Article

Title: Carbon fractions in the world's dead wood

Authors and Affiliations:
Adam R. Martin[1,*], Grant M. Domke[2], Mahendra Doraisami[1], Sean C. Thomas[3]
[1] Department of Physical and Environmental Sciences, University of Toronto Scarborough, Canada.
[2] USDA Forest Service, Northern Research Station, St. Paul, Minnesota, USA
[3] Graduate Department of Forestry, Daniels Faculty of Architecture, Landscape, and Design, University of Toronto, Toronto, Ontario, Canada

Corresponding author contact information:
Email: adam.martin@utoronto.ca, Phone: 001-647-607-7058

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Alarming increases in tree mortality due to environmental change suggest that contributions of dead wood to global carbon (C) cycles are rapidly increasing [1-3], with dead wood C flux estimates already approximating total annual anthropogenic C emissions [4]. Quantifying C in dead wood critically depends on accurate estimates of dead wood C fractions (CFs) to convert dead woody biomass into C. Most C accounting protocols, including those recently revised by the IPCC [5], utilize a default dead wood CF of 50%, but live tree studies suggest this assumption results in substantial bias in forest C estimates [6]. Here we compile and analyze a global database of dead wood CFs in trees, showing that dead wood CFs average 48.5% across forests worldwide, deviating significantly from 50%, with systematic variation among biomes, plant phyla, tissue types, and decay classes. Accounting for data-driven dead wood CFs corrects systematic overestimates in global dead wood C stock estimates of ~1.6 Pg C, an estimate approaching annual C flux estimates from land-use change globally [7]. Our analysis provides, for the first time, robust empirical CFs for dead wood globally to inform global terrestrial C accounting protocols, and revise estimates of forest C stocks and fluxes.

Forests are a large and dynamic part of the global carbon (C) cycle with estimates indicating an annual average net global forest C sink of 1.1-1.4 Pg C y^{-1} in recent decades [7,8]. Global forest C sinks owe to high net uptake in regenerating forests of ~1.3 Pg C year^{-1}; intact forests contribute an additional sink of 0.85-2.4 Pg C year^{-1} [7,8], though with evidence of a declining trend in the tropics [1]. These sinks are offset by losses of C due to deforestation and forest degradation, particularly in tropical regions where forest loss accounts for ~0.43-1.3 Pg C year^{-1} on average [7,9].

Estimates of C stocks and fluxes in woody debris – i.e., fallen and standing dead trees, branches, and other woody tissues – are a critical component of forest C dynamics. Dead wood accounts for ~8% (or 73 Pg) of total C pool in forests globally [7], and global fluxes of C due to woody decomposition range from 2-11 Pg C y^{-1}, e.g. [10]; the upper estimates of this range approximate the 2008-17 decadal average of total anthropogenic C emissions (~9.4 Pg C year^{-1} [4]). There is also wide biogeographic variability in dead wood C stocks and fluxes. For instance, dead wood C stocks represent ~3-25% of total forest C storage depending on biome, with this variability attributable to differences in primary production, tree mortality, and decomposition rates that are linked with climate and species' wood traits [10-12]. Dead wood C dynamics are also sensitive to fine-scale disturbances such as harvesting, windstorm impacts, and pest or pathogen outbreaks e.g. [13,14].

Given its importance in the global C cycle, robust methods for quantifying C in woody debris are critical for estimating forest C stocks and fluxes at multiple scales. One important consideration in estimating dead wood C fluxes that has received limited attention, is the proportion of C in dead wood, as is used to convert dead wood biomass into C stocks [15]. Assessments of dead wood C have most often utilized a single generalized C fraction (CF) – that wood is comprised of 50% C on a mass/mass basis – when converting woody debris mass to C [16-20]. Recent studies have made clear that 50% is a poor approximation of CFs in live trees: the best available live wood CF average is ~47.6%, and this estimate ranges from 28-65% across biomes, species, and tissue types [6,21]. In live trees, accounting for variability in wood CF corrects major systematic errors in forest C stocks [6,21,22]. For example, accounting for live wood CF refines existing over-estimates of up to 20.1 Pg C in tropical forests [6]. Nevertheless, generalized dead wood CFs have not been obtained for the purposes of global forest C estimation. Instead dead wood CF estimates remain scattered throughout multiple individual studies e.g. [23], making calculations of robust dead wood CFs, and their integration into forest C accounting protocols, highly challenging.

Identifying the factors explaining differences in woody debris CFs has also remained elusive in the absence of data consolidation. Arguably the most important factor driving dead wood CF variability is the decay process, commonly discretized as wood decay class (DC). There is disagreement in the literature as to the magnitude and direction of changes in CF through decomposition. For instance, studies from temperate and tropical forests have detected little to no change in CFs through decomposition [24-26], others have found increases in CFs [27,28], while others report both decreasing and increasing trends depending on phyla (i.e., conifers vs. angiosperms) and tissue type [23,29-33]. In the absence of a global data compilation and analysis, these contrasting patterns pose a challenge for estimating "generic" changes in CFs through wood decay.

Data on CF from live trees also suggests tissue-specific variability in dead wood CF will be pronounced. Specifically, there is likely to be especially high CFs in bark vs. other tissues, due to their high concentrations of C-rich and recalcitrant compounds such as lignin, suberin, and tannins [34-36]. Finally, the position of dead wood – i.e., standing vs. downed – may also influence CFs [15], but hypotheses and findings related to this are mixed with some research suggesting that standing dead wood has higher CFs vs. downed wood [23], while other lines of evidence suggest the opposite [37]. Whether or not these differences are systematic and/or independent of other factors such as biome, species identity, and DC, is unclear, as is the relative importance of these factors.

Here we develop, for the first time, a novel global dataset of 973 dead wood CF observations from 112 species and all forested biomes, to inform forest C estimation and to identify the primary factors determining dead wood CFs in trees. We specifically evaluate: 1) Do dead wood CFs differ from (a) the generalized 50% CF value commonly employed in forest C accounting, and (b) live wood CFs? As a corollary we also assess: 2) if live wood CFs predict dead wood CFs within species, 3) is there systematic and generalizable variability in dead wood CFs across biomes, species, position, and decay classes, and 4) how do dead wood CFs change through decomposition?

