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Trait-Based Response of Deadwood and Tree-Related Microhabitats to Decline in Temperate Lowland and Montane Forests

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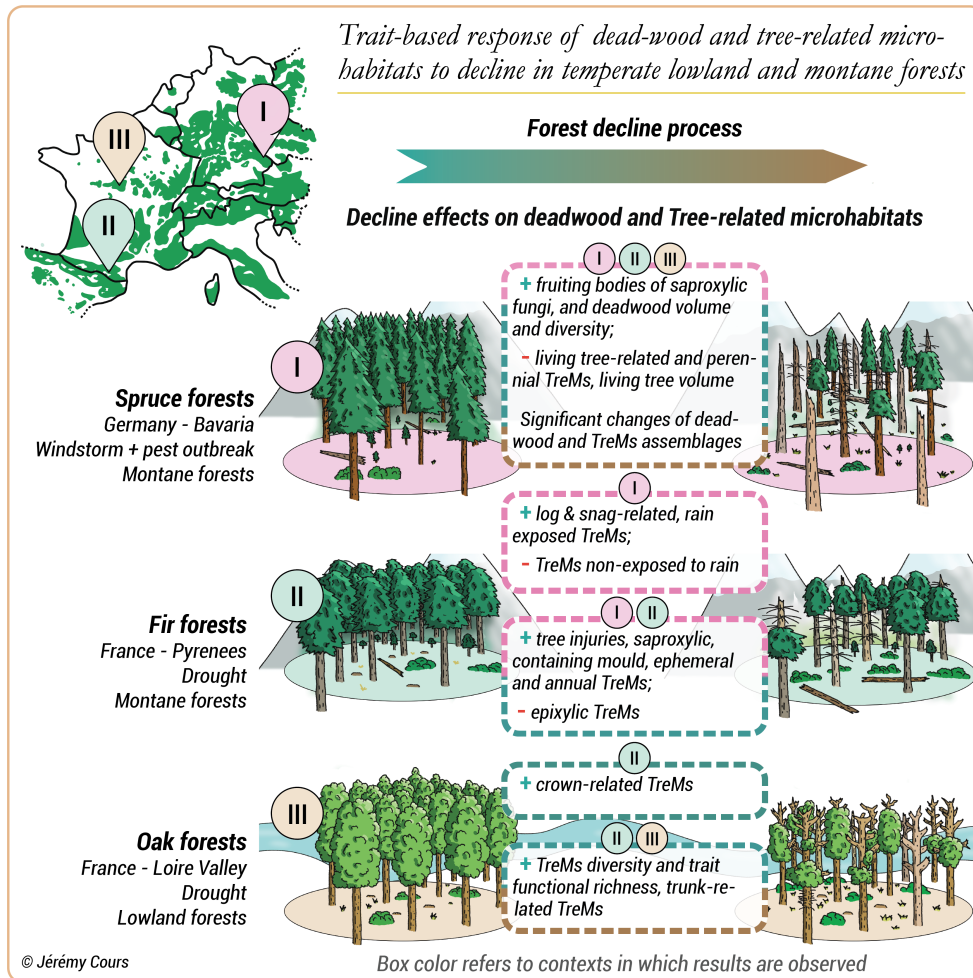
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Abstract

Forest decline caused by climate change has been a growing challenge for European foresters for decades. The accumulation of tree-related microhabitats (TreMs) and deadwood during decline can enhance stand structural heterogeneity and provide crucial habitat features for many forest ecological guilds. We analysed changes in deadwood and TreM assemblages using a trait-based approach in three case studies: drought-induced decline in highland Pyrenean fir and lowland oak forests, and windstorm/pest-induced dieback in highland Bavarian spruce forests. Decline caused significant changes in deadwood and TreM characteristics and composition in three forest contexts. However, tree density with cavities, exudates, or crown deadwood was not linked to decline intensity. Declining conifer forests had more large deadwood and downed woody debris, and their TreM assemblages were more saproxylic, less epixylic, and included more cracks and exposed sapwood. TreM assemblages in drought-declining forests had higher diversity, functional richness, and more dead tops than healthy stands. In Bavarian spruce forests, there was more decayed downed deadwood, and the TreM assemblages were more associated with the base of the tree, snags, and logs. Overall, forest decline significantly boosts ecological niche resources, typically scarce in managed forests, which could benefit many forest biodiversity groups. Though post-disturbance management should respect tree species-dependent economic balance and avoid phytosanitary risks, it should also consider the ecological benefits of decline-induced heterogeneity.

Keywords: dieback; drought; windstorm; pest outbreak; disturbance legacies; saproxylic

Graphical abstract



1 Introduction

Forest decline and dieback have increased in frequency and severity across Europe in recent decades (Seidl et al., 2011, 2014b). Forest decline could lead to tree crown dieback and, ultimately, to tree mortality (Senf et al., 2021). Decline refers to a general set of symptoms associated with loss of tree vigour including slower growth, foliage reduction, twig and branch death and potentially tree death. Dieback is part of the decline syndrome and refers more specifically to branch death associated with climatic stress, pests or pathogens (Ciesla and Donaubauer, 1994).

Decline and dieback are mainly perceived as a threat to forest continuity and, although they pose a considerable challenge to foresters (Jandl et al., 2019), they may also be considered key processes that enhance structural heterogeneity and the supply of habitat for biodiversity (for example, Ojeda et al. (2007)). Along a wide scale gradient, from large-scale stand replacing disturbances to small-scale gap dynamics (Franklin et al., 2002), natural disturbances and their cascading effects on forest stand decline create specific microhabitats, called "disturbance legacies", over multiple time scales (Cours et al., 2023; Swanson et al., 2011). They allow transient accumulations of deadwood to occur and result in a diversification of deadwood and microhabitat

types (Kulakowski et al., 2017; Sallé et al., 2021), and may induce potential changes in resource dynamics in line with the pulse dynamics theory (Jentsch and White, 2019). For instance, droughts and windstorms promote perched dead branches in the canopy, standing dead trees and downed logs, and some specific tree-related microhabitats (TreMs) such as the fruiting bodies of saproxylic fungi (Cours et al., 2021; Swanson et al., 2011; Zemlerová et al., 2023). Loss of tree vigour, associated with increased canopy openness, favours the formation of certain TreMs (Larrieu et al., 2022) while disrupting canopy buffer. Tree mortality also leads to reduction of TreMs borne by living tree while, in parallel, standing dead trees are known to host both higher TreM abundance and diversity (Paillet et al., 2019). Concurrently, deadwood and most TreMs are less abundant and less diverse in managed forests (Asbeck et al., 2022; Bouget et al., 2014).

Deadwood and TreMs are key habitats and trophic resources for a large proportion of forest biodiversity (for example, Larrieu et al. (2019)). Consequently, changes in the availability and distribution of post-disturbance microhabitats and resources are likely to affect biotic communities in declining forests, both in the short and long term (Basile et al., 2020; Cours et al., 2023; Kozák et al., 2021).

The response of deadwood and TreM patterns to the severity of forest stand decline has been rather poorly described to date. Deadwood patterns can be addressed by deadwood profiles, subdividing the local deadwood stock in classes based on size, position and decay stage, and previously used to assess forest disturbance history on forest characteristics (Halme et al., 2019; Stokland, 2001). Furthermore, variations in deadwood composition and TreM assemblages in response to disturbance could be analysed with a trait-based approach, that is, thanks to a database of eco-morphological traits describing deadwood pieces (Parisi et al., 2018) and TreMs. For deadwood, traits such as vertical position, decay stage and size, or for TreMs, type of bearing substrate or position in the tree can link these features to the type of disturbance. Generalizations from traits provide insights into understanding community responses (Qiu et al., 2023), that is, deadwood and TreM assemblages here. Our question here is whether, and if so, how forest decline can be seized as an opportunity to increase stand heterogeneity in deadwood and TreMs. Our study aimed to examine if deadwood substrates and TreMs accumulate and diversify in a predictable manner following decline and dieback events, in diverse forest contexts. We analysed three case studies: drought-induced decline in Pyrenean fir and lowland oak forests, and windstorm/pest-induced dieback in Bavarian spruce forests. In each case study, we explored a gradient of decline intensity (Johnstone et al., 2016), from "almost healthy" stands, where dynamics is dominated by small-scale gap dynamics associated with background mortality (McCarthy, 2001), to "severely disturbed and declining" stands.

We sought to establish whether different declining forest ecosystems (lowland vs montane, deciduous vs conifer, drought-induced versus windstorm/pest-induced decline) provided similar or dissimilar habitat conditions for forest organisms, according to common or contrasted features in terms of dominant tree species, management, response to disturbance and TreM ontogeny. We therefore aimed (i) to quantify the generic (all case studies) or idiosyncratic (that is, dependent on the case study or group of case studies) effects of the intensity of decline and mortality on the local quantity of deadwood substrates and TreMs, (ii) on the local diversity of substrates and (iii) on the composition of local assemblages of deadwood and TreM types. We also intended to specify whether accumulation patterns for disturbance legacies depend on their eco-morphological traits (e.g., decay stage of deadwood, saproxylic nature of TreMs, and so on).

2 Materials and Methods

2.1 Sampling Design and Case Studies

The study was conducted in three regions, that is, two French regions, the Loire valley and the French Pyrenees, and one German region, the Bavarian mountains, as part of two research projects whose data have been aggregated here (Table 1, Figure 1).

