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RESEARCH ARTICLE

From forest stand decline to salvage logging: Cascading impacts on saproxylic beetle diversity

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Abstract

1. Understanding the cascading effects of stand decline on saproxylic communities, via the induced changes in deadwood and tree-related microhabitats (TreMs), is fundamental for optimizing the management of disturbed forests. We postulated that these cascading effects would vary along decline gradients—from stand decline (proportion of declining trees) to mortality (proportion of dead trees) and subsequent salvage logging—mediated by the shifts in habitat conditions.
2. This study was conducted across three representative European forest contexts: fir forests in the Pyrenees and oak forests in the Loire Valley affected by drought disturbance, and Norway spruce forests in Bavaria affected by windstorm and bark beetle outbreak. We assessed how the taxonomic and functional α-diversity of saproxylic beetles responded to variations in the diversity and density of deadwood and TreMs, using structural equation modelling.
3. Our analysis confirmed an overall positive influence of decline processes on saproxylic beetles in conifer-dominated forests. TreM and deadwood diversity played a central role in structuring saproxylic beetle communities in stand decline contexts. The increase in TreM heterogeneity associated with stand decline or mortality enhanced saproxylic abundances, with exposed wood and trunk injuries, and deadwood-associated TreMs identified as particularly influential. Snags and large deadwood elements, especially in spruce forests, and deadwood diversity further contributed to sustaining high levels of beetle abundance.

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4. Conversely, salvage logging exerted detrimental effects, especially on the saproxylophagous guild, primarily through reductions in TreM heterogeneity, and the depletion of deadwood-associated and exposed wood and trunk injury types of TreMs.
5. Given the pronounced context dependency of the processes driving these cascading community dynamics, and considering the increasing frequency, severity and spatial extent of forest disturbances and global stand decline, it is imperative to integrate this complexity into management and conservation frameworks. Addressing these mechanisms with greater precision will be critical for maintaining biodiversity within rapidly changing forest ecosystems.

KEYWORDS
climate change, forest dieback, forest die-off, highland forest, lowland forest, montane forest, natural disturbances, temperate forest

1 | INTRODUCTION

Natural disturbances are major drivers of forest dynamics, shaping landscape heterogeneity, microclimates and biodiversity (Cours et al., 2022, 2023; Pickett & White, 1985; Viljur et al., 2022). Climate change is intensifying these events, with, for instance, increasingly severe and frequent drought in Europe (Samaniego et al., 2018; Seidl et al., 2017; Turner, 2010), exceeding many tree species physiological tolerance and triggering widespread mortality (Allen et al., 2015).

Severe disturbances affect tree condition (Senf et al., 2018, 2020), initiating progressive loss of vigour and eventually mortality—collectively described as stand decline or dieback. In cascade, these processes abruptly or gradually increase deadwood quantities and alter tree-related microhabitat (TreMs) profiles (Bouget et al., 2024; Bouget & Cours, 2025; Chowdhury et al., 2024; Zemlerová et al., 2023). Disturbance legacies—such as bark loss, fruiting bodies of saprophytic fungi or crown deadwood—modify microclimates and create distinct habitats that can positively affect certain functional guilds, for example, saproxylic beetles (Cours et al., 2023; Le Souchu, Cours, et al., 2024). Saproxylic beetles—that is, species dependent on dead or decaying wood and associated TreMs—are key contributors to nutrient cycling, forest trophic webs and pollination (Stokland et al., 2012), yet ongoing global declines highlight their sensitivity to environmental changes (Calix et al., 2018; Harvey et al., 2023; Seibold et al., 2019). Their taxonomic and functional diversity often benefit from stand decline (Beudert et al., 2015; Cours et al., 2021; Wermelinger et al., 2002), although their responses may be scale-dependent, non-linear and transient (Cours et al., 2022; Viljur et al., 2022; Wermelinger et al., 2025). Dying and dead trees can also support distinct guilds along the stand decline–mortality succession—that is, xylophagous species on dying trees and saproxylophagous species on dead trees (Le Souchu, Bouget, & Sallé, 2024).

Furthermore, forest context modulates biodiversity responses to stand decline: disturbance type, stand structure and dominant tree species shape the diversity and quantity of disturbance legacies leading to varied biodiversity outcomes (Cours et al., 2023; Turner & Seidl, 2023). For instance, windstorm and drought differently affect deadwood and TreM provision—for example, windstorm creating brief but large impulse of resources while droughts affect tree condition over longer period of time (Bouget et al., 2024). Such differences seem to differently affect biodiversity (Cours et al., 2023; Viljur et al., 2022)—for example, windstorm being more prone to benefits flower-visiting beetles than drought (Cours et al., 2021).

Salvage and sanitary logging, frequently implemented to recover timber value and mitigate pest risks (Lindenmayer et al., 2008), removes the disturbance legacies shortly after their formation. As a compounded disturbance (Bouget et al., 2024; Cours et al., 2023), it often reduces deadwood resources, negatively affecting deadwood-dependent taxa (Georgiev et al., 2022; Thorn et al., 2018), though it may benefit guilds benefiting from open habitats (Cours et al., 2021; Thorn et al., 2018; Wermelinger et al., 2025).

Although many studies have examined direct biodiversity responses to disturbance severity (see e.g. meta-analysis from Viljur et al. (2022)), the cascading pathways—define as the multiple, indirect ecological routes where stand decline alters structural legacies (e.g. deadwood and TreMs) which in turn reshape saproxylic beetle communities—connecting disturbance legacies to community responses remain poorly understood. Clarifying these pathways is essential for improving biodiversity predictions and guiding conservation-oriented forest management.

Here, we aimed to better understand the consequences of stand decline on saproxylic beetle communities via the cascading changes in deadwood and TreMs. To achieve that, we examined how saproxylic beetle α-diversity responds to stand decline across three European forest contexts: fir-dominated Pyrenean montane forests affected by drought disturbances, spruce-dominated Bavarian montane forests affected by windstorm and subsequent bark beetle outbreaks and oak-dominated lowland forests in the French Loire Valley affected by drought disturbances. We quantified stand decline and mortality, deadwood diversity and volumes and TreMs diversity and density, in order to test the following hypotheses:

(i) taxonomic and functional α-diversity, and abundance of total and guild-specific saproxylic beetles increase with the quantity (i.i) and diversity (i.ii) of deadwood and TreMs;
(ii) declining trees primarily promote xylophagous species, whereas dead trees promote saproxylophagous species;
(iii) cascading pathways differ among forest contexts due to variations in disturbance legacies—that is, drought versus bark beetle outbreak disturbance and fir versus spruce versus oak-dominated species—and timing among the study cases;
(iv) by depleting the disturbance legacy resources, salvage logging negatively affects the guilds promoted by stand decline.

2 | MATERIALS AND METHODS

2.1 | Sampling design

Our sampling design is the result of the opportunistic combination of three different forest contexts. Two were in France: the silver fir-dominated forests (*Abies alba* Mill.) in French Pyrenees, hereafter in text 'fir-dominated forests', and the oak-dominated forests (mix of *Quercus petraea* and *Quercus robur*) in Loire valley. In addition, one was set up in Germany: the Norway spruce-dominated forests (*Picea abies*) in Bavaria, hereafter in text 'spruce-dominated forests' (Figure 1, Table 1). They originated from three different projects: CLIMTREE for the two montane coniferous contexts (spruce context was also funded via BIOKLIM project; Bässler et al., 2009; Thorn et al., 2017), while the oak-dominated forest context was funded via CANOPEE project (Sallé et al., 2020). Although they all share the same methodology to describe the forest structure, that is, deadwood and TreMs, they show differences in sampling design and beetle trapping methods (see Table 1). The three projects shared the common objective of studying the consequences of forest decline on the biodiversity (with an important focus on saproxylic beetles). Along a gradient of stand decline, we selected 56 study plots in fir-dominated forests (28 in Aure valley (Central Pyrenees; 854–1570 m a.s.l.; 42°51′46.8″ N, 0°36′08.9″ E) and 28 on Sault plateau (Eastern Pyrenees; 705–1557.3 m a.s.l.; 42°50′58.7″ N, 2°00′41.3″ E)), 15 plots in oak-dominated forests (6 in Orleans forest (107–174 m a.s.l.; 48°00′28″ N, 2°09′39″ E) and 9 in Vierzon forest (120–190 m a.s.l.; 47°15′53.9″ N, 2°05′55.4″ E)) and 28 plots in spruce-dominated forests (660–1352 m a.s.l.; 49°1′24.96″ N

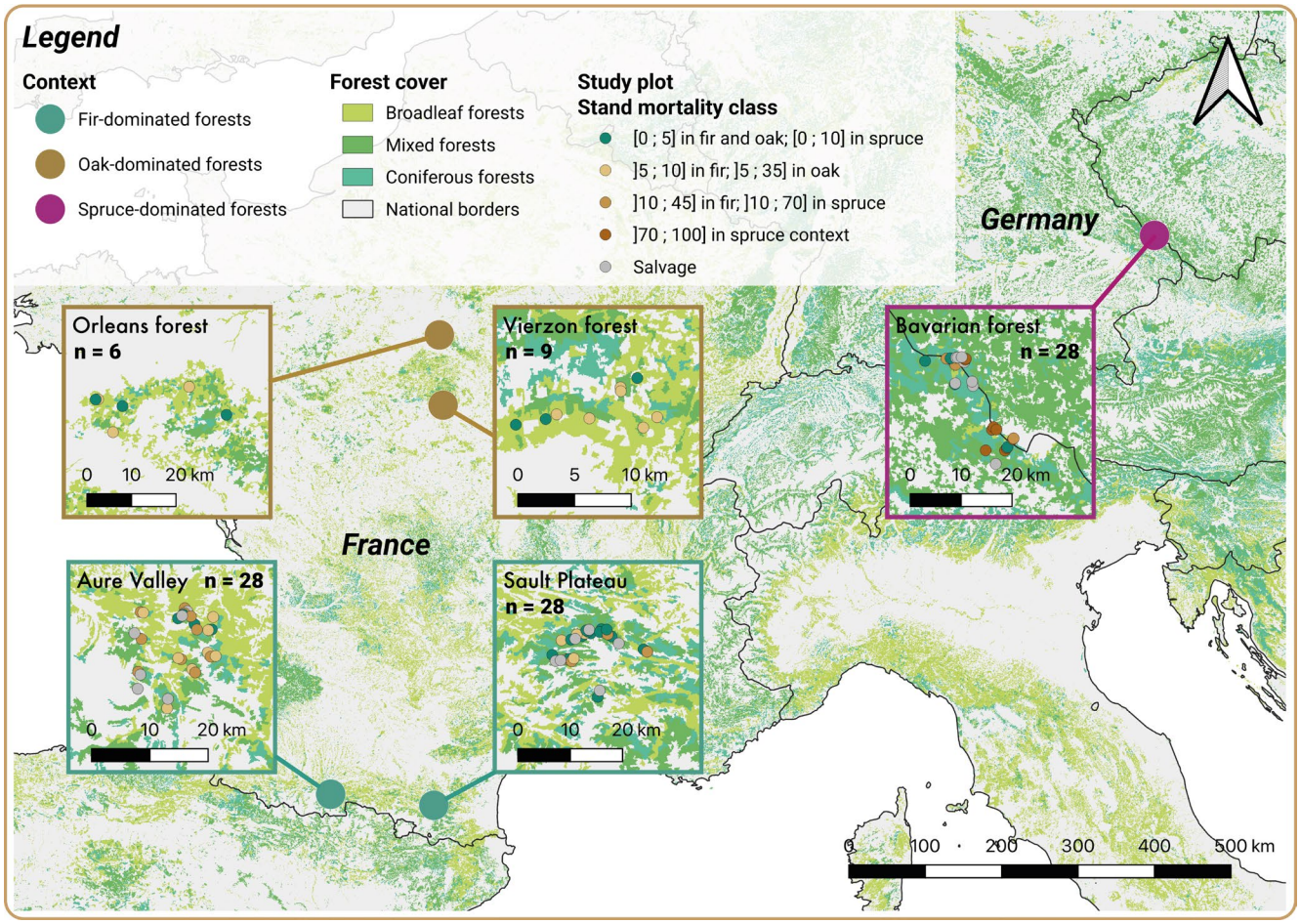

FIGURE 1 Map of the study plots and of the different study contexts. Numbers in brackets are showing mortality classes—for example, 70%–100% of mortality for the most severe class in spruce forests.