Dead wood carbon fractions compared to IPCC protocols and live wood

Dead wood CFs ranged widely from 29.4-60.2% across the compiled dataset, with an average CF estimate of 48.5±0.8% (s.e.). Dead wood CFs are significantly lower than the widely assumed 50% CF estimate by 1.5% on average (two-sided z=-6.2, p<0.001). Average estimated dead wood CFs are also significantly larger than live wood CF which average 47.2±0.8% ($F_{1,\,3392.7}$=67.7, p<0.001; Fig. 1). Across 63 species with both dead and live wood CFs, average live wood CFs were significantly and strongly related to average dead wood CFs (r^2=0.462, p<0.001, Fig. S1). This relationship differed significantly from a 1:1 relationship across the entire species pool (model slope=0.7±0.1 (s.e.), linear hypothesis test p=0.011). The intercept of the live-dead wood CF relationship, but not the slope, differed significantly across groups (p<0.001; Fig. S2, Tables S5, S6, S7). Including phyla-specific intercepts in the linear model (i.e., for angiosperms and conifers individually) explained an additional ~15% of the variation in dead wood CFs (i.e., model r^2 when including plant phyla-specific intercept terms=0.601).

Factors explaining variation in dead wood carbon fractions

Dead wood CFs varied significantly across biomes, phyla (i.e., conifers and angiosperms), tissue types, and DC (ANOVA $p<0.001$; Table S1). ANOVA revealed significant interactions between biome and phylum, tissue type, and DC, as well as between position and tissue type (Table S1). Variance partitioning indicated that the largest proportion of variability in dead wood CFs was associated with biome (23.1% of variance explained), with systematic and significant differences across all of the biomes represented (Fig. 2, Tables 1, S2, S3). Accounting for all other factors, dead wood CFs in temperate and boreal biomes (49.3±0.8% and 48.8±0.8%, respectively) were ~1.7-3.1% greater than those observed in subtropical/Mediterranean and tropical biomes (46.2±0.8 and 47.2±0.8, respectively; Fig. 2, Table 1). Tissue type was also a significant factor explaining 18.9% of variability in dead wood CFs (Fig. 2, Tables 1, S2). Bark, fine tissue, and stem wood showed the largest average dead wood CFs (48.1-48.8%), roots being intermediate (47.8%), and branches showing the lowest average dead wood CF estimates (45.7%; Fig. 2, Tables 1, S2).

Phylum also explained a significant proportion (7.6%) of the variability in dead wood CFs ($p<0.001$; Tables S2, S3), with gymnosperms dead wood CFs being 2.0% higher on average compared to angiosperms (Fig. 2, Table 1). Decay class explained 8.8% of the variation ($p<0.001$, Tables S2, S3), with systematic increases in dead wood CFs occurring across DCs 1-3 (average dead wood CF 47.5-48.0%), to DCs 4 and 5 (average dead wood CFs 48.7% and 48.6, respectively; Fig. 2, Table 1). There were only slight differences in the CFs of standing vs. downed wood ($p=0.05$; Fig. 2, Table 1). In total, the factors considered here accounted for 58.6% of the variance in dead wood CFs (Table S2).

In the subset of data ($n=431$) for which coarse wood debris (CWD) size was available, dead wood CFs did vary widely across size categories with diameter accounting for 7.4% of the variability (Table S2). When CWD diameter was included in the variance partitioning model, biome, tissue type, and DC class accounted for the largest proportion of explained variation (31.8%, 14.4%, and 14.7%, respectively), and variance explained by the model increased to 68.3% (Table S2).

Dead wood carbon fractions across decay classes

Based on a large subset of data (i.e., species with dead wood CFs from at least four DCs; where n=728 observations across n=56 species; Table S4) patterns of change in dead wood CFs with increases in DC varied widely. The majority of species (41 of 56) showed increases in dead wood CF with increasing DC, with species-specific slopes ranging from 0.03-1.64; these changes were statistically significant (i.e., slope $p \leq 0.05$) in only 5 species (Fig. 3, Table S5). In these 41 species, across DCs 1-5 dead wood CF was predicted to increase on average from 0.15-8.2% (Fig. 3). The remaining 15 species showed trends of declining dead wood CF with increasing DC (slope $p \leq 0.05$ in six instances), with slopes ranging from -0.04 to -4.14% (Fig. 3). The five species with the strongest negative trends (slope $p \leq 0.002$ in all cases) were all subtropical/ Mediterranean angiosperm species (Fig. 3, Table S5).

Dead wood carbon fractions and forest C accounting

Prominent forest C protocols, namely those of the IPCC [5], are a critical tool in compiling forest C budget data globally, and support the implementation and monitoring of critical climate change policies and programs. Reducing uncertainty in forest C estimates is therefore a key priority, with the most recent updates to the IPCC protocols updating key C accounting variables such as tree biomass stocks and growth rates (e.g., Tables 4.4 and 4.7 in [5]). However, the 2019 Refinement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories [5] included no updates to dead wood CFs – or wood CFs in general, despite considerable research on this topic [6] – and instead only recommend a 50% CF as the default value for dead wood in temperate forests; there is no IPCC-recommended CF estimate suggested for dead wood in tropical or subtropical forests.

While deviations in dead wood CFs from the widely used 50% assumption appear small (i.e., 1.5% on average; Fig. 2, Table 1), our findings suggest that existing estimates of dead wood (and hence forest) C stocks are significantly overestimated. For example, global forest C inventories that assumed a 50% dead wood CF, reported a global dead wood C stock of 72.9 Pg C in 2007 [7]. However, in employing our average dead wood CF of 48.5%, we would estimate this number at 70.7 Pg C. This difference of ~2.2 Pg C is equivalent to 2/3 of the total dead wood C stock in the entire temperate forest biome, which was estimated for the year 2007 as 3.3 Pg C by Pan et al. [7]. This overestimate of 2.2 Pg C also falls well within estimated error bounds for total C fluxes from land-use change annually [4].

When compared to other sources of uncertainty in forest C assessments, dead wood CFs can be a minor consideration [38]. Yet these biases are systematic and easily corrected. Our findings of systematic variation in dead wood CFs across biomes, tissue types, and DCs (and to lesser extent taxonomic groups and size classes; Table S2), support the calculation and promulgation of generalized dead wood CFs for the purposes of forest C accounting (Table 1). The dead wood CF data compiled here, along with CFs from live wood [6], provide a basis for better supported approximations of CFs in trees and wood globally as compared to current IPCC protocols [5].

