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Research article

Effects of forest dieback on deadwood patterns: Large scale trends from a cross-analysis of European databases

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ABSTRACT

Despite its importance as a key element for forest biodiversity and ecosystem functioning, uncertainties remain on how deadwood may change due to increasing forest dieback and subsequent management.

The opportunistic cross-analysis of two large-scale, never-before-crossed forest databases, based on the spatially representative 16 × 16 km European grid, provided a dataset of 1804 plots in 17 countries with 10-year time series of annual measurements of tree defoliation followed by punctual assessment of deadwood volumes. Generalized linear mixed models and magnitude analyses quantified the relative influence of site environmental factors and 16 metrics of the current, recent and mid-term dynamics of local decline severity on plot-level deadwood volumes across European forests.

The average level of dieback over the last five years and, to a lesser extent, the time elapsed since the last peak defoliation, were more important for deadwood stocks than were older levels of defoliation, the intensity or the frequency of extreme past declines. In Europe overall, total deadwood volume was 33% higher when the average level of decline over the previous five years increased by 10%. The significance and magnitude of the effects of past defoliation on deadwood were stronger in lowland forests than in upland forests, in coniferous forests than in broadleaf forests, in young stands than in mature stands, and for standing deadwood than for total deadwood, and varied with management.

Retaining small, declining patches, excluded from salvage or sanitary logging within managed forests, could be an integrative opportunistic forestry tool for spontaneous restoration of deadwood.

1. Introduction

Deadwood is a key element in all forests and provides microhabitats and trophic resources for a large proportion of the local forest biodiversity (Harmon et al., 1986). Deadwood also shapes soil properties and plays an important role in the carbon, nutrient and hydrological cycles (Krajick, 2001), and is recognized as an indirect indicator of biodiversity in European forests (Lassauce et al., 2011). Preserving deadwood is therefore a cornerstone of sustainable forest management.

Millennia of human activity, e.g., timber production, have considerably affected the structure of European forests. Whereas deadwood accumulates over time in unmanaged forests, the amounts of dead standing trees and lying coarse woody debris have been strongly reduced in managed forest landscapes (Siitonen, 2001; Bouget et al., 2014; Bujoczek et al., 2021) and is now limited to, on average, <10% of the natural amount (Müller and Bütler, 2010). As a result of these structural changes, managed forests are generally less biodiverse than old-growth forests or forests set-aside for conservation (Langridge et al., 2023), particularly in terms of the saproxylic insects and saprotrophic fungi responsible for the carbon and nutrient cycles. Consequently, strategies to increase primary levels of deadwood are receiving particular attention in biodiversity-friendly management practices in European forestry (Bauhus et al., 2009).

Forest decline and dieback, i.e., the syndromes associated with loss of tree vigour, which includes slower growth, foliage reduction, twig and branch death, dieback, i.e., specific symptoms of branch death associated with climatic stress, pests or pathogens, and potentially even tree death, is a key process that enhances structural heterogeneity and

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the supply of deadwood microhabitats for biodiversity (Ojeda et al., 2007; Bouget et al., 2024; Chowdhury et al., 2024). Natural disturbances and their cascading effects on forest stand decline often generate "biological legacies" (Cours et al., 2023), including transient accumulations of deadwood (Kulakowski et al., 2017; Sallé et al., 2021). Several case studies have highlighted that local deadwood significantly increased with locally increasing dieback level (Cours et al., 2021, 2022; Zemlerová et al., 2023). As drivers of deadwood dynamics (Garbarino et al., 2015), natural disturbances alter the availability and distribution of deadwood-related microhabitats and resources, which is likely to affect biotic communities in declining forests, both in the short and long term (Cours et al., 2023).

In European forests, natural disturbances have increased in extent, frequency and severity over recent decades, with climate change driving declines and tree crown dieback, and ultimately, increasing tree mortality (Senf et al., 2018). In southern European forests, Carnicer et al. (2011) reported a widespread increase in drought-induced crown defoliation from 1987 to 2007, alongside significant increases in tree mortality rates.

Despite deadwood's importance as a legacy refuge for biodiversity, uncertainties remain as to what drives its potential deadwood volumes and deadwood spatial distribution in European forests (but see Augustynczik et al., 2024). How deadwood levels may change in the future due to management and climate change also remains uncertain. How forest disturbance history influences deadwood patterns has been rather poorly described to date (Stokland, 2001; Halme et al., 2019). Whether and how a succession of repeated diebacks affects deadwood stocks has not been studied. Yet, the dynamics of disturbance legacies (e.g., deadwood) may involve time-cumulative or time-lagged (i.e., delayed) effects, such as those advanced by classical concepts of historical ecology (Tappeiner et al., 2021). The time elapsed since the most severe decline is known to affect the relative abundance of forest substrates and microhabitats in interaction with disturbance severity (Zemlerová et al., 2023). By reconstructing disturbance history, Langbehn et al. (2021) and Kozák et al. (2021) also demonstrated that communities of epiphyte lichen and saproxylic beetles were strongly determined by old-growth features, and were affected by current forest structure but also disturbance regimes in the previous 250 years. It also remains to be determined whether the conservation of small, declining patches within a managed forest could represent an opportunity for passive rewilding to restore larger quantities of deadwood (Gustafsson et al., 2020).

Our opportunistic correlative study between past crown conditions and current deadwood volumes investigated the structural effects of a succession of tree dieback events in European forests. For a subset of level-I, monitoring plots located on a systematic 16 × 16-km grid throughout Europe, data were available on both (i) deadwood measurements carried out within the framework of the Forest Focus Biosoil Project (Galluzzi et al., 2019), pre-processed into a consistent and harmonized deadwood dataset by Puletti et al. (2019); and (ii) defoliation assessments provided yearly since 1989 by the International Co-operative Program on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests), the most comprehensive European monitoring network for the large-scale assessment of forest ecosystem health (Vitale et al., 2014). Biosoil deadwood data were recently used by Augustynczik et al. (2024) to model the effects of climate and management on the distribution of deadwood in European forests. Defoliation data have been used to relate crown defoliation to environmental conditions in several European countries: Switzerland (Zierl, 2004), Germany (Seidling et al., 2012), France (Ferretti et al., 2014), Italy (Iacopetti et al., 2019) and Spain (de la Cruz et al., 2014). However, Biosoil data on deadwood and ICP data on defoliation have never been crossed before.

Defoliation level was considered as a proxy for the severity of stand dieback. Our aim was to mobilise available data on site factors and long-term monitoring of crown-vitality indicators in Europe to investigate the influence of current and recent local defoliation levels on plot-level deadwood volumes. Deadwood patterns can be addressed through deadwood profiles, which subdivide local deadwood stocks into classes based on size, position and decay stage. The cross-analysis of these two large-scale European forest databases (defoliation and deadwood) addressed the following three research questions (RQ). First, do metrics related to dieback dynamics significantly influence current deadwood stocks while compared with other environmental variables (stand age, management intensity, altitude …) (RQ1). Secondly, since forest dieback is a dynamic process that progressively increases deadwood (e.g., as the effect of droughts and heatwaves), how do plot-level deadwood volumes relate to past dynamics of local decline severity (RQ2)? Do deadwood amounts correlate more to the time-accumulation effect of the average multi-year level of dieback in the past or to the time-lagged effect of extreme past dieback events? As an extension of this question, are deadwood stocks more related to dieback level in the semi-distant past (mid-term effect) than in the recent past (short-term effect)? Moreover, due to the natural process of succession of deadwood types caused by decay (i.e. from fresh vs decayed, from standing vs lying), the nature of the influential dieback metrics as well as the significance and magnitude of the dieback effects on deadwood may indeed differ between deadwood types. Thirdly, is the deadwood-dieback relationship context-dependent across all European forests, and how (RQ3)? In fact, it is worth noting that heat waves, droughts, windstorms and pest epidemics affected lowland and highland forests, deciduous and coniferous forests, differently over the period studied. It should also be remembered that, in older and unmanaged stands, deadwood levels are naturally dependent on ageing and dying processes, regardless of the intensity of forest dieback. Therefore, do the significance and magnitude of the effects of dieback on deadwood vary with stand dynamics (e.g., stand age), management context (e.g., management intensity), forest type (e.g., broadleaf vs coniferous) and environmental factors (e.g., elevation)?

