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

Christophe Bouget, Jérémy Cours, Laurent Larrieu, Guillem Parmain, J. Müller, V. Speckens, A. Sallé

▶ **To cite this version:**

Christophe Bouget, Jérémy Cours, Laurent Larrieu, Guillem Parmain, J. Müller, et al.. Trait-Based Response of Deadwood and Tree-Related Microhabitats to Decline in Temperate Lowland and Montane Forests. Ecosystems, 2023, 10.1007/s10021-023-00875-9 . hal-04193240v1

HAL Id: hal-04193240

https://hal.inrae.fr/hal-04193240v1

Submitted on 1 Sep 2023 (v1), last revised 12 Jan 2024 (v2)

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Trait-based response of deadwood and tree-related microhabitats to decline in temperate lowland and montane forests

Short title: *Forest decline changes habitat conditions*

Bouget, C.[1*#], **Cours, J.** [1,2,3*], **Larrieu, L.**[4,5], **Parmain, G.**[1], **Müller, J.**[6,7], **Speckens, V.** [1], **Sallé, A.**[8]

1 INRAE, UR EFNO, Domaine des Barres, Nogent-sur-Vernisson, France christophe.bouget@inrae.fr; guilhem.parmain@inrae.fr

2 Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland jeremy.cours@outlook.com

3 School of Resource Wisdom, University of Jyväskylä, Jyväskylä, Finland

4 University of Toulouse, INRAE, UMR DYNAFOR, Castanet-Tolosan, France laurent.larrieu@inrae.fr

5 CNPF-CRPF Occitanie, Tarbes, France

6 Department of Nature Conservation and Research, Bavarian Forest National Park, Grafenau, Germany Joerg.Mueller@npv-bw.bayern.de

7 Ecological Field Station, University of Würzburg, Germany

8 Laboratoire de Biologie des Ligneux et des Grandes Cultures, INRAE, Université d'Orléans, F-45067 Orléans, France aurelien.salle@univ-orleans.fr

* These authors contributed equally

corresponding author: christophe.bouget@inrae.fr

Author contributions

CB, LL, JM and AS conceived the ideas and designed methodology; LL, JM, GP and JC collected the data; VS and JC analysed the data; CB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Keywords

Dieback; drought; windstorm; pest outbreak; disturbance legacies; saproxylic

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 analyzed 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.

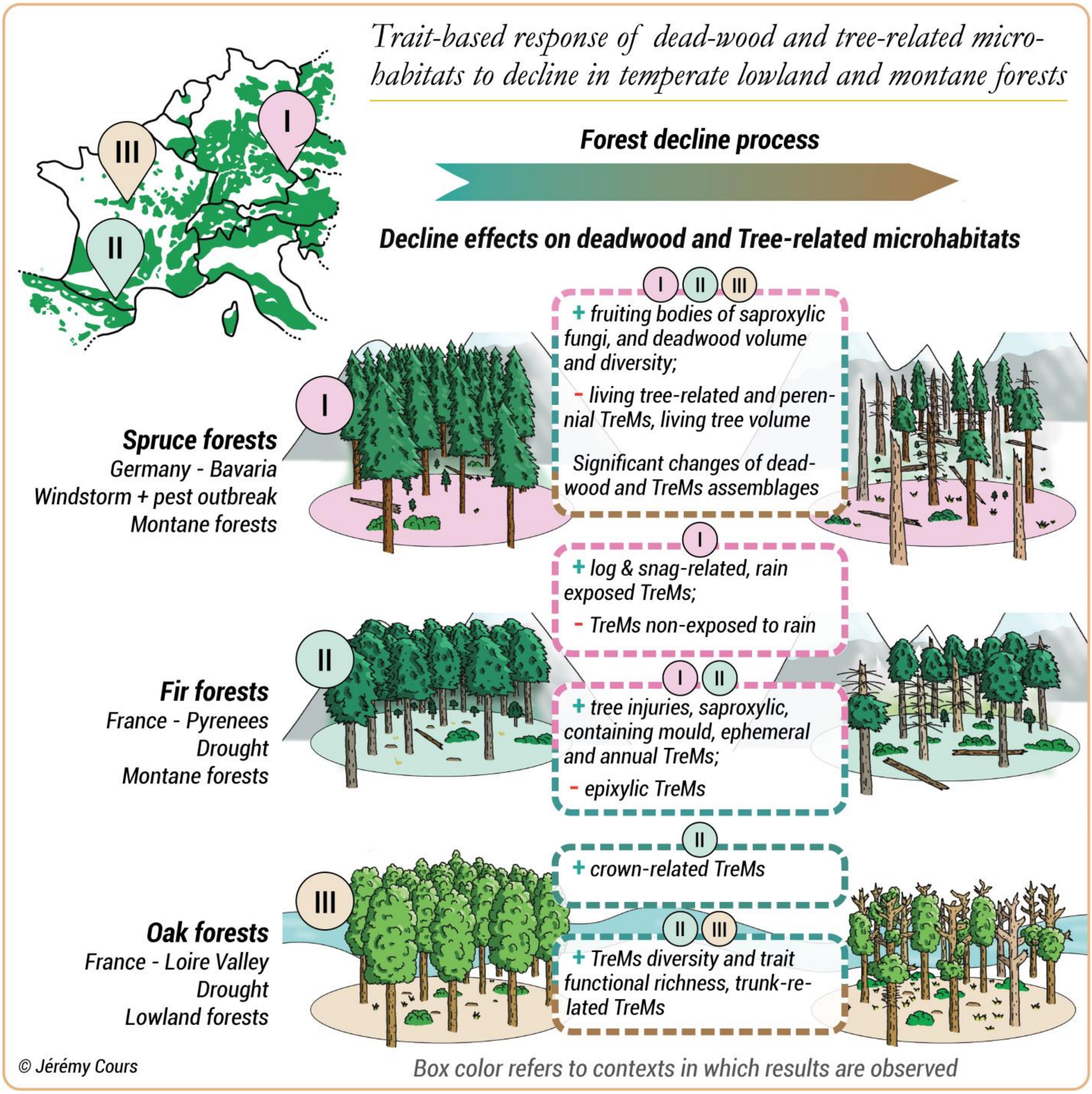
Decline caused significant changes in deadwood and TreM characteristics and composition in three forest contexts. However, tree density with cavities, exudates, or crown deadwood was not linked to decline intensity. Declining conifer forests had more large deadwood and downed woody debris, and their 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.

