståhl, Ringvall, & Fridman, 2001). The corrected wood mass loss (WML_4) was finally calculated by Equation 4:

$$WML_4 = 1 - \frac{M_4 \times (1 - S_v)}{\rho_0 \times V_r}, \quad (4)$$

V_r: reconstructed T_0 volume (cm^3); S_v: volumetric shrinkage value; M_4: wood dry mass at T_4 (g).

2.6 | Comparing bark and wood decay

To provide a comprehensive test whether there is a correlation between bark and wood decay rates, 10 additional angiosperm species incubated in the same trial in February 2013 (named 2013 cohort, name list see Table 1) were added. Furthermore, for calibration between incubation years, *Fraxinus excelsior* was both incubated in 2012 (named FEX cohort) and 2013 (named 2FEX cohort). These trees had been extracted from and incubated in site F. The decay study started in February 2013 and were harvested after 4 years incubation (February 2017). The experimental design, incubation, sampling and analysis methods were the same as that of 2012 cohort. Area-based bark mass loss and volume-corrected wood mass loss were also measured for these logs. Since wood and bark mass losses between FEX and 2FEX were rather similar for both cohorts (Table S1), we combined all species from 2012 and 2013 cohorts for comparison of bark and wood mass loss.

2.7 | Net mass loss

In order to compare the total mass loss of bark versus wood across tree species (i.e. the bark contribution to log mass loss), we calculated the net mass loss as mass loss multiplied by log biomass (bark + wood). For bark biomass at T_0, it equals area-specific mass of disc A (or E) multiplied by the surface area of the wood (length × circumference). For the wood biomass at T_0, it equals density of disc A (or E) multiplied by V_r.

3 | RESULTS

In our study, all angiosperms (BET, FEX, FSY, POP, PTR and QRO) and two gymnosperms (AGR and PAB) of the 2012 cohort showed a thicker inner bark than outer bark (Figure S1). Within the 2012 cohort species, LKA and FSY showed the highest and lowest outer bark thickness, whereas QRO and PAB showed the highest and lowest inner bark thickness. FEX, FSY and QRO showed a denser wood than bark, LKA and PME showed a similar density between wood and bark, while the other species showed a denser bark than wood (Figure S2).

3.1 | Bark mass loss

There was a significant difference in average bark mass loss estimation across species between BML_2 (ranging from 0.13 to 0.70) and BML_1 (ranging from −0.22 to 0.45) (Figure 2, $p < 0.05$). The averaged BML_2 were **2.99-fold** (Flevoland) and **3.45-fold** (Schovenhorst) higher than the corresponding averaged BML_1 at each site across species. Specifically, all the angiosperm species except FSY showed a significantly higher BML_2 compared with BML_1, whereas all the gymnosperm species except PAB showed a significant difference between BML_2 and BML_1. The average deviation (Figure 3) of bark mass loss between the two methods showed a positive correlation with inner bark thickness (R^2 = 0.176 Flevoland, R^2 = 0.523 Schovenhorst), whereas the outer bark thickness showed no significant effect on the measuring deviation as evidenced by the evenly scattered points of the different thickness classes around the regression line in Figure 3. The deviation also varied with higher taxa: angiosperms showed a stronger deviation than gymnosperms (Figures 3 and 4).

Including the fraction of bark cover had a strong effect ($p < 0.05$) on the bark mass loss based on the averaged BML_3 across species at