2. Material and methods

2.1. Joining databases and calculating metrics

The International Cooperative Program to assess and monitor air pollution effects on the forest (ICP Forests) is responsible for an extensive large-scale level-I monitoring system of forest sites (Hauβmann and Fischer, 2004), made up of dense, spatially representative, 16 × 16 km virtual grid of plots throughout European forests. The sampling points encompass ca. 6,000 monitoring plots in 42 countries. Since 1989, a standardized procedure for surveying forest health status has been applied annually (http://icp-forests.net/page/largescale-forest-condition) to 24 selected dominant and co-dominant trees (minimum height of 60 cm, showing no significant mechanical damage) in each plot. The defoliation and discoloration level of each tree crown is visually assessed as the percentage of needle/leaf loss in the assessable crown as compared to a reference tree with full foliage. Mean defoliation at the plot scale was defined as the proportion of trees with a defoliation rate of more than 25%, and used as a proxy for plot decline level. All data are available upon request to the Programme Co-ordinating Centre (PCC) of ICP Forests in Eberswalde, Germany. In the ICP database, the factors related to natural disturbances or management (i.e., vertebrate or insect herbivory, fungal or fire damage, drought impacts, removal of coarse woody debris) were not recorded in a sufficiently standardized way to be used as covariates in our models. Similarly, the presumably surveyed plot-level living-tree density and above-ground biomass for standing living trees (expressed in kg.ha^{-1}) were not available.

In the framework of the large collaborative European Forest Focus BioSoil-Biodiversity Project, additional data on stand structure and biodiversity were collected around certain ICP level-I plots (Galluzzi et al., 2019) between 2005 and 2007 (Fig. 1). Overall, a total of 3,243 geocoded Level-I plots were considered in 19 European countries (Puletti et al., 2017): Austria, Belgium (Flanders only), Cyprus, the Czech Republic, Denmark, Finland, France, Germany (eight federal

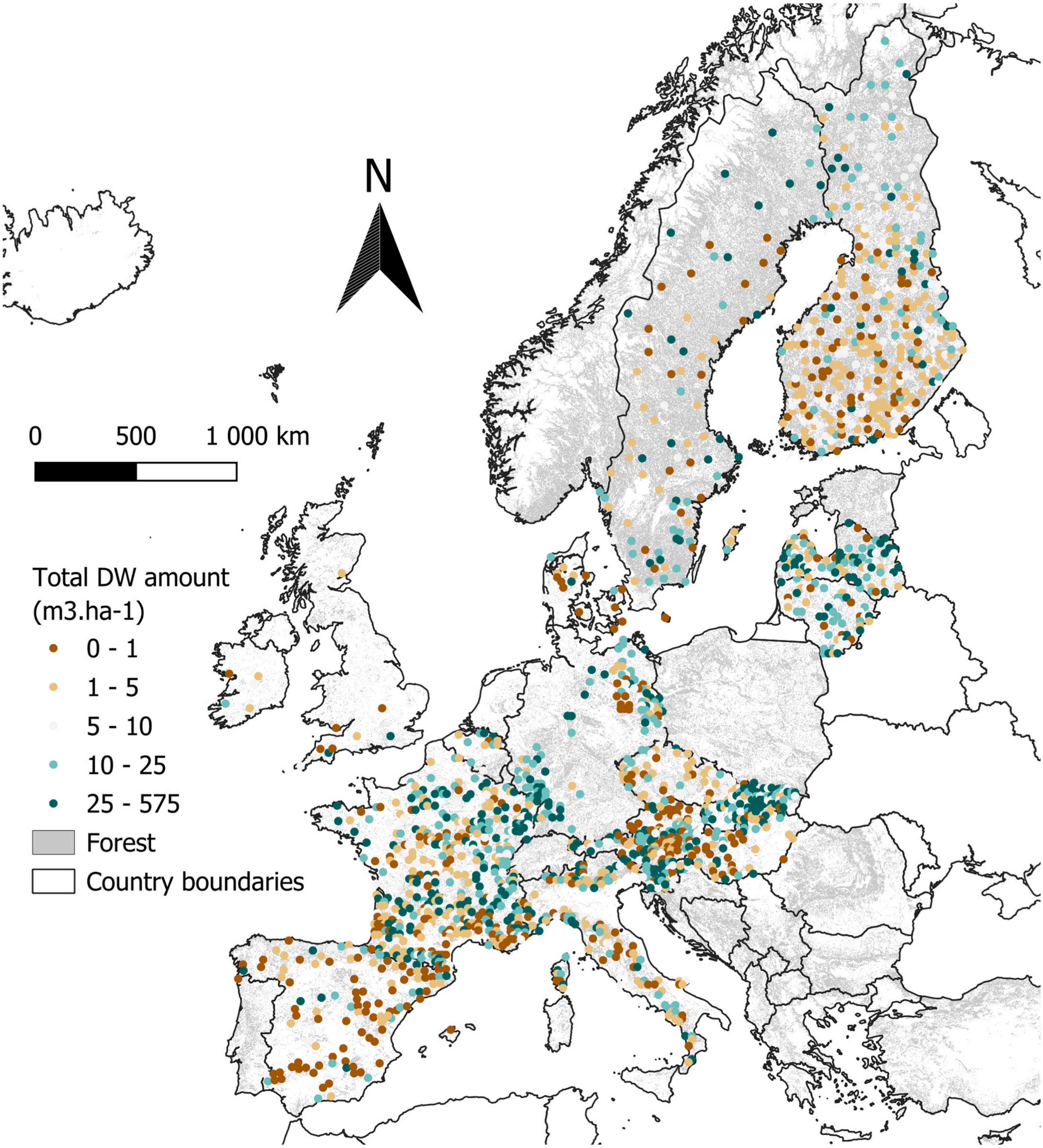


Fig. 1. Overview of the plots used for our cross-analysis of European ICP-defoliation and Biosoil-deadwood datasets.

states only), Hungary, Ireland, Italy, Latvia, Lithuania, Poland, Slovakia, Slovenia, Spain, Sweden and the United Kingdom (Fig. 1). BioSoil Project results are recorded in the multi-dimensional LI-BioDiv geodatabase, which contains the raw data on forest structure used to calculate simple plot-level forest variables (e.g., deadwood volume; Bastrup-Birk et al., 2007; Hiederer and Durant, 2010). At each plot, deadwood, i.e., coarse woody debris (including lying dead trees), snags (more than 130 cm in height, including standing dead trees) and stumps more than 10 cm in diameter, was quantified on a 400 m^2 area (Puletti et al., 2017). The raw ICP deadwood data (i.e., diameter, length or height, tree species, decay class for each deadwood piece) were processed by Puletti et al. (2017, 2019) into a consistent and harmonized pan-European deadwood dataset, providing total deadwood volume and the volume of several deadwood types for each plot, which we used in this study. Further details can be found in the ICP Forests manual (http://icp-forests.net/page/icp-forests-manual), Puletti et al. (2019) and