Factors explaining systematic variation in dead wood carbon fractions

Our study uncovers the following general patterns in CFs across dead wood globally: A) lower dead wood CFs in tropical vs. other forest biomes, B) lower dead wood CFs in angiosperms vs. gymnosperms, and C) higher dead wood CFs in bark vs. other tissues (Table 1). These results are consistent with studies on live wood CF variability [6,34,35,39], and perhaps are not surprising given the strong relationship between dead and live wood CFs observed in a subset of tree species evaluated here (Fig. S2). Based on similarities in how dead and live wood CFs vary across and within species, our study indicates that live wood chemical traits (along with their environmental and evolutionary drivers) also play a deterministic “afterlife” role *sensu* [40] in driving dead wood C dynamics.

There is considerable variability in patterns of dead wood CF change through decay (Fig. 3), suggesting that multiple mechanisms operate across different species and forest regions. Cellulose and hemicellulose generally decompose more rapidly than lignin [23,41], and lignin has a considerably higher C concentration (~60-70% C mass mass^{-1}) than cellulose/ hemicellulose (~40-44% C mass mass^{-1}) [42]; thus CFs would be expected to increase through decomposition as a function of increasing lignin concentrations. Our data on generalized CFs across DCs qualitatively correspond to this expectation (Fig. 1). Quantitatively, in assuming an average C concentration of 62.5% for lignin and 41.2% for cellulose, then our observed changes in dead wood CFs from DC 1 (47.5%) to DC 5 (48.6%) correspond to an increase in lignin concentrations through decomposition from ~27% to 33% (mass mass^{-1}). These approximate changes in lignin concentrations match patterns observed in wood decomposition experiments [41,43,44], and support the findings of increases in CFs with decomposition in the majority of tree species (Fig. 3).

However, certain species deviate from this pattern and instead show non-significant changes or significant declines in CFs through decomposition (Fig. 3). That these species are disproportionately observed in certain biomes, suggests there are mechanisms other than the degradation of cellulose and lignin that drive chemical changes in decomposition globally. One possible mechanism is the import of soil particles and soluble nutrients into dead wood by soil macrofauna – in particular termites [45] – which would reduce dead wood CFs through the decomposition process primarily in tropical and subtropical forests.

Similarly, there is an expectation that the import of soluble nutrients and particles from soils into woody debris should decrease dead wood CFs in downed wood, as compared to standing necromass [23]. Support for this expectation has been observed in temperate and boreal forests, where standing dead trees express significantly greater CFs vs. downed wood (i.e., on the order of ~1.6-2.0%) at later stages of decay (i.e., DC 4) [23]. This is consistent with our findings of dead wood CFs being higher in standing vs. downed wood, though the magnitude of the average differences in our pooled analysis is lower (~0.4%; Fig. 1). Disentangling how these and other mechanisms drive variability in CFs through decomposition will likely require detailed experimental studies that evaluate long-term decay patterns [46], account for species differences in wood functional traits [36], incorporate emerging environmental analytical techniques e.g. [47], and test for biochemical changes in wood such as the accumulation of anaerobic metabolic products [48].

At global scales, accurate estimates of CF in dead wood are critical for refining global C budgets, quantifying potential changes in dead wood fluxes under global change scenarios, mechanistically understanding the drivers of decomposition and predicting how they change in the future. Recent troubling observations of increased tree mortality in multiple forest biomes [2,3] suggest that a synthetic understanding of dead wood chemistry dynamics is especially critical for all of these avenues of forest ecological and global change science.

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Author Contributions

A.R.M conceived the study, lead data compilation and analysis, and wrote the manuscript; G.M.D. helped write and edit the manuscript; M.D. contributed to data compilation and helped write and edit the manuscript; S.C.T. contributed to data compilation and analysis, and helped write and edit the manuscript.

Author Contributions

The authors declare no competing interests.

References

1 Hubau, W. *et al*. Asynchronous carbon sink saturation in African and Amazonian tropical forests. *Nature* **579**, 80-87, (202).

2 Brando, P. M. *et al*. Abrupt increases in Amazonian tree mortality due to drought–fire interactions. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 6347-6352, (2014).

3 Van Mantgem, P. J. *et al*. Widespread increase of tree mortality rates in the western United States. *Science* **323**, 521-524, (2009).

4 Le Quéré, C. *et al*. Global carbon budget 2018. *Earth Sys. Sci. Dat.* **10**, 2141-2194, (2018).

5 IPCC. in *2019 Refinement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories. (Vol. 4): Agriculture, Forestry and Other Land Use* (eds D. Blain, F. Agus, M.A. Alfaro, & H. Vreuls) 68 (2019).

6 Martin, A. R., Doraisami, M. & Thomas, S. C. Global patterns in wood carbon concentration across the world's trees and forests. *Nat. Geosci* **11**, 915-922, (2018).

7 Pan, Y. *et al*. A large and persistent carbon sink in the world's forests. *Science* **333**, 988-993, (2011).

8 Pugh, T. A. *et al*. Role of forest regrowth in global carbon sink dynamics. *Proc. Natl. Acad. Sci. U.S.A*. **116**, 4382-4387, (2019).

9 Baccini, A. *et al*. Tropical forests are a net carbon source based on aboveground measurements of gain and loss *Science* **358**, 230-234, (2017).

10 Luyssaert, S. *et al*. CO_2 balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biol*. **13**, 2509-2537, (2007).

11 Harmon, M. E. *et al*. Ecology of coarse woody debris in temperate ecosystems. In *Adv. Ecol. Res*. Vol. 15 133-302 (Academic Press, 1986).

12 Weedon, J. T. *et al*. Global meta-analysis of wood decomposition rates: a role for trait variation among tree species? *Ecol. Lett*. **12**, 45-56, (2009).

13 McGee, G. G. The contribution of beech bark disease-induced mortality to coarse woody debris loads in northern hardwood stands of Adirondack Park, New York, USA. *Can. J. For. Res*. **30**, 1453-1462, (2000).

14 Woodall, C. W. *et al*. Net carbon flux of dead wood in forests of the Eastern US. *Oecologia* **177**, 861-874, (2015).

15 Russell, M. B. *et al*. Quantifying carbon stores and decomposition in dead wood: a review. *For. Ecol. Manage*. **350**, 107-128, (2015).

