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RESEARCH ARTICLE

Broad-scale wood degradation dynamics in the face of climate change: A meta-analysis

Catherine Chagnon[1] | **Guillaume Moreau**[2,3] | **Christine Bombardier-Cauffopé**[2] | **Julie Barrette**[4] | **Filip Havreljuk**[4] | **Alexis Achim**[1,2]

[1]Département des Sciences du Bois et de la Forêt, Faculté de foresterie, de géographie et de géomatique, Université Laval, Québec City, Québec, Canada

[2]Département des sciences du bois et de la forêt, Centre de recherche sur les matériaux renouvelables, Université Laval, Québec City, Québec, Canada

[3]Daniels Institute of Forestry and Conservation, University of Toronto, Toronto, Ontario, Canada

[4]Direction de la recherche forestière, Ministère des Forêts, de la Faune et des Parcs du Québec, Québec City, Québec, Canada

Correspondence
Guillaume Moreau, Département des sciences du bois et de la forêt, Centre de recherche sur les matériaux renouvelables, Pavillon Abitibi-Price, 2405 rue de la Terrasse, Université Laval, Québec City, QC G1V0A6, Canada.
Email: guillaume.moreau.3@ulaval.ca

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Abstract

In the context of global change, a better understanding of the dynamics of wood degradation, and how they relate to tree attributes and climatic conditions, is necessary to improve broad-scale assessments of the contributions of deadwood to various ecological processes, and ultimately, for the development of adaptive post-disturbance management strategies. The objective of this meta-analysis was to review the effects of tree attributes and local climatic conditions on the time since death of coarse woody debris ranging in decomposition states. Results from our meta-analysis showed that projected warming will likely accelerate wood decomposition and significantly decrease the residence time in decay stages. By promoting such a decrease in residence time, further climate warming is very likely to alter the dynamics of deadwood, which in turn may affect saproxylic biodiversity by decreasing the temporal availability of specific habitats. Moreover, while coarse woody debris has been recognized as a key resource for bioenergy at the global scale, the acceleration of decay-stages transition dynamics indicates that the temporal window during which dead trees are available as feedstock for value-added products will shrink. Consequently, future planning and implementation of salvage harvesting will need to occur within a short period following disturbance, especially in warmer regions dominated by hardwood species. Another important contribution of this work was the development of a harmonized classification system that relies on the correspondence between the visual criteria used to characterize deadwood decomposition stages in locally developed systems the literature. This system could be used in future investigations to facilitate direct comparisons between studies. Our literature survey also highlights that most of the information on wood decay dynamics comes from temperate and boreal forests, whereas data from subtropical, equatorial and subarctic forests are scarce. Such data are urgently needed to allow broader-scale conclusions on global wood degradation dynamics.

KEYWORDS

climate change, coarse woody debris, deadwood, decay classification system; downed woody debris, forest management; meta-analysis; standing dead wood

1 | INTRODUCTION

Forest ecosystems are shaped by natural disturbances that help maintain heterogeneous forest landscapes and promote species diversity (Buma & Schultz, 2020; Thom & Seidl, 2016). However, there is growing evidence that climate change is accelerating disturbance rates, thereby inducing broad-scale forest die-off in many regions (Anderegg et al., 2020; Millar & Stephenson, 2015; Trumbore et al., 2015). For example, an increase in the frequency and severity of droughts has induced extensive tree mortality globally (Allen et al., 2010, 2015). Global warming is also contributing to altering fire regimes in several forest ecosystems, leading to a generalized increase in fire-killed forests (Andela et al., 2017; Herawati et al., 2015; Pausas & Keeley, 2014). Outbreaks of (often invasive) insects and pathogens are also being amplified (Battisti et al., 2005; Klapwijk et al., 2012; Robinet & Roques, 2010), which can lead to compound disturbances of unprecedented severity and to broad-scale disruptions of forest ecosystems (McDowell et al., 2020; Millar & Stephenson, 2015). The increasing amount of dead trees that results from global alterations in disturbance regimes calls for the development of adaptive post-disturbance management strategies in which prioritization must be made between biomass recovery by the forest industry, or its conservation for biodiversity (Barrette et al., 2013).

The International Panel on Climate Change (IPCC) has recognized trees killed by natural disturbances as a potential key resource for bioenergy at the global scale (Chum et al., 2011). When used as a substitute for fossil fuels, biomass from dead trees has the potential to reduce net greenhouse gas emissions over time (Gustavsson et al., 2015; Lamers et al., 2013, 2014), although the net carbon balance depends on multiple factors, including the type of substituted fossil fuels, wood feedstock, and post-disturbance forest growth, which in turn can be affected by silvicultural treatments (Laganière et al., 2017). Recently dead trees may also supply both the sawlog and the wood pellet industries (Barrette et al., 2015), thereby providing services to society and substituting emission-intensive materials (Bogdanski et al., 2011). The worldwide demand for wood biomass is constantly increasing as a result of renewable energy policies that have recently been implemented in various jurisdictions (Goh et al., 2013; Lamers et al., 2014; Stupak et al., 2007).

Coarse woody debris also contributes to the structural complexity and heterogeneity of forests globally, and is thus considered a key ecological attribute involved in several ecosystem processes (Jonsson & Kruys, 2001). Post-disturbance forests are recognized as biodiversity hotspots as they provide suitable nesting, sheltering, and breeding environments for multiple animal species (Harmon et al., 1986; Thomas, 1979), as well as substrates for the proliferation of vascular plants, cryptogams, and fungi (Chećko et al., 2015; Dittrich et al., 2014; Lassauce et al., 2011; Ódor et al., 2006; Rajala et al., 2015). Deadwood also plays an essential role in the global carbon cycle through carbon stocking in forest soils and nutrient cycling processes (Denman et al., 2007; Laiho & Prescott, 2004). Salvage harvesting in forests affected by natural disturbances may thus undermine the ecological benefits of deadwood retention (Lindenmayer et al., 2004; Lindenmayer & Noss, 2006; Nappi et al., 2004), which leaves forest managers in the middle of competing expectations.

One limitation to the development of broad-scale post-disturbance management strategies is the lack of knowledge on the global dynamics of tree degradation. Weedon et al. (2009) produced a global meta-analysis of wood decomposition dynamics, which can provide key insights for carbon emission models, for example Wang et al. (2010). However, salvage harvesting decisions must be based not only on the level of degradation of the woody material itself, but also on the more general degradation state of the trees, which can be described using visual criteria (i.e., Aakala et al., 2008; Barrette et al., 2015; Mäkinen et al., 2006). To date, most studies focusing on degradation state dynamics have been limited in geographical scope and number of tree species (see Table 1). Despite being based on similar criteria, several classification systems have been locally developed to visually estimate the state of decomposition of dead trees. The multiplicity of systems used in the literature limits the possibility to compare results at a larger scale. Without a broader understanding of wood degradation dynamics, the range of wood products that could be provided by post-disturbance forests over time remains unclear, and so are the management practices that would ensure the supply of fiber for these processing pathways (Barrette et al., 2015) while ensuring the maintenance of ecological processes associated with deadwood.