Augustynczik et al. (2024). In this study, we considered the following deadwood variables: (i) total deadwood volume, (ii) standing deadwood (snags) volume, (iii) volume of ground-lying deadwood, (iv) fresh deadwood volume (i.e., cumulative volume of slightly decayed dead wood in decay classes 1 and 2, i.e., hard deadwood with bark), and (v) decayed deadwood volume (i.e., cumulative volume of highly decayed dead wood in decay classes 3 and 4, i.e., soft and debarked deadwood). Several environmental covariates were also collected from the Biosoil dataset: (i) management intensity (recently harvested, i.e., with management evidence within the last 10 years; and not recently harvested, i.e., unmanaged (no management evidence) or managed only a long time ago (management evidence but more than 10 years previously)); (ii) average stand age (young [1–40 yrs], mid-aged [41–100 yrs], mature [>100 yrs]); (iii) elevation (above sea level, a.s.l.), as a continuous quantitative variable or subdivided into three classes (lowland [0–300 m a.s.l.[; hilly [300–600 m a.s.l.[; highland [≥600 m a.s.l.]); (iv) dominant tree genus (*Quercus* spp., *Fagus* spp., *Betula* spp., other broadleaf, *Pinus* spp., *Picea* spp., other conifer including e.g., *Abies alba*); and (v) forest type, depending on the dominant tree species: coniferous, deciduous or mixed (see Table 1 and Supp. Mat. Fig. S1).

After harmonizing plot names and coordinates in the two datasets (i.e., ICP-defoliation and Biosoil-deadwood), only plots with matched data in both datasets were selected. Plots with discontinuities in defoliation measurements of two years or more were deleted. In plots with a 1-year discontinuity, the missing values were reconstructed from the average values in contiguous years. We matched defoliation measurements for the Biosoil-ICP datasets from 1989 to 2007 and finally obtained 2,070 five-year, 1,804 ten-year and 1,399 fifteen-year time series. This approach made it possible to define three 10-year time series [1995–2005, 1996–2006 and 1997–2007] with plots in 17 countries.

From these 10-year time series prior to the Biosoil deadwood measurements, we calculated 16 univariate metrics to summarize changes in defoliation throughout the 10-year period. Some of the selected parameters describe the immediate possible effects of defoliation severity in the recent past for a given year: (i) defoliation level of the year before the deadwood measurement (n-1), (ii) defoliation level of the year two years before the given year (n-2), (iii) defoliation level of the year three years before the given year (n-3). Other defoliation metrics relate to the

Table 1
Overview of deadwood response variables, dieback predictors and environmental covariates in the 10-year time series dataset.

Metrics	Meaning	Min-max	Mean ± se
Deadwood response variables			
Total DW	Volume of all deadwood pieces ($m^3.ha^{-1}$)	[0.00–574.45]	17.86 ± 0.87
Standing DW	Volume of standing deadwood (standing dead trees + snags) ($m^3.ha^{-1}$)	[0.00–555.74]	7.36 ± 0.62
Lying DW	Volume of ground-lying deadwood (lying dead trees + coarse woody debris, excluding Fine Woody Debris less than 10 cm in diameter) ($m^{3.h}a^{-1}$)	[0.00–307.11]	8.15 ± 0.50
Fresh DW	Volume of fresh deadwood (decay class 1 or 2 in the Biosoil protocol) ($m^3.ha^{-1}$)	[0.00–342.42]	7.94 ± 0.53
Decayed DW	Volume of decayed deadwood (decay class 4 or 5 in the Biosoil protocol) ($m^3.ha^{-1}$)	[0.00–291.46]	5.03 ± 0.32
Dieback parameters			
Dieback -1yr	Dieback level the year before deadwood sampling.	[0.00–100.00]	20.61
Dieback -2yr	Dieback level two years before deadwood sampling.	[0.00–100.00]	20.20
Dieback -3yr	Dieback level three years before deadwood sampling.	[0.00–100.00]	19.66
Avg. Dieback -2yrs	Average dieback level over the previous 2 years.	[0.00–78.13]	20.40
Avg. Dieback -3yrs	Average dieback level over the previous 3 years.	[0.00–80.00]	20.16
Avg. Dieback -5yrs	Average dieback level over the previous 5 years.	[0.08–69.25]	19.50
Avg. Dieback –5-10yrs	Average dieback level over the first 5 years of the 10-year time series.	[0.00–61.56]	17.56
Arith. Avg. Dieback −10yrs	Arithmetic average of annual dieback level.	[0.05–57.99]	18.72
Geom. Avg. Dieback −10yrs	Geometric average of annual dieback level.	[0.00–56.88]	17.82
Area Under the Curve	Area Under the Curve.	[0.05–51.73]	16.98
Time from last peak	Time elapsed since last peak dieback.	[0.00–16.00]	7.95
Maximum dieback lvl.	Maximum dieback level.	[0.42–100.00]	27.73
Nb. of peaks	Number of dieback peaks.	[0.00–4.00]	0.88
Nb. Yrs beyond peak lvl.	Total number of years elapsed since the peak level.	[0.00–11.00]	2.93
Duration longest peak	Duration of the longest peak period.	[0.00–11.00]	2.46
Slope dieback x time	Slope estimate of the linear regression line for dieback level versus time.	[-2.94–5.11]	0.37
Environmental covariates		**Sampling**	
Management intensity	Recent harvest, i.e., with evidence of management within the previous 10-years.	1017 plots	
	No recent harvest, i.e., unmanaged (no management evidence) or managed a long time before (management evidence but more than 10 years old).	707 plots	
Average stand age	Irregular	43 plots	
	Young [1–40 yrs]	315 plots	
	Middle-aged [41–100 yrs]	1059 plots	
	Mature [>100 yrs]	379 plots	
Elevation	a.s.l. in meters, continuous quantitative data	[0–2489]	438.38 ± 0.23
	Lowland, i.e., less than 300 m above sea level (a.s.l.)	980 plots	
	Hilly, i.e., between 300 and 600 m a.s.l.	354 plots	
	Highland, i.e., more than 600 m a.s.l.	470 plots	
Dominant tree genus	Quercus spp.	332 plots	
	Fagus spp.	180 plots	
	Betula spp.	71 plots	
	Other broadleaf spp.	151 plots	
	Pinus spp.	574 plots	
	Picea spp.	408 plots	
	Other conifer spp.	88 plots	
Forest type (dominant tree group)	Coniferous	947 plots	
	Broadleaf	656 plots	
	Mixed	201 plots	

cumulative effects of defoliation levels in the near or distant past: (i) average defoliation level over the last two years, (ii) average defoliation level over the last three years, (iii) average defoliation level over the last five years, (iv) average defoliation level over the first five years of the 10-year time series, and (v) time elapsed since last peak defoliation. Several other parameters depict general trends in the level of defoliation over the 10-year time series: for cumulative metrics: (i) arithmetic mean of annual defoliation level; (ii) geometric mean of annual defoliation level; (iii) Area Under the defoliation time Curve (AUC), i.e., the cumulative sum of defoliation levels; and for the overall trend, (iv) the estimated slope of the linear regression line for defoliation level over time. Finally, some of the metrics reflect defoliation severity and repetition along the 10-year time series, and potential time-lagged effects: (i) maximum defoliation level; (ii) total number of years elapsed, whether successive or not, after the peak dieback level, whether successive or not; (iii) the number of peaks, consecutive or discontinuous, i.e., the number of severe defoliation events and defoliation frequency; and (iv) the duration of the longest peak, i.e., the longest continuous time during which the level of defoliation was greater than the relative threshold (Table 1, Supp. Mat. Fig. S2 on between-variable correlations).