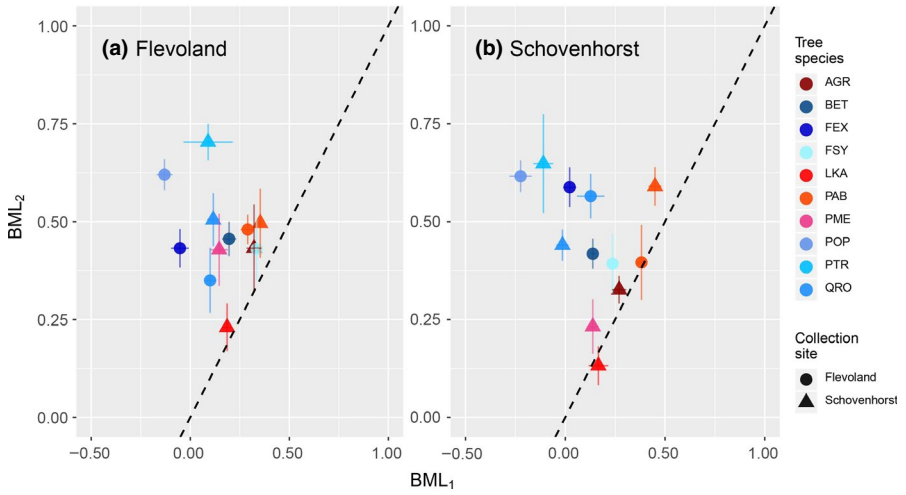

FIGURE 2 Comparison of area-based (BML_2) versus density-based (BML_1) bark mass loss over 4 years of decomposition. The dashed line is the 1:1 line. Each point with error bar indicates $M \pm SE$ ($N = 5$). Tree species are categorized into angiosperms (blue colours) and gymnosperms (red colours). See Table 1 for full names relating to species codes. Panels (a) and (b) show results at two environmentally contrasting incubation sites. There is a significant difference between BML_2 and BML_1 for tree species BET ($p = 0.017$), FEX ($p = 0.004$), PAB ($p = 0.002$), POP ($p < 0.001$), PTR ($p = 0.043$) and QRO ($p = 0.001$) in Flevoland, and BET ($p = 0.003$), FEX ($p < 0.001$), POP ($p < 0.001$) and QRO ($p < 0.001$) in Schovenhorst based on paired sample t tests, $df = 4$ for each species

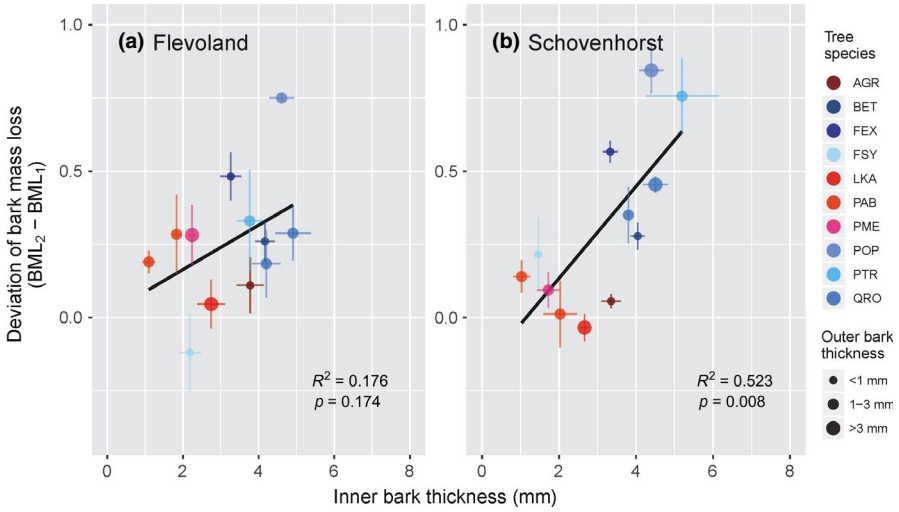

FIGURE 3 Correlations between the deviation of (BML_2 − BML_1) and inner bark thickness, for different categories of outer bark thickness, across species. Each point with error bar indicates $M \pm SE$ ($N = 5$). Panels (a) and (b) show results at two environmentally contrasting incubation sites. The correlation is at the species level