In the Loire valley, we studied two lowland sites in oak-dominated (both *Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) forests, one in the Orleans State Forest (107-174 m a.s.l.) and one in the Vierzon State Forest (120-190 m a.s.l.), which had undergone several decline events due to successive droughts, aggravated by edaphic factors especially in the Vierzon forest. The severe summer drought of 2003 had significant effects on oak tree mortality (Cours et al., 2022). The main secondary tree species were hornbeam (*Carpinus betulus* L.) and Scots pine (*Pinus sylvestris* L.). In 2020, we selected nine plots to represent a gradient of increasing decline in mature stands in each of these managed forests. The forest landscape surrounding the plots was also predominantly managed, with repeated sanitation harvesting of the most valuable oak trees during the decline process (Table 1).

In the Pyrenees, we studied two sites in montane forests dominated by silver fir (*Abies alba* Mill.), whose decline is mainly due to successive droughts occurring since the 1980's, recently accentuated by the severe drought of 2003 (Cours et al., 2022), and resulting in patch dynamics (Andrew et al., 2016). Norway spruce (*Picea abies* (L.) H. Karst) and European beech (*Fagus sylvatica* L.) were secondary species. In 2017, we selected 43 plots in managed mature stands: (i) 21 plots in the Aure Valley (854-1570 m a.s.l.) and (ii) 22 plots on the Sault Plateau (705-1557 m a.s.l.). Our plots excluded salvage logging operations (Table 1).

Finally, we studied 19 plots of Bavarian montane forest, dominated by Norway spruce (*Picea abies* (L.) H. Karst) with European beech and silver fir as the main secondary species (Bässler et al., 2009). The dieback was due to several cycles of windstorms followed by bark beetle (*Ips typographus* (L.)) outbreaks (Müller et al., 2010), the dominant drivers of forest dynamics in Norway spruce forests in temperate Europe (Zemlerová et al., 2023). This dieback phenomenon resulted in stand-replacing dynamics with greater tree mortality (Thorn et al., 2017), in a more severe way than either of the aforementioned drought-induced declines (Cours et al., 2021). Our plots were set up in 2017 in mature stands, both within the core area of the Bavarian Forest National Park, and in the surrounding zone (BIOKLIM project), with little or no human intervention, without salvage logging operations (Table 1, Müller et al. (2010)).

In each region, plots were selected in mature stands, with an equivalent tree composition. The sampling design was stratified by the intensity of decline to cover a gradient of decline level, from healthy to strongly declining plots. Across the decline gradient, mortality rates at the plot scale were higher on average and covered a wider range in the Bavarian spruce forests (52%) [± 19 [95% CI]; 4-100%] than in the Pyrenean fir forests (23%) [± 4 [95% CI]; 0-67%], followed by the lowland oak forests (9%) [± 4 [95% CI]; 0-33%].

2.2 Field Measurements

Table 1: Overview of the Three Case Studies Included in the Sampling Design.

Dataset	Data source project	Declining tree species	Secondary tree species	Source of decline	Disturbance type	Sampling year	Number of plots	Forest management	Altitudinal level
Loire valley	CANOPEE project	Sessile and pedunculate oaks	Hornbeam and Scots pine	Successive droughts	Gap dynamics	2020	Vierzon forest (n = 9), Orleans forest (n = 9)	managed stands, salvage logging	Lowland (107-190m a.s.l.)
French Pyrenees	CLIMTREE project	Silver fir	Norway spruce and European beech	Successive droughts	Gap dynamics	2017	Aure Valley (n = 21), Sault plateau (n = 22)	managed stands, no salvage logging	Highland (705-1570 m a.s.l.)
Bavarian National Park	CLIMTREE project	Norway spruce	European beech and Silver fir	Several wind-storms + successive pest outbreaks	Stand-replacing dynamics	2017	n = 19	mainly unmanaged stands, no salvage logging	Highland (660-1352 m a.s.l.)

The forest structure of plots in each region was described using the same standardized protocols. Plots were set up with a Bitterlich relascope with an opening angle corresponding to counting factor $n^\circ 1$ (ratio 1/50), and mean plot area was about 0.3 ha. For each tree within the plot, we recorded its status (that is, dead, living, snag, log), tree species and diameter at breast height (DBH; minimum DBH recorded = 17.5 cm for living trees and logs, 7.5 cm for snags, 67.5 cm for very large trees). We took the proportion of dead trees in basal area (that is, the ratio of the cumulative basal area of standing and lying dead trees to the basal area of all the trees in the plot), hereinafter referred to as "mortality rate", as a proxy for the level of local stand decline. Note that this "mortality rate" does not reflect true overall mortality rate in managed oak forests, as foresters removed most valuable declining trees. We visually inventoried TreMs on living trees, logs and snags, using the hierarchical TreM typology by Larrieu et al. (2018), describing 17 TreM groups and 53 TreM types (Suppl. Material Table S.1). For each deadwood item (length > 1 m) in the plot, we measured its decay stage (from 1 = hard deadwood fully covered with bark to 4 = soft wood without bark), length, diameter at mid-length for logs and snags < 4 m long, and DBH for dead trees and snags > 4 m. Deadwood was classified in the following categories: ground-lying (logs and uprooted dead trees) versus standing (snags and standing dead trees); small and mid-size (less than 40 cm in diameter) versus large and very large (more than 40 cm in diameter); and fresh (decay class 1 and 2) versus decayed (decay stage 3 and 4). We calculated the total number of items per hectare by allocating a coefficient N_d related to diameter (d) to each item observed in the relascope sampling: $(N_d = \pi 10^8 [\text{ArcTan}(1/50)/(\pi d)]^2)$. We estimated TreM diversity and the number of deadwood types per plot. We compiled a list of eco-morphological traits for woody elements (that is, life status (living, dead) and vertical position (downed, standing), decay stage and diameter) and for TreMs detected in the field (TreM nature, association with deadwood (saproxylic, epixylic, mould), type of bearing substrate (that is, living tree, dead tree or snag, and log), position in the tree (that is, base, trunk, crown), degree of wetness, life span or ontogenesis; Table 2 and Supplementary Material Table S.1).

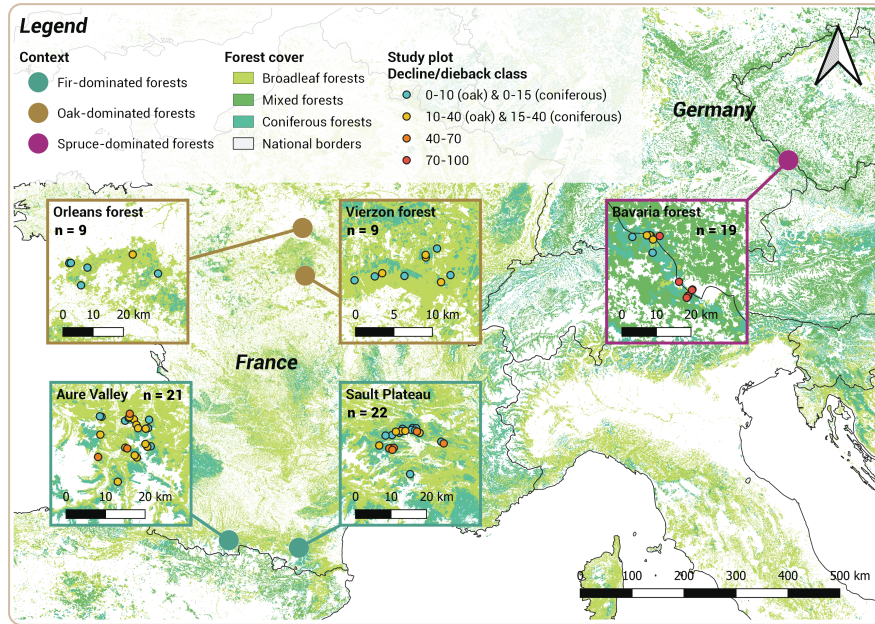


Figure 1: Map of study plots in different forest contexts.

Table 2: Overview of the Eco-morphological Traits Used to Describe Woody Elements and Tree-Related Microhabitats (TreMs).