A peak in defoliation was defined as a year in which the level of defoliation exceeded a relative threshold, i.e., the third quartile value. In our 10-year time series, the peak value was 25% and above. The defoliation level was greater than 25% throughout the whole 10-year time series for 8% of the plots, and lower than 25% throughout the whole 10-year time series for 48% of the plots. On average, the level of defoliation exceeded the 25% threshold value around 2.5 years in each time series.

2.2. *Modelling strategy*

We assessed the relative effects of (i) the metrics depicting defoliation dynamics, (ii) altitude, (ii) forest type (i.e., family of the dominant tree species) and tree genus, (iii) other environmental covariates related to forest management (i.e., stand age, management intensity), and (v) the interactions between all the independent variables explored, on deadwood. The data analysis was conducted with the R software 4.1.2. Data analysed in this study are available in the Zenodo repository at https://doi.org/10.5281/zenodo.13992861.

To test the effect of predictors on each of the five deadwood response variables, we used generalized linear mixed models (GLMM), with Biosoil year and country as random variables on the intercept, and a structure of spatial autocorrelation that decayed exponentially with distance between plots, to account for the sampling design. We looked for a family of distributions best fitted to the distribution of continuous, positive, non-Gaussian 0-inflated variables, and chose the Tweedie distribution from the class of compound Poisson–Gamma models (with log as a link function). We implemented the residual diagnostic method from the DHARMa R-package to test the accuracy of the chosen distributions. We handled over-dispersion in the residues by adding plot ID as a random effect.

We used the glmmTMB function from the glmmTMB R-package to build the models, and the *dredge* function from the *MuMIn* R-package to include fixed effects (i.e., dieback parameters and environmental covariates) alternatively in the univariate models, and sequentially in the multiplicative models considering interactions. We took predictor collinearity into account. For each response variable, we used both AIC and BIC criteria to compare the models and identify the best ones.

For each response variable and for most of the predictors, we not only analysed significance, but also magnitude (Gosselin et al., 2017), for the global dataset and for every plot subset defined by forest context categories. We simulated an increase ΔX in the predictor *dieback* and studied the magnitude of the consecutive change in the mean of the response variable *deadwood*. The simulated increase was chosen as the standard deviation of the predictor. This resulted in a 10,000-sample distribution of the relative increase in the response variable under consideration, from which we extracted the mean and the 95% confidence interval.

3. Results

3.1. *Influential covariates of dieback vs environment explaining deadwood volumes*

Average dieback in the previous five years was the best predictor of total deadwood volume, but its effect was weaker than the effect of stand age (Table 2, Supp. Mat. Table S1). The second best explanatory dieback variable was time from the last peak, which was a better predictor than all the environmental variables other than stand age (Table 2, Supp. Mat. Table S1). The best multivariate model explaining total deadwood volume included average dieback in the previous five years, time form the last peak and stand age, but also elevation and dominant tree genus as well as the interaction between average dieback in the previous five years and stand age (Table 2). Management intensity was never implicated in the best explanatory models for deadwood.

3.2. *Time-lagged vs cumulative and short-term vs mid-term effects of defoliation level on deadwood*

From the global parameters describing the dynamics of tree dieback over the 10-year period prior to the deadwood measurements, two main variables had the lowest AIC and BIC for most of the deadwood variables: the average dieback level over the previous five years, and the time elapsed since last peak defoliation (Table 1 and Fig. 2, see Supp. Mat. Figs. S3, S4, S5 and S6 for model diagnostics). In addition, we found that deadwood amount was more closely related to the level of dieback in the recent past (i.e., 5–10 years before) than in the more distant past (Fig. 2). Nonetheless, all of the dieback parameters had positive effects on deadwood amount (Fig. 2). The number of dieback peaks, the cumulative number of years after the peak value and the duration of the longest dieback period all showed significant, though weaker, effects (i.

Table 2

Best model for each deadwood variable. For each deadwood variable, delta AIC is based on the difference between the model with dieback and environmental variables and the null models including only random effects and exponential spatial covariance structures. A negative ΔAIC value means that the model including predictors better fits the data than the null model. For decayed deadwood, all the variables increased the AIC compared to the null model (see Table 1). All estimates in the table are based on scaled variables and therefore are different from the ones used to calculate magnitude.

Delta AIC	Dieback variable	Estimate ± SE	p.value
Total DW			
−90	Avg. Dieback -5yrs	+0.15 ± 0.06	**0.017** *
	Time from last peak	−0.13 ± 0.06	**0.021** *
	Age	+0.24 ± 0.04	**3.82e-10** ***
	Altitude	+0.17 ± 0.05	**0.002** **
	Dominant tree genus	Categories	
	Age × Avg. Dieback -5yrs	−0.13 ± 0.03	**0.0003** ***
Standing DW			
−52	Avg. Dieback -5yrs	+0.51 ± 0.07	**5.02e-12** ***
Lying DW			
−136	Time from last peak	−0.17 ± 0.06	**0.002** **
	Age	+0.31 ± 0.05	**1.31e-08** ***
	Dominant tree genus	Categories	
Fresh DW			
−74	Avg. Dieback -5yrs	+0.30 ± 0.09	**0.0005** ***
	Time from last peak	−0.16 ± 0.08	**0.047** *
	Age	+0.16 ± 0.06	**0.005** **
	Dominant tree genus	Categories	
	Age × Avg. Dieback -5yrs	−0.09 ± 0.05	0.063.
Decayed DW			
−71.5	Age	+0.3 ± 0.05	**1.02e-09** ***
	Altitude	+0.34 ± 0.08	**5.22e-05** ***
	Dominant tree genus	Categories	