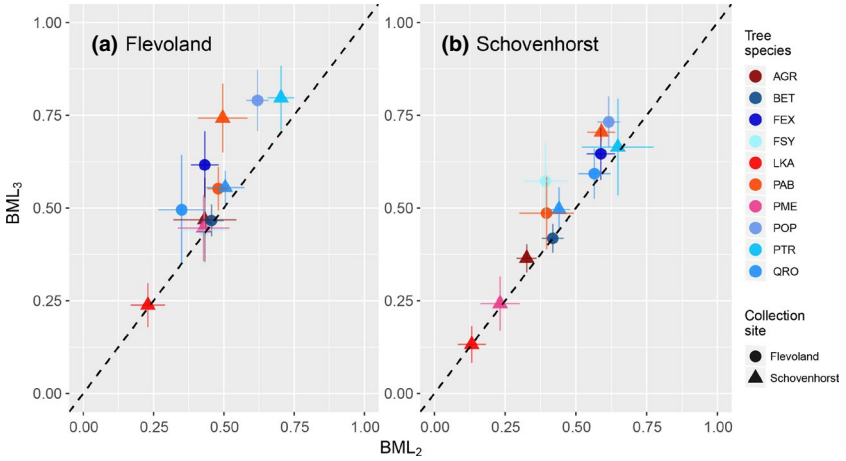

FIGURE 4 The comparison of including (BML_3) versus excluding (BML_2) bark coverage loss on measuring area-based bark mass loss over 4 years of decomposition. The dashed line is the 1:1 line. Each point with error bar indicates $M \pm SE$ ($N = 5$). So the vertical length from each point to the 1:1 line along *y* axis represents the real bark mass loss range of each species. Panel (a) and (b) showed results at two environmentally contrasting incubation sites. There is a significant difference between the BML_3 and BML_2 for tree species POP ($p = 0.025$) and PAB ($p = 0.026$) in Flevoland, and AGR ($p = 0.027$), PAB ($p = 0.002$), FSY ($p = 0.018$) and QRO ($p = 0.044$) in Schovenhorst based on paired sample *t* tests, $df = 4$ for each species

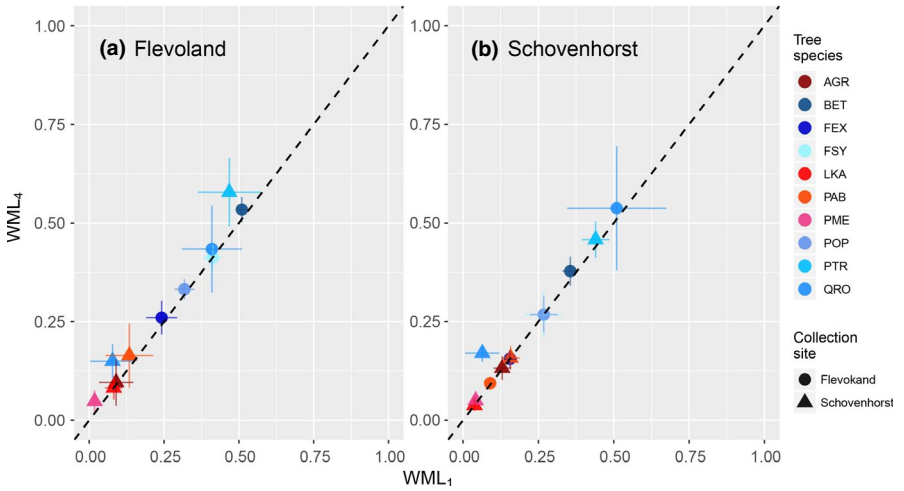

FIGURE 5 Comparison of volume-corrected (WML_4) versus density-based (WML_1) wood mass loss over 4 years of decomposition. The dashed line is the 1:1 line. Each point with error bar indicates $M \pm SE$ ($N = 5$). Panel (a) and (b) showed results at two environmentally contrasting incubation sites. There is a significant effect of volume reconstruction on wood mass loss mainly for PTR ($p = 0.012$) and PAB ($p = 0.053$) in Flevoland, and QRO ($p = 0.041$) in Schovenhorst based on paired sample *t* tests, $df = 4$ for each species

both sites, with **1.20-fold** higher values at Flevoland and **1.13-fold** at Schovenhorst than BML_2. Specifically, gymnosperm PAB and AGR, and angiosperm FSY, POP and QRO showed a significant increase in bark mass loss when bark cover was taken into account in the calculation (BML_3).

3.2 | Wood mass loss

Compared to bark mass loss, there was a relatively minor but still significant influence of the reconstruction method for wood mass loss (WML_5) across species, ranging from **1.12-fold** higher values at Flevoland to **1.08-fold** higher values at Schovenhorst than WML_1 (Figure 5). The reconstruction method mainly affected species POP, PAB and QRO.

3.3 | Cross-species comparison of bark and wood in mass loss and net mass loss

The averaged BML_2 was **2.00-fold** higher than WML_4 across all species (2012 and 2013 cohort, Figure 6). There was a positive albeit rather weak correlation ($R^2 = 0.26$, $p = 0.006$) between BML_2 and WML_4. There is also a similar correlation between BML_3 and WML_4 ($R^2 = 0.13$, $p = 0.032$). Specially, the angiosperms showed relatively higher BML_2 (ranging from **0.35** to **0.75**) coupled with higher WML_4 (ranging from **0.15** to **0.56**), while gymnosperms had a large variation in BML_2 (ranging from **0.16** to **0.58**), and a constraint and low WML_4 (ranging from **0.00** to **0.15**).