In this study, we gathered data from 23 studies, representing 2493 trees from 42 sites across Europe and the Americas, with the aim to better understand broad-scale variation in wood degradation dynamics following tree death. Using a meta-analysis approach, we reviewed the effects of a complementary set of tree attributes and local climatic conditions on the time since death of both standing dead trees and downed woody debris ranging in degradation levels. As a second objective of this study, we developed an integrated, synthetic decay class system for deadwood that could relate to locally developed systems and facilitate comparisons between studies. Finally, in support of the implementation of adaptive forest management practices, we also highlight gaps in current

TABLE 1 Summary of the 23 published studies used in the meta-analysis

#	Reference	Location	DC	Species	CWD types	Stand	Sites	Trees
1	Aakala (2010)	FI, RU	1, 2	PiA	DWD, SDT	S	3	461
2	Aakala et al. (2007)	CA	NM	AbB, PiM	SDT	S	1	190
3	Alexander et al. (2018)	US	3	FaG, Fr, LiT, QuE, QuL	DWD	H	1	94
4	Angers et al. (2012)	CA	1	AbB, PiM, PnB, PoT	SDT	S	2	211
5	Barrette et al. (2015)	CA	4	PiM	SDT	S	1	158
6	Brown et al. (1998)	US	NM	PiE, PnC,	DWD	S	1	43
7	Campbell and Laroque (2007)	CA	5 (6)	AbB, PiM	DWD, SDT	S	2	75
8	Daniels et al. (1997)	CA	6	ThP	DWD, SDT	S	1	29
9	DeLong et al. (2005)	CA	7 (6)	AbL, PiGxE	DWD	S	1	97
10	DeLong et al. (2008)	CA	BO	AbL, PiGxE	SDT	S	1	158
11	Holeksa et al. (2008)	PL	8 (9)	PiA	DWD	S	1	106
12	Huggard (1999)	CA	6	PiE	SDT	S	1	138
13	Kahl et al. (2012)	DE	NM	FaS	DWD	H	1	5
14	Kruys et al. (2002)	SE	8 (9)	PiA	DWD	S	1	90
15	Lombardi et al. (2008)	IT	4	AbA, FaS	SDT	H, S	2	103
16	Lombardi et al. (2011)	CL	4	NoB	DWD	H	1	35
17	Petrillo, Cherubini, Fravolini, et al. (2016)	IT	4	LaD, PiA	DWD	A, M, S	5	21
18	Ruel et al. (2010)	CA	O	PiM	DWD	S	1	17
19	Saine et al. (2018)	FI	10	PnS	SDT	S	13	55
20	Storaunet (2004)	NO	BO	PiA	SDT	S	1	107
21	Storaunet and Rolstad (2002)	NO	11 (12)	PiA	DWD	S	2	113
22	Waskiewicz et al. (2007)	US	6	PnP	SDT	S	1	79
23	Zielonka (2006)	PL	13	PiA	DWD	S	1	107

Notes: Location: CA, Canada; CL, Chile; DE, Germany; FI, Finland; IT, Italy; NO, Norway; PL, Poland; RU, Russian Federation; SE, Sweden; US, United States. DC: Decay classification(s) used in the reference study before we standardized it; 1, Imbeau and Desrochers (2002); 2, Lännenpäa et al. (2008); 3, Pyle and Brown (1998); 4, Hunter (1990); 5, Daniels et al. 1997; 6, Thomas et al. (1979); 7, Newberry et al. 2004; 8, Söderström (1988); 9, McCullough's (1948); 10, Renvall (1995); 11, Hofgaard (1993); 12, Arnborg (1942); 13, Holeksa (1998); BO, Branch order classification; NM, Not mentioned; O, Own classification. Tree species: AbA, *Abies alba*; AbB, *Abies balsamea*; AbL, *Abies lasiocarpa*; FaG, *Fagus grandifolia*; FaS, *Fagus sylvatica*; Fr, *Fraxinus* sp.; LaD, *Larix decidua*; LiT, *Liriodendron tulipifera*; NoB, *Nothofagus betuloides*; Pi, *Picea* sp.; PiA, *Picea abies*; PiE, *Picea engelmannii*; PiGxE, *Picea glauca* × *Picea engelmannii*; PiM, *Picea mariana*; PnB, *Pinus banksiana*; PnC, *Pinus contorta*; PnP, *Pinus ponderosa*; PnS, *Pinus sylvestris*; PoT, *Populus tremuloides*; QuE, *Quercus* subgenus *erythrobalanus*; QuL, *Quercus* subgenus *lepidobalanus*; ThP, *Thuja plicata*. Coarse Woody Debris (CWD): DWD, downed woody debris; SDT, standing dead trees. Stand: A, Alpine grassland; H, Hardwood; M, Mixedwood; S, Softwood. Sites is the number of geolocalized sites in the study. Trees: the number of trees sampled.

knowledge that should be addressed by future studies to better assess wood degradation dynamics and their inclusion into modeling efforts.

2 | MATERIALS AND METHODS

2.1 | Literature survey and study selection

Peer-reviewed articles documenting time since death (TSD) of coarse woody debris (CWD) were obtained from Google Scholar using the following keywords: "snag", "standing dead tree", "log", "downed woody debris", "coarse woody debris" or "deadwood" + "time since death" or "year of death" + "decomposition class", "degradation class" or "decay class". Abbreviations were included in the search strings and the literature cited in every study was checked for potential relevance. To be included in this meta-analysis, studies had to meet the following criteria: (1) TSDs were obtained from dendrochronology methods using crossdated ring-width series statistically validated with quality control programs such as COFECHA (Holmes, 1983); (2) TSDs were specified by decay classes (DCs), by species and by CWD type, that is, standing dead trees (SDTs) or downed woody debris (DWD); (3) statistical information, that is, mean, standard deviation, and sample sizes were clearly reported for each group of interest; (4) the study was peer-reviewed and published in English or in French and; and (5) the study was the original source of the data being reported (see Appendix I for more details on excluded studies). The final dataset is described in Table 1 and Figure 1.

2.2 | Data assembly

Candidate explanatory variables affecting TSD were selected based on literature and according to their availability either in open-source databases or directly withing the selected studies. Two types of independent variables were tested: (1) tree-level variables, that is, decay class, CWD type, wood density, and phylogeny (softwood or hardwood); (2) site-level climatic conditions, that is, mean maximum summer temperature and mean total annual precipitation (Table 2).

We first constructed an integrated decay-class system allowing us to comprehensively compile and classify data from all selected studies. Current systems typically segregate dead trees into several DCs based on various individual stem attributes, such as the firmness or presence of bark, the presence or absence of remaining foliage, the presence of twigs or branches, etc. We thus developed a harmonized three-class system describing the state of decomposition of both DWD and SDT (Figure 2 and Table S1). We have excluded the more advanced stages of decay for which dating tree death by dendrochronology is generally unapplicable as a result of an absence of bark or due to excessive wood decomposition. Whenever there was uncertainty when assigning data according to one category of our classification system, priority was given to the hardness of the wood, followed by the state of decomposition and the order of branches (Figure 2). Following the attribution of a new DC based on our integrated system, we extracted TSD means, standard deviations and sample sizes per CWD type, species and DC for each study site (Figure S1). WebPlotDigitizer (V.4.0., Rohatgi, 2018) was used if the data were presented as figures in the publications.

Species- and region-specific mean wood density (WD) values were obtained from the Global wood density database (Zanne et al., 2009). The database reports values collected from the literature of wood density as oven-dry mass divided by green volume (Chave et al., 2009), or specific gravity. Most species found correspondence in the database, but in the few cases where species- and region-specific values were not available in the database, the mean density of species of the same genus for the region of interest was used.