= $p < 0.01$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

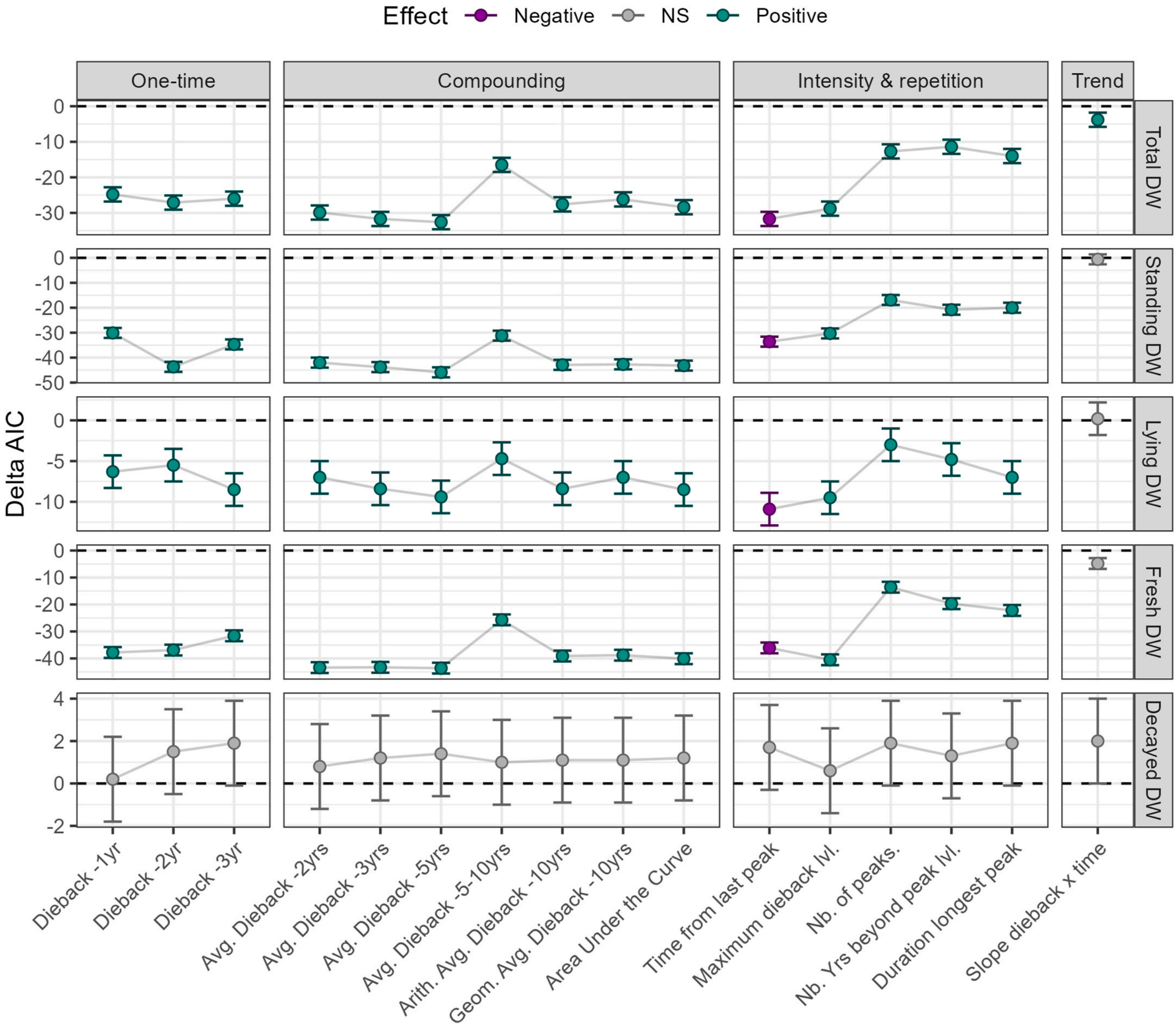


Fig. 2. Generalized Linear Mixed modelling (Tweedie fitting) for deadwood ~ dieback relationships. Delta AIC is based on the differences between the model with dieback variables and the null models including only random effects and exponential spatial covariance structures. Selection criteria for the models were AIC and BIC (since the AIC and BIC results were quite similar, we only present AIC values in this figure). "Avg." = "Average", "yrs" = "years", "Arith" = "Arithmetic", "Geom" = "Geometric", "lvl." = "level", "Nb." = "Number".

e., individual models with higher AIC values). The slope of dieback over time had no significant effect on most deadwood metrics, with the exception of total deadwood amount, whose ΔAIC was very close to −2 (Fig. 2).

3.3. Variations in the dieback-deadwood relationship with deadwood type

Average dieback in the previous five years also had the most influence on fresh deadwood volume, and a stronger positive effect than the more general environmental variables such as stand age, management intensity or forest type (Table 2, Supp. Mat. Table S1). The second key dieback variable explaining fresh deadwood was time from the last peak, which also had a stronger negative effect than the environmental variables (Table 2, Supp. Mat. Table S1). The best multivariate model included average dieback in the previous five years and time from the last peak, as well as stand age, dominant tree genus and interactions between average dieback in the previous five years and dominant tree genus, and between stand age and average dieback in the previous five years (Table 2).

Average dieback in the previous five years was the only variable to affect standing deadwood volume; no other dieback or environmental variables had a significant effect (Table 2, Supp. Mat. Table S1). The higher the average level of dieback over the previous five years, the greater the volume of standing deadwood on the plot. The best multivariate model explaining lying deadwood volume included stand age, dominant tree genus and time from the last peak (Table 2). Stand age and dominant tree genus had the strongest individual effects on lying deadwood volume, followed by time from the last peak and forest type (Supp. Mat. Table S1). The more time elapsed between the last dieback peak and the deadwood measurement, the lower the volume of deadwood lying in the plot.

Decayed deadwood volume was not significantly affected by any of the parameters describing dieback dynamics over the previous 10-year period. However, it was influenced by stand age, elevation and dominant tree genus, which were all included in the best multivariate model (Table 2, Supp. Mat. Table S1).

Overall, standing deadwood or fresh deadwood volumes were best explained by dieback metrics, while total, lying or decayed deadwood volume was best determined by environmental parameters (Table 2, Supp. Mat. Table S1).

Across all the European plots studied, total deadwood, standing deadwood and fresh deadwood volumes were higher on average (+33% [IC95% 22–45%], +66% [IC95% 43–91%] and +54% [IC95% 36–72%], respectively; Fig. 3) when the dieback index value over the previous five years increased by 10% (i.e. the standard deviation value of the predictor). Local volumes for total deadwood, standing deadwood and fresh deadwood doubled when the average level of dieback over the previous five years increased by 24%, 14%, and 17%, respectively. Local volumes of total, lying and fresh deadwood were lower on average (−21% [IC95% 15–27%], −17% [IC95% 8–25%] and −29% [IC95% 21–36%], respectively) when the time elapsed since peak dieback increased by seven years.

3.4. Variations in the dieback-deadwood relationship with forest context

3.4.1. The influence of dieback on deadwood varies with stand dynamics

Consistent with the significant interaction between average dieback in the previous five years and stand age for total and fresh deadwood, stand age class affected the significance and strength of several dieback-deadwood relationships. The relationship between dieback parameters (Avg. Dieback -5yrs and Time from peak) and total deadwood was stronger in young stands than in middle-aged stands, and not significant in mature stands (Fig. 3). The dieback metrics (Avg. Dieback -5yrs and Time from peak) were correlated with fresh deadwood in middle-aged and mature stands, while the models based on data from the young age class did not converge (except for Time from peak; Fig. 3). Time from the last peak was not related to lying deadwood for any of the stand age classes (Fig. 3, Supp. Mat. Table S4), and only standing deadwood in middle-aged stands was affected by average dieback in the previous five years (Fig. 3, Supp. Mat. Table S4).

3.4.2. The influence of dieback on deadwood varies with management intensity

The relationship between dieback and deadwood was significant in each of the management intensity classes and for each deadwood category (except for decayed deadwood; Fig. 3). Although it should be noted that magnitude CIs overlapped between classes, the relationship tended to be stronger in recently-logged stands than in unharvested stands for total and fresh deadwood (Fig. 3, Supp. Mat. Tables S2 and S3). In contrast, it tended to be weaker in recently-logged stands than in unharvested stands for standing and lying deadwood (Fig. 3, Supp. Mat. Table S4).