Highlights

- Forest decline increased and diversified deadwood substrates in every context.
- Decline-induced changes in tree-related microhabitats were context-dependant.
- Eco-morphological traits drive the accumulation patterns for disturbance legacies

Graphical abstract



Introduction

Forest decline and dieback have increased in frequency and severity across Europe in recent decades (Seidl and others, 2011; Seidl and others, 2014b). Forest decline could lead to tree crown dieback and, ultimately, to tree mortality (Senf and others, 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 & Donaubauer, 1994).

Decline and dieback are mainly perceived as a threat to forest continuity and, although they pose a considerable challenge to foresters (Jandl and others, 2019), they may also be considered key processes that enhance structural heterogeneity and the supply of habitat for biodiversity (e.g. Ojeda and others, 2007). Along a wide scale gradient, from large-scale stand replacing disturbances to small-scale gap dynamics (Franklin and others, 2002), natural disturbances and their cascading effects on forest stand decline create specific microhabitats, called "disturbance legacies", over multiple time scales (Swanson and others, 2011; Cours and others, 2023). They allow transient accumulations of deadwood to occur and result in a diversification of deadwood and microhabitat types (Kulakowski and others, 2017; Sallé and others, 2021), and may induce potential changes in resource dynamics in line with the pulse dynamics theory (Jentsch & 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 (Swanson and others, 2011; Cours and others, 2021; Zemlerová and others, 2023). Loss of tree vigour, associated to increased canopy openness, favours the formation of certain TreMs (Larrieu and others, 2022) while disrupting canopy buffer. Tree mortality also lead 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 and others, 2019). Concurrently, deadwood and most TreMs are less abundant and less diverse in managed forests (Bouget and others, 2014; Asbeck and others, 2022).

Deadwood and TreMs are key habitats and trophic resources for a large proportion of forest biodiversity (e.g. 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 (Cours and others, 2023, Kozák and others, 2021; Basile and others, 2020).

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 (Stokland 2001; Halme and others, 2019). Furthermore, variations in deadwood composition and TreM assemblages in response to disturbance could be analysed with a trait-based approach, i.e, thanks to a database of eco-morphological traits describing deadwood pieces (Parisi and others, 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 and others, 2023), i.e. dead wood 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 dead wood and TreMs. Our study aimed to examine if dead wood 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 and others, 2016), from "almost healthy" stands, where dynamics is dominated by small-scale gap dynamics associated to 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 vs 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 (i.e. dependent on the case study or group of case studies) effects of the intensity of decline and mortality on the local quantity of dead wood substrates and TreMs, (ii) on the local diversity of substrates and (iii) on the composition of local assemblages of dead wood 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 dead wood, saproxylic nature of TreMs, etc.).

Material and methods

Sampling design and case studies

The study was conducted in three regions, i.e. 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, Fig. 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 and others, 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.

In the Pyrenees, we studied two sites in montane forests dominated by silver fir (*Abides alba* Mill.), whose decline is mainly due to successive droughts occurring since the 1980’s, recently accentuated by the severe drought of 2003 (Cours and others, 2022), and resulting in patch dynamics (Andrew and others, 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.

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 and others, 2009). The dieback was due to several cycles of windstorms followed by bark beetle (*Ips typographus* (L.)) outbreaks (Müller and others, 2010), the dominant drivers of forest dynamics in Norway spruce forests in temperate Europe (Zemlerová and others, 2023). This dieback phenomenon resulted in stand-replacing dynamics with greater tree mortality (Thorn and others, 2017), in a more severe way than either of the aforementioned drought-induced declines (Cours and others, 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 (Müller and others, 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%].

Field measurements

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° 1 (ratio 1/50), and mean plot area was about 0.3 ha. For each tree within the plot, we recorded its status (i.e. 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 (i.e. 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 S1).

For each deadwood item (length > 1 m) in the plot, we measured its decay stage (from 1 = hard dead wood 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) vs standing (snags and standing dead trees); small and mid-size (less than 40 cm in diameter) vs large and very large (more than 40 cm in diameter); and fresh (decay class 1 and 2) vs 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: ($N_d = \pi\ 10^8\ [\mathrm{ArcTan}(1/50)/(\pi\ d)]^2$). We estimated TreM diversity and the number of deadwood types per plot.

We compiled a list of eco-morphological traits for woody elements (i.e, 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 (i.e, living tree, dead tree or snag, and log), position in the tree (i.e. base, trunk, crown), degree of wetness, life span or ontogenesis; Table 2 and Supplementary Material Table S1).

Data analysis

Univariate analysis

Analyses were conducted using the R software 4.1.2. (R Core Team, 2022). First, in order to obtain a general idea of forest conditions in non-declining 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 (i.e, 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 (i.e, 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, i.e. 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 to 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 and others, 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 (i.e. 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%-pvalue 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.

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 (i.e, by combining tree species, substrate, decay stage and diameter class, and (ii), TreM types (Larrieu and others, 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 (i.e. in a fir context: Aure and Sault; in an oak context: Orleans and Vierzon).

In parallel, we distributed our plots equally among decline classes, i.e. [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, indicspecies 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 & Jackson, 2001; protest function, vegan R-package).

Results

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 S2). 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 S2). 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.

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 (Fig. 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; Fig. 2a). However, the density of TreMs associated with bark injuries (i.e, exposed sapwood and heartwood) increased significantly with decline level in both the fir and spruce plots (Fig. 3). We also measured a significant increase in the density of trees bearing the fruiting bodies of lignicolous fungi (Fig. 3), i.e. 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 (Fig. 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 (Fig. 3). Furthermore, the TreM multi-trait functional richness increased with decline level in the fir and oak stands (respectively by +47% and +79%; Fig. 4), but significantly decreased in the spruce forests (-16%; Fig. 4).

Effect of decline level on assemblage composition of substrate types

The decline severity had a significant effect on dead wood and TreM assemblage composition in all three forests (Table 3). In the fir forests, medium and large decayed lying deadwood and large decayed standing dead wood 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 to 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).