16 Campbell, J., Alberti, G., Martin, J. & Law, B. E. Carbon dynamics of a ponderosa pine plantation following a thinning treatment in the northern Sierra Nevada. *For. Ecol. Manage*. **257**, 453-463, (2009).

17 Chambers, J. Q. *et al*. Response of tree biomass and wood litter to disturbance in a Central Amazon forest. *Oecologia* **141**, 596-611, (2004).

18 Domke, G. M., Woodall, C. W. & Smith, J. E. Accounting for density reduction and structural loss in standing dead trees: Implications for forest biomass and carbon stock estimates in the United States. *Carbon Balance Manag*. **6**, 14, (2011).

19 Janisch, J. E. & Harmon, M. E. Successional changes in live and dead wood carbon stores: implications for net ecosystem productivity. *Tree Physiol*. **22**, 77-89, (2002).

20 Keith, H., Mackey, B. G. & Lindenmayer, D. B. Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proc. Natl. Acad. Sci. U.S.A*. **106**, 11635-11640, (2009).

21 Thomas, S. C. & Martin, A. R. Carbon content of tree tissues: a synthesis. *Forests* **3**, 332-352, (2012).

22 Martin, A. R. & Thomas, S. C. A reassessment of carbon content in tropical trees. *PLoS One* **6**, e23533, (2011).

23 Harmon, M. E., Fasth, B., Woodall, C. W. & Sexton, J. Carbon concentration of standing and downed woody detritus: effects of tree taxa, decay class, position, and tissue type. *For. Ecol. Manage*. **291**, (2013).

24 Weggler, K., Dobbertin, M., Jüngling, E., Kaufmann, E. & Thürig, E. Dead wood volume to dead wood carbon: the issue of conversion factors. *Eur. J. For. Res.* **131**, 1423-1438, (2012).

25 Gorgolewski, A., Rudz, P., Jones, T., Basiliko, N. & Caspersen, J. Assessing coarse woody debris nutrient dynamics in managed northern hardwood forests using a matrix transition model. *Ecosystems*, 1-14, (2019).

26 Moreira, A. B., Gregoire, T. G. & do Couto, H. T. Z. Wood density and carbon concentration of coarse woody debris in native forests, Brazil. *For. Ecosyst.* **6**, 18, (2019).

27 Sandström, F., Petersson, H., Kruys, N. & Ståhl, G. Biomass conversion factors (density and carbon concentration) by decay classes for dead wood of *Pinus sylvestris*, *Picea abies* and *Betula* spp. in boreal forests of Sweden. *For. Ecol. Manage.* **243**, 19-27, (2007).

28 Cousins, S. J., Battles, J. J., Sanders, J. E. & York, R. A. Decay patterns and carbon density of standing dead trees in California mixed conifer forests. *For. Ecol. Manage.* **353**, 136-147, (2015).

29 Köster, K., Metslaid, M., Engelhart, J. & Köster, E. Dead wood basic density, and the concentration of carbon and nitrogen for main tree species in managed hemiboreal forests. *For. Ecol. Manage.* **354**, 35-42, (2015).

30 Clark, D. B., Clark, D. A., Brown, S., Oberbauer, S. F. & Veldkamp, E. Stocks and flows of coarse woody debris across a tropical rain forest nutrient and topography gradient. *For. Ecol. Manage.* **164**, 237-248, (2002).

31 Yang, F. F. *et al*. Dynamics of coarse woody debris and decomposition rates in an old-growth forest in lower tropical China. *For. Ecol. Manage.* **259**, 1666-1672, (2010).

32 Chao, K. J. *et al*. Carbon concentration declines with decay class in tropical forest woody debris. *For. Ecol. Manage.* **391**, 75-85, (2017).

33 Guo, J., Chen, G., Xie, J., Yang, Z. & Yang, Y. Patterns of mass, carbon and nitrogen in coarse woody debris in five natural forests in southern China. *Ann. For. Sci.* **71**, 585-594, (2014).

34 Martin, A. R., Gezahegn, S. & Thomas, S. C. Variation in carbon and nitrogen concentration among major woody tissue types in temperate trees. *Can. J. For. Res.* **45**, 744-757, (2015).

35 Gao, B., Taylor, A. R., Chen, H. Y. & Wang, J. Variation in total and volatile carbon concentration among the major tree species of the boreal forest. *For. Ecol. Manage.* **375**, 191-199, (2016).

36 Dossa, G. G. *et al*. The cover uncovered: bark control over wood decomposition. *J. Ecol.* **106**, 2147-2160, (2018).

37 Fukasawa, Y. The geographical gradient of pine log decomposition in Japan. *For. Ecol. Manage.* **349**, (2015).

38 Campbell, J. L. *et al*. Estimating uncertainty in the volume and carbon storage of downed coarse woody debris. *Ecol. Appl.* **29**, e01844, (2019).

39 Ma, S. *et al*. Variations and determinants of carbon content in plants: a global synthesis. *Biogeosciences* **15**, 693, (2018).

40 Cornelissen, J. H. C. *et al*. Leaf digestibility and litter decomposability are related in a wide range of subarctic plant species and types. *Funct. Ecol.* **18**, 779-786, (2004).

41 Ganjegunte, G. K., Condron, L. M., Clinton, P. W., Davis, M. R. & Mahieu, N. Decomposition and nutrient release from radiata pine (*Pinus radiata*) coarse woody debris. *For. Ecol. Manage.* **187**, 197-211, (2004).

42 Pettersen, R. C. The Chemical Composition of Wood. In *The Chemistry of Solid Wood* (ed R. Rowell) 57-126 (American Chemical Society, 1984).

43 Berg, B., Ekbohm, G. & McClaugherty, C. Lignin and holocellulose relations during long-term decomposition of some forest litters. Long-term decomposition in a Scots pine forest. IV. *Can. J. Bot.* **62**, 2540-2550, (1984).

44 Schowalter, T. D., Zhang, Y. L. & Sabin, T. E. Decomposition and nutrient dynamics of oak *Quercus* spp. logs after five years of decomposition. *Ecography* **21**, 3-10, (1998).

45 Buxton, R. D. Termites and the turnover of dead wood in an arid tropical environment. *Oecologia* **51**, 379-384, (1981).

46 Moore, T. R., Trofymow, J. A., Prescott, C. E., Titus, B. D. & Group, C. W. Can short-term litter-bag measurements predict long-term decomposition in northern forests? *Plant Soil* **416**, 419-426, (2017).