Local climatic conditions were obtained at a 1-km^2 spatial resolution from the WorldClim database (V.2, Fick & Hijmans, 2017). Mean maximum summer temperature and mean total annual precipitation for 1970–2000 were extracted for each site according to their coordinates using

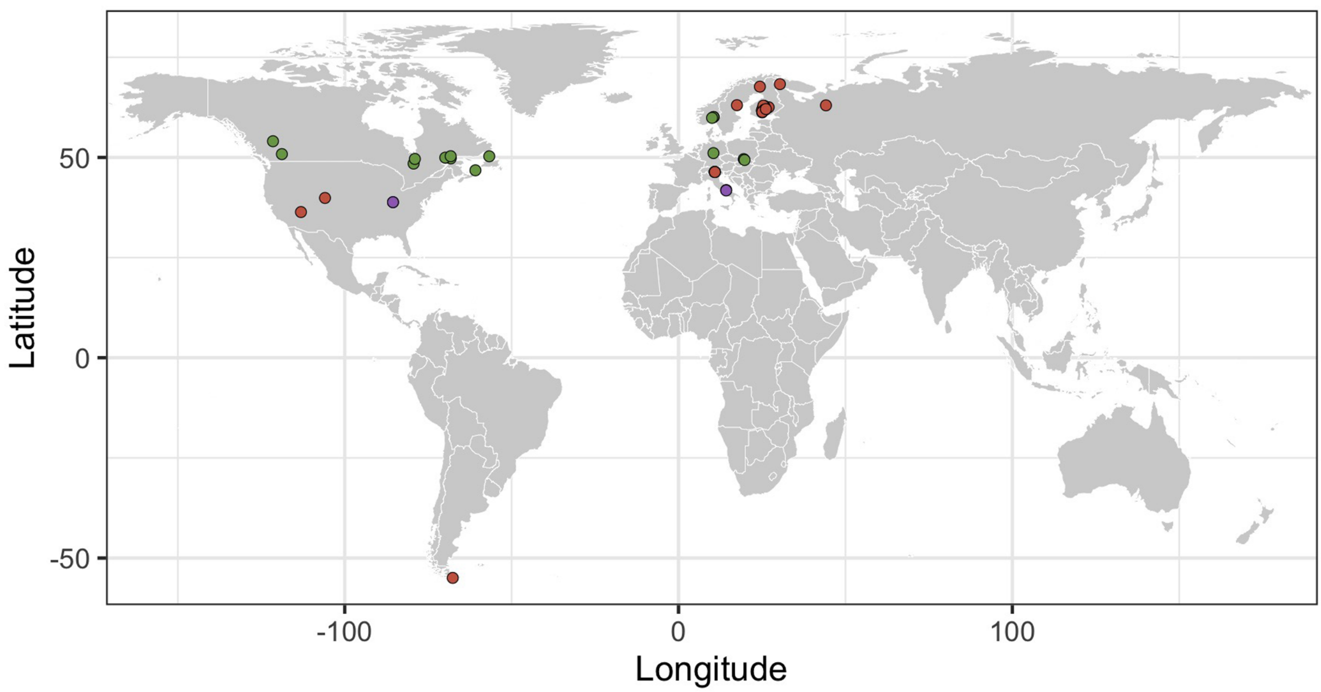

FIGURE 1 Localization of the 42 sites of the 23 studies included in the present meta-analysis. The colors refer to the results of a clustering analysis based on site- and tree-level variables that were found to affect wood debris decomposition. Cluster A (red) is mainly composed of softwoods exposed to cold and dry environments, cluster B (green) is composed of softwoods in cold but wet environments and cluster C (purple) consists of hardwood in warmer environments

TABLE 2 List of candidate explanatory variables included in the modeling process

Variable	Description
DC	Decay class: 1, 2 or 3
CWD	Coarse woody debris type: standing dead tree (SDT) or downed woody debris (DWD)
TreePhyl	Tree phylogeny; hardwood or softwood
WD (g/cm^3)	Species- and region-specific wood density (Global wood density database (Zanne et al., 2009)
Prec (cm)	Mean total annual precipitation for 1970–2000 (WorldClim database (V.2, Fick & Hijmans, 2017)
MaxTemp (°C)	Mean maximal temperatures in January (Southern Hemisphere) and July (Northern Hemisphere) for 1970–2000 (WorldClim database (V.2, Fick & Hijmans, 2017)

the "raster" package (V. 2.9-5, Hijmans et al., 2015) in R statistical programming software (R Core Team, 2019).

2.3 | Meta-analysis

The influence of the selected candidate variables on TSD was tested using mixed-effect meta-regressions. Raw TSD mean was used as the outcome measure for the meta-analysis, as this measure is provided on a meaningful scale and was available throughout all selected studies. Mixed models (Table 3) were implemented using the "rma.mv" function of the "metafor" package (Viechtbauer, 2010) in R. Given that methods and sample characteristics are likely to be somewhat different throughout the set of studies included in the meta-analysis, the study of origin was added as a random effect in each model (Viechtbauer, 2010). The sensitivity of our models to outliers was tested using the "influence" function of the "metafor" package (Viechtbauer, 2010).

We performed a model selection to identify the best predictors of TSD using the "MuMIn" package (Bartoń, 2019) in R. Because preliminary analyses of the dataset suggested strong interactions between DC and climate variables, they were included as interactions in the candidate models (i.e., DC × MaxTemp and DC × Prec). Preliminary analyses also suggested a potential interaction between DC and WD so they were included both as additive and interaction terms in the candidate models. No correlations were found between independent variables ($r < 0.7$; Figure S2), allowing us to include a full model in the model selection. We fitted a total of eight candidate models that were included in the model selection process, including a null (intercept-only) model (Table 3). The performance of the candidate models was assessed with the corrected Akaike information criterion (AICc). Because the AICc weight of the best model was <0.9, it was not possible to select a unique model to explain TSD. Therefore, we evaluated the effects of each variable included in the best models through model averaging using the "MuMIn" package. Estimates and confidence intervals were calculated using a "full" average, which is a type of shrinkage estimator that prevents biasing values away from zero (Bartoń, 2019). *p*-values were used to assess the significance of the considered explanatory variables.

To summarize the woody debris dynamics at a broad scale, we performed a cluster analysis considering the significant explanatory variables previously identified in the model selection. This analysis allowed us to first identify patterns in wood debris dynamics, and then relate these patterns to site characteristics. We used mixed reduced *K*-means (mixed RKM), which implements a joint dimension reduction (principal component analysis for mixed data) and clustering method for mixed-type variables, using the "clustrd" package in R (Markos et al., 2019). This method is well-suited for mixed datasets such as ours, which include both discrete and metric values (van de Velden et al., 2019). Mixed RKM also performs better than a two-step analysis in which a cluster analysis is applied to the results of dimension reduction (i.e., tandem analysis), an approach that proved unsuitable for the clustering step (van de Velden et al., 2017, 2019; Vichi & Kiers, 2001). The appropriate number of clusters and the stability of the solution were evaluated using 20 bootstrap replicates through the "clustrd" package.

To better evaluate the implications of the variables identified as affecting TSD on the woody debris dynamics, we modeled decay-class distributions of woody debris over time for each cluster identified in the mixed RKM analysis using the stage-based matrix method developed by Kruys et al. (2002). Only tree species for which DCs 1 to 3 were sampled were included in the mean residence time calculation. Given that all selected studies did not contain longitudinal data (i.e., decay of woody debris was not measured over time), slow-decaying trees are more likely to have been sampled than quick-decaying ones. To account for this bias, we calculated the mean residence time in each DC using a Horwitz–Thompson estimator, as suggested by Kruys et al. (2002). The mean residence times for each decay class within each cluster were then used to compute transition probabilities. The probabilities were calculated using a 5-year time step, within which a tree could either remain in the same DC, move to the next DC, or move to the second next DC (Kruys et al., 2002). Trees were considered "out" of the system when they reached a DC > 3. Computations were implemented in the R statistical programming environment.