The averaged percentage of bark dry mass relative to whole-log dry biomass was 19.9% in undecomposed dead trees (Figure 7). The net mass loss of bark relative to the whole-log mass loss during the

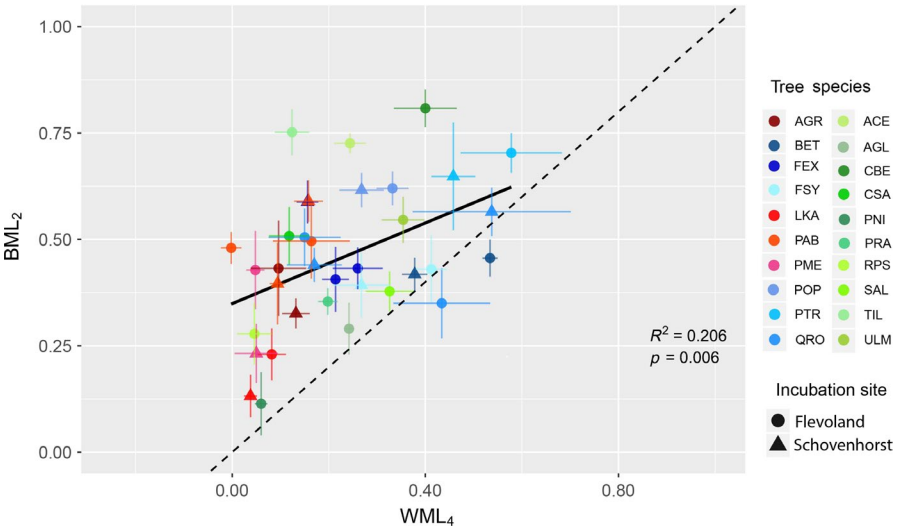

FIGURE 6 Comparison of minimum bark mass loss (BML_2) and volume-corrected wood mass loss (WML_4) across species over 4 years of decomposition. The dashed line is the 1:1 line. Each point with error bar indicates $M \pm SE$ ($N = 5$). Tree species with green colours are the 2013 cohort. See Table 1 for full names relating to species codes. The correlation is at the species level

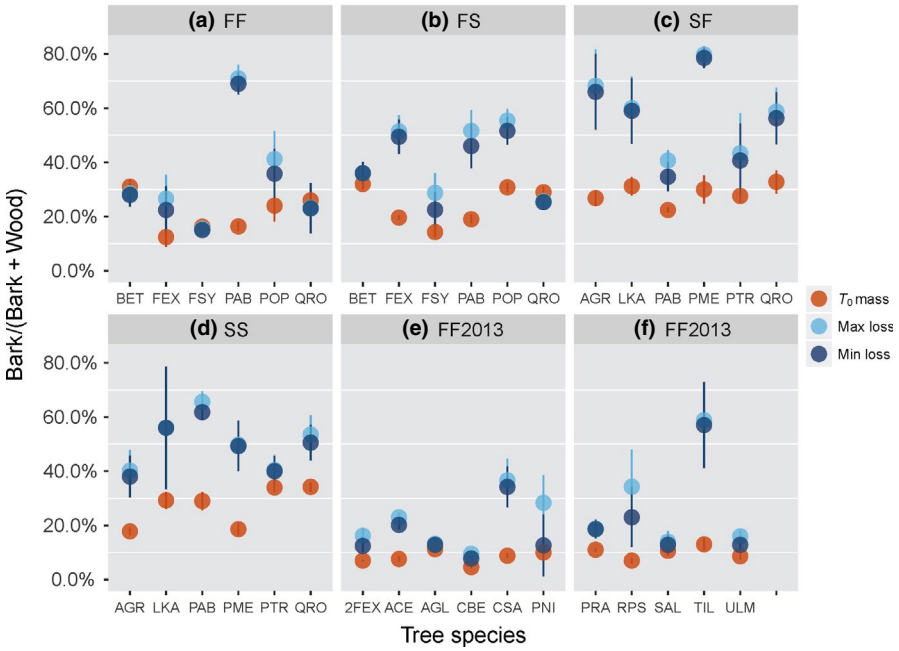

FIGURE 7 Percentage of the bark relative to total stem dry biomass before decomposition (T_0 mass) and net bark mass loss to whole stem mass loss (gram, bark + wood) over 4 years of decomposition. Each point with error bar indicates $M \pm SE$ ($N = 5$). Max loss: maximum bark net mass loss to whole stem loss; Min loss: minimum bark net mass loss to whole stem loss. Panels (a)–(d) show species of the 2012 cohort, and (e)–(f) show species of the 2013 cohort. The two capitals on top of each panel give information of the collection site (first capital) and incubation site (second capital). F, Flevoland; S, Schovenhorst

4 years of decomposition was 36.1% without considering bark fragment loss (Min loss) and the percentage increased to 39.3% when including bark fragment loss (Max loss). Specifically, gymnosperm bark contributed 57.8% (Max loss) and 55.3% (Min loss) to whole-log mass loss, whereas angiosperm bark contributed 32.3% (Max loss) and 28.9% (Min loss).