47 Frey, S. D., Nadelhoffer, K. J., LeMoine, J. M., Lajtha, K. & Simpson, M. J. Molecular-level changes in soil organic matter composition after 10 years of litter, root and nitrogen manipulation in a temperate forest. *Biogeochemistry* **141**, 183-197, (2018).

48 Warner, D. L., Villarreal, S., McWilliams, K., Inamdar, S. & Vargas, R. Carbon dioxide and methane fluxes from tree stems, coarse woody debris, and soils in an upland temperate forest. *Ecosystems* **20**, 1205-1216, (2017).

Tables

Table 1. Generalized mean dead wood carbon fractions (CF) across five different factors. Mean values here were calculated as least squares means, derived from five different linear-mixed effects models (all fit as modified versions of Equation 1). Values here correspond to data presented in Fig. 2, while linear mixed effects model diagnostics are presented in Table S3.

Factors	Value	Mean CF	S.E.	Lower C.I.	Upper C.I.
Biomes	Boreal	48.84	0.76	40.69	56.98
	Subtropical/ Medit.	46.24	0.83	37.38	55.09
	Temperate	49.29	0.74	41.29	57.28
	Tropical	47.16	0.79	38.66	55.66
Phyla	Angiosperm	47.18	0.79	44.59	49.77
	Gymnosperm	49.19	0.79	46.58	51.79
Tissues	Branch	45.67	1.14	42.13	49.21
	Root	47.79	1.14	44.25	51.33
	Stem	48.07	1.07	44.75	51.4
	Bark	48.73	1.08	45.38	52.09
	Fine tissue	48.8	1.23	44.97	52.63
Position	Downed	47.81	1.05	44.32	51.31
	Standing	48.22	1.06	44.7	51.74
Decay class	1	47.53	1.03	44.16	50.9
	2	47.55	1.03	44.18	50.93
	3	47.98	1.03	44.61	51.36
	4	48.68	1.04	45.28	52.08
	5	48.61	1.05	45.17	52.04

Figures and Figure Legends

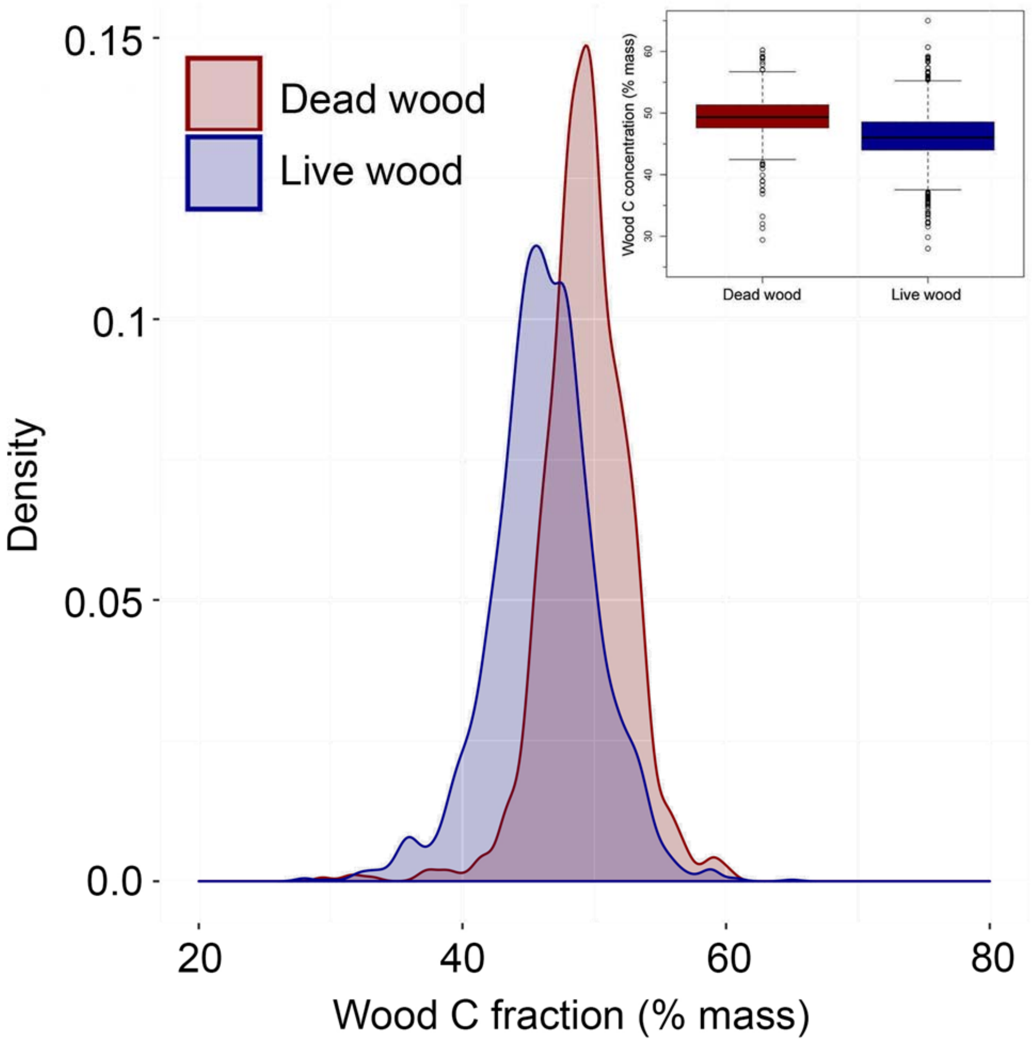

Fig. 1. Carbon fractions (CF) in dead vs. live wood in a global wood CF database. Histograms correspond to kernel density estimates fit for CF values from dead (*n*=973) and live wood (*n*=2,437) separately, with corresponding boxplots (showing medians, 25-75th percentiles, outliers, and range excluding outliers) inset.