TABLE 1 Information about the different study cases.

	Context	Fir-dominated forests	Spruce-dominated forests	Oak-dominated forests
	Location	French Pyrenees	Bavaria (Germany)	Central France
	Mean altitude	1160 m a.s.l.	1077 m a.s.l.	150 m a.s.l.
	Plot number	56	28	15
Environmental gradients	Stand mortality (proportion)	0.1 (0–0.42)	0.55 (0–1)	0.07 (0–0.33)
	Stand decline (proportion)	0.68 (0.15–1)	NA	0.33 (0–0.9)
	Salvage logging	12 plots	9 plots	NA
Insect data set	Sampling method (traps/plot)	2 transparent flight-interception traps	1 transparent flight-interception traps	2 green Lindgren traps +1 black baited Lindgren
	Saproxylic beetles—abundance	487 (67–2699)	75 (7–260)	978 (208–1891)
	Saproxylic beetles—Species richness	47 (13–75)	25 (1–66)	53 (6–81)
Disturbance legacies	Deadwood volume ($m^3.ha^{-1}$)	50 (0–258)	136 (2–438)	21 (0–103)
	Deadwood diversity	4 (0–12)	5 (1–9)	1 (0–3)
	TreM diversity	12 (6–21)	7 (1–15)	8 (1–13)

Note: For continuous gradients, mean, minimum and maximum values are presented, while for salvage logging, the numbers of plots treated are presented. For more detailed information, see Figures S1 and S2.

13°38′5.222″ E; Figure 1). Fir and spruce forests included 12 and 9 plots, respectively, which have been salvage logged (Figure 1, Table 1), while the most valuable oak trees were regularly harvested during the decline process, which reduced the volume of deadwood in this context. In fir and oak forests, plots were set up in managed forests and the forests around were also predominantly managed. Plots in spruce forests were set up in the Bavarian Forest National Park, which is characterized by large areas of unmanaged disturbance areas but also by intervention sites with salvage logging in the buffer and former development zones of the National Park (see Müller et al., 2010; Thorn et al., 2016). Stand decline in fir and oak forests were mainly the result of drought events (the 2003 drought being a major event in the occurrence of these declines), which mainly resulted in patch dynamics (Sallé et al., 2020). In spruce forests, the decline studied was the result of windstorms and bark beetle outbreaks, which mainly resulted in stand-replacing dynamics (Thorn et al., 2017). The most recent impactful event for the spruce forests was the effect of the windstorm Kyrill in 2007, from which most of the decline in our studied plots was the results, compounded by the subsequent bark beetle outbreaks.

2.2 | Environmental conditions

To assess the dendrometric characteristic of each plot, we implemented a sampling protocol using relascope with 1/50 ratio (factor 1). For each tree sampled, we recorded the type (i.e. living tree, standing dead tree and lying deadwood), the tree species, the diameter, and the decay stage for deadwood (from 1 = fresh deadwood with full cover of bark, to 4 = soft wood with no more remaining barks). The diameter was recorded at breast height (dbh) on living trees and standing dead trees higher than 4 m, and at mid-height (or length) on standing trees lower than 4 m and on lying deadwood. In addition, for each recorded tree, we noted the tree-related microhabitats (TreMs) on living and standing dead trees, based on the 47 types described by Larrieu et al. (2018). Mean plot area was approximately of 0.3 ha and depended on the dbh of the largest trees and their location from the centre. Finally, we converted plot data into 1 ha densities by allocating the coefficient N_d to every measured tree and deadwood piece (Pardé & Bouchon, 1988) We calculated the coefficient N_d as $N_d = \pi \times 10^8 \times ((arctan(1/50))/(\pi \times dbh))^2$. Such allocation is important for the better representation of tree diameter classes (small trees being under evaluated with relascopic sampling protocol [and vice versa with larger trees]), and result comparability (standardization at the scale of 1 ha). Field data were collected in 2017 in the fir and spruce forests and in 2020 in oak forests.

In parallel, we used eco-morphological traits related to each ligneous substrates (i.e. living trees and deadwood) and TreM, to describe their changes. For ligneous substrates, we directly used field measurements, that is, type of substrate (as an ordinal scale: 1 = 'lying deadwood', 2 = 'standing deadwood', 3 = 'living trees'), decay stage (from 1 = 'hard deadwood fully covered by bark' to 4 = 'very soft wood out of bark') and diameter classes (see Bouget et al., 2024).

In addition, we used a list of two eco-morphological traits characterizing each TreM found in the field, that is, (i) type of substrate bearing the TreM (as an ordinal scale: 1 = 'lying deadwood', 2 = 'standing deadwood', 3 = 'living trees') and (ii) its association with deadwood (whether the TreM contains decaying deadwood, mould or neither, hereafter named 'saproxylic TreMs'; for additional information, see Bouget et al., 2024; data updated).

We used the quantitative eco-morphological traits from ligneous substrates and TreMs to compute community-weighted means (CWM), functional dispersion (FDis) for each of them and overall functional dispersion, using FD R-package (Laliberté et al., 2014; for more information, see Bouget et al., 2024). We used the sum of weight N_d as abundance measure. We also calculated the volume of the different types of deadwood, that is, standing and lying, low and high decay level (i.e. level ≥3 on a scale from 1 to 4), small and large (dbh ≥40 cm) and deadwood diversity combining all these features with tree species (Siitonen et al., 2000). Volumes were calculated using length and diameter for all logs and standing deadwood of less than 4 m tall, and we used Schaeffer's volume equations for living trees and standing deadwood of more than 4 m tall—using the equation $volume = 0.000138 \times (\pi \times dbh)^2 - 0.0066 \times \pi \times dbh + 0.0955$ for coniferous trees and $volume = 0.000203 \times (\pi \times dbh)^2 - 0.0097 \times \pi \times dbh + 0.1194$ for broadleaf trees. In addition, we calculated the total TreM diversity (based on the 47 types described by Larrieu et al., 2018) and the density per hectare of trees bearing fruiting bodies of saproxylic fungi, tree injuries and exposed sapwood, rot-holes and saproxylic TreMs known to be important for saproxylic beetles (Larrieu et al., 2018; Stokland et al., 2012).

To account for the two successive processes of tree decline and death, we measured two gradients, that is, stand decline and mortality. First, in all forest contexts, we quantified plot-level 'stand mortality' as the proportion of standing dead tree basal area relative to the total basal area of both standing dead and living trees. Second, we quantified the plot-level 'stand decline' using ARCHI protocol (Drénou, 2025). This method uses tree architecture to classify tree on a decline gradient, from healthy fully functioning tree to dead tree, including three decline stages in between, that is, resilient, stressed and irreversible death. We applied the method on the 20 closest dominant trees from the centre of each plot in fir- and oak-dominated forests. ARCHI protocol has not been employed in spruce-dominated forests and therefore has not been calculated in this context (Table 1). We used the proportion of dying trees—that is, stressed and irreversible death categories, therefore not adding dead trees—as a measure of 'stand decline'. The use of both metrics provides a dynamic perspective where trees are first declining due to the disturbances and are ultimately dead. Along the manuscript, we specifically refer to stand decline and mortality as it is used by foresters, only focusing on trees.

2.3 | Beetle sampling, identification and characterization

We sampled saproxylic beetles using different types of traps in each study context. In fir- and spruce-dominated forests, we used flight-interception traps (©Polytrap). They consisted in crossed pair of transparent plastic panes (40×60 cm) above a funnel conducting into a container filled with an unbaited preservative (50% propylene glycol and 50% water with a drop of detergent). There were two interception traps in fir forests, each at least 20 m from the other, placed around the centre of each study plot (Cours et al., 2022), while there was only one interception trap in spruce forest, placed at the centre of each study plot (Cours et al., 2021). The traps were suspended roughly 1.5 m above the ground and were sampled every month from mid-May to mid-September 2016 in spruce forests and 2017 in fir forests. In oak forests, we used a combination of two types of traps in each plot, two green unbaited multi-funnel traps and one black multi-funnel trap baited with volatiles (a blend of cerambycid pheromones, ethanol and alpha-pinene, hooked to the trap, see Roques et al., 2023) to sample different families of saproxylic beetles (mostly Buprestidae beetles with the two unbaited green multi-funnel traps, and both Curculionidae and Cerambycidae species with the baited black multi-funnel trap; Sallé et al., 2020). The baited traps have an attractive effect decreasing with distance and mostly help capturing nearby individuals (Turchin & Odendaal, 1996). As in fir and spruce forests, collectors were filled with unbaited preservative. Each trap was installed in a separate tree at least 50 m from each other, around the plot centre. In oak forests, the project objective was to sampled canopy fauna specifically (CANOPEE project). Therefore, these traps were suspended in the tree canopy, approximately 15 m above the ground. The traps were sampled every month from mid-May to the end of August 2020. All the captured saproxylic beetles were identified at the highest possible taxonomic level—that is, 87% at the species level, 1% at the genus level and 12% at the family level. We retained the genera in which 100% of regional species are known to be saproxylic, and families in which at least 75% of regional species are known to be saproxylic (Bouget et al., 2019). Since we could not identify most of Staphylinidae species, and since their exclusion is not considered to have a significant impact on the analysis of the response of saproxylic beetles (Parmain et al., 2015), we excluded them from the data sets.