Finally, we computed spatially explicit projections of how the mean TSD of deadwood may evolve over time when

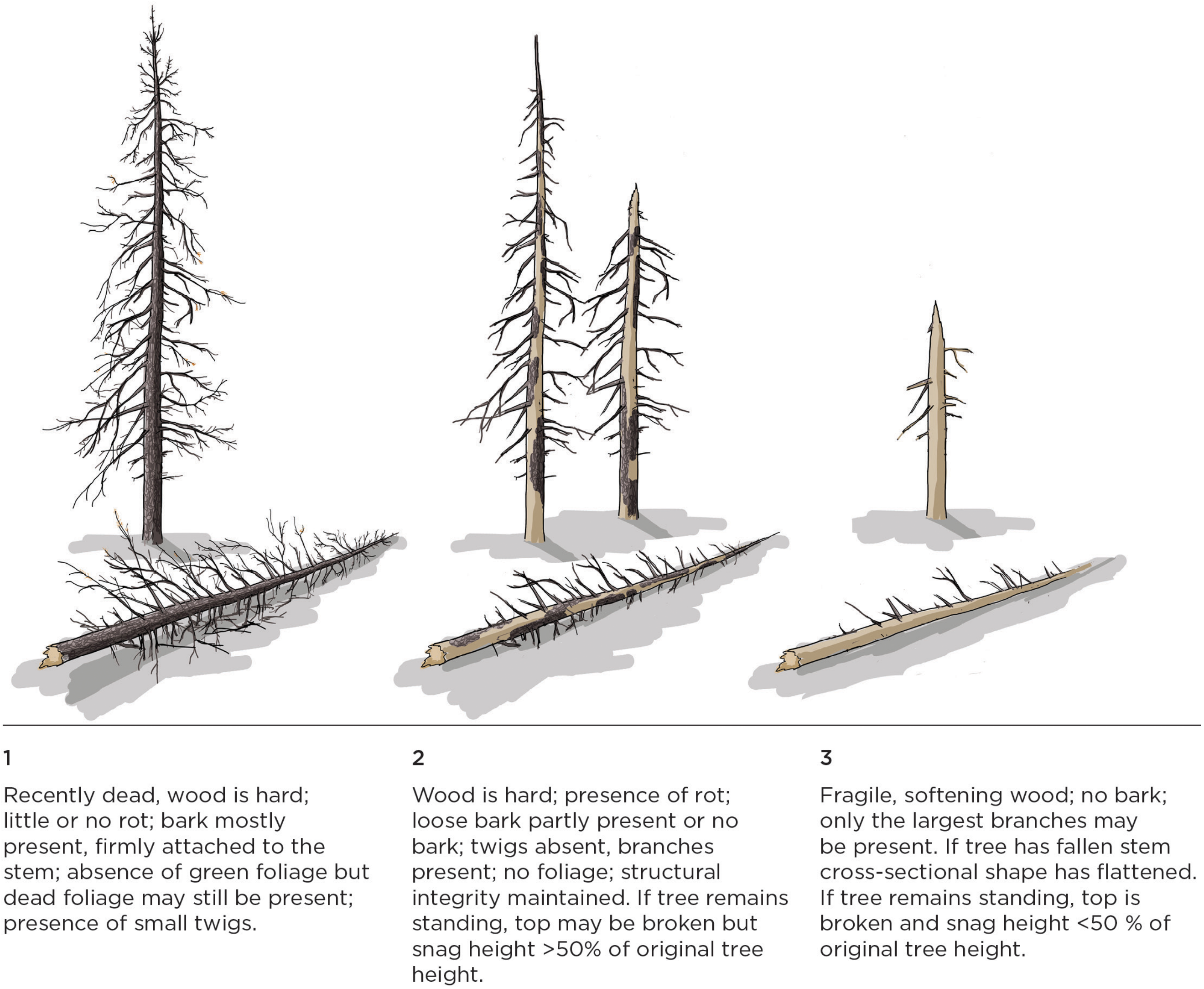

FIGURE 2 Integrating decay classification developed for this meta-analysis allowing the inclusion of both standing dead trees and downed woody debris. Advanced decay stages were not considered when building this classification system as dendrochronology methods are generally impracticable on such debris

considering two scenarios of future climate in comparison to a reference climate. For the purpose of the paper, we focused on the first decay class, as the time window within which trees can be used as feedstock for bioenergy is limited (Barrette et al., 2015). Projections were computed for Europe where we had the highest density of sites included in the meta-analysis. First, forest composition was acquired using the EU-Forest database (Mauri et al., 2017), a high resolution (1-km-cell grid) dataset compiling tree occurrence from European National Forest Inventories. Species occurrences were compiled using a one-degree-cell grid overlying the area covered by the EU-Forest database. Species with less than 50 occurrences across Europe were removed. Second, species-specific wood density (g/cm^3) for Europe was obtained from the Global wood density database (Zanne et al., 2009). Species for which wood density was not available were attributed the mean density of the corresponding genus in Europe. The average wood density for each one-degree cell was then calculated as the mean wood density weighted by the species abundances. Finally, baseline (1970–2000) and projected (2080–2100) maximum temperatures and total annual precipitation according to shared socio-economic pathways (SSPs) 2–4.5 and 5–8.5 were obtained from Worldclim (V.2, Fick & Hijmans, 2017). Downscaled (10-min resolution) projections for eight models of the CIMP6 (Coupled Model Intercomparison Project Phase 6; Eyring et al., 2016) multi-model ensemble that were available at the time of running the analyses (see Table S2 for detailed information on these models). Baseline maximum temperatures and total annual precipitation were averaged for each one-degree cell. Projected climate variables were calculated considering the outputs of the eight GCMs. Spatially explicit projections of the TSD of woody debris were computed using the best model identified through the model selection process and

TABLE 3 Model selection table of the eight multiple linear meta-regression models built for predicting time since death (TSD), where K is the total number of parameters, (including an intercept), Δ_i is the difference in Akaike information criteria, corrected for small sample sizes (AICc) with the best model, and W_i is the ratio of the Δ_i for a given model to that of the whole set of candidate models. Dependent variables included in the models are described in Table 2

Explanatory variable	ID	LL	K	AICc	Δ_i	W_i
DC × MaxTemp + DC × Prec + TreePhyl + DC × WD	6	−957.0	14	1945.3	0.0	0.72
DC × MaxTemp + DC × Prec + CWD + TreePhyl + DC × WD	8	−956.9	15	1947.6	2.3	0.23
DC × MaxTemp + DC × Prec + TreePhyl + WD	5	−962.4	12	1951.3	6.0	0.01
DC × MaxTemp + DC × Prec + CWD + TreePhyl + WD	7	−962.3	13	1953.5	8.2	0.00
DC × MaxTemp + DC × Prec	3	−974.5	10	1970.8	25.5	0.00
DC × MaxTemp + DC × Prec + CWD	4	−974.4	11	1972.8	27.6	0.00
DC	2	−1126.0	4	2260.4	315.1	0.00
Intercept only	1	−1913.3	2	3830.7	1885.4	0.00

mapped across Europe using the "predict.rma" function of the "metafor" package. As our model is linear and based on a normal distribution, the projected values associated with the warmer sites were sometimes slightly below zero (~20% of the 1-km cells across Europe). We assigned these cells a predicted value of 0 to remain biologically meaningful.

3 | RESULTS

Our meta-analysis indicated that both climatic conditions and tree-level variables were good indicators of the time since death of woody debris. Model selection revealed that the most plausible model (wAICc = 0.72) included the interaction between DC and maximum summer temperature, the interaction between DC and total annual precipitation, the interaction between DC and WD and the tree phylogeny (Model 6, Table 3). The second most plausible model (wAICc = 0.23) included the same variables as well as the CWD type.