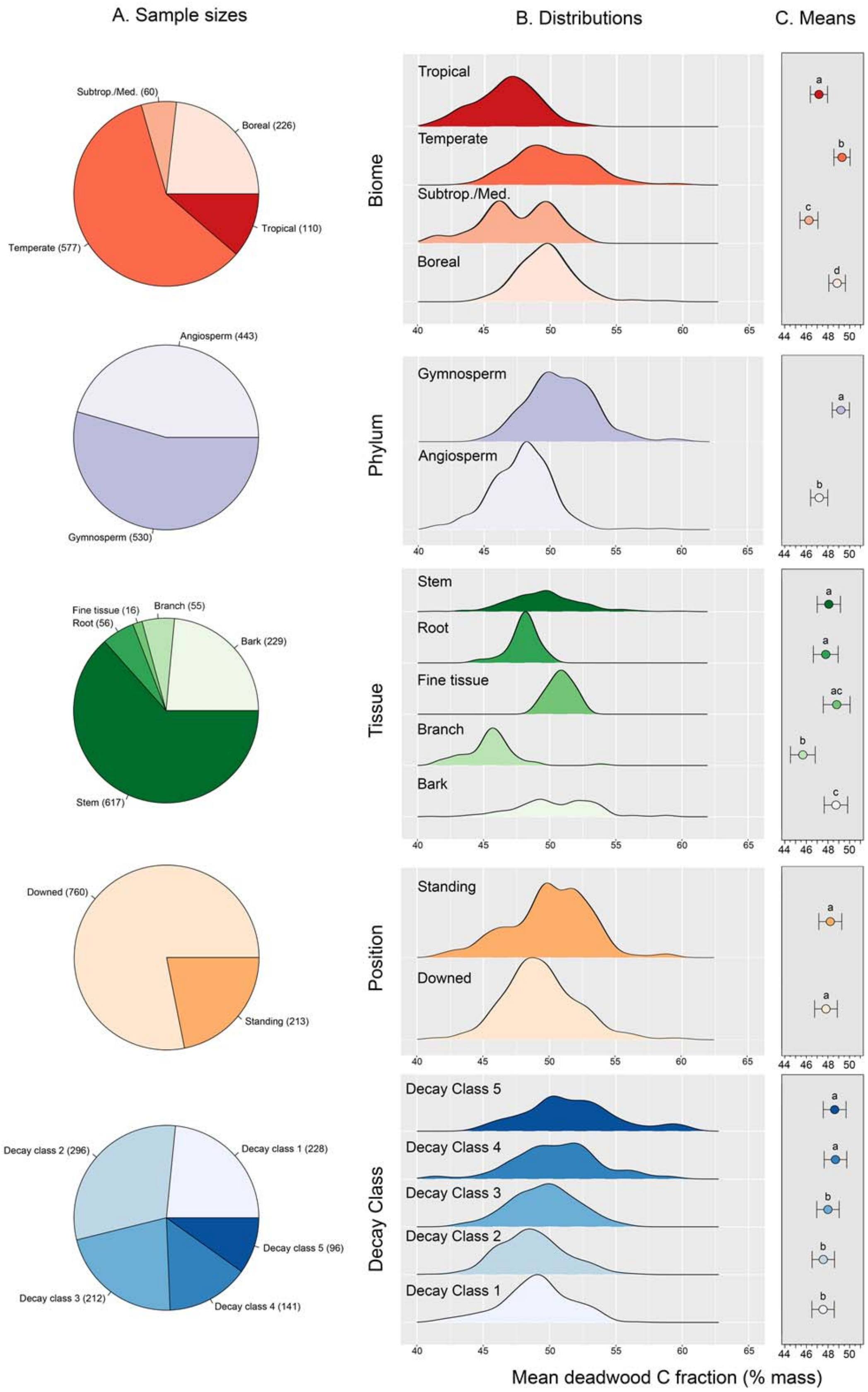
A. Sample sizes
B. Distributions
C. Means
Subtrop./Med. (60)
Boreal (226)
Tropical (110)
Temperate (577)
Angiosperm (443)
Gymnosperm (530)
Fine tissue (16)
Root (56)
Branch (55)
Bark (229)
Stem (617)
Downed (760)
Standing (213)
Decay class 2 (296)
Decay class 1 (228)
Decay class 5 (96)
Decay class 3 (212)
Decay class 4 (141)
Biome
Tropical
Temperate
Subtrop./Med.
Boreal
a
b
c
d
Phylum
Gymnosperm
Angiosperm
a
b
Tissue
Stem
Root
Fine tissue
Branch
Bark
a
a
ac
b
c
Position
Standing
Downed
a
a
Decay Class
Decay Class 5
Decay Class 4
Decay Class 3
Decay Class 2
Decay Class 1
a
a
b
b
b
40
45
50
55
60
65
44
46
48
50
Mean deadwood C fraction (% mass)

Fig. 2. Sample sizes, distributions and mean dead wood carbon fraction (CF) values across biomes, phyla, tissue type, dead wood position, and decay class. Middle panels (B) represent kernel density estimates fit to subsets of dataset (based on the sample sizes presented in pie charts). Right panels (C) represent least square mean values (± s.e.) estimated from a linear mixed effects model fit to the entire dead wood dataset (*n*=973). Within a given data subset, different letters above mean values denotes statistically significant differences (at $p<0.05$) in mean dead wood C values.