We characterized each saproxylic beetle species by seven functional traits: the preferred (i) deadwood diameter, (ii) stage of decay, (iii) canopy closure, (iv) the mean body size, (v) their trophic regime, (vi) the used TreM and (vii) whether they are flower visitors or not. The first three indices were niche traits based on species occurrence data, that is, class of deadwood diameter and stage of decay in which species were recorded (see Gossner et al., 2013; Janssen et al., 2017). Mean body size was based on direct measurements from the FRISBEE database (Bouget et al., 2019) as well as the larval feeding guild, the larval microhabitat and the adult floricolous behaviour. For further analysis, we specifically focused on 'Xylophagous' and 'Saproxylophagous' regarding the larval feeding guild and on 'Xylofungicolous' and 'Cavicolous' species regarding the TreM used by the larva (Table 2).

The beetle capture has been done after the acquisition of necessary permits. No other ethical approval was needed for the conduct of this study. We did not need a licence or permit to achieve fieldwork that has been done simply in accordance with owners (both public and private, see Acknowledgements).

TABLE 2 The different guilds studied in abundance and species richness, used abbreviations in figures and their definitions (Bouget et al., 2005).

Guilds	Abbreviation	Definition
Xylophagous	Xylo.	Saproxylic beetle species with larvae foraging all the woody tissues in living dying, or recently dead trees
Saproxylophagous	Saprox.	Saproxylic beetle species with larvae foraging decayed, rotten deadwood
Mycetophagous	Myceto.	Saproxylic beetle species with larvae foraging saproxylic fungi
Xylofungicolous	Xylofun.	Saproxylic beetle species with larvae inhabiting fruiting bodies of saproxylic fungi
Cavicolous	Cavic.	Saproxylic beetle species with larvae inhabiting tree cavities
Floricolous	Floric.	Saproxylic beetle species with adults visiting flowers

2.4 | Statistical analysis

Data analysis was conducted with R software 4.5.1 (R Core Team, 2025).

Regarding the response variables, we used the saproxylic beetle community matrices and the trait databases—that is, the preferences in deadwood diameter, stage of decay and canopy closure and the mean body size—to calculate the functional indices. First, we removed vagrant species that are only associated with broadleaf tree species in both coniferous-dominated forests (and vice versa for oak-dominated forests), based on Bouget et al. (2019).

The functional richness (FRic), Rao's entropy index (RaoQ) and evenness (FEve) were calculated using the *FD* R-package, implementing abundance community matrices (Laliberté et al., 2014). We also calculated the CWM and FDis of each of the quantitative traits used for the functional indices (i.e. preferences in deadwood diameter, stage of decay and canopy closure and the mean body size). To isolate non-random assembly processes from the potential sampling effects associated with species richness, we calculated standardized effect sizes (SES) for all functional diversity indices (FRic, RaoQ, FEve, FDis). We employed a null model approach, generating 999 randomized indices by randomly swapping trait values between species across each context species pool. The SES for each index was calculated as follows: $SES=(I_{obs}-\text{mean}(I_{null}))/\text{sd}(I_{null})$, where I_{obs} represents the observed index value, and $\text{mean}(I_{null})$ and $\text{sd}(I_{null})$ represent the mean and standard deviation of the null distribution, respectively. This standardization ensures that the resulting values reflect functional assembly (convergence or divergence) independent of taxonomic richness.

In addition, we calculated the taxonomic diversity and abundance for the entire communities but also for each ecological guilds (Bouget et al., 2019), defined by larval feeding guild (i.e. xylophagous, saproxylophagous and mycetophagous), larval microhabitat (i.e. xylofungicolous and cavicolous) and adult behaviour (i.e. floricolous, see Table 2). Finally, we used *iNEXT* R-package (Hsieh & Chao, 2020) to calculate standardized species richness—that is, Hill number $q=0$—therefore disentangling from the effect of abundance. We also included the calculation of Shannon diversity index for all species—that is, Hill number $q=1$. Due to inherent variations in sampling completeness across contexts and bird guilds, we standardized our comparisons using community-specific coverage levels (Table S2). Following the guidelines of Chao et al. (2014), we set the target coverage for each group at a level that required, at most, an extrapolation to double the observed sample size, thereby ensuring the reliability of our richness estimates. Consequently, one plot was excluded in spruce-dominated forests from the final analysis due to insufficient sampling completeness—that is, sample coverage = 33% (see Table S1).

Finally, to calculate the cascading effects of stand decline and mortality, and of salvage logging on environmental conditions and saproxylic beetles, we employed piecewise structural equation modelling (SEM), using the *piecewiseSEM* R-package, version 4.1.2 (Lefcheck et al., 2020). In our SEMs, hierarchical relationships were the direct effects of stand decline and mortality, and salvage logging on trees (i.e. ligneous substrates) and subsequently on TreMs, which all may had effects on saproxylic beetles—that is, the cascading pathway. We constructed SEM for each forest context, to account for the different sampling schemes. The models implemented in the SEM were a mix of linear mixed models, for which we log-transformed the variables that required it, and generalized linear mixed models for the abundance and species richness of saproxylic beetles. In generalized linear mixed models, we used the negative binomial (after testing for residual over-dispersion, using 'check_overdispersion' function from *performance* R-library, Lüdecke et al., 2020) and Poisson distribution families. We also added a random variable using site—that is, Aure and Sault in fir context, and Orléans and Vierzon in oak context; Figure 1—, and the plot altitude as fixed covariable when significant in model to account for the within-site biogeographic context. We tested each model using the function 'check_model' from *performance* R-package (Lüdecke et al., 2020), to test for residual normality, predictor collinearity and potential outliers. We applied a selection of best SEM by the selection of predictors in each model that reduce overall SEM AIC by at least two. We divided the analysis in two datasets: (i) a first dataset for testing both the effects of stand decline (only in fir- and oak-dominated forests) and mortality, therefore not using salvage logged plots, and (ii) a second dataset for testing the effect of salvage logging, therefore using only salvage logged plots and unsalvaged plots from the most severe mortality class in each coniferous

context, that is, 10%–45% in fir-dominated forests and 70%–100% in spruce-dominated forests (Figure 1). In models, salvage logging has been used as a binary variable, that is, absence–occurrence of salvage logging. In spruce-dominated forests, since we only tested the effect of either stand mortality or salvage logging—that is, only one tested effect in each part of analysis—on ligneous substrates, we used the 5% α-error *p*.value to determine the significant effects. In fir- and oak-dominated forests, we used a 2.5% α-error *p*.value to test the effects of both stand decline and mortality effects as a strict adjustment of the *p*.value (0.05/2). For TreMs, we tested either stand mortality and decline or salvage logging as well as the ligneous substrate predictors (i.e. 14 or 15 tested effects in total). Likewise for biodiversity, we tested for the potential effects of all predictors (i.e. 23 or 24 tested effects). Therefore, we respectively adjusted the α-error *p*.value to 0.0036 or 0.0033 (as the result of 0.05/14 and 0.05/15) and 0.0022 or 0.0021 (as the result of 0.05/23 and 0.05/24). In addition, we also tested for the direct effect of stand decline and mortality, and salvage logging on the abundance of the species summing at least 10 individuals and occurring in at least 10% of the plots in each of the three contexts (Figure 5). We used the same model structure as in the SEM for the species abundance, that is, the tested predictor, a random site factor in fir- and oak-dominated forests, and the negative binomial distribution family.

3 | RESULTS

We found 27,299 individuals from 127 beetle species in fir-dominated forests, 2341 individuals from 103 species in spruce-dominated forests and 14,676 individuals from 238 species in oak-dominated forests.

3.1 | Cascading effects of stand decline and mortality and salvage logging on taxonomic and functional α-diversity of saproxylic beetles

3.1.1 | Cascading effects mediated by TreMs

TreM trait dispersion was promoted by stand decline in fir-dominated forests and by stand mortality in spruce-dominated forests, promoting both xylophagous and mycetophagous in fir context, and overall beetle abundance in spruce forests (Figures 2 and 3).

In addition, the density of trees bearing certain types of TreMs, also promoted by either stand decline or mortality, positively influenced certain guilds of beetles and community traits. In both coniferous-dominated forests, the density of trees bearing saproxylic TreMs promoted the overall Shannon index (Figures 2 and 3).

Changes in TreM trait values also led to changes in saproxylic beetle communities. The decrease in value of substrate type bearing TreMs—that is, less TreMs borne by living trees—had a negative effect on the abundance of xylofungicolous species in fir context (Figure 2), and xylophagous species in spruce forests (Figure 3).

3.1.2 | Cascading effects mediated by ligneous substrates

In addition to the numerous cascading effects observed via TreMs, many other observed paths were directly due to changes in ligneous substrates. In fir-dominated forests, we found that the decrease in volume of living trees caused by stand mortality has negatively affected the abundance of xylophagous beetles (Figure 2). Such living tree volume reduction in spruce forests led to a decrease in dispersion of the community preference in deadwood diameter (Figure 3).

Deadwood diversity promoted the abundance of xylofungicolous species in fir forests (Figure 2). In oak-dominated forests, the increasing deadwood diversity caused by stand mortality promoted the average community body size (Figure 4).

The increased volume of standing deadwood in fir-dominated forests benefited the flower-visitor richness (Figure 2). In spruce-dominated forests, while the volume of logs negatively affected the overall beetle abundance, the increasing volume of standing deadwood due to stand mortality markedly benefited the overall abundance as well as the abundances of xylophagous, mycetophagous, xylofungicolous and floricolous species (Figure 3).

In addition, the increasing amount of large and very large deadwood promoted the abundance of saproxylophagous in spruce-dominated forests (Figure 3), while the reduction in very large trees caused by stand mortality might have slightly reduced the overall Shannon index (Figure 3). In contrast, in oak-dominated forests, the increasing amount of large and very large deadwood has negatively affected the abundance of mycetophagous species (Figure 4).

Moreover, in oak-dominated forests, the increasing amount of less decayed deadwood due to stand mortality led to a reduction in abundance and species richness of saproxylophagous species (Figure 4). Similarly, we found that overall deadwood volume negatively affected the xylofungicolous guild in the same context (Figure 4).

Furthermore, in spruce-dominated forests, the substrate changes towards fewer living trees and more deadwood—that is, CWM substrate—led to an average community preference for more closed forest environments (Figure 3). Such shift in woody substrate led to higher functional evenness in oak-dominated forests (Figure 4). The more diverse substrates—that is, FDis substrate—found in high mortality stands, favoured the species richness of mycetophagous and xylofungicolous in spruce forests (Figure 3) and the abundance of flower visiting beetles in oak context (Figure 4).

3.2 | Cascading effects of salvage logging

We found that most of the negative effects of salvage logging on saproxylic beetle guilds were linked to a reduction in certain TreMs.