Trait group	Trait	Description
Woody elements		
	Status/position	Combination of life status (alive vs dead) and vertical position (standing vs lying on the ground): 3 = living tree; 2 = snag or dead tree; 1 = log
	Decay stage	From 1 (= hard deadwood fully covered by bark) to 4 (= soft wood with no bark)
	Diameter	Diameter at mid-length for logs; diameter at mid-height for snags less than 4 m tall; diameter at breast height otherwise
Tree-related microhabitats		
Association to deadwood	Saproxyllic	Containing decaying deadwood (e.g., rot-holes, dead branches)
	Epixylic	Containing no decaying deadwood (e.g., bryophytes, lichens, mistletoe)
	Mould	Containing mould (e.g., mainly rot-holes)
Bearing substrate	Living tree	Mainly borne by living trees (e.g., burrs, epicormic shoots)
	Snag	Mainly borne by snags and dead trees (e.g., bark pockets and shelters)
	Log	Mainly borne by logs (e.g., root plates)
Position in tree	Base	Mainly or strictly occurring at the base of the tree (e.g., bryophytes, root buttress concavities)
	Trunk	Mainly or strictly occurring on the trunk of the tree (e.g., sap runs, trunk rot-hole)
	Crown	Mainly or strictly occurring in the tree crown (e.g., dead tops and branches)
Wetness	Dry	That are never wet inside since they are protected from precipitation (e.g., perennial polypores)
	Wet	Exposed to precipitation (e.g., chimney trunk base rot-holes) or intrinsically wet (for example, active sap run)
Life span	Ephemeral	Maintain their function for less than a year (e.g., pulpy agarics, slime moulds)
	Annual	Maintain their function about a year (e.g., annual polypores)
	Perennial	Maintain their function for more than a year (e.g., rot-holes, perennial polypores)
Ontogenesis	Slow	Replacement rate of about decades (e.g., chimney trunk base rot-hole, lichens)
	Fairly slow	Replacement rates of about a decade (e.g., root plates, root buttress concavities)
	Fairly rapid	Replacement rate of less than a decade (e.g., woodpecker breeding cavities, bark losses)
	Rapid	Replacement rate of about a year (e.g., slime moulds, vertebrate nests)

2.3 Data Analysis

2.3.1 Univariate Analysis

Analyses were conducted using the R software 4.1.2. (R Core Team, 2023). First, to obtain a general idea of forest conditions in nondeclining stands in each region, we calculated mean values for the woody elements and TreMs variables for plots in the lowest dieback class separately. Second, we tested the direct effect of forest stand decline (that is, mortality rate) on each univariate metric with a generalized linear mixed model (glmmTMB function from the glmmTMB R-package and mixed-model function from the GLMMadaptive R-package), including site as a random variable (that is, Aure and Sault in the Pyrenees, and Orleans and Vierzon in the Loire Valley). In addition to volume and diversity for the woody elements (living trees, total deadwood, deadwood categories), and abundance and diversity for TreM groups, we used community-weighted means (CWM) and functional dispersion (FDis; dbFD function, FD R-package) values for each eco-morphological trait describing woody elements and TreMs, and the multi-trait functional richness (FRic) of the 42 TreM types observed in the study plots, as plot-scale response variables in univariate analyses. We tuned the fit function to the distribution of each response variable, using Gaussian (mostly for CWM and FDis metrics), Poisson and negative binomial distributions (the latter mostly for volume, diversity and density of woody elements and TreMs, that is, countable, sometimes overdispersed, response variables). We tested the goodness-of-fit of the selected distribution with the residual diagnostic method from the DHARMA R-package.

We then estimated the magnitude of a standardised increase in decline on the successfully modelled response variables. For this purpose, we first extracted each estimate (or β -coefficient) associated with the effect of forest decline on each response variable modelled and its standard deviation. Then, we simulated a Gaussian distribution of each estimate, based on its value and standard deviation. We simulated an increase of 27% in forest decline (namely, the standard deviation of the mortality rate) and studied the magnitude of the consecutive change in the mean of each response variable (Barbier et al., 2009). We extracted mean and 95% confidence intervals in the resulting 10,000-sample distribution of the relative increase in each response variable.

Finally, we used Structural Equations Modelling (SEM, R-package piecewiseSEM) to test both the direct and indirect effects (that is, deadwood-mediated effects, since TreMs are borne by woody elements) of forest decline on TreMs. SEM provides a unique network of multiple predictors and response variables, at multiple hierarchical levels, where deadwood variables can be both response variables (y) in a first set of models, and predictors (x) in a second set of models. We tested 17 individual relationships and adjusted 5%-p value to 0.00294. We validated the piecewise SEM with Shipley's test of directed separation (or d-separation), and checked that when $p > 0.05$, there were no missing relationships.

2.3.2 Multivariate Analysis

In a second step, we performed a multivariate analysis of the composition of two community matrices: (i) the woody element species, based on different characteristics (that is, by combining tree species, substrate, decay stage and diameter class, and (ii), TreM types (Larrieu et al., 2018). As abundance variables, we used (i)

the calculated volume per hectare for the woody elements, and (ii) the density per hectare for TreM-bearing trees. We then computed between-plot Bray–Curtis distances (vegdist function, vegan R-package) and ran non-metric multidimensional scaling (metaMDS R-function) for both matrices in each forest context. Next, we tested the effect of forest decline on both matrix composition, using PERMANOVA (adonis2 R-function) with the "site" effect as a constraint (that is, in a fir context: Aure and Sault; in an oak context: Orleans and Vierzon).

In parallel, we distributed our plots equally among decline classes, that is, [0–15],]15–40],]40–70] and]70–100] classes in the fir- and spruce-dominated forests, and [0–10] and]10–40] classes in the oak-dominated forests. We then searched for characteristic types of woody elements and TreMs in each decline class and for each tree species, through an indicator-species analysis (multipatt function, indicpecies R-package). For TreMs, we used the detailed TreM type, and not the coarser TreM group as in glmm. Finally, we tested the co-variation between the matrices of woody elements and TreMs, according to the Procrustes methodology (Peres-Neto and Jackson (2001); protest function, vegan R-package).

3 Results

3.1 Variations in Decline Level and Forest Conditions Among the Case Studies

Local deadwood diversity, deadwood and living-tree volumes and the density of trees bearing rot-holes or epiphytes were all lower in the oak stands than in the coniferous stands. On the other hand, the density of trees bearing woodpecker cavities or crown deadwood was higher in the oak forests than in either of the coniferous forests (Suppl. Material Table S.2). The number of very large living trees was greater in the fir forests, and the density of exudate-bearing trees and the volume of fresh deadwood were higher in the spruce forests than in the two other two contexts. For deadwood, the number of very large pieces, and the volume of highly decayed pieces, large pieces and lying pieces were higher in fir forests than in spruce forests, followed by oak forests. This was also the case for the TreM diversity, and the density of trees bearing sporocarps, burrs, cankers, exposed sapwood and concavities (Suppl. Material Table S.2). Spruce stands hosted higher volumes of standing deadwood and mid-sized deadwood pieces, and higher densities of TreM-bearing trees than did fir stands, followed by oak stands.

3.2 Effect of Decline Level on Substrate Quantity

The level of local decline had a strong positive effect on the volume of total deadwood (+265% in fir, +217% in spruce, +291% in oak), fresh deadwood (+87% in spruce, +316% in oak), decayed deadwood (+321% in fir, +367% in spruce), mid-sized deadwood (+305% in fir, +161% in spruce), large deadwood (+224% in fir, +428% in spruce), standing deadwood (+194% in fir, +354% in spruce, +308% in oak), ground-lying deadwood (+351% in fir, +145% in spruce).

With increasing levels of decline, we did not observe any increase in local density of all TreM-bearing trees in any forest context (Figure 3). In relation to this point, we observed a significant decrease in living wood volume in the fir, spruce and oak forests (respectively –37%, –30% and –49%, for a 27% increase in local

decline level; Figure 2a). However, the density of TreMs associated with bark injuries (that is, exposed sapwood and heartwood) increased significantly with decline level in both the fir and spruce plots (Figure 3). We also measured a significant increase in the density of trees bearing the fruiting bodies of lignicolous fungi (Figure 3), that is, ephemeral fungi in fir forests, and perennial fungi in spruce and oak forests. Conversely, the density of trees bearing epiphytes, burrs, cankers or concavities decreased with increasing decline level in spruce forests (Figure 3).

3.3 Effect of Decline Level on Substrate Diversity

We observed a significant increase in deadwood diversity with decline level in all forest contexts (+79% in fir, +13% in spruce, +179% in oak). In addition, we observed a significant increase in local diversity of TreM-bearing trees with increasing levels of decline in both the fir and oak forests (Figure 3). Furthermore, the TreM multi-trait functional richness increased with decline level in the fir and oak stands (respectively by +47% and +79%; Figure 4), but significantly decreased in the spruce forests (−16%; Figure 4).

3.4 Effect of Decline Level on Assemblage Composition of Substrate Types

The decline severity had a significant effect on deadwood and TreM assemblage composition in all three forests (Table 3). In the fir forests, medium and large decayed lying deadwood and large decayed standing deadwood were characteristic of severely declining stands whereas large living trees were characteristic of very low levels of decline (Table 4). In the spruce forests, medium and large decayed standing deadwood was characteristic of highly declining stands (Table 4). No specific deadwood type was significantly associated with either healthy or declining stands in the oak forests (Table 4). A few TreMs were characteristic of severely declining stands: bark pockets in all the forest contexts, cracks and polypores in both spruce and fir forests, and bark shelters and dead tops in fir stands only (Table 4). No particular TreM was characteristic of healthy or weakly declining stands.

The composition of deadwood and TreM assemblages clearly co-varied along the decline gradient at the plot level; the co-variation was very strong in spruce (Procrustes matrix correlation = 0.84, permutation test p value < 0.001) and less so in fir (Procrustes matrix correlation = 0.55, p < 0.001) and oak forests (Procrustes matrix correlation = 0.67, p = 0.013).