All variables included in the most plausible model were significant predictors of TSD according to model averaging, while CWD type had no effect (Table 4). We found that DC was strongly related to TSD with woody debris of DC2 and DC3 having mean TSD values (±SE) 9.45 ± 2.43 ($p < 0.0001$) and 35.65 ± 3.83 ($p < 0.0001$) greater than that of DC1, respectively. In the interaction between maximum summer temperature and DC, we found that the magnitude of the negative effect of temperature on TSD tended to increase in more advanced DCs ($p < 0.0001$, Figure 3a). Conversely, our results indicated a positive effect of total annual precipitation on TSD, which was higher for DC2 and DC3 than DC1 ($p < 0.0001$, Figure 3b). Wood density also had a positive effect on TSD, which again was greater in more advanced DCs ($p = 0.012$, Figure 3c). Finally, we found that TSD tended to be on average 4.42 ± 1.40 years higher in softwoods than in hardwoods for all DCs ($p = 0.002$).

Wood debris dynamics were successfully clustered considering significant variables influencing TSD, that is, maximum summer temperatures, total annual precipitation, wood density, and tree phylogeny. According to bootstrapping, the most stable solution contained three clusters, which accounted for 83.6% of the variance observed between the observations. The resulting clusters and dimension reduction were represented on a two-dimensional biplot (Figure 4). The first axis of the resulting ordination was mainly associated with maximum summer temperature and tree phylogeny, while the second was associated with a precipitation gradient. Cluster A contained 48.4% of all site-level means and was mainly composed of softwoods of low wood densities that were exposed to cold and dry environments. Cluster B contained 42.2% of all site-level means and was mainly characterized by softwoods of higher wood densities that were exposed to cold and wet environments. Cluster C contained 9.4% of all site-level means and was characterized by hardwoods that had the highest wood densities and that were exposed to warmer environments.

A decay-class transition rate model was produced for each of the three clusters identified considering the mean residence time in each DC within each cluster and allowed us to visualize the changes in the proportions of each decay class over time (Figure 5). Cluster A, mainly characterized by softwoods in cold and dry environments, showed slow transitions between DCs, with 75% of the trees being out of the system (i.e., decay class >3) ~50 years after tree death. The transition model for cluster B, mainly characterized by softwoods of higher wood densities in cold but wetter environments, showed an even slower decay process, with 75% of the trees being out of the system ~65 years after tree death. In cluster C, characterized by hardwoods from warmer environments, the modeled wood degradation was much faster, with 75% of the trees being out of the system after ~30 years.

TABLE 4 Model-averaged coefficients based on the model selection described in Table 3 using a full average estimator (similar to shrinkage estimator). Estimate, standard error (SE), *z*- and *p*-value (*z*, *p*), and lower and upper boundaries of the 95% confidence intervals are reported (ci.Lb and ci.Ub). The categorical variables, that is, decay class (DC), tree phylogeny (TreePhyl), and coarse woody debris type (CWT) are compared to their respective reference levels: Decay class 1 (DC1), hardwood, and downed woody debris (DWD, in opposition to standing dead wood (SDW)

	Estimate	SE	*z*	*p*	Ci.Lb	Ci.Ub
Intercept	15.24	9.01	1.90	0.0572	−0.46	30.95
DC2	9.45	2.43	3.89	<0.0001	4.69	14.21
DC3	35.65	3.83	9.31	<0.0001	28.15	43.17
MaxTemp	−1.49	0.51	2.92	0.0036	−2.50	−0.49
Prec	0.19	0.05	3.68	0.0002	0.09	0.29
(TreePhyl)Softwood	4.42	1.40	3.16	0.0016	1.68	7.16
WD	22.01	5.72	3.68	0.0001	10.80	33.22
DC2:MaxTemp	−0.82	0.15	5.56	<0.0001	−1.12	−0.53
DC3:MaxTemp	−2.20	0.24	9.28	<0.0001	−2.66	−1.73
DC2:Prec	0.17	0.02	10.17	<0.0001	0.14	0.20
DC3:Prec	0.16	0.03	5.58	<0.0001	0.10	0.22
DC2:WD	4.67	8.84	0.53	0.5973	−12.65	21.99
DC3:WD	29.98	11.93	2.51	0.0120	6.59	53.37
(CWT) SDW	−0.06	0.29	0.22	0.8238	−0.64	0.51

Finally, the spatially explicit projections of TSD for deadwood corresponding to the DC1 category ranged between 0.0 and 61.0 years (with a 95% confidence interval around prediction ranging from 0.0 to 100.0 years) when using the baseline climate across Europe (Figure 6). The lower values of predicted TSD were obtained around the Mediterranean, whereas the highest TSD predictions were concentrated in the Alps, in Scotland and in southwestern coast of Norway. The mean predicted TSD (±SD) across the modeled territory was 9.6 ± 9.0 years. Projected TSD values for the 2080–2100 period under SSP2-4.5 showed a similar range of 0.0 to 59.0 years (95% CI: 0.0 to 97.5) across Europe, but values showed a general decreasing trend, with a mean value of 5.8 ± 8.4 years. Under SSP5-8.5, projected TSD values ranged between 0.0 and 62.2 years (95% CI: 0.0 to 101.7) for the 2080–2100 period, but the mean value decreased to 3.9 ± 7.9 years. A slight increase in TSD was observed in the southwestern coast of Norway, whereas most of the territory was characterized by a reduced TSD. Under this scenario, projected values of TSD neared zero in most of continental Europe.

4 | DISCUSSION

4.1 | Factors influencing wood debris decomposition dynamics

Our results show that the decomposition rates of both standing dead trees and downed woody debris increase with temperature but tend to decrease with annual precipitation. The association between higher temperatures and increased decomposition rates is well-established in the literature (Campbell & Laroque, 2007; Hararuk et al., 2020; Přívětivy et al., 2016; Russell et al., 2015). The optimal temperature for saproxylic fungal activity has been reported to range between 24 and 38°C for several species in the United States (Panshin & de Zeeuw, 1980), which is in line with our findings. Increased fungal activity is also promoted by wood moisture content (ratio of the mass of water to that of the oven-dry wood) values in the range of 30–45% (Panshin & de Zeeuw, 1980; Rayner & Boddy, 1988), beyond which oxygen becomes limiting (Hararuk et al., 2020; Olajuyigbe et al., 2012; Wang et al., 2002; Zell et al., 2009). Such a relationship may seem to contrast with the negative impact of precipitation on decay rates that we observed, but total annual precipitation alone may not be a good predictor of wood debris moisture (Liu et al., 2013). Debris characteristics such as standing or downed debris (Hararuk et al., 2020; Petrillo, Cherubini, Sartori, et al., 2016; Přívětivy et al., 2016), wood density (Mackensen et al., 2003; Petrillo, Cherubini, Sartori, et al., 2016) and soil moisture, which in turn is influenced by aspect, slope, and soil properties (Bardelli et al., 2018; Petrillo, Cherubini, Sartori, et al., 2016), are also important drivers of wood debris moisture. Moreover, because most of the included studies are located at relatively high latitude, high precipitation may be representative of high snowfall and extended snow cover, which may slow down the decomposition process