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 (Fig. 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; Fig. 2b) while dispersion increased significantly with decline (Fig. 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 (Fig. 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 to live trees, and were less perennial and more associated with the trunk (Fig. 4). In contrast, many eco-morphological traits influenced TreM responses to increasing decline levels in both the fir and spruce forests (Fig. 4). TreM assemblages were more ephemeral and less perennial in declining plots compared to healthy ones (Fig. 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 (Fig. 4). Likewise, declining plots provide more TreMs containing mould (respectively +70% and +105%; Fig. 4). In all three forest types, TreMs were less associated to living trees (ca -10%; Fig. 4), and in spruce, they were significantly more associated to snags and logs (+24% and +14%; Fig. 4). In the fir forests, TreMs were less associated to the base of the tree (Fig. 4); they were slightly, but significantly, more related to the crown and trunk- (ca +10%; Fig. 4). In contrast, in the spruce forests, they were more associated to the tree base (+6%; Fig. 4). Finally, in the spruce forests, TreMs were significantly less protected from humidity (more exposed to weather or intrinsically wetter; Fig. 4) and their ontogenesis was somewhat slower in the declining plots than in the healthy ones (Fig. 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 Fig. S1, S2, S3). Some TreMs were significantly associated to 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.

Discussion

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 (Kulakowski and others, 2017; Thom and others, 2017; Cours and others, 2021). 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 dead wood 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 (Paillet and others, 2019; Ojeda and others, 2007; Kozák and others, 2018). In spruce forests, Zemlerová and others (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 and others, 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 & 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, Zemlerova 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 and others, 2018), especially in the upper part of tree crown, more vulnerable to soil drought (Chakraborty and others, 2017); and crown dieback can be further amplified during the subsequent loss of tree vigour (Sallé and others, 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 and others, 2022) and trunk cavities (Ojeda and others, 2007; Larrieu and others, 2022). Degree of crown dieback is a primary factor explaining woodpecker tree selection for cavity excavation (Ojeda and others, 2007; Dudinszky and others, 2021) 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 and others, 2023). Woodpecker-breeding-holes and rot-holes are related to slowly active biological processes on large trees, especially in oaks (Courbaud and others, 2022). For such TreMs, the time elapsed since the last major disturbance may be crucial (Cours and others, 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 and others, 2023). In our case, this may be because a certain combination of necessary processes did not occur (e.g, bark injuries, pest attacks, bacterial activity, root pressure; Weber 2006).

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 to living trees, in line with the increasing proportion of dead trees and subsequent reduction in living trees number (Zemlerová and others, 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 to 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 to the base of the tree and more associated to 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 to the base of tree and to snags and logs, and to 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.

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 (Viljur and others, 2022; Cours and others, 2023). Natural disturbances generate structural complexity (Kulakowski and others, 2017; Gough and others, 2022; Turner, 2010) and spatial heterogeneity from the individual tree to whole landscapes (Seidl and others, 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 and others, 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 (Larrieu & Cabanettes, 2012; Paillet and others, 2019; Asbeck and others, 2022). 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.

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 and others, 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.

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 to decline-generated substrates (Bouget & Duelli, 2004; Thom & Seidl, 2016; Cours and others, 2021; 2022, 2023; Basile and others, 2020). 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 and others, 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 and others, 2021). Selective post-disturbance logging (Priewasser and others, 2013) and retaining patches of declining or dead trees (Angelstam, 1998), based on benchmark retention targets (Thorn and others, 2020), could take advantage of disturbance and decline to maintain ecologically important structural characteristics, or even to restore old-growth conditions, within managed landscapes.

Acknowledgements and funding information

The authors would like to thank C. Moliard and B. Nusillard for their help in data collection, S. Ladet for managing the GIS data, W. Heintz, L. Burnel, J. Molina, J. Willm, G. Sajdak for field work, C. Lopez-Vaamonde, L. Sire and S. Thorn for fruitful interactions within the CLIMTREE project. This research is part of i) the CLIMTREE project, “Ecological and Socioeconomic Impacts of Climate-Induced Tree Dieback in Highland Forests”, included in the Belmont Forum call for collaborative research action: “Mountains as Sentinels of Change”, funded by the French National Research Agency

(ANR) (ANR-15-MASC-002-01); and (ii) the CANOPEE project, supported by the Région Centre-Val de Loire (Project no. 2018-00124136).

Compliance with Ethical Standards

The authors declare that they have no financial conflicts of interest in relation to the content of the article.

Data availability

Data have been posted on the Zenodo repository (https://doi.org/10.5281/zenodo.7816953). R code for statistical analyses is available on https://github.com/J-Cours/Forest_decline_deadwood_TreMs.git.

References

Aakala T. 2010. Coarse woody debris in late-successional *Picea abies* forests in northern Europe: variability in quantities and models of decay class dynamics. Forest Ecology and Management 260(5): 770-779

Andrew ME, Ruthrof KX, Matusick G, Hardy GESJ. 2016. Spatial configuration of drought disturbance and forest gap creation across environmental gradients. PLoS One, 11(6), e0157154.

Angelstam PK. 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. Journal of Vegetation Science, 9(4): 593-602

Asbeck T, Kozak D, Spinu AP, Mikoláš M, Zemlerova V, Svoboda M. 2022. Tree-Related Microhabitats Follow Similar Patterns but are More Diverse in Primary Compared to Managed Temperate Mountain Forests. Ecosystems, 25(3): 712-726

Barbier S, Chevalier R, Loussot P, Bergès L, Gosselin F. 2009. Improving biodiversity indicators of sustainable forest management: tree genus abundance rather than tree genus richness and dominance for understory vegetation in French lowland oak hornbeam forests. Forest Ecology and Management, 258 (Supplement): S176-S186

Basile M, Asbeck T, Jonker M, Knuff AK, Bauhus J, Braunisch V, Mikusinski G, Storch I. 2020. What Do Tree-Related Microhabitats Tell Us about the Abundance of Forest-Dwelling Bats, Birds, and Insects? Journal of Environmental Management, 264: 110401

Bässler C, Förster B, Moning C, Müller J. 2008. The BIOKLIM Project: Biodiversity Research between Climate Change and Wilding in a temperate montane forest–The conceptual framework. Waldökologie, Landschaftsforschung und Naturschutz, 7: 21-33.