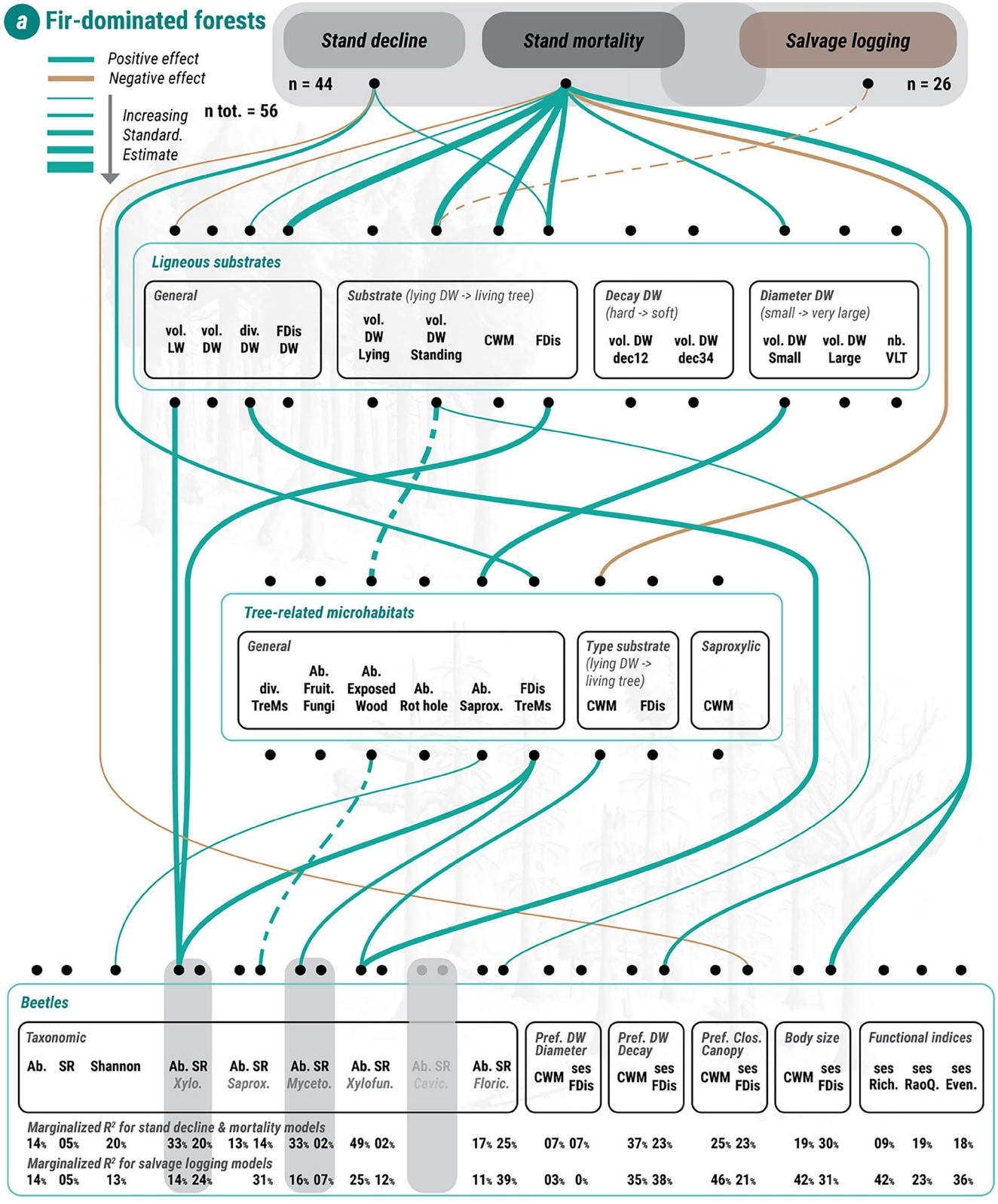

FIGURE 2 Results from structural equation modelling (SEM) for fir-dominated forests (Pyrenees region, drought disturbance). The structure of SEM is 'stand decline -> ligneous substrates -> tree-related microhabitats -> saproxylic beetles'. *p*.values are adjust based on the number of potential effects—see Methods. Green lines show positive effects and brown lines negative ones. Solid lines show effects from stand decline & mortality models, while dashed lines show effects from salvage logging ones. Line widths illustrate the magnitude of effects (standardized estimates). The percentages are the marginalized R-squared for stand decline & mortality models (top) and salvage models (bottom). '*vol.*' = '*volume*'; '*LW*' = '*Living Wood*'; '*DW*' = '*Deadwood*'; '*Ab.*' = '*Abundance*'; '*SR*' = '*Species Richness*'; '*FDis*' = '*Functional Dispersion*'; '*FRic*' = '*Functional Richness*'; '*Rich.*' = '*Richness*'; '*Even*' = '*Evenness*'; '*ses*' = '*standardized effect size*'.

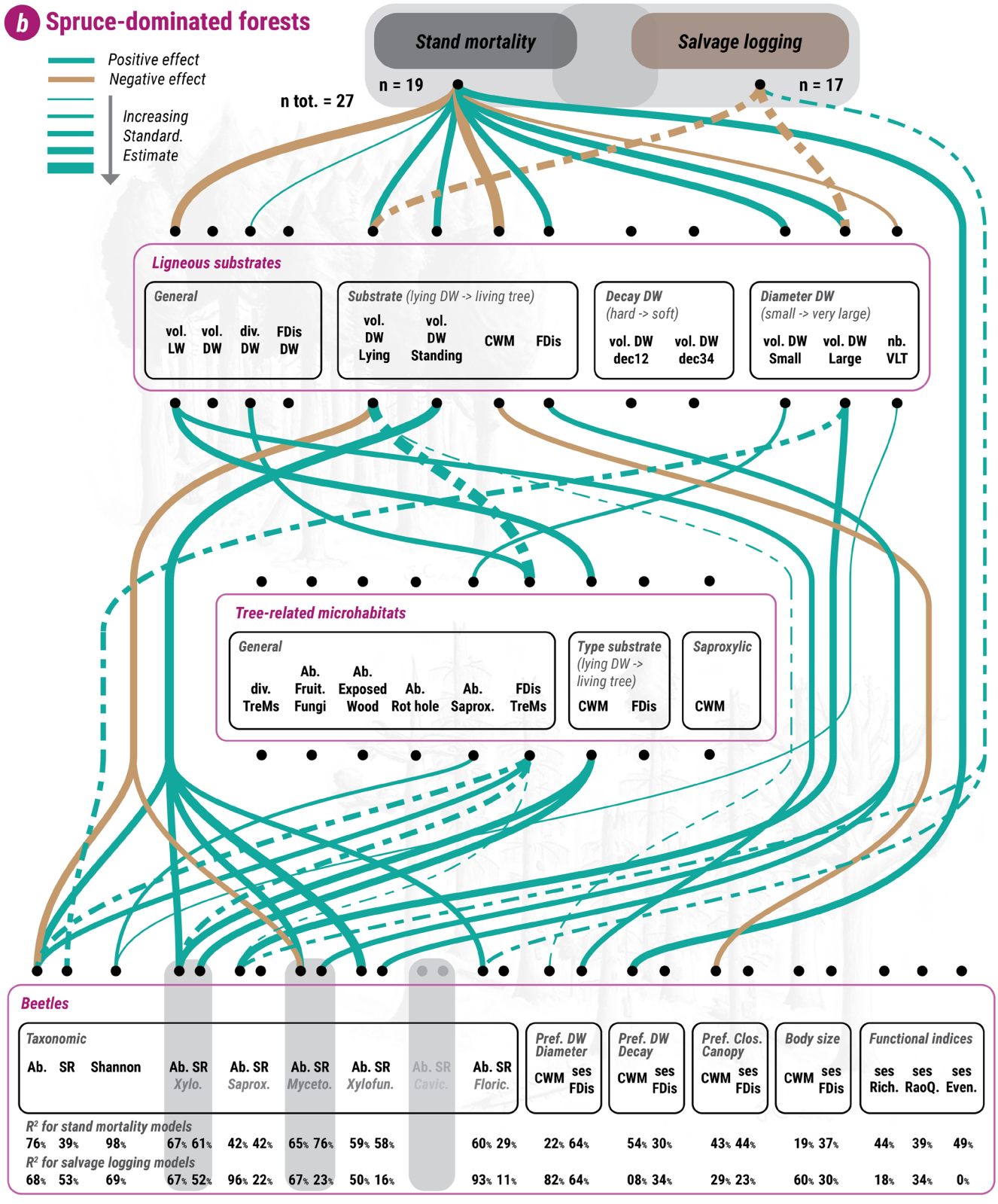

FIGURE 3 Results from structural equation modelling (SEM) for spruce-dominated forests (Bavaria region, windstorm and insect-outbreak disturbances). For additional information, see legend of Figure 2.

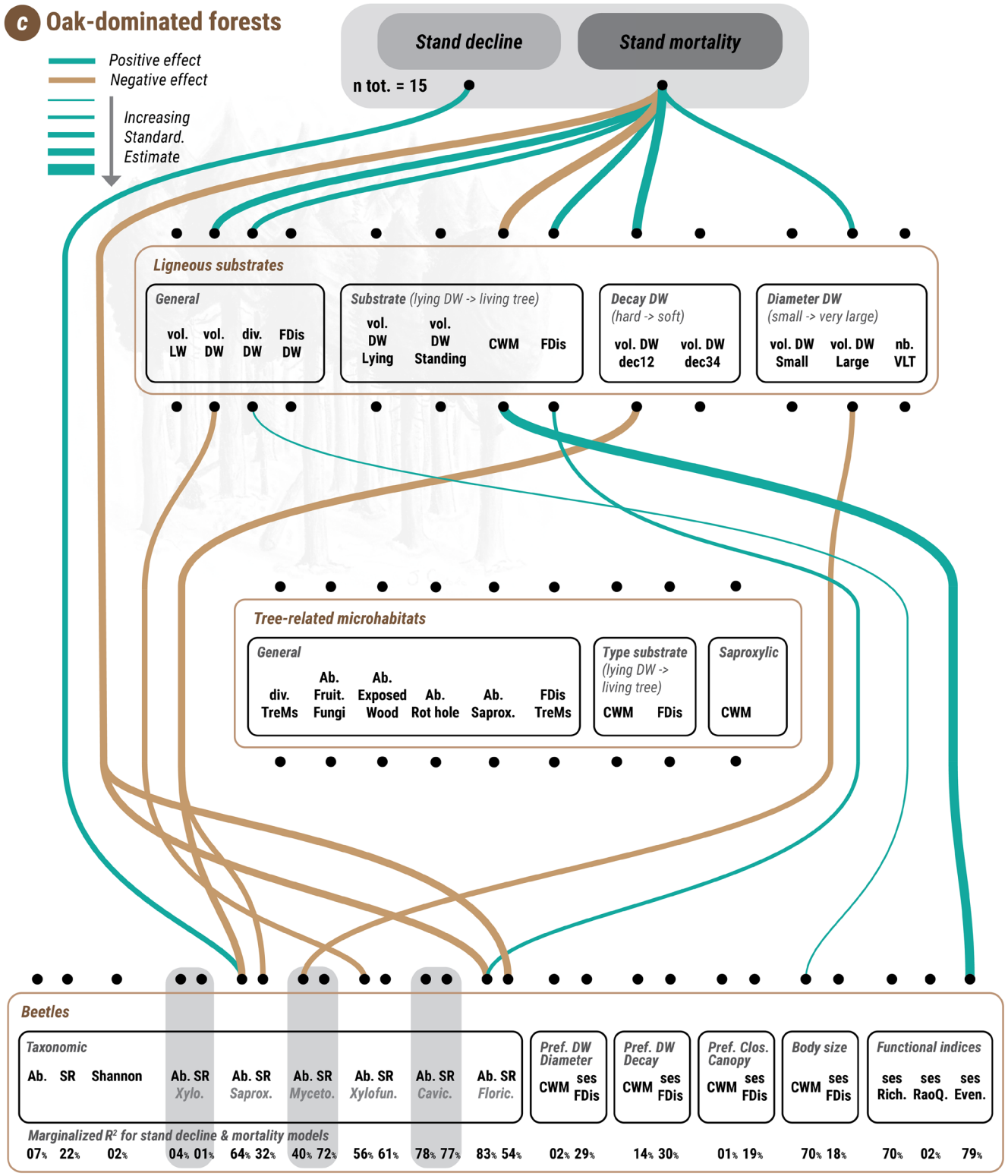

FIGURE 4 Results from structural equation modelling (SEM) for oak-dominated forests (Loire region, drought disturbance). For additional information, see the legend of Figure 2.