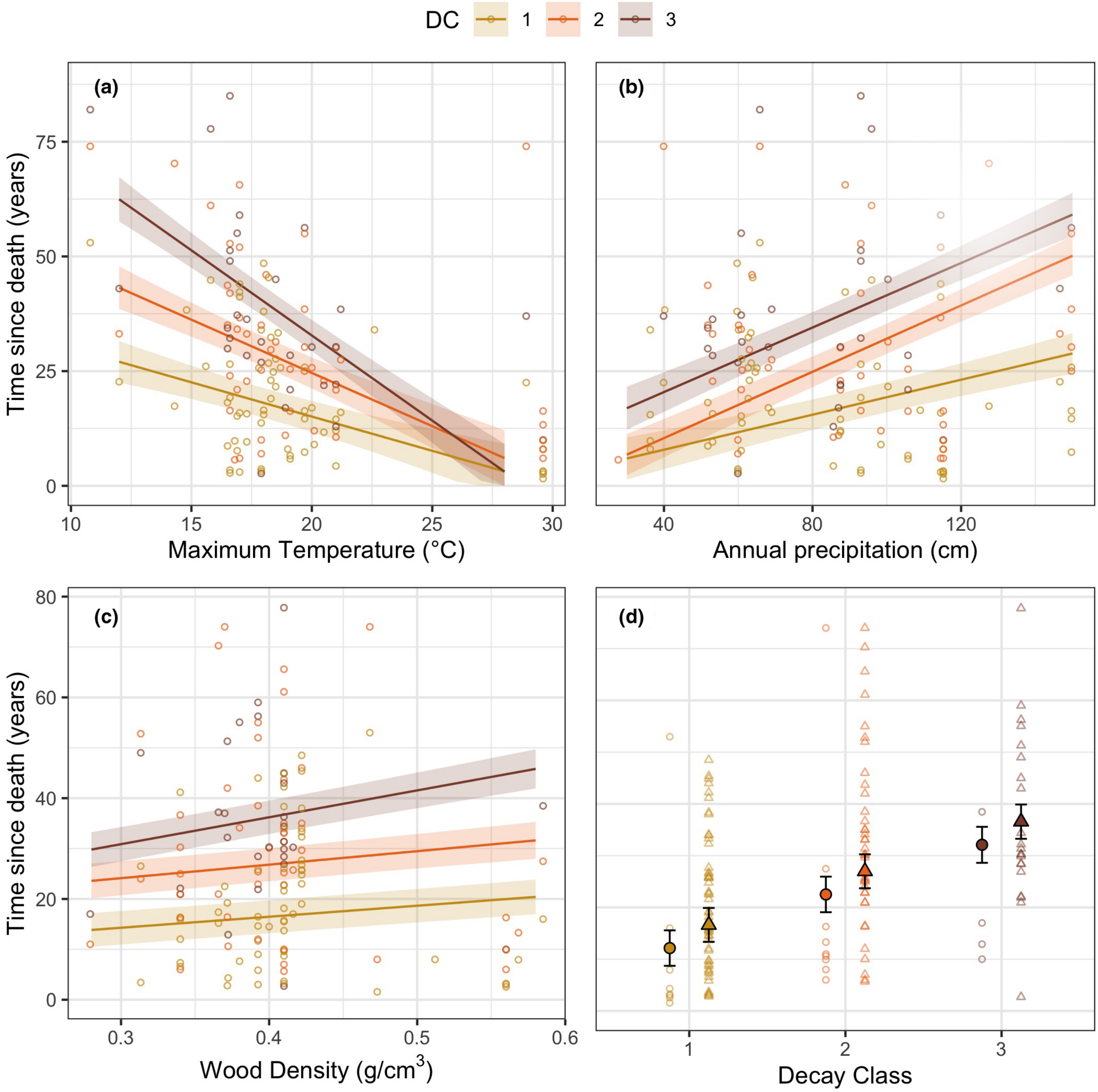

FIGURE 3 Predicted time since death of coarse wood debris in relation to decay class (DC) and (a) annual maximum temperature (°C; as in July for the Northern Hemisphere and January for the Southern Hemisphere), (b) total annual precipitation (cm) and (c) wood density (g/cm^3) and (d) tree phylogeny where triangles represent softwood and circles hardwood. Lines and filled symbol represent model predictions computed using a meta-regression approach, with the mean of the explanatory variables other than the one of interest used as a constant. Open symbols represent the observations from the included studies. Shaded areas and error bars represent standard error (SE)

(Gómez-Brandón et al., 2020). The impact of precipitation on decay rates may also interact with temperature, saproxylic fungi assemblage composition as well as the current decay state of the considered woody debris (A'Bear et al., 2014; Herrmann & Bauhus, 2013; Olajuyigbe et al., 2012; Venugopal et al., 2017; Wang et al., 2002). As highlighted by our cluster analysis, precipitation may not be considered in isolation of these other factors.

The areas covered by this meta-analysis are projected to undergo an important warming phase in the next decades, with projected increases in mean annual temperatures ranging from 2 to 5°C by 2100 in North America and western Europe (IPCC, 2013). Our results are in line with a previous assessment (Russell et al., 2014), which suggested that such warming will likely accelerate wood decomposition. Based on our model, the estimated TSDs

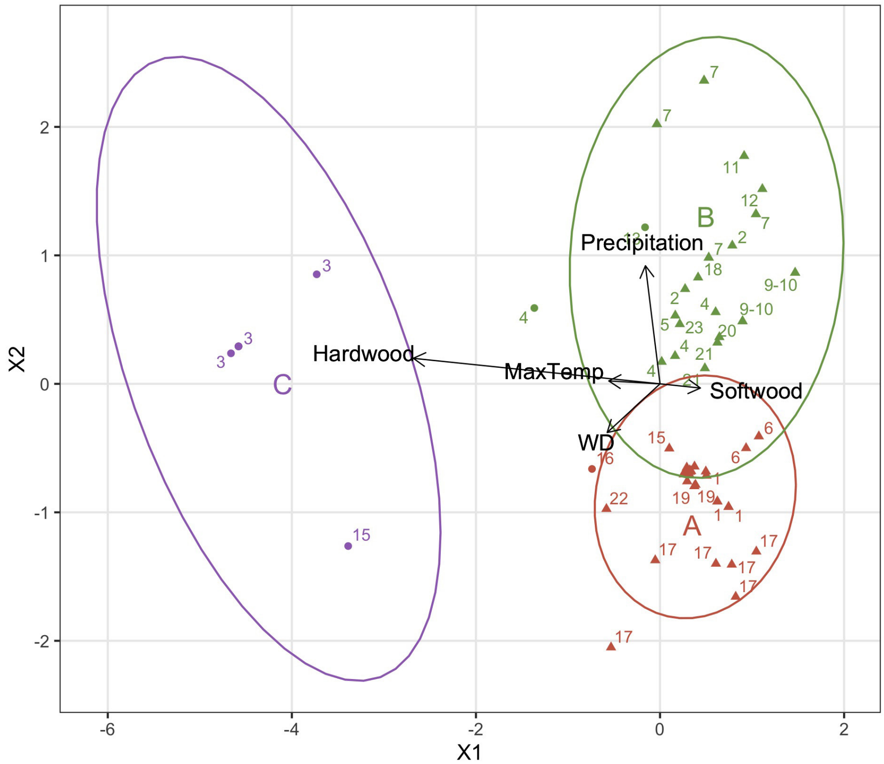

FIGURE 4 Mixed reduced *k*-means biplot of samples included in the meta-analysis considering site maximum summer temperature, site total annual precipitation (cm), wood density and tree phylogeny (triangles represent softwood and circles hardwood.) of the sampled species. The three ellipses represent the three clusters (labelled A, B, and C) identified through the analysis, and the color of the symbols indicates the associated cluster. The number associated with each symbol indicates the study to which the observation belongs according to Table 1. Note that the concentrated symbols in cluster A all belong to study 19, but that labels were not shown to keep the figure legible. Arrows indicate the magnitude and direction of the increasing values of climatic conditions and tree-level variables. Accordingly, the first axis (X1) is associated with a gradient from warmer to colder maximum temperatures, and with a shift from hardwood to softwood species. The second axis (X2) is associated with increasing precipitation. Wood density is associated with both axes and increases toward the upper right of the plot

of the three DCs were almost equivalent at maximum temperatures >25°C and overlapped when considering the associated standard errors in Figure 3. Although not biologically meaningful, our model seemed to indicate younger deadwood in DC3 than in DC2 in warm sites. While this highlights the uncertainty around these estimates, the similar TSD values predicted for the three DCs are in fact indicative of an overall faster decomposition rate.