Bouget C, Duelli P. 2004. The effects of windthrow on forest insect communities: a literature review. Biological conservation, 118(3): 281-299

Bouget C, Parmain G, Gilg O, Noblecourt T, Nusillard B, Paillet Y, Pernot C, Larrieu L, Gosselin F. 2014. Does a set-aside conservation strategy help the restoration of old-growth forest attributes and recolonization by saproxylic beetles? Animal Conservation, 17(4): 342-353.

Chakraborty T, Saha S, Matzarakis A, Reif A. 2017. Influence of multiple biotic and abiotic factors on the crown die-back of European beech trees at their drought limit. Flora, 229: 58-70.

Choat B, Brodribb TJ, Brodersen CR, Duursma RA, López R, Medlyn BE. 2018. Triggers of tree mortality under drought. Nature, 558(7711): 531-539

Ciesla WM, Donaubauer E. 1994. Decline and dieback of trees and forests: a global overview, FAO Forestry Paper 120

Courbaud B, Larrieu L, Kozak D, Kraus D, Lachat T, Ladet S, Müller J, Paillet Y, Sagheb-Talebi K, Schuck A, Stillhard J, Svoboda M, Zudin S. 2022. Factors influencing the rate of formation of tree-related microhabitats and implications for biodiversity conservation and forest management. Journal of Applied Ecology, 59(2): 492-503

Cours J, Larrieu L, Lopez-Vaamonde C, Müller J, Parmain G, Thorn S, Bouget C. 2021. Contrasting responses of habitat conditions and insect biodiversity to pest- or climate-induced dieback in coniferous mountain forests. Forest Ecology and Management, 482: art. 118811.

Cours J, Sire L, Ladet S, Martin H, Parmain G, Larrieu L, Moliard C, Lopez-Vaamonde C, Bouget, C. 2022. Drought-induced forest dieback increases taxonomic, functional, and phylogenetic diversity of saproxylic beetles at both local and landscape scales. Landscape Ecology, 37(8): 2025-2043

Cours J, Bouget C, Barsoum N, Horak J, Le Souchu E, Leverkus AB, Pincebourde S, Thorn S, Sallé A. 2023. Surviving in changing forests: key contributions of legacies from abiotic disturbances to the resilience of arthropod communities, Current Forestry Reports

Dudinszky N, Ippi S, Kitzberger T, Cerón G, Ojeda V. 2021. Tree size and crown structure explain the presence of cavities required by wildlife in cool-temperate forests of South America. Forest Ecology and Management, 494: 119295

Franklin JF, Spies TA, Pelt RV, Carey AB, Thornburgh DA, Berg DR, Lindenmayer DB, Harmon ME, Keeton WS, Shaw DC, Bible K, Chen J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management, 155:399-423

Gough C. M, Atkins JW, Fahey RT, Curtis PS, Bohrer G, Hardiman BS, Hickey LJ, Nave LE, Niedermaier KM, Clay C, Tallant JM, Bond-Lamberty B. 2022. Disturbance has variable effects on the structural complexity of a temperate forest landscape. Ecological Indicators, 140: 109004

Halme P, Purhonen J, Marjakangas E.-L, Komonen A, Juutilainen K, Abrego N. 2019. Dead wood profile of a semi-natural boreal forest – implications for sampling. Silva Fennica, 53, 4: 10010.

Holec J, Kučera T, Běťák J, Hort L. 2020. Macrofungi on large decaying spruce trunks in a Central European old-growth forest: what factors affect their species richness and composition? Mycological Progress, 19: 53-66

Jandl R, Spathelf P, Bolte A, Prescott CE. 2019. Forest adaptation to climate change—is non-management an option? Annals of forest science, 76(2): 1-13

Jentsch A, White P. 2019. A theory of pulse dynamics and disturbance in ecology. Ecology, 100(7): e02734

Johnstone JF, Allen CD, Franklin JF, Frelich LE, Harvey BJ, Higuera PE, Mack MC, Meentemeyer RK, Metz MR, Perry GL, Schoennagel T, Turner MG. 2016. Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment 14:369–378

Kneeshaw DD, Sturtevant BR, DeGrandpé L, Doblas-Miranda E, James PM, Tardif D, Burton PJ. 2021. The vision of managing for pest-resistant landscapes: Realistic or utopic? Current Forestry Reports, 7: 97-113

Kozák D, Mikoláš M, Svitok M, Bače R,…, Svoboda M. 2018. Profile of tree-related microhabitats in European primary beech-dominated forests. Forest Ecology and Management, 429: 363–374

Kozák D, Svitok M, Wiezik M, Mikoláš M, Thorn S, Buechling A,…, Svoboda M. 2021. Historical disturbances determine current taxonomic, functional and phylogenetic diversity of saproxylic beetle communities in temperate primary forests. Ecosystems, 24(1): 37-55.

Kulakowski D, Seidl R, Holeksa J, Kuuluvainen T, Nagel TA, Panayotov M, Svoboda M, Thorn S, Vacchiano G, Whitlock C, Wohlgemuth T, Bebi P. 2017. A walk on the wild side: Disturbance dynamics and the conservation and management of European mountain forest ecosystems. Forest Ecology and Management, Ecology of Mountain Forest Ecosystems in Europe, 388: 120–131

Larrieu L, Cabanettes A. 2012. Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech–fir forests. Canadian Journal of Forest Research, 42(8): 1433-1445

Larrieu L, Courbaud B, Drénou C, Goulard M, Bütler R, Kozák D, Kraus D, Krumm F, Lachat T, Müller J, Paillet Y, Schuck A, Stillhard J, Svoboda M, Vandekerkhove K. 2022. Key factors determining the presence of Tree-related Microhabitats: A synthesis of potential factors at site, stand and tree scales, with perspectives for further research. Forest Ecology and Management, 515: 120235

Larrieu L, Gosselin F, Archaux F, Chevalier R, Corriol G, Dauffy-Richard E, Deconchat M, Gosselin M, Ladet S, Savoie J.M, Tillon L, Bouget C. 2019. Assessing the potential of routine stand variables from multi-taxon data as habitat surrogates in European temperate forests. Ecological Indicators, 104: 116-126

Larrieu L, Paillet Y, Winter S, Bütler R, Kraus D, Krumm F, Lachat T, Michel A.K, Regnery B, Vandekerkhove K. 2018. Tree related microhabitats in temperate and Mediterranean European forests: A hierarchical typology for inventory standardization. Ecological Indicators, 84: 194-207

Lindenmayer DB, Franklin JF, Lõhmus A, Baker SC, Bauhus J, Beese W, Brodie A, Kiehl B, Kouki J, Martínez Pastur G, Messier C, Neyland M, Palik B, Sverdrup-Thygeson A, Volney J, Wayne A, Gustafsson L. 2012. A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. Conservation letters, 5(6): 421-431.