4 | DISCUSSION

Methods for assessing woody debris decay rates have been of high priority in forest ecology and management for a long while (Harmon et al., 2008). Our approach of measuring bark mass loss using an area-based method and wood mass loss using volume reconstruction of initial dimensions for decaying logs can help reduce the error and uncertainty of estimation. Compared with previous approaches, our easy methodology can be applied to field investigations and experimental laboratory field studies, such as climate chamber incubation, common garden experiments and reciprocal exchange incubations, for various research purposes, and it can cover a wide range of decay stages and size classes of woody debris. The classification using decay classes has been widely used in chronosequence and decomposition-vector studies, even though it is rather subjective and the number of decay classes used ranges from 2 to 13 (Freschet et al., 2012; Kubartova, Ottosson, Dahlberg, & Stenlid, 2012), making comparisons among studies difficult. Our suggested methodology enables a more reliable comparison between bark and wood decay within and across species, which is important for making better predictions of whole-log decomposition rates with changing forest tree composition. Our results, based on 20 tree species of

wide-ranging phylogenetic and ecological position, showed that on average, over 4 years, bark decomposed twice as fast as wood across species. Furthermore, bark and wood mass loss were significantly positive correlated albeit rather weakly (R^2 = 0.26, p = 0.006). More work still needs to be done to understand which internal or external factors affect this bark-wood decay correlation as well as the substantial scatter around it.

4.1 | Considerations for measuring bark and wood decay

The functional difference between inner and outer bark also showed a strong afterlife effect on dead bark decay. Asynchronous volume loss of inner and outer bark makes estimation of bark mass loss via density loss highly questionable, as we demonstrated. This difference between the two kinds of mass loss was especially strong for the angiosperms both in our field experimental condition and in a previous field monitoring investigation (Shorohova et al., 2016). Compared with the temperate tree species tested in our study, relatively thick inner barks are expected in tropical humid regions because of more vigorous growth of the trees and because the climate permits more or less continuous growth almost throughout the year (Roth, 1981). Thus, we strongly recommend the area-based method to estimate bark mass loss across different climatic regions. Previous studies found that different decay rates between cellulose-rich parenchymatous cells and more recalcitrant lignified and suberized cells in *Picea abies* and *Fagus sylvatica* barks resulted in strong inner bark thickness loss within 6 weeks of decay followed by a slight outer bark thickness loss by the end of the third year (Parameswaran & Wilhelm, 1979). In our study, we found an increased bark mass loss using the area-based method for both species, moreover, other species with thicker inner bark showed much stronger measurement deviation (Figure 3). The asymmetric loss of volume between inner and outer bark makes estimation of whole-bark mass loss difficult with previous methods. In litterbag studies with pre-weighed bark samples detached from the wood, mass loss can be measured directly and accurately (Dossa et al., 2018). However, this direct method cannot be used for bark that remains attached to the log, which makes it difficult to provide data to prove how accurate our new method is. Still, as area should be a much more stable expression base for bark mass loss than volume, we consider the area-based method to be a reliable approach. Our method also provides the possibility to better study mass loss in inner and outer bark separately. Another disadvantage of our method might be the destruction of the bark sample, although in our specific decomposition experiment the sequential sampling of logs pre-empted the need for re-using the bark samples.

Wood mass loss starts with density loss, followed by volume loss years later for most tree species. Especially species with less decay-resistant sapwood tend to show volume loss soon after decay has started. Thus, the selective choice of these species for volume reconstruction is necessary and we suggest that this choice should also include decay period and log size. We only found a slight volume loss for *Picea abies*, *Populus tremula* (POP) and *Quercus robur* (QRO) over the first 4 years of decomposition, while the other species still had a largely intact structure. Another study monitoring volume loss of *Picea abies* (Harmon et al., 1999) and *Fagus sylvatica* (Müller-Using & Bartsch, 2009) found significant volume depletion after 8 and 6 years of decay, respectively, which showed no conflict with our result. We broadly infer from these findings that studies using a decay model that estimates a decay constant based on density loss get large underestimations when the coarse woody material decays for more than 5 years. Compared with our user-friendly method, using a trunk shape function to calculate the green volume (Müller-Using & Bartsch, 2009) requires quantities of background datasets collected from the same species and similar site, which is not always possible especially for investigations in protected forest. Other methods based on the circle area formula may give large errors when the cross-section is irregular in shape, which is very common. Moreover, none of these methods consider bark mass loss separately. Our method of calculating wood cross-section area directly can effectively avoid such errors and also enable a separate focus on the bark and wood decay.