The presence of very old DC3 debris in cold environments contributed to steepening the slope of the linear relationship between temperature and the time since death. Nonlinear models may have been better suited to such data (Oberle et al., 2020) but the implementation of such models using meta-regression is not possible with current tools, to our knowledge. Moreover, given that observations are much scarcer in warmer environments, the uncertainty increases toward warmer sites. Considering the available datasets, our model must be seen as mainly representative of boreal and temperate conditions. Still, the faster decomposition rate that can be expected with higher temperatures is well in line with the results of the decay-class transition rate models. The total residence time of deadwood (considering 75% of the sample trees) in DCs 1 to 3 was reduced by ~45%–60% in the cluster associated with warmer study sites compared to those associated with colder sites. Conversely, the projected increase in precipitation regime across most of the areas covered by our meta-analysis (IPCC, 2013) could have mitigating effects on the expected increase in wood degradation rates, according to our results. Yet, spatially explicit projections of TSD for deadwood of the DC1 category across Europe indicate a strong generalized trend toward an increased decomposition rate, with slight decreases in decay rates being projected only in very limited areas. However, these projections should be interpreted with caution, as local factors may be accountable for an important part of the variability in wood decomposition dynamics (Bradford et al., 2014, 2017; Hu et al., 2018) and may interfere with the apparent generalized trend shown by broad-scale

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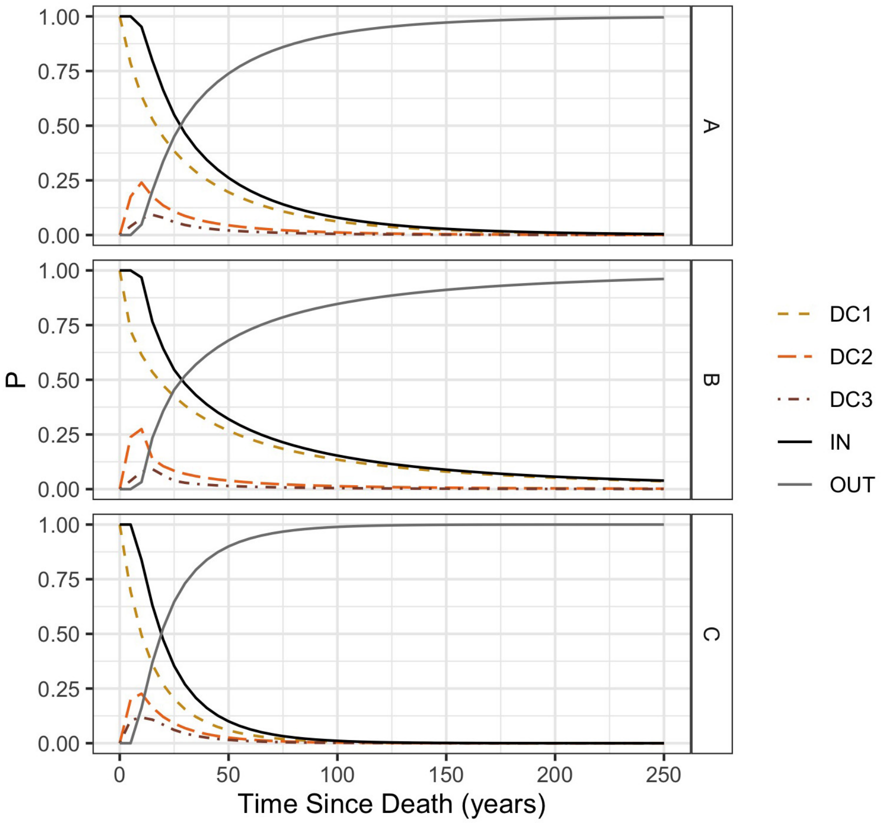

FIGURE 5 Proportion of trees within each decay class (P) in relation to the time since death for the three clusters identified by the mixed reduced k-means analysis. Cluster A is composed of softwoods exposed to cold and dry environments, cluster B is composed of softwoods in cold but wet environments and cluster C consists of hardwood in warmer environments. Decay-class transition probabilities were based on a 5-year period. "IN" refers to the proportion of trees that are inside the system (i.e., DC $\leq$ 3), while "OUT" refers to the proportion of trees that are out of the system (i.e., DC > 3)

projections. Moreover, one limitation of our spatially explicit projections is that they do not consider changes in forest composition and wood density that are likely to result from climate warming (e.g., Buras & Menzel, 2019).

Regarding the influence of tree-level factors on wood decomposition, we found that tree phylogeny and wood density had a significant effect on TSD for a given decay class. Softwood debris were found to be generally older than hardwood debris, a result in line with that of previous studies. The higher nitrogen and phosphorous concentration of hardwoods (Hu et al., 2018; Weedon et al., 2009) could explain the higher decomposition rate, whereas the higher lignin content in softwoods is known to slow decay (Freschet et al., 2012). In addition, the xylem anatomy of hardwoods, characterized by the presence of large vessels, is likely to promote faster fungi colonization (Weedon et al., 2009) that the more continuous structure of softwood xylem (Harmon et al., 1986). Our results also indicate that TSD increases with wood density, which may seem surprising as hardwoods are usually denser than softwoods (Weedon et al., 2009). Yet, we believe this relationship to be attributable to the fact that most of our data are from softwoods, in which denser wood contains more lignin (Weedon et al., 2009), whereas the opposite relationship is true for hardwoods.

We found no effect of CWD type on TSD, which contrasts with previous results indicating a faster decomposition of downed woody debris compared to snags (Hararuk et al., 2017; Oberle et al., 2018; Storaunet & Rolstad, 2002). Faster colonization of downed debris by micro-organisms (Boddy, 2001) and a favorable moisture content resulting from a direct contact with the soil are thought to promote faster decomposition (Oberle et al., 2018). The non-significance of the CWD type in our study may arise from the fact that the timing of the fall (transition from SDW to DWD), known to influence wood decay rate (Storaunet & Rolstad, 2002), was not considered herein given its scarce availability within the datasets.

4.2 | Implications for conservation and management

By promoting a decreased residence time in each decay stage, further climate warming may alter the dynamics of deadwood, which in turn may affect saproxylic biodiversity (Brunet & Isacsson, 2009; Buse, 2012; Lachat et al., 2013). As deadwood represents a dynamic habitat evolving over time, specific habitat features must be available at the right time to allow successful colonization and ensure the maintenance of saproxylic diversity (Lachat et al., 2013; Müller & Bütler, 2010). Species associated with narrow ecological niches or characterized by a limited dispersal ability may be critically affected by a reduced residence time of deadwood in response to warmer conditions (Lachat et al., 2013; Müller & Bütler, 2010).