In fir-dominated forests, the reduction in exposed wood TreMs caused by standing deadwood harvest negatively affected the richness of saproxylophagous (Figure 2). In spruce-dominated forests, the marked decrease of TreM trait dispersion caused by log harvesting negatively affected overall beetle abundance, as well as the abundances in xylophagous and saproxylophagous (Figure 3).

FIGURE 5 Species-scale responses (species or genus) in abundance to the decline and mortality severity, and salvage logging. Selection of taxa present in at least 10% of sites and summing at least 10 individuals in each context. Results extracted from negative binomial glmm including site random factor. Number of captured individuals next to taxa name. '*Xyl.*' = '*Xylophagous*'; '*Saprox.*' = '*Saproxylophagous*'; '*Sap*' = '*Sap-feeders*'.

3.3 | Direct effects of stand decline and salvage logging on the most abundant saproxylic beetle species in each context

In fir-dominated forests, effects of both stand decline and mortality were generally positive on the abundances of the most abundant saproxylic species, with negative effects only found for several taxa—that is, mainly *Epuraea* species and *Pediacus dermestoides* (Figure 5a). We also noticed that only *Nacerdes gracilis* positively responded to both stand decline and mortality (Figure 5a). In addition, we found that salvage logging had positive effects on *Pityophthorus pityographus* and *Trypodendron lineatum* (Figure 5a), and therefore, no negative effect was observed on the most abundant species.

In spruce-dominated forests, we mostly found positive effects of stand mortality (e.g. for *Oxymirus cursor* or *Rhagium bifasciatum*) but also negative effects on *Microbregma emarginatum* and *Micrambe abietis* (Figure 5b). Salvage logging in spruce-dominated forests promoted the abundances of *Ampedus nigrinus* and *Dasytes obscurus*, while also decreased abundances of *Peltis ferruginea* and *Acrotrichis* species (Figure 5).

In oak-dominated forests, stand decline had an overall positive effect on the most abundant taxa while stand mortality had an

inverse effect, negatively affecting the abundance of most of the taxa, except *Lymexylon navale* (Figure 5c).

4 | DISCUSSION

4.1 | Cascading effects of stand decline on beetle taxonomic and functional diversity

Stand decline and mortality generally promoted saproxylic beetle abundances in conifer-dominated forests, partially supporting our first hypothesis and previous findings (Cours et al., 2021, 2022; Sallé et al., 2020; Viljur et al., 2022). In oak forests, however, stand decline only has shown a positive effect, whereas mortality mostly had negative effects, consistent with Le Souchu, Cours, et al. (2024) on hymenoptera. Our study advances earlier work by explicitly identifying how stand decline and mortality affect saproxylic beetle communities through changes in TreM and deadwood substrates—that is, the cascading pathways.

4.1.1 | The consistent importance of deadwood and TreM diversity for saproxylic beetle abundance in context of forest stand decline

Deadwood diversity emerged as a key factor in all forest contexts, promoting beetle abundances or community average size. Previous studies have identified deadwood diversity as a consistent predictor of saproxylic beetle diversity in temperate forests (Bouget et al., 2013). A diverse deadwood pool provides high-quality substrates for specialist species (e.g. large diameter logs; Lachat et al., 2013; Similä et al., 2003).

TreMs were also central for explaining cascading effects during stand decline in coniferous forests, especially supporting overall abundance and dominant species. The relationship between habitat heterogeneity and biodiversity is well established. The *habitat-heterogeneity hypothesis* predicts that diverse habitats promote species richness through niche differentiation, whereas the *more-individuals hypothesis* suggests that increased resource availability first boosts abundance, which then secondarily enhances species richness (Clarke & Gaston, 2006; Müller et al., 2018; Seibold et al., 2016). Our results rather support the more individual mechanism since most cascading pathways promoted beetle abundance: higher deadwood diversity and TreM trait dispersion likely reflecting greater resource availability for saproxylic beetles (Müller et al., 2018). For instance, the standardized Shannon index primarily tracked changes in dominant species, highlighting an effect on abundance rather than species richness.

Saproxylic TreMs were especially influential, promoting dominant species. They are known to be among the central microhabitats produced during the stand decline process (Bouget et al., 2024; Chowdhury et al., 2024; Przepiora & Ciach, 2025). Our results demonstrate that, in addition to deadwood, TreMs are great support for the saproxylic biodiversity and therefore need to be better recognized in conservation.

4.1.2 | Snags as key habitat in declining spruce-dominated forests

Snags emerged as a major driver of abundance of almost all trophic guilds in spruce forests, reflecting their central role in supporting saproxylic biodiversity in this context (Bouget et al., 2014). Snags are known to provide high-quality habitat supporting saproxylic beetle assemblages (Bouget et al., 2012, 2014; Cours et al., 2021; Kozák et al., 2021; Parisi et al., 2018). Their importance is particularly pronounced in coniferous forests, where snags are often the primary source of cracks and polypores, microhabitats that are rare on living trees (Larrieu & Cabanettes, 2012). In fir forests, in the context of salvage logging, snags supported saproxylophagous richness by bearing exposed wood TreMs. For instance, *Cis punctulatus*, a mycetophagous species preferring tall snags (Hjältén et al., 2010), responded positively to spruce stand mortality.

In contrast, lying deadwood exhibited opposite effects in spruce-dominated forests. Despite similar decay stages and diameters to standing deadwood (Figure S7), greater log volumes were associated with lower overall abundance, particularly among mycetophagous species. This finding is unexpected given that logs typically complement snags in enriching local species pools (Bouget et al., 2012; Graf et al., 2022; Hjältén et al., 2010; Jonsell & Weslien, 2003). Because snag and log volumes were not negatively correlated (Figure S3c), reduced abundance associated with logs likely reflects unmeasured ecological processes, such as resource specialization or species interactions. Future work should assess species-level preferences for snags versus logs and investigate potential negative interactions—for example, competition or habitat exclusion—that may structure communities in declining spruce stands.

4.2 | Contrasts between the effects of canopy decline and tree mortality

Our results support the hypothesis that stand decline and stand mortality exert distinct influences on saproxylic beetle communities. In fir-dominated forests, stand decline indirectly favoured xylophagous species. In oak-dominated forests, although overall responses of the xylophagous community were not significant, higher proportions of declining trees promoted several early-stage xylophagous species, that is, *Agrilus biguttatus*, *A. laticornis* or *A. sulcicollis* and *Coraebus undatus* (Le Souchu, Bouget, & Sallé, 2024; Sallé et al., 2020). Decline thus represents an early successional stage where stressed living trees provide abundant resources for opportunistic colonizers (Stokland et al., 2012; Thorn et al., 2016; Wermelinger et al., 2025), particularly in drought-affected systems where tree death unfolds slowly.

In contrast, stand mortality generated divergent cascading effects depending on forest context. In coniferous-dominated forests,

mortality advanced succession dynamics by promoting saproxylophagous species (e.g. *Nacerdes gracilis*, *Rhagium bifasciatum*) that typically colonize after xylophagous pioneers (Lettenmaier et al., 2026). In oak-dominated forests, however, mortality seems to have stopped the species succession by reducing saproxylophagous abundance and richness. The harvest of valuable trees in this context may have had confounded effects that led to the observed negative results.

These contrasting patterns may stem from inherent differences in wood physical and chemical properties. Oak decomposition is slower and shaped by distinct wood-decay fungal pathways (mostly fibrous white-rot) compared with conifers, which typically mostly host cubic brown-rot (Kahl et al., 2017). Although short-term effects of fungal communities on beetles appear limited (Sbaraglia et al., 2025), they could exert long-term effects via priority effects (Weslien et al., 2011). Microclimatic context likely further amplifies these contrasts: in coniferous forests at high altitudes and/or latitudes, canopy openings may warm deadwood while abundant precipitation maintains wood moisture—conditions favourable for colonization (Harmon et al., 2020; Sbaraglia et al., 2025; Seibold et al., 2016). Conversely, in warm, dry lowland oak forests, openings likely accelerate deadwood desiccation, reducing suitability for many saproxylic taxa (Harmon et al., 2020). Additionally, continued logging in oak forests may have negatively affected saproxylic beetles and confound results (Thorn et al., 2018).

4.3 | Context dependency of stand decline and mortality effects

Stand mortality was most severe in spruce-dominated stands, which showed the highest deadwood volumes—up to 438 $m^3.ha^{-1}$ (Figure S1)—and the sharpest contrast between low and high stand decline levels (see Table 1). In contrast, TreMs diversity was greatest in fir-dominated forests (Figure S1). Although oak-dominated forests displayed high TreM trait diversity, mean TreMs abundances were consistently lower than in coniferous forests (Figure S1), despite oak's general tendency to host more TreMs and in higher diversity (Courbaud et al., 2022; Vuidot et al., 2011). This discrepancy likely reflects the effects of ongoing salvage logging in the oak context. These structural contrasts generated distinct cascading effects on saproxylic beetle communities across forest contexts (Cours et al., 2021, 2023; Sallé et al., 2021; Viljur et al., 2022).

Each declining context also supported distinct beetle communities aligned with different successional stages. In spruce-dominated forests, the rapid and severe mortality triggered by *Ips typographus* occurred several years before sampling. Consequently, we observed only one dominant xylophagous species—*Pityophthorus pityographus*—and a negative effect of mortality on xylophagous richness due to the loss of TreMs borne by living trees. This pattern parallels observations from Switzerland, where xylophagous beetles peak in the 5 years following windstorm and subsequently collapse to near-zero levels (Wermelinger et al., 2025). In contrast, slow drought-driven decline in fir and oak forests allowed overlap between early- and late-successional beetle groups.