3.4.3. The influence of dieback on deadwood varies with dominant tree species

The positive effect of the average dieback in the previous five years on total, fresh and standing deadwood volumes was significant for all forest types (i.e., broadleaf, coniferous and mixed forests) (except for standing deadwood in mixed forests, which we were unable to test; Fig. 3). The positive effect was stronger in coniferous than in broadleaf forests for total and standing deadwood, while mixed forests fell in between (Fig. 3, Supp. Mat. Table S2 and S4). The effect of time from the last peak on total deadwood was significant in all forest types, but not for ground-lying or fresh deadwood in broadleaf forests (Fig. 3, Supp. Mat. Tables S3 and S4). The confidence intervals (CIs) associated with the magnitude values overlapped between forest types.

Consistent with the significant interaction between average dieback in the previous five years and dominant tree genus in the best multivariate model for fresh deadwood, the dieback-deadwood relationship varied with dominant tree species (Fig. 3). The dieback parameters (Avg. Dieback -5yrs and Time from peak) had significant effects on total and fresh deadwood in oak, pine and spruce forests, but not in birch and beech forests, which were also less represented in the dataset (Supp. Mat. Tables S2 and S3). Similarly, the effect of time from the last peak on ground-lying deadwood was significant in oak, pine and spruce forests, but not in birch or beech forests (Fig. 3, Supp. Mat. Table S4). Average dieback in the previous five years significantly affected standing deadwood in pine and spruce forests only (Fig. 3, Supp. Mat. Table S4). Overall, the magnitude of the effects were stronger in oak forests than in spruce forest, followed by pine forests, but the CIs of the values overlapped (Supp. Mat. Table S4).

3.4.4. The influence of dieback on deadwood varies with altitude

The dieback-deadwood relationship was significant in lowland forests for total, fresh, standing and lying deadwood, and in highland forests for total and fresh deadwood. The dieback-deadwood relationship was never significant at intermediate elevations (Fig. 3, Supp. Mat. Tables S2, S3 and S4).

4. Discussion

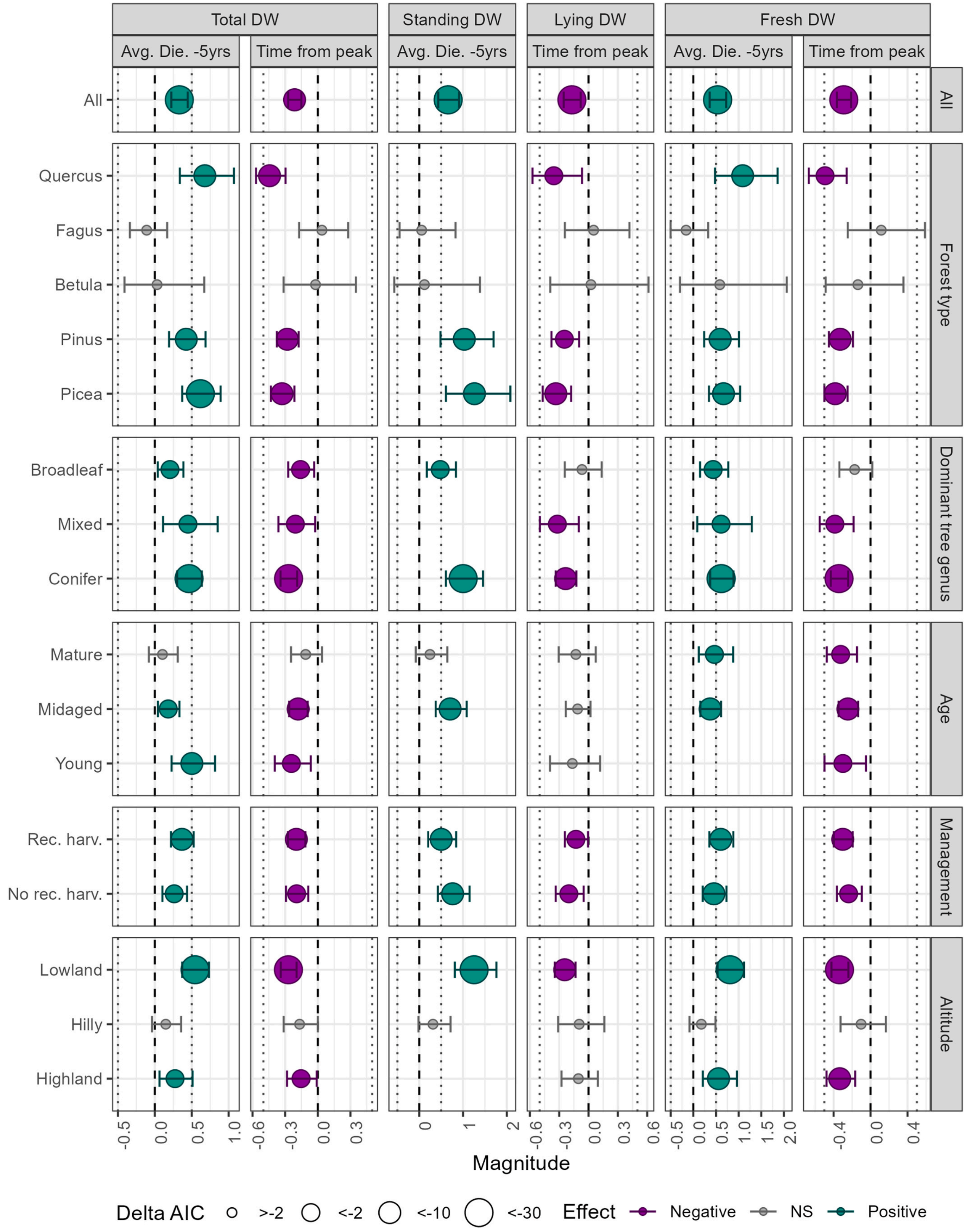
4.1. Influential covariates of dieback vs environment explaining deadwood volumes

This study confirms the significant structuring effects, compared with other environmental variables, of recently occurring dieback on current deadwood stocks in various European forest contexts (in answer to RQ1). Similarly, Bujoczek & Bujoczek (2022) demonstrated that the extent of damage to living trees by pathological symptoms adversely affecting their health was one of the main factors influencing deadwood stocks in Polish forests. Dieback caused by windstorms, drought, parasites or pathogens can lead to profound changes in forest structure, and is likely to leave a biological legacy in the form of increased deadwood stocks (Cours et al., 2023). Tree crown dieback can ultimately bring about the death of perched branches and even whole standing trees (Senf et al., 2021; Cours et al., 2022), and this reinforces the deadwood complex on the ground by promoting the fall of dead branches or dead trees (Bouget et al., 2024; Chowdhury et al., 2024).

Even if defoliation level (used here as the proxy for forest dieback) only indirectly and incompletely reflects the vitality of the crown and the disturbance level in the stand (Bussotti et al., 2024), dieback level and deadwood volume were significantly and positively linked at the stand scale (RQ1). This response was non-linear, since the Tweedie distribution, a compound Poisson-Gamma distribution for exponential dispersion models, was chosen to best fit this relationship. In our case studies, the other explanatory factors for total deadwood volume were stand age, altitude, forest type and tree species identity, which are classic drivers of global deadwood patterns (Stokland et al., 2012; Augustynczik et al., 2024).