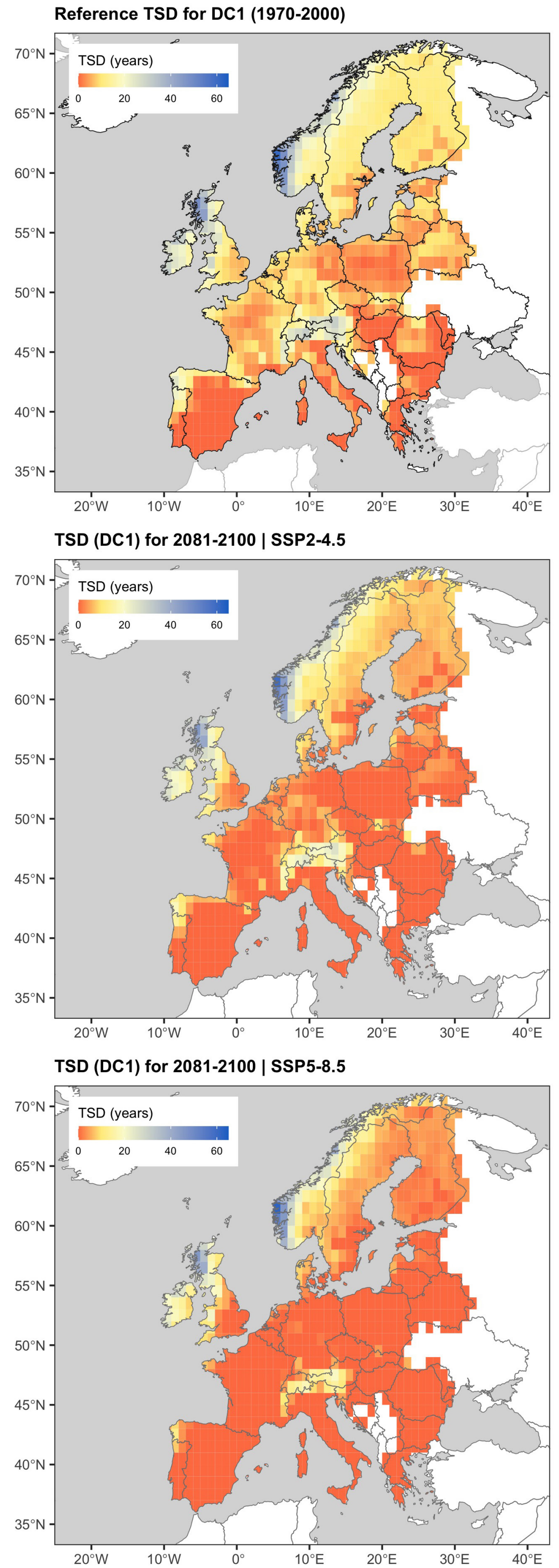

FIGURE 6 Modeled time since death (TSD, in years) of deadwood of decay class 1 across Europe. Top panel shows the reference TSD modeled using the baseline climate (1970–2000). Middle and bottom panels refer to TSD for the 2080–2100 period modeled according to climatic projections for SSP2-4.5 and SSP5-8.5, respectively

However, as climate change is expected to increase the frequency and magnitude of tree mortality events worldwide (Anderegg et al., 2020; Millar & Stephenson, 2015; Trumbore et al., 2015), the increased amount of dead trees could counteract the effect of increased temperature on deadwood decomposition rates. Moreover, as higher temperature is associated with increased species richness, warming could compensate, a least partly, for the diversity loss associated with the reduced availability of deadwood at different decomposition stages (Müller et al., 2015). Still, the ecological thresholds in deadwood quantities necessary to ensure the maintenance of saproxylic species diversity depends on local forest attributes as well as on the dispersal potential of the associated species assemblage (Lachat et al., 2013, Müller & Bütler, 2010). Locally informed thresholds could thus be used in conjunction with our decay-class transition rate models to better inform forest managers and conservationists on the potential impact of warming on saproxylic biodiversity.

Considering global warming, the increase in both the frequency and severity of natural disturbances and the acceleration of decay-stages transition dynamics also highlights the necessity to adapt salvage logging strategies. Indeed, the harvesting of woody debris may represent a great opportunity to value the carbon stocked in deadwood either for bioenergy or into long-lived end-products such as lumber (Lamers et al., 2013, 2014). Indeed, forests are estimated to contain around 50% of the terrestrial biosphere carbon (Malhi, 2002), of which up to 20% is in the form of standing dead trees and downed woody debris (Delaney et al., 1998; Harmon et al., 1990). However, such use of deadwood requires a targeted harvesting of lightly decayed wood, whose persistence is strongly influenced by both climatic conditions and tree-level attributes. For example, our results indicated that the mean residence time of trees in the first decay class will shift from a mean of ~10 years to 4–6 years in 2080 across Europe. Hence, as climate gets warmer, the "shelf life" of dead trees as feedstock for value-added products will considerably shrink. This is especially true for hardwoods species, for which the planning and implementation of salvage harvesting will need to occur within a short period following disturbance. The relevance of salvage harvesting has not only been considered in terms of financial viability (e.g., Barrette et al., 2017; Béland et al., 2020; Bogdanski et al., 2011; Kumar et al., 2008), but also according to its climate change mitigation potential (e.g., Laganière et al., 2017; Lamers et al., 2013, 2014). The latter depends on a multitude of (sometimes interacting) factors, such as the type of end-product (Barrette et al., 2015) and its expected lifespan (Kurz et al., 1993), the carbon footprint of the substituted product (e.g., Laganière et al., 2017), the carbon sequestration rate of the post-disturbance forest (Paquette & Messier, 2010), and the timing and quantity of emissions related to the decomposition the dead trees. To increase the climate change mitigation potential of salvage harvesting, special attention should be given to the factors that may help reduce the time needed to achieve atmospheric benefits (Mansuy et al., 2018). As such, dead trees that decompose at a faster rate, in warmer regions, may be seen as a better source of feedstock to increase greenhouse gas mitigation (Laganière et al., 2017).

5 | CONCLUSIONS

In the context of global change, understanding and modeling broad-scale dynamics of wood degradation, with the goal to improve projections of their contributions to various ecological processes and global carbon cycle is an ongoing challenge. The objective of this meta-analysis was to review the effects of tree attributes and local climatic conditions on the time since death of coarse woody debris ranging in degradation levels. In the first place, an important contribution of this meta-analysis is the development of a synthetic decay-class system that integrates the multiple classification used in the literature to classify deadwood decomposition state according to visual criteria. This standardized system should be prioritized in future investigations to allow direct comparisons between studies, which is a key to improve our understanding of the broad-scale dynamics of tree degradation. In the second place, our analysis showed that projected warming will likely accelerate wood decomposition and significantly decrease the residence time in each decay stage. Because the impact of such dynamics on the biodiversity is still poorly understood, the development of locally explicit ecological thresholds in deadwood quantities necessary to ensure the maintenance of saproxylic species diversity should be a research priority. Moreover, while coarse woody debris has been recognized as a key resource for bioenergy at the global scale (Chum et al., 2011), the acceleration of decay-stages transition dynamics indicates that the window of time to harvest dead trees targeted as feedstock will shrink. Consequently, future planning and implementation of salvage harvesting will need to occur within a short period following disturbance, especially in warmer regions dominated by hardwood species. As highlighted by Weedon et al. (2009), global climate-vegetation models predicted an expansion of forest area dominated by hardwood species in many regions (IPCC, 2007). These projections further highlight the need to develop strategies allowing rapid planning and implementation of adaptive silvicultural treatments to succeed in increasing greenhouse gas mitigation. Finally, our literature survey emphases that the majority of the available information on wood decay comes from temperate and boreal forests of North America and Western Europe, whereas data from subtropical, equatorial, and subarctic forests are scarce. Such data are urgently needed to allow broader-scale conclusions (Weedon et al., 2009) and to produce representative carbon pools models capable of informing adaptive management strategies with respect to the global carbon cycle.

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CONFLICT OF INTEREST

All authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

ORCID

Catherine Chagnon https://orcid.org/0000-0002-2854-3360
Guillaume Moreau https://orcid.org/0000-0002-3522-6988
Filip Havreljuk https://orcid.org/0000-0003-1436-8730
Alexis Achim https://orcid.org/0000-0003-0118-1651

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