Wider landscape contexts likely participated in the observed differences between regions through varying colonization dynamics. For instance, decline in conifer-dominated forests occurred within a less intensively managed matrix—specifically, the unmanaged stands in spruce forests and the presence of high-altitude old-growth remnants in the Pyrenees fir forests (Barredo et al., 2021). These areas likely served as regional species pools (or 'continents' sensu MacArthur & Wilson, 1967), facilitating the colonization of the newly available resource patches in these two contexts and supporting the robust cascading responses we observed (Busse et al., 2022). In contrast, the more isolated and scattered unmanaged oak patches in the Loire Valley landscape may have limited the immigration of specialized saproxylic guilds, thereby dampening the community-level response to stand decline.

Flower-visiting beetles also showed strong context dependency, likely reflecting variations in canopy openness among them. Their relative abundance was lowest in fir-dominated forests compared with the two other contexts. Slow drought-driven decline in fir-dominated forests produces limited canopy opening compared with the more severe decline in spruce forests, and the more actively logged oak forests (Cours et al., 2021). Moreover, many shade-tolerant seedlings and saplings occur in such small canopy openness in fir forests that could have further reduced flower abundances. Canopy openness is a key driver of beetle assemblages (Bouget et al., 2013), and more broadly, forest insect communities (Sire et al., 2022), as sun-exposed deadwood typically hosts more species than shaded substrates (Lettenmaier et al., 2022; Seibold et al., 2016).

Tree mortality in spruce-dominated forests unexpectedly favoured species preferring shadier environments. Although canopy loss should increase solar exposure, the dense tree regeneration might have recreated shaded conditions that benefited this beetle community (Sbaraglia et al., 2025).

Overall, our results underscore the strong context dependency of stand decline and mortality effects (Catford et al., 2022). Cascading ecological responses varied depending on dominating tree species, biogeographical and landscape settings and the natural disturbance type (Cours et al., 2023). Methodological differences—most notably, distinct trapping methods and sampled vertical stratum between oak and conifer contexts—likely contributed to some of the observed contrasts. Nevertheless, our study clarifies how interacting structural and ecological factors drive divergent saproxylic beetle responses across European forest contexts. Given the rising frequency, severity and extent of natural disturbances and forest stand decline globally (Allen et al., 2015; McDowell et al., 2020; Samaniego et al., 2018; Seidl et al., 2017; Viljur et al., 2022), addressing this complexity is increasingly crucial for conserving biodiversity in rapidly changing forest landscapes.

4.4 | Salvage logging had contrasting effects across saproxylic guilds

We partly confirmed our hypothesis that salvage logging negatively affects local saproxylic beetle community via resource depletion

(Lindenmayer et al., 2008; Thorn et al., 2018). Salvage logging primarily reduced TreM trait dispersion and exposed wood ones, leading to declines in several saproxylic guilds in both coniferous contexts. These findings further emphasize the central role of TreMs in sustaining saproxylic beetle communities, both under conditions of habitat enrichment and habitat loss. Salvage logging specifically impacts saproxylophagous beetles because it removes decayed deadwood—a critical resource that is harvested before it can form (Priewasser et al., 2013).

However, salvage logging also promoted the abundances of floricolous and saproxylophagous species in spruce-dominated forests. Because many adult saproxylophagous beetles are also floricolous (e.g. numerous *Cerambycidae* species; see Figure S5), this positive effect is likely driven by this adult-related trait—that is, saproxylophagous trophic trait being related to larval stage. This pattern agrees with previous studies showing that salvage logging promotes floricolous species (Heil & Burkle, 2018; Thorn et al., 2016; Wermelinger et al., 2025). In montane forests, salvage logging creates canopy openings and soil disturbances that promote the establishment of flowering plants such as *Epilobium angustifolium*, as well as species from the *Apiaceae*, *Asteraceae* or *Campanulaceae* families, thereby enhancing pollinator resources (Orczewska et al., 2019; Swanson et al., 2011; Thorn et al., 2016; Wermelinger et al., 2025).

5 | CONCLUSION

Our study shows that forest stand decline generally enhances saproxylic beetles in European coniferous forests and identifies the cascading habitat-mediated mechanisms driving these responses. Increased diversity in deadwood and tree-related microhabitats generally boosted overall beetle abundance, and standing dead trees played a key role in spruce-dominated forests affected by windstorm and bark beetle outbreaks. Decline and mortality triggered different successional pathways depending on forest context. These mechanisms were strongly context dependent, underscoring the need to better understand how decline processes vary across forest contexts under a rapidly changing climate.

Conversely, the harvest during salvage logging of habitat trees that developed rich diversity of TreMs and deadwood after natural disturbance bears most of the detrimental effects. These findings are consistent with earlier evidence of the detrimental impacts of salvage logging on forest biodiversity (Lindenmayer et al., 2008; Thorn et al., 2018, 2020).

We therefore advocate for the conservation of declining forest stand patches as temporary biodiversity refugia for saproxylic beetles. At minimum, retaining TreM-rich large snags during salvage logging operations can provide essential 'lifeboats' for saproxylic beetles and help sustain biodiversity.

AUTHOR CONTRIBUTIONS

Jérémy Cours, Christophe Bouget and Aurélien Sallé conceived the ideas and designed methodology; Laurent Larrieu, Guilhem Parmain, Jörg Müller, Simon Thorn, Alain Rocques and Jérémy Cours collected the data; Jérémy Cours analysed the data; Jérémy Cours, Christophe Bouget and Aurélien Sallé led the writing of the manuscript. Carlos Lopez-Vaamonde, Aurélien Sallé, Jörg Müller and Alain Rocques were the leaders of projects that have funded this research (see Acknowledgments). All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and codes available from the Zenodo Repository https://doi.org/10.5281/zenodo.17927769 (Cours et al., 2026).

STATEMENT ON INCLUSION

This study brings together authors based in France and Germany, where the study was conducted, to address a global and timely

question. The data have been collected in both public and private forest areas, and we acknowledge every land owners and managers who helped us in the selection of plots in the field and allowing us the access to them to collect data for the time of the different projects. All authors were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent were considered from the onset. Whenever relevant, literature published by scientists from the region was cited.

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REFERENCES

Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, *6*(8), art129. https://doi.org/10.1890/ES15-00203.1

Barredo, J., Brailescu, C., Teller, A., Sabatini, F., Mauri, A., & Janouskova, K. (2021). *Mapping and assessment of primary and old-growth forests in Europe: EUR 30661*. Publications Office of the European Union. https://doi.org/10.2760/797591

Bässler, C., Förster, B., Moning, C., & Müller, J. (2009). The BIOKLIM project: Biodiversity research between climate change and wildling in a temperate montane forest—The conceptual framework. *Waldökologie, Landschaftsforschung und Naturschutz*, *7*, 21–33.

Beudert, B., Bässler, C., Thorn, S., Noss, R., Schröder, B., Dieffenbach-Fries, H., Foullois, N., & Müller, J. (2015). Bark beetles increase biodiversity while maintaining drinking water quality. *Conservation Letters*, *8*(4), 272–281. https://doi.org/10.1111/conl.12153

Bouget, C., Brustel, H., & Nageleisen, L.-M. (2005). Nomenclature of wood-inhabiting groups in forest entomology: Synthesis and semantic adjustments. *Comptes Rendus Biologies*, *328*(10–11), 936–948. https://doi.org/10.1016/j.crvi.2005.08.003

Bouget, C., Brustel, H., Noblecourt, T., & Zagatti, P. (2019). *Les Coléoptères saproxyliques de France: Catalogue écologique illustré*. Editions du MNHN.

Bouget, C., & Cours, J. (2025). Effects of forest dieback on deadwood patterns: Large scale trends from a cross-analysis of European databases. *Journal of Environmental Management*, *375*, 124315. https://doi.org/10.1016/j.jenvman.2025.124315

Bouget, C., Cours, J., Larrieu, L., Parmain, G., Müller, J., Speckens, V., & Sallé, A. (2024). Trait-based response of deadwood and tree-related microhabitats to decline in temperate lowland and montane forests. *Ecosystems*, *27*, 90–105. https://doi.org/10.1007/s10021-023-00875-9

Bouget, C., Larrieu, L., & Brin, A. (2014). Key features for saproxylic beetle diversity derived from rapid habitat assessment in temperate forests. *Ecological Indicators*, *36*, 656–664. https://doi.org/10.1016/j.ecolind.2013.09.031

Bouget, C., Larrieu, L., Nusillard, B., & Parmain, G. (2013). In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. *Biodiversity and Conservation*, *22*(9), 2111–2130. https://doi.org/10.1007/s10531-013-0531-3

Bouget, C., Nusillard, B., Pineau, X., & Ricou, C. (2012). Effect of deadwood position on saproxylic beetles in temperate forests and conservation interest of oak snags. *Insect Conservation and Diversity*, *5*(4), 264–278. https://doi.org/10.1111/j.1752-4598.2011.00160.x

Busse, A., Cizek, L., Čížková, P., Drag, L., Dvorak, V., Foit, J., Heurich, M., Hubený, P., Kašák, J., Kittler, F., Kozel, P., Lettenmaier, L., Nigl, L., Procházka, J., Rothacher, J., Straubinger, C., Thorn, S., & Müller, J. (2022). Forest dieback in a protected area triggers the return of the primeval forest specialist *Peltis grossa* (Coleoptera, Trogossitidae). *Conservation Science and Practice*, *4*(2), e612. https://doi.org/10.1111/csp2.612

Calix, M., Alexander, K. N. A., Nieto, A., Dodelin, B., Soldati, F., Telnov, D., Vazquez-Albalate, X., Aleksandrowicz, O., Audisio, P., Istrate, P., Jansson, N., Legakis, A., Liberto, A., Makris, C., Merkl, O., Pettersson, R. M., Schlaghamersky, J., Bologna, M. A., Brustel, H., … Purchart, L. (2018). *European red list of saproxylic beetles*. IUCN. https://portals.iucn.org/library/node/47296

Catford, J. A., Wilson, J. R. U., Pyšek, P., Hulme, P. E., & Duncan, R. P. (2022). Addressing context dependence in ecology. *Trends in Ecology & Evolution*, *37*(2), 158–170. https://doi.org/10.1016/j.tree.2021.09.007

Chao, A., Chiu, C.-H., & Jost, L. (2014). Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through hill numbers. *Annual Review of Ecology, Evolution, and Systematics*, *45*(1), 297–324. https://doi.org/10.1146/annurev-ecolsys-120213-091540

Chowdhury, F. I., Lloret, F., Jaime, L., Margalef-Marrase, J., & Espelta, J. M. (2024). Deadwood and tree-related Microhabitat's abundance and diversity are determined by the interplay of drought-induced die-off and local climate. *Forest Ecology and Management*, *563*, 121989. https://doi.org/10.1016/j.foreco.2024.121989

Clarke, A., & Gaston, K. J. (2006). Climate, energy and diversity. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1599), 2257–2266. https://doi.org/10.1098/rspb.2006.3545

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. https://doi.org/10.1111/1365-2664.14068

Cours, J., Bouget, C., Barsoum, N., Horák, J., Le Souchu, E., Leverkus, A. B., Pincebourde, S., Thorn, S., & Sallé, A. (2023). Surviving in changing forests: Abiotic disturbance legacy effects on arthropod communities of temperate forests. *Current Forestry Reports*, *9*, 189–218. https://doi.org/10.1007/s40725-023-00187-0

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*, 118811.