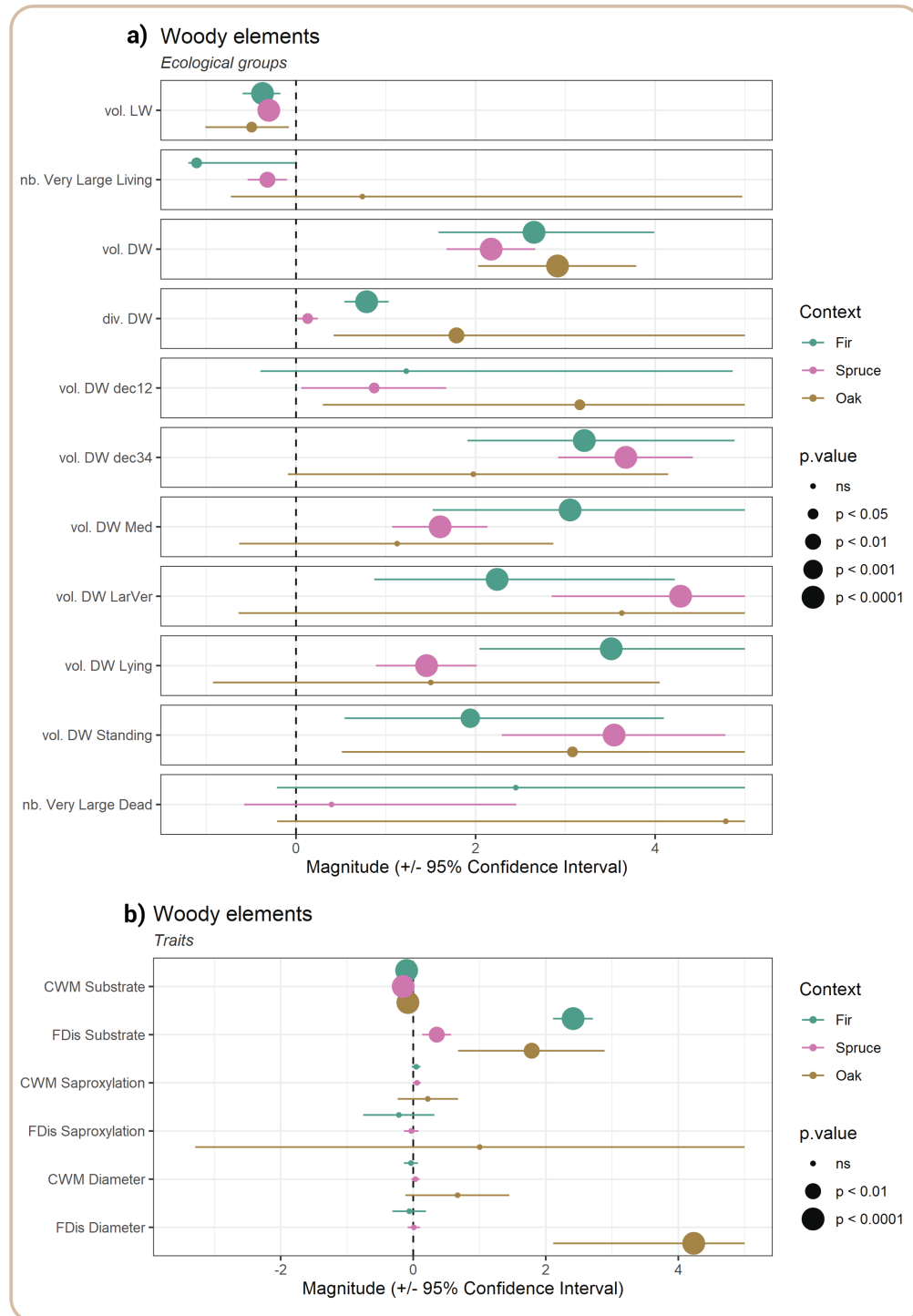


Figure 2: Magnitude of the effects of the level of forest stand decline on the ecological groups of woody elements (top) and mean (CWM) or variance (FDis) of the traits describing the woody elements (bottom). Magnitude was calculated as the subsequent relative increase or decrease in each woody ecological group for a 27% (= SD value) increase in the level of forest decline. The size of the dots increases with the significance of the model. "LW": "living wood", "DW": "deadwood", "vol.": "volume", "dec": "decay", "Med": "Mid-size deadwood", "LarVer": "Large and Very large deadwood"; the CWM and FDis of the Substrate variable include both living and deadwood while the CWM and FDis of the decay stage and diameter variables include only deadwood items.

3.4 Effect of Decline Level on Assemblage Composition of Substrate Types

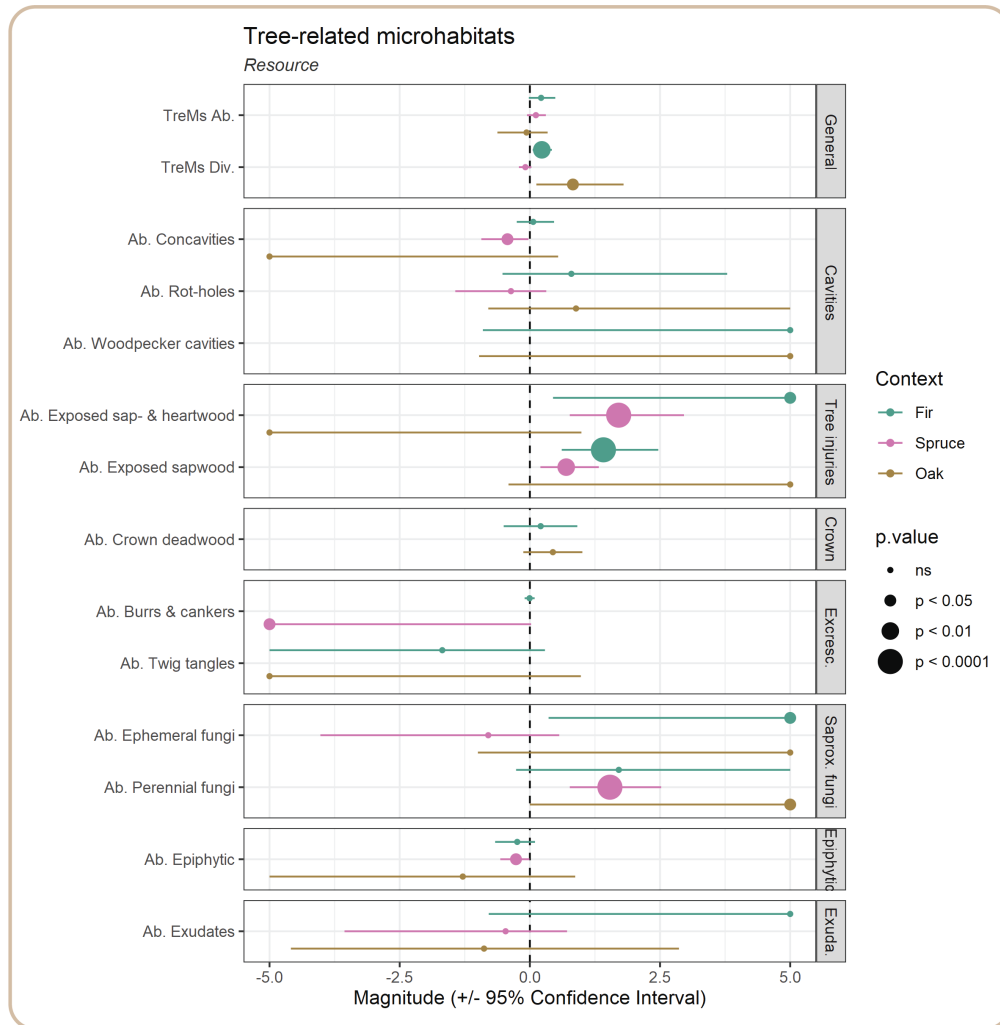


Figure 3: Magnitude of the effects of forest stand decline level on tree-related microhabitats (TreMs) (see legend Figure 2).