McCarthy J. 2001. Gap dynamics of forest trees: A review with particular attention to boreal forest. Environmental Reviews, 9, 1–59

Meigs GW, Morrissey RC, Bače R, Chaskovskyy O, Čada V, Després T, Donato D.C, Janda P, Lábusová J, Seedre M, Mikoláš M, Nagel TA, Schurman JS, Synek M, Teodosiu M, Trotsiuk V, Vítková L., Svoboda M. 2017. More ways than one: Mixed-severity disturbance regimes foster structural complexity via multiple developmental pathways. Forest Ecology and Management, 406: 410–426

Müller J, Noss RF, Bussler H, Brandl R. 2010. Learning from a “benign neglect strategy” in a national park: Response of saproxylic beetles to dead wood accumulation. Biological Conservation, 143: 2559–2569

Ojeda VS, Suarez ML, Kitzberger T. 2007. Crown dieback events as key processes creating cavity habitat for magellanic woodpeckers. Austral Ecology, 32: 436–445

Paillet Y, Debaive N, Archaux F, Cateau E, Gilg O., Guilbert E. 2019. Nothing else matters? Tree diameter and living status have more effects than biogeoclimatic context on microhabitat number and occurrence: An analysis in French forest reserves. PLoS One, 14(5): e0216500.

Parisi F, Pioli S, Lombardi F, Fravolini G, Marchetti M, Tognetti R. 2018. Linking deadwood traits with saproxylic invertebrates and fungi in European forests - a review. iForest 11: 423-436.

Peres-Neto PR, Jackson DA. 2001. How well do multivariate data sets match? The advantages of a Procrustean superimposition approach over the Mantel test. Oecologia 129: 169-178.

Priewasser K, Brang P, Bachofen H, Bugmann H, Wohlgemuth T. 2013. Impacts of salvage-logging on the status of deadwood after windthrow in Swiss forests. European Journal of Forest Research, 132: 231– 240

Qiu T, Bell AJ, Swenson JJ, Clark JS. 2023. Habitat–trait interactions that control response to climate change: North American ground beetles (Carabidae). Global Ecology and Biogeography, in press

Sallé A, Cours J, Le Souchu E, Lopez-Vaamonde C, Pincebourde S, Bouget C. 2021. How climate change-induced alterations of canopies reshape temperate forest arthropod communities? The need for integrative approaches. Frontiers in Forests and Global Change, 4: 710854.

Seidl R, Schelhaas MJ, Lexer MJ. 2011. Unraveling the drivers of intensifying forest disturbance regimes in Europe. Global Change Biology, 17(9): 2842-2852

Seidl R, Rammer W, Spies TA. 2014a. Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning. Ecological Applications, 24: 2063-2077.

Seidl R, Schelhaas MJ, Rammer W, Verkerk PJ. 2014b. Increasing forest disturbances in Europe and their impact on carbon storage. Nature climate change, 4(9): 806-810.

Senf C, Sebald J, Seidl R. 2021. Increasing canopy mortality affects the future demographic structure of Europe's forests. One Earth, 4(5): 749-755

Stokland JN. 2001. The coarse woody debris profile: an archive of recent forest history and an important biodiversity indicator. Ecological Bulletins 49: 57–70.

Swanson ME, Franklin JF, Beschta RL, Crisafulli CM, DellaSala DA, Hutto RL, Lindenmayer DB, Swanson FJ. 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment 9: 117–125.

Thom D, Rammer W, Dirnböck T, Müller J, Kobler J, Katzensteiner K, Helm N, Seidl R. 2017. The impacts of climate change and disturbance on spatio-temporal trajectories of biodiversity in a temperate forest landscape. Journal of Applied Ecology, 54(1): 28-38

Thom D, Seidl R. 2016. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. Biological Reviews, 91(3): 760-781

Thorn S, Bässler C, Svoboda M, Müller J. 2017. Effects of natural disturbances and salvage logging on biodiversity–Lessons from the Bohemian Forest. Forest Ecology and Management, 388, 113-119.

Thorn S, Chao A, Georgiev KB, Müller J, Bässler C, Campbell JL, Castro J, Chen YH, Choi CY, Cobb TP, Donato DC, Durska E, Macdonald E, Feldhaar H, Fontaine JB, Fornwalt PJ, Hernández RMH, Hutto RL, Koivula M, Lee EJ, Lindenmayer D, Mikusiński G, Obrist MK, Perlík M, Rost J, Waldron K, Wermelinger B, Weiß I, Żmihorski M, Leverkus AB. 2020. Estimating retention benchmarks for salvage logging to protect biodiversity, Nature Communications, 11, 1: 4762

Turner MG. 2010. Disturbance and landscape dynamics in a changing world. Ecology, 91: 2833-2849

Viljur ML, Abella SR, Adámek M, Alencar JBR, Barber NA, Beudert B, …, Thorn S. 2022. The effect of natural disturbances on forest biodiversity: an ecological synthesis. Biological Reviews, 97(5): 1930-1947

Weber RWS. 2006. On the ecology of fungal consortia of spring sap flows. Mycologist, 20: 140-143

Zemlerová V, Kozák D, Mikoláš M,…, Svoboda M. 2023. Natural Disturbances are Essential Determinants of Tree-Related Microhabitat Availability in Temperate Forests. Ecosystems, in press.