Cours, J., Sallé, A., Larrieu, L., Lopez-Vaamonde, C., Müller, J., Parmain, G., Thorn, S., Roques, A., & Bouget, C. (2026). Data & codes - From forest stand decline to salvage logging: Cascading impacts on saproxylic beetle diversity [Dataset]. *Zenodo*. https://doi.org/10.5281/zenodo.17927769

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*, 2025–2043. https://doi.org/10.1007/s10980-022-01453-5

Drénou, C. (2025). The ARCHI method, a key to understanding trees. *Forêt et Innovation*, *12*, 10–34.

Georgiev, K. B., Bässler, C., Feldhaar, H., Heibl, C., Karasch, P., Müller, J., Perlik, M., Weiss, I., & Thorn, S. (2022). Windthrow and salvage logging alter β-diversity of multiple species groups in a mountain spruce forest. *Forest Ecology and Management*, *520*, 120401. https://doi.org/10.1016/j.foreco.2022.120401

Gossner, M. M., Lachat, T., Brunet, J., Isacsson, G., Bouget, C., Brustel, H., Brandl, R., Weisser, W. W., & Müller, J. (2013). Current near-to-nature Forest management effects on functional trait composition of saproxylic beetles in beech forests. *Conservation Biology*, *27*(3), 605–614. https://doi.org/10.1111/cobi.12023

Graf, M., Lettenmaier, L., Müller, J., & Hagge, J. (2022). Saproxylic beetles trace deadwood and differentiate between deadwood niches before their arrival on potential hosts. *Insect Conservation and Diversity*, *15*(1), 48–60. https://doi.org/10.1111/icad.12534

Harmon, M. E., Fasth, B. G., Yatskov, M., Kastendick, D., Rock, J., & Woodall, C. W. (2020). Release of coarse woody detritus-related carbon: A synthesis across forest biomes. *Carbon Balance and Management*, *15*(1), 1. https://doi.org/10.1186/s13021-019-0136-6

Harvey, J. A., Tougeron, K., Gols, R., Heinen, R., Abarca, M., Abram, P. K., Basset, Y., Berg, M., Boggs, C., Brodeur, J., Cardoso, P., de Boer, J. G., De Snoo, G. R., Deacon, C., Dell, J. E., Desneux, N., Dillon, M. E., Duffy, G. A., Dyer, L. A., … Chown, S. L. (2023). Scientists' warning on climate change and insects. *Ecological Monographs*, *93*(1), e1553. https://doi.org/10.1002/ecm.1553

Heil, L. J., & Burkle, L. A. (2018). Recent post-wildfire salvage logging benefits local and landscape floral and bee communities. *Forest Ecology and Management*, *424*, 267–275.

Hjältén, J., Stenbacka, F., & Andersson, J. (2010). Saproxylic beetle assemblages on low stumps, high stumps and logs: Implications for environmental effects of stump harvesting. *Forest Ecology and Management*, *260*(7), 1149–1155. https://doi.org/10.1016/j.foreco.2010.07.003

Hsieh, T. C., & Chao, K. H. M. a. A. (2020). *iNEXT*: *Interpolation and extrapolation for species diversity* (Version 2.0.20) [Computer software]. https://CRAN.R-project.org/package=iNEXT

Janssen, P., Fuhr, M., Cateau, E., Nusillard, B., & Bouget, C. (2017). Forest continuity acts congruently with stand maturity in structuring the functional composition of saproxylic beetles. *Biological Conservation*, *205*, 1–10. https://doi.org/10.1016/j.biocon.2016.11.021

Jonsell, M., & Weslien, J. (2003). Felled or standing retained wood—It makes a difference for saproxylic beetles. *Forest Ecology and Management*, *175*(1), 425–435. https://doi.org/10.1016/S0378-1127(02)00143-3

Kahl, T., Arnstadt, T., Baber, K., Bässler, C., Bauhus, J., Borken, W., Buscot, F., Floren, A., Heibl, C., Hessenmöller, D., Hofrichter, M., Hoppe, B., Kellner, H., Krüger, D., Linsenmair, K. E., Matzner, E., Otto, P., Purahong, W., Seilwinder, C., … Gossner, M. M. (2017). Wood decay rates of 13 temperate tree species in relation to wood properties, enzyme activities and organismic diversities. *Forest Ecology and Management*, *391*, 86–95. https://doi.org/10.1016/j.foreco.2017.02.012

Kozák, D., Svitok, M., Wiezik, M., Mikoláš, M., Thorn, S., Buechling, A., Hofmeister, J., Matula, R., Trotsiuk, V., Bače, R., Begovič, K., Čada, V., Dušátko, M., Frankovič, M., Horák, J., Janda, P., Kameniar, O., Nagel, T. A., Pettit, J. L., … 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. https://doi.org/10.1007/s10021-020-00502-x

Lachat, T., Bouget, C., Bütler, R., & Müller, J. (2013). Deadwood: Quantitative and qualitative requirements for the conservation of saproxylic biodiversity. In *Integrative approaches as an opportunity for the conservation of forest biodiversity* (p. 92). European Forest Institute.

Laliberté, E., Legendre, P., & Shipley, B. (2014). *FD*: *Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology* (Version 1.0-12) [Computer software]. https://CRAN.R-project.org/package=FD

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 forests1This article is one of a selection of papers from the international symposium on dynamics and ecological services of deadwood in forest ecosystems. *Canadian Journal of Forest Research*, *42*(8), 1433–1445. https://doi.org/10.1139/x2012-077

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. https://doi.org/10.1016/j.ecolind.2017.08.051

Le Souchu, E., Bouget, C., & Sallé, A. (2024). Environmental drivers of local and temporal variations in the community of oak-associated borers (Coleoptera: Buprestidae). *European Journal of Forest Research*, *143*(2), 603–616. https://doi.org/10.1007/s10342-023-01644-y

Le Souchu, E., Cours, J., Cochenille, T., Bouget, C., Bankhead-Dronnet, S., Braet, Y., Burguet, P., Gabard, C., Galkowski, C., Gereys, B., Herbrecht, F., Joncour, B., Marhic, E., Michez, D., Buhl, P. N., Noblecourt, T., Notton, D. G., Penigot, W., Rasplus, J.-Y., … Sallé, A. (2024). Responses of the hyper-diverse community of canopy-dwelling Hymenoptera to oak decline. *Insect Conservation and Diversity*, *17*, 430–448. https://doi.org/10.1111/icad.12708

Lefcheck, J. S., Byrnes, J., & Grace, J. (2020). *piecewiseSEM*: *Piecewise structural equation modeling* (Version 2.1.2) [Computer software]. https://CRAN.R-project.org/package=piecewiseSEM

Lettenmaier, L., Bässler, C., Decker, O., Hagge, J., Heibl, C., Mamadashvili, G., Seibold, S., Thorn, S., & Müller, J. (2026). 12 years of assembly patterns in saproxylic beetles suggest early decay wood as ephemeral resource patch. *Journal of Animal Ecology*, *95*(2), 282–295. https://doi.org/10.1111/1365-2656.70183

Lettenmaier, L., Seibold, S., Bässler, C., Brandl, R., Gruppe, A., Müller, J., & Hagge, J. (2022). Beetle diversity is higher in sunny forests due to higher microclimatic heterogeneity in deadwood. *Oecologia*, *198*(3), 825–834. https://doi.org/10.1007/s00442-022-05141-8

Lindenmayer, D. B., Burton, P. J., & Franklin, J. F. (2008). *Salvage logging and its ecological consequences*. Island Press. https://agris.fao.org/agris-search/search.do?recordID=US201300128956

Lüdecke, D., Makowski, D., Waggoner, P., & Patil, I. (2020). *performance*: *Assessment of regression models performance* (Version 0.4.6) [Computer software]. https://CRAN.R-project.org/package=performance

MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton University Press.

McDowell, N. G., Allen, C. D., Anderson-Teixeira, K., Aukema, B. H., Bond-Lamberty, B., Chini, L., Clark, J. S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurtt, G. C., Jackson, R. B., Johnson, D. J., Kueppers, L., Lichstein, J. W., Ogle, K., Poulter, B., Pugh, T. A. M., Seidl, R., … Xu, C. (2020). Pervasive shifts in forest dynamics in a changing world. *Science*, *368*(6494), eaaz9463. https://doi.org/10.1126/science.aaz9463

Müller, J., Brandl, R., Brändle, M., Förster, B., de Araujo, B. C., Gossner, M. M., Ladas, A., Wagner, M., Maraun, M., Schall, P., Schmidt, S., Heurich, M., Thorn, S., & Seibold, S. (2018). LiDAR-derived canopy structure supports the more-individuals hypothesis for arthropod diversity in temperate forests. *Oikos*, *127*(6), 814–824. https://doi.org/10.1111/oik.04972

Müller, J., Noss, R. F., 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*(11), 2559–2569. https://doi.org/10.1016/j.biocon.2010.06.024

Orczewska, A., Czortek, P., & Jaroszewicz, B. (2019). The impact of salvage logging on herb layer species composition and plant community recovery in Białowieża Forest. *Biodiversity and Conservation*, *28*(13), 3407–3428. https://doi.org/10.1007/s10531-019-01795-8

Pardé, J., & Bouchon, J. (1988). *Dendrométrie* (2nd ed.). Ecole Nationale du génie rural, des Eaux et Forêts.