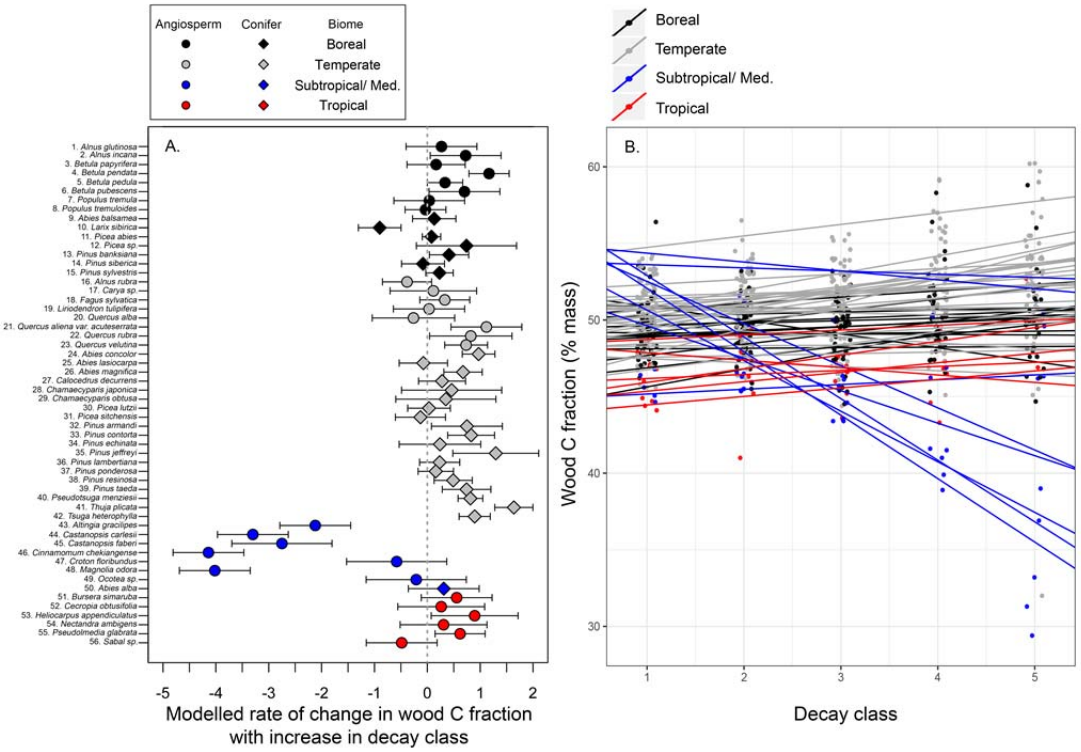

Fig. 3. Changes in dead wood carbon fractions (CF) as a function of wood decomposition stage. Panel A presents modeled rates of change in dead wood CFs as a function of decay class, which are the slope estimates derived from a mixed effect model. Panel B presents the species-specific models predicting dead wood CFs as a function of decay class.

Methods

Literature review

We built on our existing wood C database [49], which consists of *n*=2,228 observations of CFs in live wood only, as the basis for dead wood CF consolidation. We first reviewed all peer-reviewed papers that were cited by our previous work i.e., [49,50,51] for records of dead wood CFs. Then we searched three peer-reviewed literature databases (Web of Science, Scopus, and Google Scholar) for papers with dead wood CF records, using the primary search terms "coarse wood debris", "dead wood", and "carbon", and "wood nutrient." Articles identified by these terms or combinations thereof, as well as papers that cited these publications, were searched for dead wood CF data. Data compilation was halted at the end of 2019.

Criteria for inclusion broadly followed that of Martin et al. [49], such that only dead wood CF data associated with species identities and tissue type identities were included in our database. This was done to maximize our sample size, while allowing analysis that was specific enough to inform forest C estimation. For each paper with species- and tissue-specific data, dead wood CF observations were then extracted from text, tables and figures, with figure-based data extracted using the Web-Plot Digitizer software [52].

For each observation, we recorded species-specific taxonomy as presented in original publications, which was then adjusted according to the Taxonomic Name Resolution Service v.4.0 [53]. Each dead wood CF observation was then classified as belonging to one of four major forested biomes including A) boreal, B) temperate, C) subtropical/ Mediterranean, and D) tropical. Tissue type was recorded as one of the following: A) bark, B) stem (inclusive of heartwood and sapwood, which were largely undifferentiated in dead wood CF studies), C) branch (inclusive of three observations reported as small "twigs"), D) roots (large and small, which were by-in-large undifferentiated in dead wood CF publications), and E) unspecified fine tissue. Two papers reported sampled material as belonging to "stems and branches", which were classified as "stems" for analysis here assuming stems contributed the larger proportion of biomass to these analyses.

Each dead wood CF observation was then categorized according to three primary factors associated with wood decomposition and related chemical change: A) decay class

(DC), B) position, C) size (diameter and length). In the majority of publications dead wood DC was reported along a conventional 1-5 scale, and was therefore included in our database as published while noting the decay class scale employed. In cases where DC for was reported as a two-category range (e.g. DC 1-2) the higher DC was used for analysis, while in cases were a multi-category DC was presented (e.g. DC 1-5) the middle DC value was used. In the few instances DC was reported along a 0-5 point scale (where DC 0 is clearly defined in the publication as dead and not live wood), dead wood reported with a DC of 0 was classified as DC 1. Lastly, in a subset of papers the number of years since tree death (instead of DC) was reported. In these cases, years since death were converted to DC based on published decay class transition matrices [e.g. 54].

Position was recorded as one of A) "standing" referring to snags, or B) "downed" referring to anything sampled from the forest floor. Values for "suspended" woody debris were combined with those for snags. A few publications did not differentiate dead wood as being standing vs. downed in the original publication, and instead classified dead wood as "standing/ downed." These few cases were classified as "downed" for analysis here, since there were very few observations in this group (particularly across multiple DCs).

Diameter measurements were available for less than 50% of dead wood CF observations, and papers presented a combination of quantitative and categorical measurements. Therefore diameter values were recorded following the original publication, and then categorized into one of seven groups that were chosen to maintain maximum resolution while balancing sample sizes. These diameter groups employed here were: 1) 0.1-1.0 cm, 2) 1.1-2.5 cm, 3) 2.51-5.0 cm, 4) 5.1-10.0 cm, 5) 10.1-20 cm, 6) 20.1-30 cm, and 7) ≥ 30.1 cm. There are two caveats to these classifications. First, in instances were publications reported size ranges that overlapped two or more of our groups (e.g., one paper reported dead wood as 7-12 cm in diameter), the mid-point of the size range was used to allocate observations into final diameter classes. Second, in cases where dead wood was reported as belonging to undefined categories (e.g. one paper reporting diameter values of ≥ 2.5 cm), all observations from that publication were placed in the next highest diameter group. Length measurements were available only for a small subset of observations, and were recorded as in the original publication and categorized as either 1) 1-100 cm, or 2) ≥ 100 cm.

Our literature-based search was augmented with a structured trait query from the TRY Functional Trait Database [55]. Specifically, we requested records for coarse woody debris C concentration (TRY Database trait number 868). However, all of the *n*=42 records for this trait were not associated with a species, and were therefore not included in our final dataset.