Table legends

Table 1 *Overview of the three case studies included in the sampling design*

Table 2 *Overview of the eco-morphological traits used to describe woody elements and tree-related microhabitats (TreMs).*

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

Tables

Table 1

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 (107-190 m 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 (107-190 m a.s.l.)
Bavarian Forest National Park	CLIMTREE project	Norway spruce	European beech and Silver fir	Several windstorms + successive pest outbreaks	Stand-replacing dynamics	2017	n=19	mainly unmanaged stands, no salvage logging	Highland (107-190 m a.s.l.)

Table 2

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 dead wood 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 4m tall; diameter at breast height otherwise
TreMs		
Association to deadwood	Saproxylic	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, byophytes, 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 (e.g. 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)

Table 3

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	**$p < 0.01$**

Table 4

Region	***Group***	***Indicator type***	***Stat***	***p.value***
Woody elements				
Fir-dominated forests	[0; 15]	*Living, Abies alba, large size*	0.7	**$p < 0.001$**
	]40; 70]	*Lying dead wood, Abies alba, mid-size, decay 3*	0.87	**$p < 0.001$**
		Standing dead wood Abies alba large size, decay 3	0.8	**$p < 0.01$**
		Lying dead wood Abies alba large size, decay 3	0.76	**$p < 0.01$**
Spruce-dominated forests	]70; 100]	*Standing dead wood, Picea abies, large size, decay 3*	0.9	**$p < 0.001$**
		Standing dead wood, Picea abies, mid-size, decay 3	0.87	**$p < 0.01$**
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	**$p < 0.001$**

Figure legends

Fig. 1 *Map of study plots in different forest contexts*

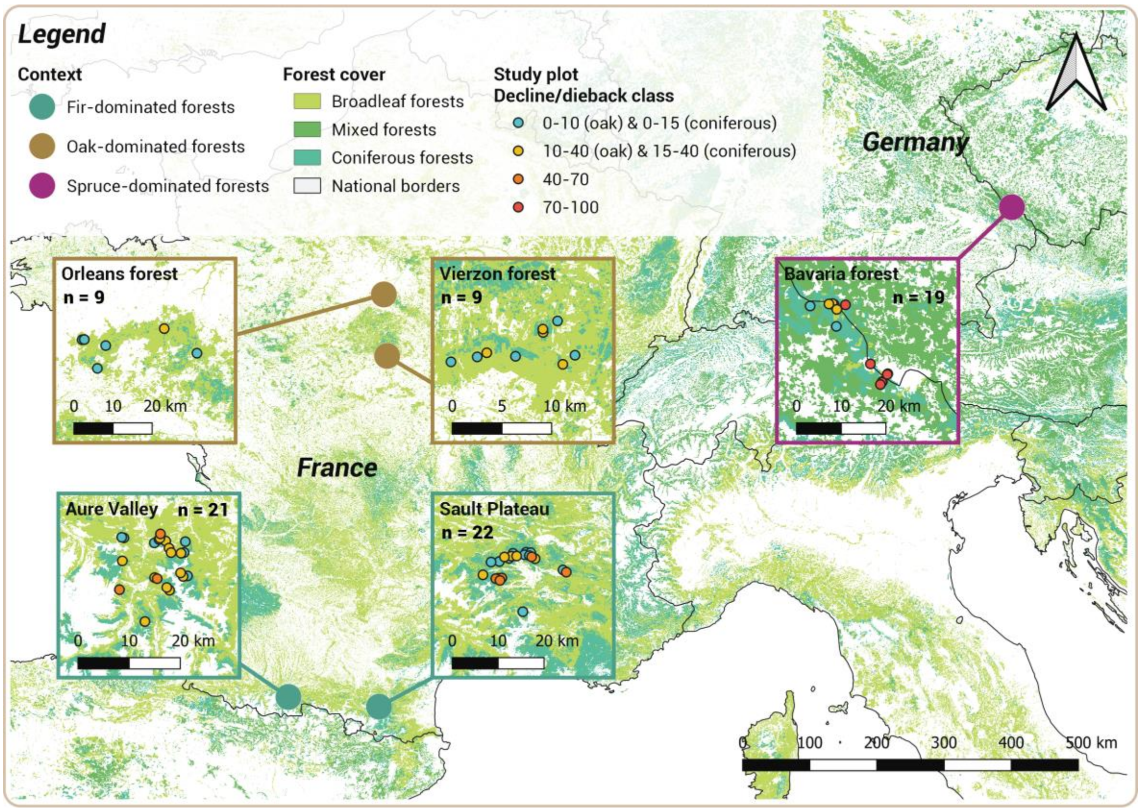
Fig. 2 *Magnitude of the effects of the level of forest stand decline on the ecological groups of woody elements (top), and mean (CWM) or variance (FDis) of the traits describing the woody elements (bottom). Magnitude was calculated as the subsequent relative increase or decrease in each woody ecological 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 dead wood while the CWM and FDis of the decay stage and diameter variables include only deadwood items.*