4.2. Time-lagged vs cumulative and short-term vs mid-term effects of defoliation level on deadwood

Plot-level deadwood volumes correlated to current forest features and to recent past levels of local forest dieback reflected by the defoliation level. Among the environmental factors tested in the decadal time series, the main predictors of total deadwood volume were (i) the average level of dieback over the previous five years, and (ii) the time elapsed since last peak defoliation over the 10-year period preceding the deadwood measurements, though their significant effects were always weaker than the effect of stand age. Deadwood stocks appear to be more related to a high average level of dieback in the recent past (time accumulation short-term effect) or to a short time elapsed since the last defoliation peak (short-term ecological lag), than to older levels of defoliation (in the semi-distant past, from five to ten years before), whether described by the intensity of extreme past decline or the



(caption on next page)

Fig. 3. Magnitudes and AIC values compared to null model AIC (i.e., delta AIC) of dieback variables from the best models for the volume of different deadwood types within each subset (full data in Suppl. Mat.). Magnitude was calculated as the increase or decrease in the response variable relative to a 10% increase in the average dieback level in the previous five years (i.e., observed standard deviation), or to a 7-year increase in the time elapsed since the last peak in dieback (i.e., observed standard deviation). The magnitude analysis was performed for each subset defined by forest context: management intensity (recently harvested and no recent harvest), average stand age (young, middle-aged and mature), elevation (lowland, hilly and highland), main dominant tree genus (*Quercus* spp., *Fagus* spp., *Betula* spp., *Pinus* spp. and *Picea* spp.), and forest type (i.e., dominant tree group: coniferous, deciduous, mixed). Dashed lines show the 0 value (i.e., no effect), while dotted lines show the magnitude value of 0.5, since scales are different for each deadwood variable. "Avg" = "Average", "Die." = "Dieback".

frequency of past decline peaks in the previous ten years (mid-term lagged effects) or the average decline in the last ten years (cumulative mid-term effect).

In other words, the cumulative short-term effect of forest decline level has a greater impact on deadwood volumes than do mid- and long-term lagged effects, at least overall in Europe (in answer to RQ2).

Ecological time-lags or time-accumulation effects refer to the time interval from the onset of an environmental change to the presence of a legacy (Chen et al., 2023), i.e., here from tree dieback related to disturbance and stress (e.g., drought, pests, pathogens, windstorms, wildfires, etc.) to deadwood creation. The different mechanisms resulting in ecological time-lags between tree dieback and deadwood creation (deadwood perched in living trees is not recorded in the Biosoil protocol) along the decline process are as follows: tree decline > branch mortality > branch fall > tree mortality > standing dead tree > fresh lying deadwood > decayed lying deadwood. Previous studies have already attested that deadwood dynamics, especially deadwood accretion, are indirectly but significantly influenced by disturbance history reflected by environmental factors, especially under natural conditions with no human intervention (e.g., Harmon et al., 1986; Sturtevant et al., 1997). According to Zemlerová et al. (2023), the relative abundance of TreMs (i.e., other disturbance legacies, remarkable for forest biodiversity) within primary temperate forests was maximized by unique interactions between past disturbance severity and elapsed time.

The time-lagged effects of past conditions on the current forest state have also been shown in studies relating climate conditions and vegetation vitality, or forest structure and current biodiversity. Modelling by Ognjenović et al. (2022) indicates a very strong influence of the previous year's drought on defoliation changes, i.e., the accumulated impact of location-specific stressful environmental conditions on beech vitality. Drought and heat have short-term cumulative and time-lag effects on subtropical vegetation growth and photosynthetic activity in China, with varying effects among different vegetation types (Ren et al., 2023). In addition, 50% of the vegetation in China showed time-lagged effects in relation to anthropogenic activities over time scales of six to ten years, proving that anthropogenic activities have triggered ecological changes, and that plant ecosystems cannot keep pace (Wang et al., 2023). Concerning plant ecosystem resilience, based on a reconstructed disturbance history, Langbehn et al. (2021) demonstrated that lichen species richness increased with time since disturbance (i.e., with long-lasting uninterrupted succession) and Kozák et al. (2021) showed that frequency of past disturbances was the most important factor influencing current saproxylic beetle communities.

4.3. *Variations in the dieback-deadwood relationship with deadwood type*

Across European forests, the significance and magnitude of the dieback effects on deadwood varies with deadwood type (in response to RQ2).

Standing deadwood is even more responsive than total deadwood to recent-past defoliation level. Indeed, the effect of average dieback level over the last five years on standing deadwood volume was twice as great as on total deadwood volume. Overall, standing deadwood volume was best explained by recent past decline metrics, while lying deadwood volume was best determined by general environmental parameters (i.e., stand age, tree species identity, forest type). In western European forests, Bouget et al. (2024) already showed that decline-induced increases in deadwood were stronger for standing deadwood than for lying deadwood, and were directly related to the number of dying and dead trees in both spruce and oak forests, though this was not the case in fir forests. This trend may depend on the length of the time series analysed here, since unsalvaged snags will eventually become logs.

A time-lag in response to stand dieback dynamics might exist between fresh and decayed deadwood. Average dieback level over the last five years and time elapsed since peak dieback had stronger effects on fresh deadwood than any general environmental variables, and the magnitude of these effects was far higher than for the total deadwood volume. On the contrary, none of the global parameters describing the past dynamics of tree decline significantly affected the local volume of decayed deadwood, which was best determined by environmental parameters. Perhaps longer time-series should be used for the study of the relationship between past dieback levels and decayed deadwood volume. However, it is worth noting that highly decomposed deadwood is very rare in European forests (Puletti et al., 2019) where it is common practice to salvage dead or dying trees that have been felled, leading to the extraction of any trees likely to result in decayed lying deadwood (Lindenmayer and Noss, 2006; Thorn et al., 2017; Cours et al., 2023). When natural disturbances lead to forest dieback, forest owners generally want to salvage their economic capital or avoid more damage (e.g., pest outbreaks). Since most European forests are managed for timber production (Barredo et al., 2021), human intervention may explain the absence of a correlation between past dieback levels and decayed deadwood volume. Human activity may also explain the absence of mid- and long-term compounding effects from dieback. Wood harvesting might also explain why time from the last peak decline was the main structuring dieback metric for lying deadwood: the longer the interval, the higher the probability that salvage logging has occurred. Therefore, more than representing the effect from a natural decaying process, time from last peak decline might simply reflect the negative effects of salvage logging on deadwood production.

Although significant relationships were demonstrated between deadwood and global variables summarizing the 10-year time series of decline, it may be instructive to explore whether deadwood stocks depend on past diebacks in a more complex way. This would require finding a way to treat longitudinal predictors for the entire time series, stabilizing variance in the statistical properties of the time series (i.e., guaranteeing stationarity), and handling defoliation with autoregressive models (Bull et al., 2020).

4.4. *Variations in the dieback-deadwood relationship with forest context*

Across European forests, the significance and magnitude of the dieback effects on deadwood also vary with stand dynamics, management intensity and other environmental context factors such as forest type and altitude.

4.4.1. *The influence of dieback on deadwood varies with stand dynamics*

Stand age class affected the significance and strength of several decline-deadwood relationships. In answer to the research question RQ3, the relationship between dieback level and total deadwood was stronger in young stands than in middle-aged stands, and not significant in mature stands. Moreover, the average level of dieback in the previous five years and the stand age had a significant negative interaction effect on total and fresh deadwood. According to Garbarino et al. (2015), stand age clearly influences the disturbance-deadwood relationship, depending on the type of disturbance: (i) in young stands, there may be a gradual input of deadwood through snag fall following insect attacks or fire, or a massive input of deadwood in case of stand replacing windstorm events, while (ii) in old stands, a gradual input of deadwood due to competition-related mortality is likely in the absence of major disturbances.