3.4 Effect of Decline Level on Assemblage Composition of Substrate Types

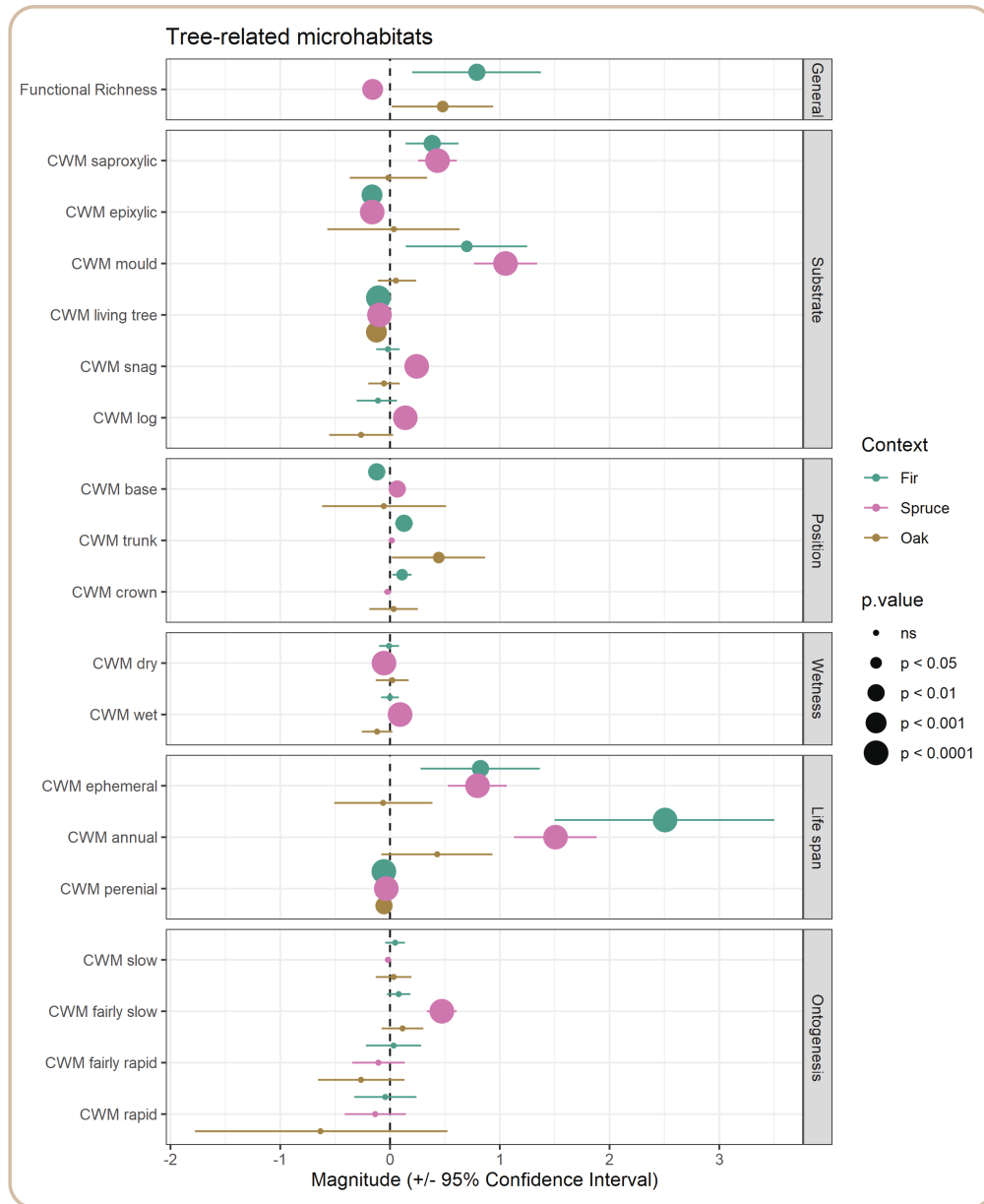


Figure 4: Magnitude of effects of forest stand decline level on tree-related microhabitats traits (TreMs) (see legend Figure 2).

3.5 Influence of the Eco-Morphological Traits of Substrates on Response Patterns to Decline

Table 3: Compositional Response of Woody Elements (Living and Dead Types; top) or TreM (bottom) Assemblages to Forest Stand Decline, Analysed by PERMANOVA (Adonis R-function).

Context	Df	F.Model	R ²	p value
Woody elements				
Fir-dominated forests	1	6.37	0.13	p < 0.001
Spruce-dominated forests	1	13.9	0.45	p < 0.001
Oak-dominated forests	1	2.2	0.12	p < 0.05
Tree-related microhabitats				
Fir-dominated forests	1	3.37	0.07	p < 0.01
Spruce-dominated forests	1	11.05	0.39	p < 0.001
Oak-dominated forests	1	2.91	0.15	p < 0.01

Analyses for each data subset were constrained by site.

Table 4: Characteristic Woody Elements or TreMs Identified in Groups Based on Decline Level by IndVal Analysis.

Region	Group	Indicator type	Stat	p value
Woody elements				
	[0; 15]	Living, Abies alba, large size	0.7	p < 0.001
Fir-dominated forests]40; 70]	Lying deadwood, Abies alba, mid-size, decay 3	0.87	p < 0.001
		Standing deadwood, Abies alba, large size, decay 3	0.8	p < 0.01
		Lying deadwood, Abies alba, large size, decay 3	0.76	p < 0.01
Spruce-dominated forests]70; 100]	Standing deadwood, Picea abies, large size, decay 3	0.9	p < 0.001
		Standing deadwood, Picea abies, mid-size, decay 3	0.87	p < 0.001
Oak-dominated forests		NA		
Tree-related microhabitats				
Fir-dominated forests]40; 70]	Bark pocket	0.92	p < 0.001
		Annual polypore	0.85	p < 0.01
		Bark shelter	0.85	p < 0.01
		Crack	0.68	p < 0.01
		Dead top	0.67	p < 0.01
Spruce-dominated forests]70; 100]	Crack	0.93	p < 0.001
		Perennial polypore	0.88	p < 0.01
		Bark pocket	0.88	p < 0.01
Oak-dominated forests]10; 40]	Bark pocket	0.82	p < 0.001

Woody elements included both deadwood and living trees. We restricted to indicator type with p < 0.01.

3.5 Influence of the Eco-Morphological Traits of Substrates on Response Patterns to Decline

Increasing the level of decline did not result in any significant changes in mean or dispersion of deadwood decay stage in any forest context (Figure 2b). Nonetheless, several eco-morphological deadwood traits responded significantly to decline. In all contexts, the mean substrate status (on a gradient from standing live trees to lying logs) decreased (−9% in fir, −8% in spruce and −15% in oak; Figure 2b) while dispersion increased significantly with decline (Figure 2b). Neither the mean value nor the dispersion for deadwood diameter changed significantly with increasing dieback in the fir and spruce forests; however, in the oak forests, the latter did increase significantly with decline (Figure 2b).

Only a few effects of decline on the mean traits of TreM assemblages were observed in the oak plots, where TreM assemblages were significantly less associated with live trees, and were less perennial and more associated with the trunk (Figure 4). In contrast, many eco-morphological traits influenced TreM responses to increasing decline levels in both the fir and spruce forests (Figure 4). TreM assemblages were more ephemeral and less perennial in declining plots compared to healthy ones (Figure 4). Moreover, epixylic TreMs decreased slightly, though significantly, in TreM assemblages in the declining plots (-16% in both fir and spruce forests), while the increase in mean saproxylic TreM trait ($+38\%$ in fir and $+43\%$ in spruce forests) was significant (Figure 4). Likewise, declining plots provide more TreMs containing mould (respectively $+70\%$ and $+105\%$; Figure 4). In all three forest types, TreMs were less associated with living trees (ca -10% ; Figure 4), and in spruce, they were significantly more associated with snags and logs ($+24\%$ and $+14\%$; Figure 4). In the fir forests, TreMs were less associated with the base of the tree (Figure 4); they were slightly, but significantly, more related to the crown and trunk- (ca $+10\%$; Figure 4). In contrast, in the spruce forests, they were more associated with the tree base ($+6\%$; Figure 4). Finally, in the spruce forests, TreMs were significantly less protected from humidity (more exposed to weather or intrinsically wetter; Figure 4) and their ontogenesis was somewhat slower in the declining plots than in the healthy ones (Figure 4).

The SEM results showed that many TreM responses were actually related to decline-induced changes in deadwood assemblages in all of the forest contexts (Suppl. Material Figures S.1, S.2, S.3). Some TreMs were significantly associated with deadwood features that were themselves affected by decline. For example, in the fir forests, (i) deadwood diversity positively influenced the mean of the saproxylic TreM trait; (ii) standing deadwood volume positively influenced the abundance and diversity of TreMs. In the spruce forests, deadwood diversity increased multi-trait dispersion of TreMs. However, several TreM responses were positively linked with changes in deadwood traits that were not significantly fostered by decline severity. For instance, in the fir forests, mean deadwood diameter increased the dispersion of TreM substrate and position.

4 Discussion

4.1 Decline-Driven Accumulation of Substrates

As expected, decline favoured the accumulation of deadwood such as fallen branches, standing and lying dead trees and snags, and resulted in large increases in total deadwood and standing deadwood volumes. The progressive loss of tree vigour during decline may translate first into crown dieback, then into tree mortality, especially on spruce but less systematically on oak and fir trees; this gradual process makes transient accumulations of different types of deadwood resources possible (Cours et al., 2021; Kulakowski et al., 2017; Thom et al., 2017). Considering the magnitude of change, as in this study, reveals that some deadwood types were more affected by the decline process than others though this is not consistent across forest contexts. For instance, decline-induced increases were stronger for standing deadwood, directly related to the number of declining trees, than to lying deadwood in both spruce and oak forests, though this was not the case in fir forests. In both declining conifer forests, deadwood assemblages contained more large deadwood and more lying deadwood compared to healthy stands, and large decayed standing deadwood was

a characteristic deadwood type.

Overall, we found no decline-induced increase in the local abundance of TreM-bearing trees. Nonetheless, we revealed significant increases in the density of fungal TreMs and bark pockets in all the forest contexts, in line with the general increase in weakened trees and snags frequently bearing these TreMs (Kozák et al., 2018; Ojeda et al., 2007; Paillet et al., 2019). In spruce forests, Zemlerová et al. (2023) have shown that ephemeral and perennial fungal fruiting bodies are significantly related to disturbance severity. The higher occurrence of fungal fruiting bodies can indicate the higher heterogeneity of habitat conditions, caused by low severity and temporal succession of disturbances, favouring a wide range of fungal species with different ecological requirements (Holec et al., 2020).

In the conifer forests (Pyrenean fir and Bavarian spruce), tree injuries increased with decline intensity, certainly resulting from bark peeling after sunburn and colonisation of subcortical arthropods, water deficits, and deadwood decay process. For instance, cracks, frequently borne by snags (Larrieu and Cabanettes, 2012), and bark pockets were characteristic of declining stands. Bark beetles, whose massive subcortical attacks rapidly cause bark peeling, colonized the declining conifer stands. In spruce forests, Zemlerová et al. (2023) also found a significant relationship of exposed sapwood occurrence with disturbance severity, in line with superficial tree injuries and bark loss caused by the fall of windthrown trees. They observed high abundance of TreM types such as bark pockets and bark shelters, associated with insect outbreaks and the presence of snags. On the contrary, in oak forests, Buprestid xylophagous beetles do not induce this type of symptom when they attack trees, at least in the short term. Decline trajectories differ among tree species and could lead to distinct TreM patterns.