4.2 | The relationship between bark and wood decay

Our finding that after 4 years bark generally decayed twice as fast as coarse wood is consistent with previous knowledge that bark is nutritious, has high water storage capacity and is more exposed to the decomposers from the external environment in comparison to the wood (Ulyshen, Müller, & Seibold, 2016), and that bark can act as physical and chemical defenses preventing decomposes accessing to the wood at early decay stages. Furthermore, the result that bark always decomposed faster than wood even though the initial density of bark is higher than wood for most species, and the result that the fast decay rate of bark is mainly positively correlated with the thickness of inner bark (Figure S4), all hint at a need to consider inner and outer bark separately to deepen our understanding of the decay dynamics of bark. A cask effect of outer bark on the total bark decay rate and predominant control of inner bark on early stage bark decay rate are apparent from our results. For instance, *Betula pendula*, with thick, fast-turnover inner bark and resinous, recalcitrant, paper-like outer bark that tends to be retained around the log for several years, first showed a similar bark and wood mass loss over 4 years of decomposition in our study (Figure 6), whereas wood decayed faster than bark later based on a 10 years' decomposition study (Johnson, Siccama, Denny, Koppers, & Vogt, 2014). This change suggests a tipping point in the bark decomposition, after which mainly outer bark remains and total bark mass loss decreases. This also suggests that the pattern of decay rate of bark versus wood would change as decay advanced, and that the variation within bark (i.e. inner vs. outer bark) matters. Tree species with a thick outer bark and relatively thin inner bark are more common in fire-prone regions (Rosell, 2016). A different decay pattern of bark decay rate and ratio of bark

to wood decay would be expected for tree species in such regions. Tree species in the same region may thus converge in inner and outer bark traits, resulting in coupled bark and wood decay rates, but this hypothesis is in need of in-depth study in order to deepen our understanding of dead tree decay dynamics.

We also found a significant positive albeit weak correlation between bark and wood mass loss. We hypothesize that there is a much tighter relationship in mass loss between inner bark and sapwood across species, as both represent the tissues involved in metabolic processes that are likely coupled. The shared ontogenetic origin (from cambium) between inner bark and (sap)wood (Evert, 2006), as opposed to the separate origin of outer bark (often from cork cambium), may link the decomposability of inner bark and sapwood via the afterlife effects of their trait coordination (such as density, stiffness and water capacity; Rosell et al., 2014). Testing this hypothesis would require separating inner bark from outer bark and sapwood from heartwood (in heartwood forming species) or inner wood, which is a practically challenging but worthwhile aim for future study. Another possible reason for the rather weak coupling between bark and wood mass loss may be that bark becomes detached as decay advances, but this process can probably be suppressed when the log is rapidly buried by litter, soil or ground vegetation after tree fall. In one of our study sites (Flevoland), some logs gradually became strongly overgrown by moss after one year of decomposition, which could have strongly affected the interaction between decomposition of bark and wood interaction (Chang et al., 2019). Furthermore, wood with low density (i.e. larger vessels, or thin-walled fibres) is easily accessible to micro-organisms and can provide a favourable environment for microbial activity in terms of moisture and oxygen conditions, thus being less affected by bark cover, especially in logs with unsealed ends which is common in the field (Ulyshen et al., 2016), as it was in our experiment.

5 | CONCLUSIONS

This study has pinpointed the best potential methods for measuring bark and wood mass loss rate across diverse woody species, and has shown that which methodology is applied really matters for comparing the relationship between bark and wood decay dynamics. Previous studies calculating a decay constant or mass half-life based on density loss probably yield strong underestimations for wood mass loss and even stronger underestimations for angiosperm bark mass loss. The fraction of bark left on the wood decreases with time and the decay degree of bark has fallen off should also be considered in estimating bark mass loss. We can define the range of bark mass losses by calculating minimum and maximum bark mass loss, even though the exact bark mass loss is hard to measure. Log wood volume reconstruction already matters somewhat to wood mass loss rates within 4 years of decomposition in a temperate region, but will become even more important as decay progresses. A positive correlation in mass loss was observed between bark and wood across species over 4 years in this study, but it was rather weak and needs to be studied in more detail. We expect this relationship to be stronger if inner and outer bark mass loss are detected separately and inner bark mass loss is compared with (sap)wood mass loss across tree species, as these are both related to metabolically active organs shortly before tree death. In general, inner and outer bark decay should be considered separately to achieve a better understanding of bark decay as the ratio of inner to outer bark thickness and the traits of inner and outer bark could alter the relative decay rates of bark to wood.