4.4.2. *The influence of dieback on deadwood varies with management intensity*

Management intensity was never included in the best models explaining deadwood amount, but in response to RQ3, the positive influence of dieback on deadwood volume was stronger in recently managed than in unmanaged plots, especially for fresh deadwood. In line with our results, Bujoczek and Bujoczek (2022) also identified stronger relationships between dieback level and deadwood volume in managed forests than in nature reserves. For Norway spruce forests in Slovakia, Potterf et al. (2022) recently showed a stronger increase in disturbances in managed than in unmanaged forests, potentially indicating stronger resistance to increasing natural disturbances in unmanaged forests.

4.4.3. *The influence of dieback on deadwood varies with dominant tree species*

In answer to RQ3, the dieback-deadwood relationship varied according to dominant tree species: the positive effects of dieback on deadwood were stronger in coniferous than in broadleaf forests. Dieback level had a significant effect on total, fresh and ground-lying deadwood in oak, pine and spruce forests, but not in birch and beech forests, which were also less represented in the dataset. Overall, the magnitude of the dieback effects tended to be slightly stronger in oak forests than in spruce, and then, pine forests.

The question arises as to whether a higher average dieback level can help explain a stronger dieback-deadwood relationship in certain tree species. On the contrary, in our database, European broadleaf forests were more defoliated than coniferous forests in the decade preceding the deadwood measurements (Supp. Mat. Fig. S1), during which the 2003 drought was a major cause of tree dieback (Lorenz et al., 2008). The average time elapsed since last peak dieback in broadleaf forests (i.e., 5.2 years) was about half the time in coniferous forests (i.e., 9.7 years), and the average dieback level in the previous ten years was 40% higher in broadleaf (on average, 21% of declining trees for all plots) than in coniferous forests (on average, 15% of declining trees for all plots). Local deadwood amounts were also higher in broadleaf (on average, 19.6 $m^3.ha^{-1}$) than in coniferous forests (on average, 16.6 $m^3.ha^{-1}$; Supp. Mat. Fig. S1).

At the tree species level, recent past dieback level was the highest in oak forests (23% of declining trees for all plots), followed by beech (18%), spruce (17%), and other conifers – including silver fir (16%) and pine (14%). Oak forests displayed the highest recent past dieback level for the period 1996–2005, but also the lowest plot-level deadwood amount in 2006 (27.1 $m^3.ha^{-1}$ for beech, 19.2 $m^3.ha^{-1}$ for spruce, 13.4 $m^3.ha^{-1}$ for pine, 25.1 $m^3.ha^{-1}$ for other conifers, but only 12.6 $m^3.ha^{-1}$ for oak; Supp. Mat. Fig. S1). It should be remembered that the progressive loss of tree vigour during decline may first translate into crown dieback, partly apprehended by our key indicator of tree condition, defoliation level, and then may sometimes, but not always, result in branch/tree mortality. There may be a poor correlation between defoliation level and branch/tree mortality which could have affected our results for oak forests. The gradual process from tree decline to tree mortality means that transient accumulations of different types of deadwood resources vary among tree species. In European forests, Bouget et al. (2024) observed that branch and tree mortality is more systematic in spruce, after a decline due to a succession of windstorms and bark beetle outbreaks, but less systematic in oak and fir, whose decline was due to drought. In Polish forests, it has been shown that deadwood volume is affected by a temporary increase in mortality for certain species in decline, the case for ash and spruce (Bujoczek and Bujoczek, 2022). Deadwood amounts increase with natural tree mortality and are dependent on tree species, due to (i) higher mortality rates of certain tree species, (ii) lower deadwood decay rates for certain tree species (Laarmann et al., 2009), (iii) contrasting dominant disturbances (e.g., wildfire, drought, pests, pathogens, windstorms, etc.) for each tree species and each bioclimatic region (Garbarino et al., 2015), and (iv) salvage or sanitary logging executed on certain tree species to recuperate the economic capital before wood depreciation and to protect the remaining forest from pest outbreaks.

4.4.4. *The influence of dieback on deadwood varies with altitude*

In response to RQ3, the effects of recent past dieback level on deadwood volumes were stronger in lowland than in highland forests. Altitude can be linked to gradients in stand structure, tree species composition, management intensity, disturbance regimes and climatic conditions. Nonetheless, in our data, lowland and highland forests were equally represented in each of the broad considered categories: conifer/broadleaf, young/mature, recently managed/unmanaged. Similarly, in our data, average dieback level in the previous five, ten or fifteen years was similar in lowland and highland forests. On the other hand, larger amounts of deadwood were found in highland forests than in lowland forests. According to Garbarino et al. (2015), deadwood volumes are the largest in cool climates, where forest productivity and deadwood accumulation are high but decomposition is slow. Across European forests, Augustynczik et al. (2024) also found deadwood hotspots in the montane forests of Central Europe. Our study confirms that highland forests, for a similar level of disturbance and decline, do have higher quantities of deadwood than lowland forests, partly due to tree decline over longer periods of time (Supp. Mat. Fig. S1).

4.5. *Practical applications*

Our study provides arguments in favour of measures designed to increase deadwood habitats beneficial to biodiversity in integrative nature conservation strategies for managed forests (Gustafsson et al., 2020). In addition to setting aside forest reserves and retention of dead trees, preserving small patches of declining woodland distributed across managed forests could be a third, complementary integration strategy and an opportunity for passive rewilding (du Toit and Pettorelli, 2019) to spontaneously restore structural heterogeneity and larger quantities of deadwood (Doerfler et al., 2018). Thorn et al. (2020) provided benchmarks for retention targets, i.e., the proportion of naturally disturbed forested areas that should be excluded from harvesting to preserve biodiversity. While values vary according to the taxonomic group considered, the above authors suggest the following two generic operational measures: maintain at least 90% of forest species diversity, and avoid salvage/sanitary logging in 75% of a naturally disturbed forest area. For instance, in Germany, Busse et al. (2022) documented the recent expansion of *Peltis grossa*, a greatly severely threatened saproxylic beetle, which is now thriving most likely due to the widespread forest decline which has occurred in the last decades, whereas before, the beetle was barely surviving in a few patches of forest reserves. Retaining declining patches based on Thorn et al. (2020)'s benchmarks would balance specific economic and phytosanitary requirements with the ecological benefits of disturbance-induced complexity and retention silviculture. Managers could take advantage of disturbance and decline to restore old-growth conditions within managed landscapes (Aszalós et al., 2022).

5. Perspectives

Our study illustrates the interest of cross-analyzing large-scale forest databases. Other data from the Biosoil LI-BioDiv database could be mobilized (canopy closure, number of tree layers, alpha diversity of vascular plant species, referring to ICP subplot 2) to study other cross-relationships between multiple forest variables (see e.g., Augustynczik et al., 2024). Mapping certain disturbance parameters (e.g., year of latest disturbance, disturbance intensity, disturbance agent) would provide another source of disturbance data at the European scale which could improve our modelling of disturbance-dieback-deadwood relationships (Senf and Seidl, 2021; Forzieri et al., 2023).

CRediT authorship contribution statement

C. Bouget: Writing – original draft, Validation, Supervision, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **J. Cours:** Writing – review & editing, Visualization, Software, Methodology, Formal analysis, Data curation.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.124315.

Data availability

The data that support the findings of this study are openly available in the Zenodo repository at https://doi.org/10.5281/zenodo.13992861.

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