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 - Biogeosciences and Forestry*, *11*(3), 423. https://doi.org/10.3832/ifor2670-011

Parmain, G., Bouget, C., Müller, J., Horak, J., Gossner, M. M., Lachat, T., & Isacsson, G. (2015). Can rove beetles (Staphylinidae) be excluded in studies focusing on saproxylic beetles in central European beech forests? *Bulletin of Entomological Research*, *105*(1), 101–109. https://doi.org/10.1017/S0007485314000741

Pickett, S. T. A., & White, P. S. (1985). *The ecology of natural disturbance and patch dynamics*. Academic Press. https://doi.org/10.1016/C2009-0-02952-3

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*(2), 231–240. https://doi.org/10.1007/s10342-012-0670-1

Przepiora, F., & Ciach, M. (2025). *Bark beetles as ecosystem engineers: Triggered tree mortality rearranges the assemblage of Tree-related Microhabitats in old-growth coniferous forest* (p. 2025.04.11.648382). bioRxiv. https://doi.org/10.1101/2025.04.11.648382

R Core Team. (2025). *R: A Language and Environment for Statistical Computing*[Computer software]. R Foundation for Statistical Computing. https://www.R-project.org/

Roques, A., Ren, L., Rassati, D., Shi, J., Akulov, E., Audsley, N., Auger-Rozenberg, M.-A., Avtzis, D., Battisti, A., Bellanger, R., Bernard, A., Bernadinelli, I., Branco, M., Cavaletto, G., Cocquempot, C., Contarini, M., Courtial, B., Courtin, C., Denux, O., … Millar, J. G. (2023). Worldwide tests of generic attractants, a promising tool for early detection of non-native cerambycid species. *NeoBiota*, *84*, 169–209. https://doi.org/10.3897/neobiota.84.91096

Sallé, A., Cours, J., Le Souchu, E., Lopez-Vaamonde, C., Pincebourde, S., & Bouget, C. (2021). Climate change alters temperate forest canopies and indirectly reshapes arthropod communities. *Frontiers in Forests and Global Change*, *4*, 120. https://doi.org/10.3389/ffgc.2021.710854

Sallé, A., Parmain, G., Nusillard, B., Pineau, X., Brousse, R., Fontaine-Guenel, T., Ledet, R., Vincent-Barbaroux, C., & Bouget, C. (2020). Forest decline differentially affects trophic guilds of canopy-dwelling beetles. *Annals of Forest Science*, *77*(3), 86. https://doi.org/10.1007/s13595-020-00990-w

Samaniego, L., Thober, S., Kumar, R., Wanders, N., Rakovec, O., Pan, M., Zink, M., Sheffield, J., Wood, E. F., & Marx, A. (2018). Anthropogenic warming exacerbates European soil moisture droughts. *Nature Climate Change*, *8*(5), 421–426. https://doi.org/10.1038/s41558-018-0138-5

Sbaraglia, C., Thorn, S., Ambrožová, L., Bässler, C., Čížek, L., Kozel, P., Procházka, J., & Drag, L. (2025). Sun exposure as a main driver influencing the arriving communities of saproxylic beetles on deadwood. *Ecological Entomology*, *50*(3), 565–576. https://doi.org/10.1111/een.13428

Seibold, S., Bässler, C., Brandl, R., Büche, B., Szallies, A., Thorn, S., Ulyshen, M. D., & Müller, J. (2016). Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *Journal of Applied Ecology*, *53*(3), 934–943. https://doi.org/10.1111/1365-2664.12607

Seibold, S., Gossner, M. M., Simons, N. K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J. C., Linsenmair, K. E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., & Weisser, W. W. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, *574*(7780), 7780. https://doi.org/10.1038/s41586-019-1684-3

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M. J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T. A., & Reyer, C. P. O. (2017). Forest disturbances under climate change. *Nature Climate Change*, *7*(6), 6. https://doi.org/10.1038/nclimate3303

Senf, C., Buras, A., Zang, C. S., Rammig, A., & Seidl, R. (2020). Excess forest mortality is consistently linked to drought across Europe. *Nature Communications*, *11*(1), 1. https://doi.org/10.1038/s41467-020-19924-1

Senf, C., Pflugmacher, D., Zhiqiang, Y., Sebald, J., Knorn, J., Neumann, M., Hostert, P., & Seidl, R. (2018). Canopy mortality has doubled in Europe's temperate forests over the last three decades. *Nature Communications*, *9*(1), 1. https://doi.org/10.1038/s41467-018-07539-6

Siitonen, J., Martikainen, P., Punttila, P., & Rauh, J. (2000). Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *Forest Ecology and Management*, *128*(3), 211–225. https://doi.org/10.1016/S0378-1127(99)00148-6

Similä, M., Kouki, J., & Martikainen, P. (2003). Saproxylic beetles in managed and seminatural scots pine forests: Quality of dead wood matters. *Forest Ecology and Management*, *174*(1), 365–381. https://doi.org/10.1016/S0378-1127(02)00061-0

Sire, L., Yáñez, P. S., Wang, C., Bézier, A., Courtial, B., Cours, J., Fontaneto, D., Larrieu, L., Bouget, C., Thorn, S., Müller, J., Yu, D. W., Monaghan, M. T., Herniou, E. A., & Lopez-Vaamonde, C. (2022). Climate-induced forest dieback drives compositional changes in insect communities that are more pronounced for rare species. *Communications Biology*, *5*(1), 1. https://doi.org/10.1038/s42003-021-02968-4

Stokland, J. N., Siitonen, J., & Jonsson, B. G. (2012). *Biodiversity in dead wood*. Cambridge University Press. https://doi.org/10.1017/CBO9781139025843

Swanson, M. E., Franklin, J. F., Beschta, R. L., Crisafulli, C. M., DellaSala, D. A., Hutto, R. L., Lindenmayer, D. B., & Swanson, F. J. (2011). The forgotten stage of forest succession: Early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment*, *9*(2), 117–125. https://doi.org/10.1890/090157

Thorn, S., Bässler, C., Bernhardt-Römermann, M., Cadotte, M., Heibl, C., Schäfer, H., Seibold, S., & Müller, J. (2016). Changes in the dominant assembly mechanism drive species loss caused by declining resources. *Ecology Letters*, *19*(2), 163–170.

Thorn, S., Bässler, C., Brandl, R., Burton, P. J., Cahall, R., Campbell, J. L., Castro, J., Choi, C.-Y., Cobb, T., Donato, D. C., Durska, E., Fontaine, J. B., Gauthier, S., Hebert, C., Hothorn, T., Hutto, R. L., Lee, E.-J., Leverkus, A. B., Lindenmayer, D. B., … Müller, J. (2018). Impacts of salvage logging on biodiversity: A meta-analysis. *Journal of Applied Ecology*, *55*(1), 279–289. https://doi.org/10.1111/1365-2664.12945

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, Ecology of Mountain Forest Ecosystems in Europe*, *388*, 113–119. https://doi.org/10.1016/j.foreco.2016.06.006

Thorn, S., Chao, A., Georgiev, K. B., Müller, J., Bässler, C., Campbell, J. L., Castro, J., Chen, Y.-H., Choi, C.-Y., Cobb, T. P., Donato, D. C., Durska, E., Macdonald, E., Feldhaar, H., Fontaine, J. B., Fornwalt, P. J., Hernández, R. M. H., Hutto, R. L., Koivula, M., … Leverkus, A. B. (2020). Estimating retention benchmarks for salvage logging to protect biodiversity. *Nature Communications*, *11*(1), 1.

Turchin, P., & Odendaal, F. J. (1996). Measuring the effective sampling area of a pheromone trap for monitoring population density of southern pine beetle (Coleoptera: Scolytidae). *Environmental Entomology*, *25*(3), 582–588. https://doi.org/10.1093/ee/25.3.582

Turner, M. G. (2010). Disturbance and landscape dynamics in a changing world. *Ecology*, *91*(10), 2833–2849.

Turner, M. G., & Seidl, R. (2023). Novel disturbance regimes and ecological responses. *Annual Review of Ecology, Evolution, and Systematics*, *54*(1), 63–83. https://doi.org/10.1146/annurev-ecolsys-110421-101120

Viljur, M.-L., Abella, S. R., Adámek, M., Alencar, J. B. R., Barber, N. A., Beudert, B., Burkle, L. A., Cagnolo, L., Campos, B. R., Chao, A., Chergui, B., Choi, C.-Y., Cleary, D. F. R., Davis, T. S., Dechnik-Vázquez, Y. A., Downing, W. M., Fuentes-Ramirez, A., Gandhi, K. J. K., Gehring, C., … Thorn, S. (2022). The effect of natural disturbances on forest biodiversity: An ecological synthesis. *Biological Reviews*, *97*(5), 1930–1947. https://doi.org/10.1111/brv.12876

Vuidot, A., Paillet, Y., Archaux, F., & Gosselin, F. (2011). Influence of tree characteristics and forest management on tree microhabitats. *Biological Conservation*, *144*(1), 441–450. https://doi.org/10.1016/j.biocon.2010.09.030

Wermelinger, B., Duelli, P., & Obrist, M. K. (2002). Dynamics of saproxylic beetles (Coleoptera) in windthrow areas in alpine spruce forests. *Forest Snow and Landscape Research*, *77*, 133–148.

Wermelinger, B., Obrist, M. K., Duelli, P., Schneider Mathis, D., & Gossner, M. M. (2025). Two decades of arthropod biodiversity after windthrow show different dynamics of functional groups. *Journal of Applied Ecology*, *62*(2), 371–387. https://doi.org/10.1111/1365-2664.14860

Weslien, J., Djupström, L. B., Schroeder, M., & Widenfalk, O. (2011). Long-term priority effects among insects and fungi colonizing decaying wood. *Journal of Animal Ecology*, *80*(6), 1155–1162. https://doi.org/10.1111/j.1365-2656.2011.01860.x

Zemlerová, V., Kozák, D., Mikoláš, M., Svitok, M., Bače, R., Smyčková, M., Buechling, A., Martin, M., Larrieu, L., Paillet, Y., Roibu, C.-C., Petritan, I. C., Čada, V., Ferenčík, M., Frankovič, M., Gloor, R., Hofmeister, J., Janda, P., Kameniar, O., … Svoboda, M. (2023). Natural disturbances are essential determinants of tree-related microhabitat availability in temperate forests. *Ecosystems*, *26*, 1260–1274. https://doi.org/10.1007/s10021-023-00830-8

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Mean and range values (bold line = confidence interval at 95%, thin line = range of the minimum and maximum values) of the explanatory variables. Deadwood volume is presented in $m^3.ha^{-1}$. The abundance of TreMs is to understand as the number of trees bearing the specific set of TreMs, in $nb.ha^{-1}$.

Figure S2. Mean and range values (bold line = confidence interval at 95%, thin line = range of the minimum and maximum values) of the response variables.

Figure S3. Spearman's correlation between the predictors (left: woody elements, right: TreMs) tested in SEMs, for each context. Only the significant correlations are shown (at $p < 0.05$).

Figure S4. Spearman's correlation between biodiversity variables in fir-dominated forests.

Figure S5. Spearman's correlation between biodiversity variables in spruce-dominated forests.

Figure S6. Spearman's correlation between biodiversity variables in oak-dominated forests.

Figure S7. Characteristics of woody substrates in each forest context. Average values and confidence interval based on substrate trait data.

Figure S8. List of species in fir-dominated forests and their abundance (log-transformed) within each studied plot. Classes of forest mortality.

Figure S9. List of species in spruce-dominated forests and their abundance (log-transformed) within each studied plot. Classes of forest mortality.

Figure S10. List of species in oak-dominated forests and their abundance (log-transformed) within each studied plot. Classes of forest mortality.

Table S1. Sampling coverage (SC) for each plot for each forest context. (In spruce forest context, T3_5 has been removed due to too low sampling coverage for the subsequent analysis).

Table S2. Sample completeness chosen for overall community and ecologic guilds in each context.

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