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AUTHORS' CONTRIBUTIONS

J.H.C.C., C.C. and R.S.P.v.L. conceived the ideas and designed the methodology; all authors made contributions to data collection via fieldwork or laboratory work; C.C. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository: Chang et al. (2020), https://doi.org/10.5061/dryad.pk0p2ngjw.

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REFERENCES

Andringa, J. I., Zuo, J., Berg, M. P., Klein, R., van't Veer, J., de Geus, R., … Cornelissen, J. H. C. (2019). Combining tree species and decay stages to increase invertebrate diversity in dead wood. *Forest Ecology and Management*, *441*, 80–88. https://doi.org/10.1016/j.foreco.2019.03.029

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

Chang, C. H., Wu, F. Z., Wang, Z., Tan, B., Cao, R., Yang, W. Q., & Cornelissen, J. H. C. (2019). Effects of epixylic vegetation removal on the dynamics of the microbial community composition in decaying logs in an Alpine Forest. *Ecosystems*, *22*, 1478–1496. https://doi.org/10.1007/s10021-019-00351-3

Chang, C., van Logtestijn, R. S. P., Goudzwaard, L., van Hal, J., Zuo, J., Hefting, M., … Cornelissen, J. H. C. (2020). Data from: Methodology matters for comparing coarse wood and bark decay rates across tree species. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.pk0p2ngjw

Cornelissen, J. H. C., Sass-Klaassen, U., Poorter, L., van Geffen, K., van Logtestijn, R. S., van Hal, J., … Hefting, M. M. (2012). Controls on coarse wood decay in temperate tree species: Birth of the LOGLIFE experiment. *Ambio*, *41*(Suppl 3), 231–245. https://doi.org/10.1007/s13280-012-0304-3

Dossa, G. G. O., Schaefer, D., Zhang, J. L., Tao, J. P., Cao, K. F., Corlett, R. T., … Harrison, R. D. (2018). The cover uncovered: Bark control over wood decomposition. *Journal of Ecology*, *106*, 2147–2160. https://doi.org/10.1111/1365-2745.12976

Evert, R. F. (2006). *Esau's plant anatomy: Meristems, cells, and tissues of the plant body: Their structure, function, and development*. Hoboken, NJ: John Wiley & Sons.

Franceschi, V. R., Krokene, P., Christiansen, E., & Krekling, T. (2005). Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytologist*, *167*, 353–375. https://doi.org/10.1111/j.1469-8137.2005.01436.x

Fraver, S., Milo, A. M., Bradford, J. B., D'Amato, A. W., Kenefic, L., Palik, B. J., … Brissette, J. (2013). Woody debris volume depletion through decay: Implications for biomass and carbon accounting. *Ecosystems*, *16*, 1262–1272. https://doi.org/10.1007/s10021-013-9682-z

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

Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S. V., Lattin, J. D., … Cummins, K. W. (1986). Ecology of coarse woody debris in temperate ecosystems. In A. MacFadyen & E. D. Ford (Eds.), *Advances in ecological research* (pp. 133–302). Orlando, FL: Academic Press.

Harmon, M. E., Krankina, O. N., & Sexton, J. (1999). Decomposition vectors: A new approach to estimating woody detritus decomposition dynamics. *Canadian Journal of Forest Research*, *30*, 76–84. https://doi.org/10.1139/x99-187

Harmon, M. E., Woodall, C. W., Fasth, B., & Sexton, J. (2008). *Woody detritus density and density reduction factors for tree species in the United States: A synthesis*. General Technical Reports No. NRS-29, 84p. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA.