Surprisingly, crown deadwood was not characteristic of declining stands in any of our case studies. Yet, drought-induced cavitation can generate dry branches, partial branch mortality and can trigger an accumulation of deadwood in the canopy in the short term (Choat et al., 2018), especially in the upper part of tree crown, more vulnerable to soil drought (Chakraborty et al., 2017); and crown dieback can be further amplified during the subsequent loss of tree vigour (Sallé et al., 2021). Therefore, crown dieback is a typical feature of declining trees. Our surprising result might stem from our TreM sampling protocol, since crown deadwood was measured only on living trees, not on dead ones, the latter being recorded as standing deadwood.

Tree decline favours the creation of several types of TreMs: crown deadwood, bark loss, cracks (Courbaud et al., 2022) and trunk cavities (Larrieu et al., 2022; Ojeda et al., 2007). Degree of crown dieback is a primary factor explaining woodpecker tree selection for cavity excavation (Dudinszky et al., 2021; Ojeda et al., 2007) in deciduous-dominated forests. However, the density of cavity-bearing trees was not related to decline intensity in any of the contexts in our study. Rot-holes are actually a TreM group which is not very common in spruce forests (Zemlerová et al., 2023). Woodpecker-breeding-holes and rot-holes are related to slowly active biological processes on large trees, especially in oaks (Courbaud et al., 2022). For such TreMs, the time elapsed since the last major disturbance may be crucial (Cours et al., 2023) and may have been insufficient in this study. Likewise, rather surprisingly, the local density of exudate-bearing trees did not vary with decline in any of the contexts in our study. However, they normally occur in spruce plots disturbed with low severities (Zemlerová et al., 2023). In our case, this may be because a certain combination of necessary processes did not occur (for example, bark injuries, pest attacks, bacterial activity, root pressure; Weber

(2006)).

4.2 Decline-Driven Changes in Habitat Composition, Partly Related To Eco-Morphological Traits of Substrates

From our ordination results, decline-induced changes in TreM- and deadwood-assemblages were significant in all three contexts. Overall, the differences among contexts were more pronounced for TreMs than for deadwood. In response to forest decline, TreM assemblages shifted towards less perennial TreMs and were less associated with living trees, in line with the increasing proportion of dead trees and subsequent reduction in living trees number (Zemlerová et al., 2023).

Beyond these common features, the contrasted contexts in our study led to contrasting dynamics in declining stands, with different TreMs and deadwood types associated with tree decline. In the conifer forests (Pyrenean fir and Bavarian spruce), TreM assemblages were more saproxylic, less epixylic, more ephemeral and contained more mould due to decline. Our results show that drought-induced decline in silver fir and oak forests had similar effects on TreM assemblages. They were less associated with the base of the tree and more associated with the crown and trunk, and included more dead tops in declining than in healthy stands. In the Bavarian spruce forests, deadwood and TreM assemblages co-varied more strongly than in the other contexts. Windstorm/pest-induced decline led to more TreMs associated with the base of tree and with snags and logs, and with a slower ontogenetic rate than in healthy stands. Slower TreM generation process in Bavarian declining stands on average than in healthy stands can probably be attributed to the strong dynamics specific to the high mortality following the compound storm and pest outbreak succession rather than the specific effect of the spruce tree species.

4.3 Decline-Driven Diversification of Substrates

Several of our results point toward increased local heterogeneity of stand structure after decline due to a diversification of deadwood and TreM assemblages, which in turn, may favour diverse forest guilds (Cours et al., 2023; Viljur et al., 2022). Natural disturbances generate structural complexity (Gough et al., 2022; Kulakowski et al., 2017; Turner, 2010) and spatial heterogeneity from the individual tree to whole landscapes (Seidl et al., 2014a). For our data, deadwood diversity and the dispersion of woody-element status increased with the level of decline in all three forest contexts, and resulted in a higher heterogeneity of woody items. This was also true for the dispersion of deadwood diameter in the oak forests. Natural disturbances have previously been shown to increase the diversity of deadwood substrates (Aakala, 2010; Swanson et al., 2011). In our study, this resulted in increasing diversity in deadwood (in the three contexts) and TreM (in fir and oak forests) assemblages with decline level. In spruce forests, Zemlerová et al. (2023) previously observed that the total TreM groups diversity did not significantly change with disturbance severity. Moreover, the diversity and multi-trait richness of TreM increased with decline level in the fir and oak forests. The decline induced by severe water constraints in silver fir and oak forests is inherently progressive. Drought-induced tree decline may therefore allow snags to accumulate diverse TreMs (Asbeck et al., 2022; Larrieu and Cabanettes, 2012; Paillet et al., 2019). In our study, the decline-induced increase in deadwood enhanced several parameters

of TreM diversity. In the conifer forests (Pyrenean fir and Bavarian spruce), the decline-induced increase in deadwood diversity (spruce) or in standing deadwood volume (fir) fostered TreM diversity. From [Meigs et al. \(2017\)](#), disturbance severity can be associated with a complex forest structure including disturbance legacies and features associated with old-growth forests such as TreM-bearing trees, snags and forest-floor deadwood.

4.4 Study Limitations

In our study, decline or dieback increased and diversified suitable deadwood substrates in every context, but the effects on TreM assemblages were more context-dependant. For example, TreMs associated with slow, gradual, drought-induced decline were associated with the tree crown, where tree decline begins. On declining conifer trees, TreMs were associated with bark beetle-induced bark peeling, which frequently exacerbates conifer decline. Nonetheless, a limitation of our study is that we have no data on the position of the study along the past dynamics of local decline or on the time elapsed since peak decline, which is known to affect the relative abundance of TreMs in interaction with disturbance severity ([Zemlerová et al., 2023](#)). In our study, significant effects of decline were observed in all three contexts but they were more diverse and intense in fir and spruce forests than in oak forests. Our comparison among tree species was nonetheless weakened by differing experimental designs. First, forest management was more intensive in the oak forests, including salvage logging operations, than in the montane conifer forests, excluding repeated sanitation harvesting. Second, in the spruce forests, the mortality rate was higher on average and covered a wider range than in the fir forests and finally in the oak forests, potentially resulting from contrasting salvage harvests of declining trees. Finally, the number of study plots was higher in the Pyrenean fir forests than in the spruce and oak forests.

5 Conclusion

Our results confirm that decline caused by drought or windstorm disturbances, considerably boosts the stocks of fallen and weakened trees, and then TreM and deadwood resources for opportunistic deadwood-dwelling organisms. Overall, the accumulation of disturbance legacies and the subsequently enhanced structural habitat heterogeneity generally benefit many groups of forest biodiversity, directly or indirectly associated with decline-generated substrates ([Basile et al., 2020](#); [Bouget and Duelli, 2004](#); [Cours et al., 2021, 2022, 2023](#); [Thom and Seidl, 2016](#)). Identifying more clearly the relative contribution of tree species on dieback processes and management strategies would be relevant to better adapt management to ongoing changes in disturbance regimes. Post-disturbance management must balance the specific economic and phytosanitary requirements with the ecological benefits of disturbance-induced complexity and retention silviculture ([Lindenmayer et al., 2012](#)). We know that the risk of large-scale pest outbreaks is much lower in oak and fir forests than in spruce forests thanks to certain management practices ([Kneeshaw et al., 2021](#)). Selective post-disturbance logging ([Priewasser et al., 2013](#)) and retaining patches of declining or dead trees ([Angelstam, 1998](#)), based on benchmark retention targets ([Thorn et al., 2020](#)), could take advantage of disturbance and decline to maintain ecologically important structural characteristics, or even to restore old-growth conditions, within managed landscapes.

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7 Data availability

Data have been posted on the Zenodo repository ([link](#)). R code for statistical analyses is available on [link](#).

8 Supplementary material

8.1 Database of eco-morphological traits for tree-related microhabitats (TreMs) and CWM-FDis calculations

Our database includes eco-morphological traits describing tree-related microhabitats (TreMs). We allocated a degree of occurrence (0 = no occurrence, 1 = rare occurrence, 2 = common occurrence, 3 = almost systematic occurrence) to each category of TreM based on a weighted score of expert opinion (co-author LL).

For TreMs, we analysed the CWM and FDis of their elementary traits in two ways. Firstly, we analysed each elementary trait separately; for example, for the bearing substrate trait, we examined TreM occurrence on living trees, snags and logs separately (see Figure 4). Secondly, we used some groups of traits as an ordinal scale. For instance, for the bearing substrate, we analysed the entire gradient from logs to living trees, as well as the status and position of the woody elements. For the bearing substrate, we assigned different values to different substrates (i.e., 3 for living trees, 2 for snags and standing dead trees, and 1 for logs). We then estimated the position of each TreM along the resulting gradient based on the mean value weighted by its occurrence on each elementary trait. We also used this method for position in the tree, wetness, life span and ontogenesis (see Figures S.1, S.2 and S.3). We only used these trait gradients for Structural Equations Modelling.

Table S.1: Database of eco-morphological traits for tree-related microhabitats (TreMs).