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

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

664 Figures

665



666

Fig. 1

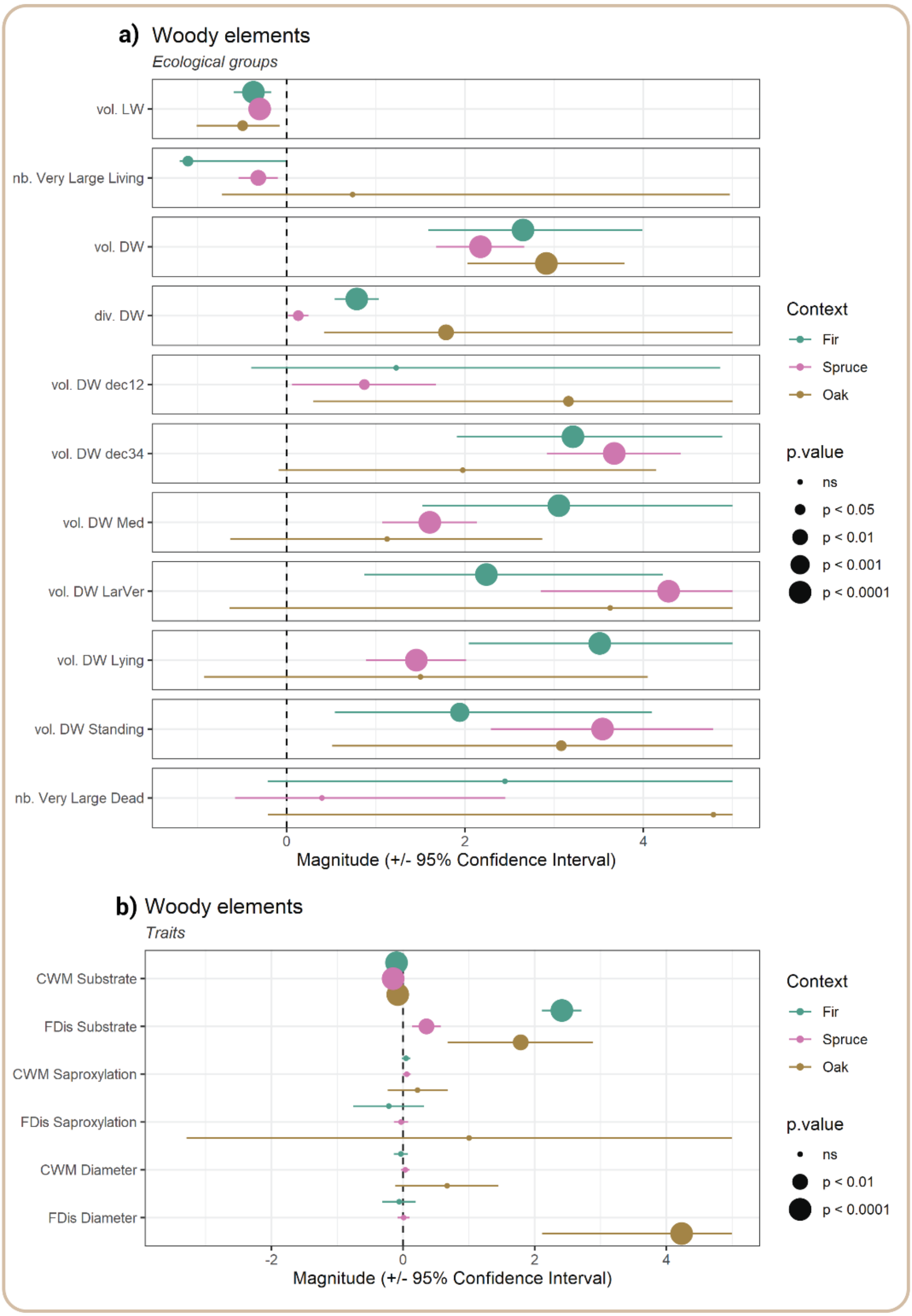

a) Woody elements
Ecological groups
vol. LW
nb. Very Large Living
vol. DW
div. DW
vol. DW dec12
vol. DW dec34
vol. DW Med
vol. DW LarVer
vol. DW Lying
vol. DW Standing
nb. Very Large Dead
0
2
4
Magnitude (+/- 95% Confidence Interval)
Context
Fir
Spruce
Oak
p.value
ns
p < 0.05
p < 0.01
p < 0.001
p < 0.0001
b) Woody elements
Traits
CWM Substrate
FDis Substrate
CWM Saproxylation
FDis Saproxylation
CWM Diameter
FDis Diameter
-2
0
2
4
Magnitude (+/- 95% Confidence Interval)
Context
Fir
Spruce
Oak
p.value
ns
p < 0.01
p < 0.0001