Hérault, B., Beauchêne, J., Muller, F., Wagner, F., Baraloto, C., Blanc, L., & Martin, J.-M. (2010). Modeling decay rates of dead wood in a neotropical forest. *Oecologia*, *164*, 243–251. https://doi.org/10.1007/s00442-010-1602-8

Johnson, C. E., Siccama, T. G., Denny, E. G., Koppers, M. M., & Vogt, D. J. (2014). In situ decomposition of northern hardwood tree boles: Decay rates and nutrient dynamics in wood and bark. *Canadian Journal of Forest Research*, *44*, 1515–1524. https://doi.org/10.1139/cjfr-2014-0221

Kahl, T., Arnstadt, T., Baber, K., Bässler, C., Bauhus, J., Borken, W., … Gossner, M. M. (2017). Wood decay rates of 13 temperate tree species in relation to wood properties, enzyme activities and organismic diversities. *Forest Ecology and Management*, *391*, 86–95. https://doi.org/10.1016/j.foreco.2017.02.012

Kubartova, A., Ottosson, E., Dahlberg, A., & Stenlid, J. (2012). Patterns of fungal communities among and within decaying logs, revealed by 454 sequencing. *Molecular Ecology*, *21*, 4514–4532. https://doi.org/10.1111/j.1365-294X.2012.05723.x

Müller-Using, S., & Bartsch, N. (2009). Decay dynamic of coarse and fine woody debris of a beech (*Fagus sylvatica* L.) forest in Central Germany. *European Journal of Forest Research*, *128*, 287–296. https://doi.org/10.1007/s10342-009-0264-8

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., … Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science*, *333*, 988–993. https://doi.org/10.1126/science.1201609

Parameswaran, N., & Wilhelm, G. E. (1979). Micromorphology of naturally degraded beech and spruce barks. *European Journal of Forest Pathology*, *9*, 103–112. https://doi.org/10.1111/j.1439-0329.1979.tb00667.x

Rijsdijk, J. F., & Laming, P. B. (1994). *Physical and related properties of 145 timbers: Information for practice*. Dordrecht, The Netherlands: Springer Science & Business Media.

Rosell, J. A. (2016). Bark thickness across the angiosperms: More than just fire. *New Phytologist*, *211*, 90–102. https://doi.org/10.1111/nph.13889

Rosell, J. A., Gleason, S., Mendez-Alonzo, R., Chang, Y., & Westoby, M. (2014). Bark functional ecology: Evidence for tradeoffs, functional coordination, and environment producing bark diversity. *New Phytologist*, *201*, 486–497. https://doi.org/10.1111/nph.12541

Roth, I. (1981). *Structural patterns of tropical barks*. Berlin, Germany: Borntraeger.

Shorohova, E., & Kapitsa, E. (2014). Mineralization and fragmentation rates of bark attached to logs in a northern boreal forest. *Forest Ecology and Management*, *315*, 185–190. https://doi.org/10.1016/j.foreco.2013.12.016

Shorohova, E., Kapitsa, E., Kazartsev, I., Romashkin, I., Polevoi, A., & Kushnevskaya, H. (2016). Tree species traits are the predominant control on the decomposition rate of tree log bark in a mesic old-growth boreal forest. *Forest Ecology and Management*, *377*, 36–45. https://doi.org/10.1016/j.foreco.2016.06.036

Ståhl, G., Ringvall, A., & Fridman, J. (2001). Assessment of coarse woody debris: A methodological overview. *Ecological Bulletins*, *49*, 57–70. https://doi.org/10.2307/20113264

Ulyshen, M. D., Müller, J., & Seibold, S. (2016). Bark coverage and insects influence wood decomposition: Direct and indirect effects. *Applied Soil Ecology*, *105*, 25–30. https://doi.org/10.1016/j.apsoil.2016.03.017

Ulyshen, M. D., & Wagner, T. L. (2013). Quantifying arthropod contributions to wood decay. *Methods in Ecology and Evolution*, *4*, 345–352. https://doi.org/10.1111/2041-210x.12012

Weedon, J. T., Cornwell, W. K., Cornelissen, J. H., Zanne, A. E., Wirth, C., & Coomes, D. A. (2009). Global meta-analysis of wood decomposition rates: A role for trait variation among tree species? *Ecology Letters*, *12*, 45–56. https://doi.org/10.1111/j.1461-0248.2008.01259.x

Zuo, J., Berg, M. P., Klein, R., Nusselder, J., Neurink, G., Decker, O., … de Briones, M. J. (2016). Faunal community consequence of interspecific bark trait dissimilarity in early-stage decomposing logs. *Functional Ecology*, *30*, 1957–1966. https://doi.org/10.1111/1365-2435.12676

Zuo, J., Hefting, M. M., Berg, M. P., van Logtestijn, R. S. P., van Hal, J., Goudzwaard, L., … Cornelissen, J. H. C. (2018). Is there a tree economics spectrum of decomposability? *Soil Biology and Biochemistry*, *119*, 135–142. https://doi.org/10.1016/j.soilbio.2018.01.019

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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