TreM group	TreM type	Association to deadwood				Position in tree			Wetness			Life span			Ontogeny										
		Saprox. Epixy.	Contains mould	Living tree linked	Snag linked	Log linked	Global	Base	Trunk	Crown	Global	Dry	Wet	Water filled	Global	Ephem. Annual	Perenn.	Global	Slow	Fairly slow	Fairly rapid	Rapid	Global		
Burs and Cankers	Burr	0	3	0	3	0	0	3	1	3	0	1.75	3	0	0	1	0	0	3	3	3	2	0	0	2.8
	Canker	3	0	1	3	1	1	2.4	1	3	1	2	2	1	0	1.333	0	0	3	3	2	3	0	0	2.7
Concavities	Dendroblehn	2	2	2	3	1	1	2.4	2	2	2	2	0	1	3	2.75	3	1	1	1.6	1	3	1	0	2.4
	Root buttress concavity	0	3	0	3	2	0	2.6	3	0	0	1	3	1	0	1.25	0	0	3	3	1	3	1	0	2.4
	Trunk bark lined cavity	0	3	0	3	0	0	3	0	3	0	2	3	1	0	1.25	0	0	3	3	3	0	0	0	3
Crown	Woodpecker foraging excavation	3	0	1	3	3	1.714	2	3	1	1.833	2	1	0	1.333	0	0	3	3	1	2	3	1	1.929	
	Dead branches	3	0	1	3	3	2	2.125	0	0	3	3	2	2	0	1.5	1	1	3	2.4	2	3	2	1	2.188
	Dead top	3	0	0	3	3	0	2.5	0	0	3	3	2	2	0	1.5	1	1	3	2.4	3	1	1	1	2.333
Ephemeral fungal fruiting bodies and slime molds	Remaining broken limb	3	0	1	3	2	0	2.6	0	0	3	3	2	2	0	1.5	0	0	3	3	2	3	1	1	2.286
	Annual polypore	3	0	0	2	3	3	1.875	2	3	1	1.833	3	1	0	1.25	0	3	1	2.25	3	1	0	0	2.875
	Pulpy agaric	0	3	0	3	2	2	2.143	2	3	2	2	1	2	0	1.667	3	0	0	1	2	3	1	0	2.5
Epiphytic or parasitic cryptogams and phanerogams	Slime mold	0	3	0	1	3	3	1.714	2	3	1	1.833	1	3	0	1.75	3	0	0	1	0	0	3	2	1.3
	Bryophyte	0	3	0	3	3	3	2	3	2	1	1.667	1	2	0	1.667	0	0	3	3	3	1	0	0	2.875
	Ferns	0	3	0	3	1	1	2.167	0	3	2	2.4	0	3	0	2	0	1	3	2.75	1	3	1	0	2.4
Exposed sapwood and heartwood	Foliose or fruticose lichens	0	3	0	3	1	1	2.4	1	3	2	2.167	2	1	0	1.333	0	0	3	3	3	0	0	0	3
	Ivy or liana	0	3	0	3	3	2	2.125	3	3	2	1.875	1	3	0	1.75	0	0	3	3	1	2	3	1	1.929
	Mistletoe	0	3	0	3	0	0	3	0	2	3	2.6	0	3	0	2	0	0	3	3	0	2	3	0	1.9
Exposed sapwood only	Crack	3	0	1	3	3	1	2.286	1	3	1	2	2	1	0	1.333	0	0	3	3	3	2	0	0	2.8
	Lightning scar	3	0	1	3	1	0	2.75	0	3	1	2.25	2	1	0	1.333	0	0	3	3	3	0	0	0	3
	Limb breakage	3	0	1	3	1	0	2.75	0	3	0	2	2	2	0	1.5	0	0	3	3	3	1	1	0	2.6
Exposed sapwood only	Stem breakage	3	0	0	3	1	0	2.75	0	3	0	2	0	3	0	2	0	0	3	3	3	2	0	0	2.8
	Bark loss	3	0	0	3	2	2	2.143	3	2	1	1.667	3	1	0	1.25	0	0	3	3	1	1	3	1	1.833

8.1 Database of eco-morphological traits for tree-related microhabitats (TreMs) and CWM-FDis calculations

	Bark pocket	1	1	2	1	3	1	2	2	2	2	0	3	0	2	1	3	2	2.167	2	3	0	0	2.7	
	Bark shelter	0	3	0	1	3	1	2	1	3	2	2.167	2	0	0	1	1	3	2	2.167	2	3	0	0	2.7
Fresh exudates	Heavy resinosis	3	0	1	3	0	0	3	1	3	1	2	0	3	0	2	0	0	3	3	1	2	3	1	1.813
	Sap run	2	0	1	3	0	0	3	1	3	1	2	0	3	0	2	1	1	3	2.4	2	3	1	1	2.286
Ground pit from windfall	Rooplate	3	0	0	0	0	3	1	3	0	0	1	1	3	0	1.75	0	0	3	3	1	3	1	1	2.167
Insect galleries and bore holes	Insect gallerie and bore holes	3	0	1	1	3	3	1.714	1	3	2	2.167	3	0	0	1	0	0	3	3	2	2	3	1	2.063
Microsoils	Crown microsoil	0	3	0	3	1	0	2.75	1	2	3	2.333	0	3	0	2	0	0	3	3	3	0	0	0	3
Nests	Invertebrate nest	2	3	1	3	2	1	2.333	2	3	2	2	3	1	0	1.25	0	3	2	2.4	2	3	1	0	2.5
	Vertebrate nest	0	3	0	3	1	1	2.4	1	1	3	2.4	1	3	0	1.75	2	3	1	1.833	1	1	2	3	1.643
Perennial fungal fruiting bodies (life span > 1 year)	Perennial polypore	3	0	0	2	3	3	1.875	2	3	1	1.833	3	1	0	1.25	0	0	3	3	3	1	0	0	2.875
Rot-holes	Chimney trunk base rot-hole	3	0	3	3	2	0	2.6	3	2	0	1.4	0	3	0	2	0	0	3	3	3	0	0	0	3
	Semi-open trunk rot hole	3	0	3	3	2	0	2.6	2	3	1	1.833	1	2	0	1.667	0	0	3	3	3	1	0	0	2.875
	Trunk base rot hole	3	0	3	3	2	0	2.6	3	0	0	1	2	1	0	1.333	0	0	3	3	3	1	0	0	2.875
	Trunk rot hole	3	0	3	3	2	0	2.6	0	3	0	2	2	1	0	1.333	0	0	3	3	3	1	0	0	2.875
Snag-base coarse woody debris	Snag-base coarse woody debris	3	0	3	0	3	0	2	3	0	0	1	0	3	0	2	0	0	3	3	3	0	0	0	3
Twig tangles	Epicormic shoots	0	3	0	3	0	0	3	0	3	0	2	0	3	0	2	0	0	3	3	1	3	2	1	2.071
	Witch broom	0	3	0	3	0	0	3	0	0	3	3	0	3	0	2	0	0	3	3	1	2	3	1	1.929
Woodpecker breeding cavities	Large woodpecker breeding cavity	3	0	1	3	2	0	2.6	0	3	2	2.4	3	1	0	1.25	0	0	3	3	0	1	3	1	1.6
	Medium-sized woodpecker breeding cavity	3	0	1	3	2	0	2.6	0	3	2	2.4	3	1	0	1.25	0	0	3	3	0	1	3	1	1.6
	Small woodpecker breeding cavity	3	0	1	3	2	0	2.6	0	3	2	2.4	3	1	0	1.25	0	0	3	3	0	1	3	1	1.6

Table S.2: Average values of stand features in each study region for healthy stands. In order to give a general idea of forest conditions in non-declining stands in each region, mean values of woody elements and TreMs variables were calculated only for plots in the lowest dieback class, i.e. [0; 15] in fir and spruce forests, and [0; 10] in oak forests. "vol." = "volume", "dec" = "decay", "dec12" = "fresh deadwood", "dec34" = "decayed deadwood", "Med" = "Mid-size deadwood", "LarVer" = "Large and Very large deadwood"; "Ab." = "Abundance". (\pm) gives standard error (SE) values.