Data analysis – dead wood CFs vs. live wood CFs and a generalized 50% CF

All analyses were performed using R v.3.2.1 (R Foundations for Statistical Computing). First, we utilized a two-tailed *z*-test to evaluate if dead wood CFs across our entire dataset (*n*=973 observations total) differed significantly from a 50% CF assumption. Then, two approaches were then taken to compare live vs. dead wood CFs. First, we fit a linear mixed effects model using the '*lmer*' function in the '*lme4*' R package [56] to our entire wood CF dataset (*n*=3,410 observations total from both dead and live wood). In this model, wood CF values were predicted as a function of an observation being "dead or live" (as a fixed effect), while accounting for biome and phylum as random effects. These random effects were incorporated in this model in efforts to better isolate "dead vs. live" differences since 1) the dead and live CF datasets differ in the number and proportion of observations per biome and phyla, and 2) wood CFs vary systematically as a function of biome and phylum; therefore failing to account for these factors statistically may have biased dead vs. live comparisons. (Note: we also sought to include tissue type as a random effect in this model, though since tissue types are reported more specifically in live wood (*n*=8 types) than in dead wood (*n*=5 types), it was not possible to parameterize the model with this random effect). Based on this model we then calculated and statistically compared least square mean CF values for both groups using the '*lsmeans*' and '*difflsmeans*' functions in the '*lsmeans*' R package [57]. Distributions for dead and live wood CF data were presented visually using kernel density estimates calculated in '*ggplot2*' [58].

Next, we tested if live wood CFs can be used to predict dead wood CFs. Using the subset that included only species with values of both, we calculated species-specific mean live wood and dead wood CFs values, and fit a linear regression to predict dead wood CF from live wood CFs. This linear model was then statistically compared to a 1:1

relationship using the '*linearHypothesis*' function in the '*car*' R package [59]. We then included both phylum and phylum-by-live wood CF interaction terms in this model to evaluate if intercepts and slopes of live-dead wood CF relationship differed among species groups (i.e., conifers vs. angiosperms).

Data analysis – factors explaining dead wood CFs

We first used an analysis of variance (ANOVA) to evaluate if dead wood CFs vary as a function of biome, phylum, tissue type, position, and DC, as well as all two-way interaction terms. We then complemented this ANOVA with a variance partitioning analysis to quantify the proportion of variability in dead wood CFs explained by biome, phylum, tissue type, position, and DC (where *n*=973 dead wood observations). This analysis followed the methods developed and employed by multiple studies evaluating functional trait variability in plants e.g. [60,61], including our own earlier work on live wood CF variability in trees [49].

Specifically, the variance partitioning analysis entailed fitting a linear mixed effects model with the '*lme*' function in the '*nlme*' R package [62] where all nested levels – namely DC, within position (i.e., standing, dead), within tissue, within phylum (i.e., conifer, angiosperm), within biome) – are entered as sequential random effects, and the overall intercept (or overall mean dead wood CF value) is the only estimated fixed effect [60]. We then used the '*varcomp*' function in the '*ape*' R package [63] to quantify and partition variation in dead wood CFs across these nested levels. (Note: the variance partitioning analysis was also performed while including size as a factor, but since this necessarily reduced our sample size by over half (to *n*=413 observations), these results are discussed only briefly).

We then estimated and compared generalized dead wood CF across DCs, positions, tissues, phyla, and biomes. Specifically, we fit five linear mixed effects models wherein one of the five variables (i.e., DC, position, tissue, phylum, biome) was included as a fixed effect, and the other four variables were included as nested random effects. Based on these five models, we then used the '*lsmeans*' function to calculate least square mean dead wood CFs individually for each DC, position, tissue type, phylum, and biome, and compared them using the '*difflsmeans*' function. (Note: this analysis did not include interaction terms since with few exceptions these were largely non-significant predictors of dead wood CFs (Table S1)).

Data analysis – changes in dead wood CFs through decomposition

We evaluated how dead wood CFs changes with DC in more specific detail, using a subset of data that included only species with wood C values from at least four DCs. For this subset of n=56 species, we then used a linear mixed effects model to evaluate how wood C changes across DC, and if/how the rate of change differs across species (subset species highlighted in Table S4). This analysis entailed using the '*lme*' function to fit species-specific models predicting dead wood CFs as a function of DC. Specifically, dead wood CFs were predicted as a function of species identity (representing a species-specific intercept) and a species-by-DC interaction term (representing a species-specific slope parameter) as fixed effects, while accounting for biome, phylum, tissue type, and position) as random effect.

Data availability

The compiled data set used in our analyses is available through the TRY Functional Trait Database (data set ID number to be determined upon article publication), and is available from the corresponding author upon request.

Code availability

The code used to perform all analyses and generate figures is available upon request to the corresponding author.

Methods References

49 Martin, A. R., Doraisami, M. & Thomas, S. C. Global patterns in wood carbon concentration across the world's trees and forests. *Nat. Geosci* **11**, 915-922, (2018).

50 Thomas, S. C. & Martin, A. R. Carbon content of tree tissues: a synthesis. *Forests* **3**, 332-352, (2012).

51 Martin, A. R. & Thomas, S. C. A reassessment of carbon content in tropical trees. *PLoS One* **6**, e23533, (2011).

52 WebPlotDigitizer v. 4.2 (San Francisco, California, USA, 2019).

53 Brad, B. *et al*. The taxonomic name resolution service: an online tool for automated standardization of plant names. *BMC Bioinformatics* **14**, 16, (2013).

54 Krankina, O. N. & Harmon, M. E. Dynamics of the dead wood carbon pool in northwestern Russian boreal forests. *Water, Air, and Soil Pollution* **82**, 227-238, (1995).

55 Kattge, J., Bönisch, G., Díaz, S. & al., e. TRY plant trait database – enhanced coverage and open access. *Global Change Biol*. **26**, 119-188, (2020).

56 Bates, D., Maechler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**, 1-48, (2015).

57 Lenth, R. V. Least-Squares Means: The R Package lsmeans. *Journal of Statistical Software* **69**, 1-33, (2016).

58 Wickham, H. *ggplot2: Elegant Graphics for Data Analysis*. (Springer-Verlag, 2009).

59 An {R} Companion to Applied Regression, Second Edition (Sage, Thousand Oaks, CA, URL: http://socserv.socsci.mcmaster.ca/jfox/Books/Companion, 2011).

60 Messier, J., McGill, B. J. & Lechowicz, M. J. How do traits vary across ecological scales? A case for trait‐based ecology. *Ecol. Lett*. **13**, 838-848, (2010).

61 Martin, A. R. *et al*. Intraspecific trait variation across multiple scales: the leaf economics spectrum in coffee. *Funct. Ecol*. **31**, 604-612, (2017).

62 nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-131 (URL: https://CRAN.R-project.org/package=nlme>, 2017).

63 Paradis, E., Claude, J. & Strimmer, K. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289-290, (2004).

Supplementary Information is available for this paper.

Correspondence and requests for materials should be addressed to Adam R. Martin.

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