Fig. 2

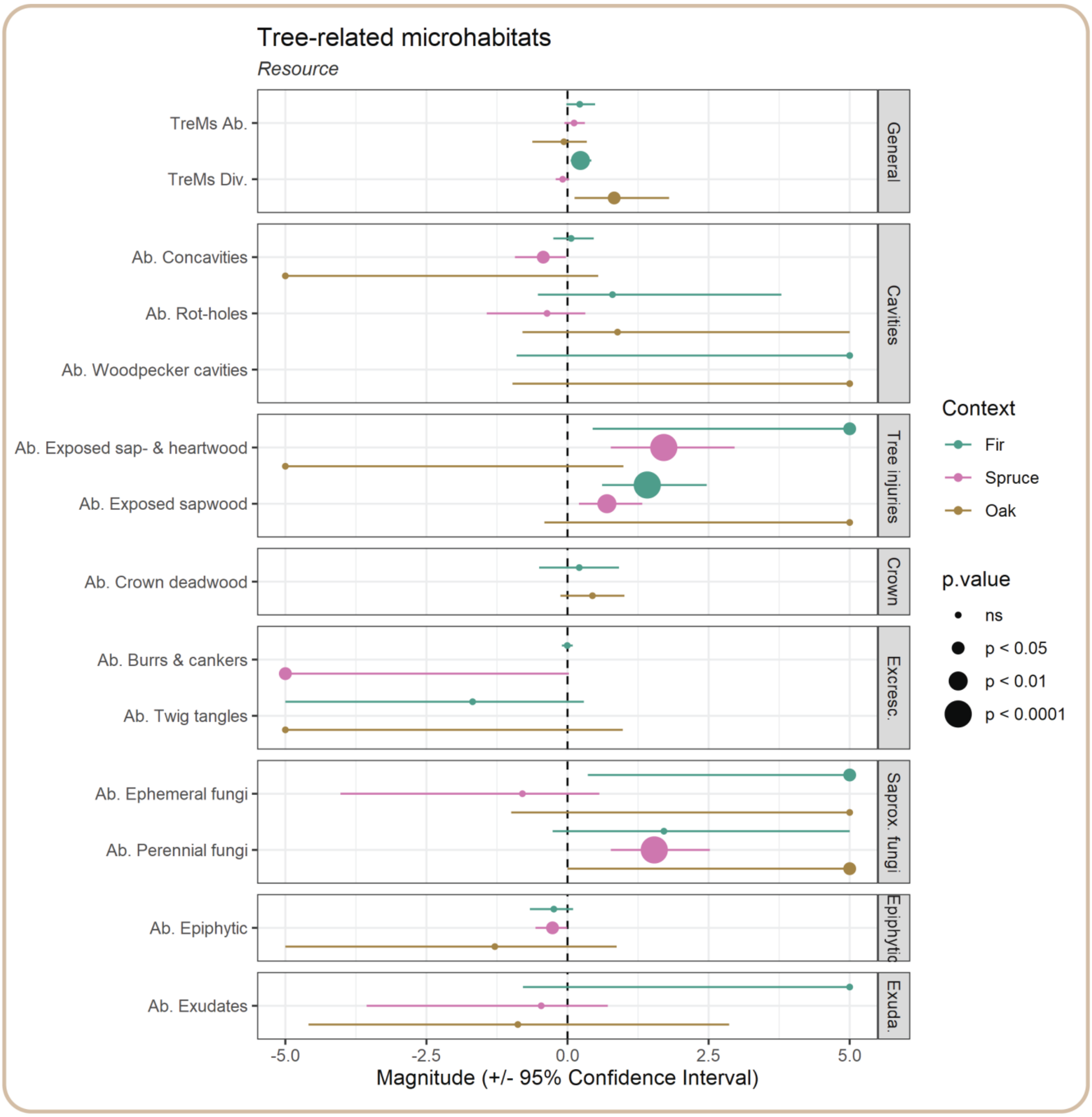
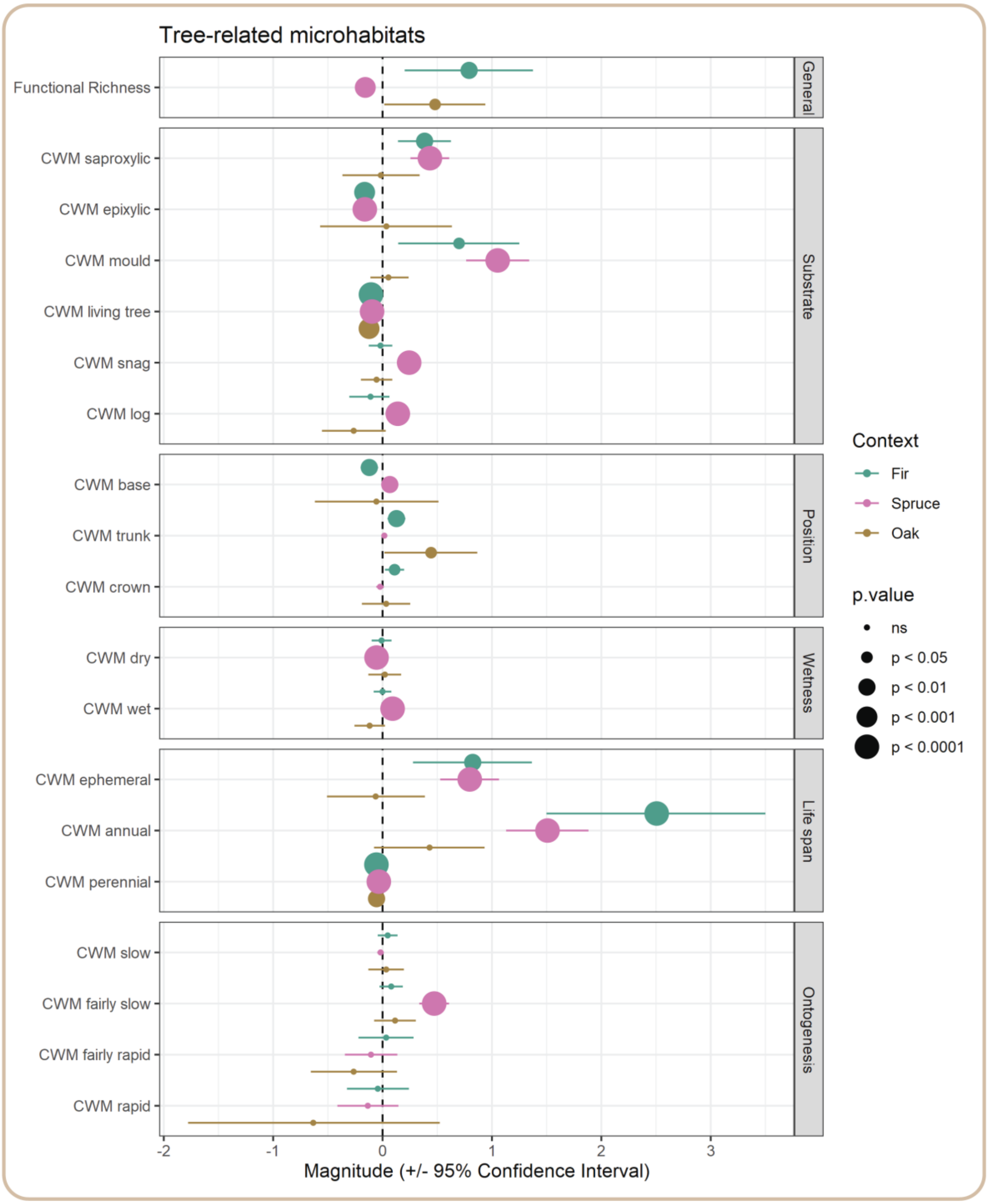

Tree-related microhabitats
Resource
TreMs Ab.
TreMs Div.
Ab. Concavities
Ab. Rot-holes
Ab. Woodpecker cavities
Ab. Exposed sap- & heartwood
Ab. Exposed sapwood
Ab. Crown deadwood
Ab. Burrs & cankers
Ab. Twig tangles
Ab. Ephemeral fungi
Ab. Perennial fungi
Ab. Epiphytic
Ab. Exudates
General
Cavities
Tree injuries
Crown
Excresc.
Saprox. fungi
Epiphytic
Exuda.
-5.0
-2.5
0.0
2.5
5.0
Magnitude (+/- 95% Confidence Interval)
Context
Fir
Spruce
Oak
p.value
ns
p < 0.05
p < 0.01
p < 0.0001

Fig. 3



Tree-related microhabitats
Functional Richness
CWM saproxylic
CWM epixylic
CWM mould
CWM living tree
CWM snag
CWM log
CWM base
CWM trunk
CWM crown
CWM dry
CWM wet
CWM ephemeral
CWM annual
CWM perennial
CWM slow
CWM fairly slow
CWM fairly rapid
CWM rapid
General
Substrate
Position
Wetness
Life span
Ontogenesis
-2
-1
0
1
2
3
Magnitude (+/- 95% Confidence Interval)
Context
Fir
Spruce
Oak
p.value
ns
p < 0.05
p < 0.01
p < 0.001
p < 0.0001

Fig. 4