Variable	Fir forests	Spruce forests	Oak forest
Woody elements			
vol. Living trees ($\text{m}^3 \cdot \text{ha}^{-1}$)	500 (± 37)	461 (± 55)	288 (± 19)
vol. Dead wood ($\text{m}^3 \cdot \text{ha}^{-1}$)	22 (± 7)	25 (± 7)	7.5 (± 2.4)
div. Dead wood ($\text{nb} \cdot \text{ha}^{-1}$)	3 (± 0.4)	4 (± 0.7)	0.5 (± 0.15)
vol. Dead wood dec12 ($\text{m}^3 \cdot \text{ha}^{-1}$)	5.5 (± 2)	13 (± 7)	6.5 (± 2)
vol. Dead wood dec34 ($\text{m}^3 \cdot \text{ha}^{-1}$)	17 (± 3)	12 (± 5)	1 (± 1)
vol. Dead wood Med ($\text{m}^3 \cdot \text{ha}^{-1}$)	12 (± 2)	19 (± 8)	3 (± 2)
vol. Dead wood LarVer ($\text{m}^3 \cdot \text{ha}^{-1}$)	10 (± 2)	6 (± 4)	4.5 (± 2)
vol. Dead wood Lying ($\text{m}^3 \cdot \text{ha}^{-1}$)	10 (± 2)	7 (± 4)	1 (± 1)
vol. Dead wood Standing ($\text{m}^3 \cdot \text{ha}^{-1}$)	12 (± 3)	18 (± 8)	6.5 (± 2.5)
nb. Very Large Living ($\text{nb} \cdot \text{ha}^{-1}$)	16 (± 4)	7 (± 3)	6.5 (± 2)
nb. Very Large Dead ($\text{nb} \cdot \text{ha}^{-1}$)	1 (± 0.3)	0.5 (± 0.3)	0 (± 0)
Tree-related microhabitats			
Abundance ($\text{nb} \cdot \text{ha}^{-1}$)	359 (± 30)	437 (± 94)	112 (± 8)
Diversity ($\text{nb} \cdot \text{ha}^{-1}$)	11 (± 0.6)	8.5 (± 1)	7 (± 1)
Ab. Concavities ($\text{nb} \cdot \text{ha}^{-1}$)	81 (± 9)	42 (± 14)	6.5 (± 2.5)
Ab. Rot-holes ($\text{nb} \cdot \text{ha}^{-1}$)	13 (± 5)	14 (± 8)	5 (± 1.4)
Ab. Woodpecker cavities ($\text{nb} \cdot \text{ha}^{-1}$)	0.4 (± 0.4)	0 (± 0)	3 (± 1.5)
Ab. Exposed sap- and heartwood ($\text{nb} \cdot \text{ha}^{-1}$)	1.7 (± 1)	1.8 (± 1)	0.5 (± 0.5)
Ab. Exposed sapwood ($\text{nb} \cdot \text{ha}^{-1}$)	84 (± 13)	39 (± 16)	8 (± 3.5)
Ab. Crown deadwood ($\text{nb} \cdot \text{ha}^{-1}$)	16.5 (± 5)	16 (± 7.5)	56 (± 7.7)
Ab. Burrs and cankers ($\text{nb} \cdot \text{ha}^{-1}$)	10 (± 3)	2 (± 1)	0.2 (± 0.2)
Ab. Twig tangles ($\text{nb} \cdot \text{ha}^{-1}$)	27 (± 9)	0.5 (± 0.5)	2 (± 1)
Ab. Ephemeral fungi ($\text{nb} \cdot \text{ha}^{-1}$)	5 (± 2)	2 (± 1.6)	0.2 (± 0.2)
Ab. Perennial fungi ($\text{nb} \cdot \text{ha}^{-1}$)	25 (± 10)	4 (± 3)	1 (± 1)
Ab. Epiphytic ($\text{nb} \cdot \text{ha}^{-1}$)	308 (± 57)	292 (± 63)	28 (± 7)
Ab. Exudates ($\text{nb} \cdot \text{ha}^{-1}$)	0.14 (± 0.14)	16 (± 10)	1.2 (± 1)

8.1 Database of eco-morphological traits for tree-related microhabitats (TreMs) and CWM-FDis calculations

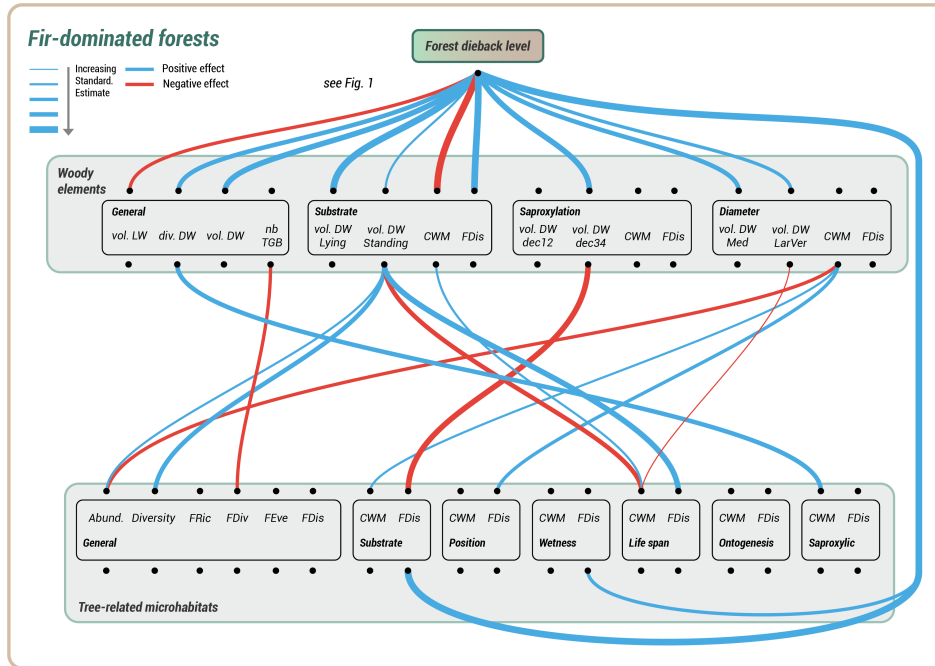


Figure S.1: Structural equation modelling (SEM) disentangling the effects of (i) forest stand decline on woody elements and (ii) forest stand decline and woody elements on tree-related microhabitats, in fir-dominated forests. Blue = positive effect, red = negative effect. Line thickness increases with standardized SEM estimates. As TreM variables were tested for 17 potential effects (of forest stand decline and woody elements), significant effects were adjusted at $p < 0.00294$. "subst." = "substrate"

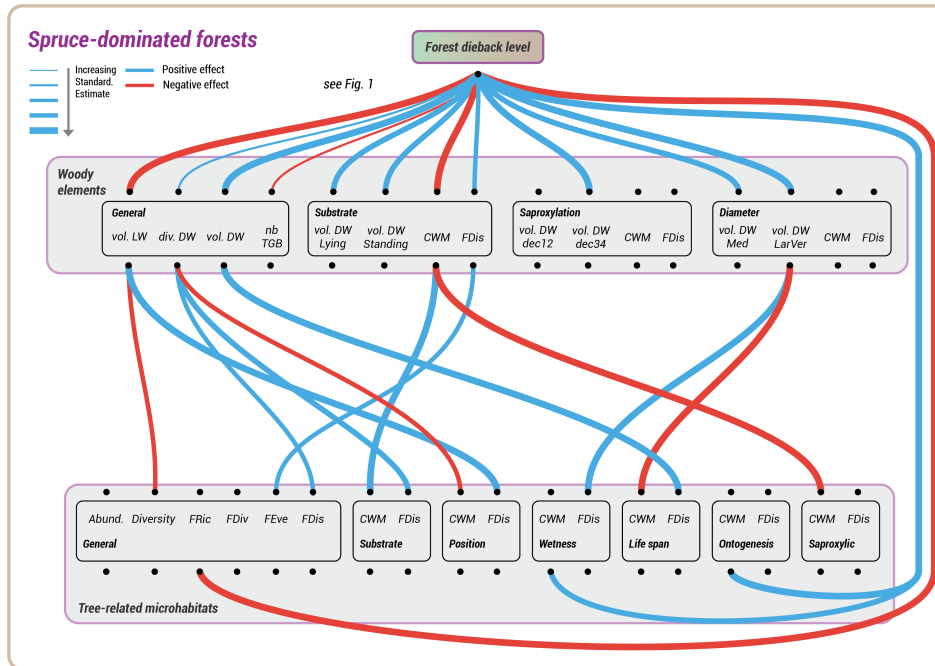


Figure S.2: Structural equation modelling (SEM) in spruce-dominated forests (see legend Figure S.1)

8.1 Database of eco-morphological traits for tree-related microhabitats (TreMs) and CWM-FDis calculations

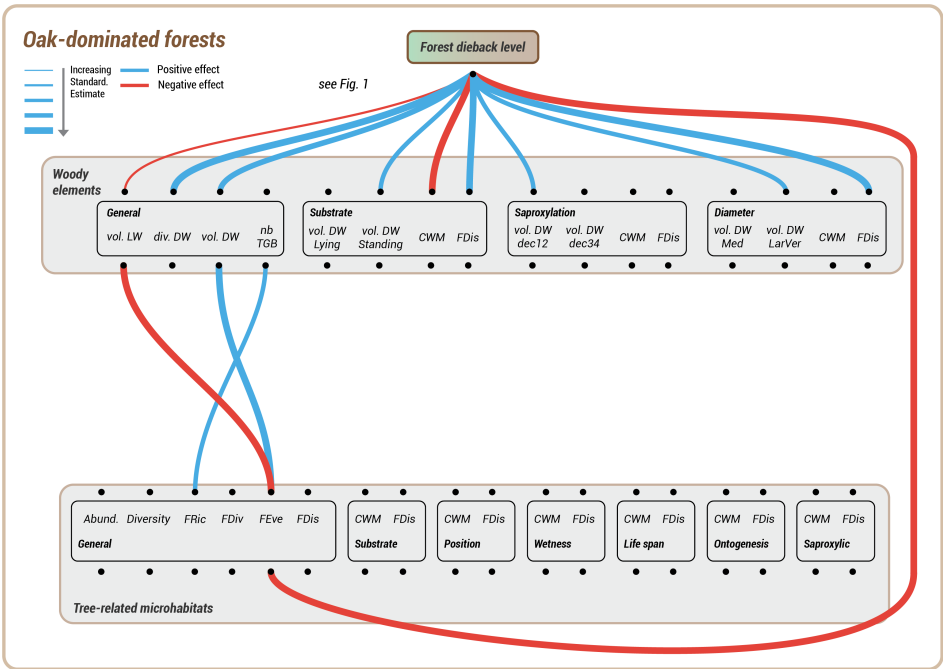


Figure S.3: Structural equation modelling (SEM) in oak-dominated forests (see legend Figure S.1)

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