Contrasting responses of habitat conditions and insect biodiversity to pest- or climate-induced dieback in coniferous mountain forests

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Highlights

- We examined effects of dieback and salvage logging in two montane coniferous forests.
- The composition of saproxylic beetles seemed highly modified by severe diebacks.
- The severity and spatial extent of diebacks seemed to influence the beetles response.
- The more severe the dieback, the greater the deadwood amount and the canopy opens.
- We invite foresters to conserve biological legacies through deadwood-rich areas.

Abstract

Natural disturbances are major drivers of forest dynamics. However, in the current context of anthropogenic global warming, shifts in disturbance regimes are expected. Natural disturbances usually leave biological or structural legacies which are important for early-successional species. Nevertheless, these legacies are usually eliminated by forest managers through salvage logging. Here, we investigated the consequences of forest dieback and the following salvage logging on both forest habitat conditions and saproxylic beetle communities.

We conducted our study in two types of conifer-dominated highland forests: Pyrenean silver fir (*Abies alba*) which has suffered drought-induced dieback and Bavarian Norway spruce (*Picea abies*) which has suffered bark beetle-induced (*Ips typographus*) dieback.

In both of the forest contexts, dieback provided a biological legacy through an increase in deadwood resources; however, this increase was much greater in the spruce forests. Nonetheless, despite this increase in resources, neither type of forest gained in total abundance or species richness after disturbance, compared to healthy stands. Nevertheless, the species composition of saproxylic beetle composition was significantly affected by dieback in spruce stands, but not in the silver fir forests. In the spruce plots, saproxylic beetles responded positively to the large increase in deadwood in the declining stands, including a very strong positive response from red-listed species. Saproxylic beetle assemblages in spruce forests were mainly drove by canopy openness and deadwood amount. In the silver fir plots, we did not observed responses from the saproxylic beetle communities to deadwood amount increase. This lack of response may be explained by the relatively low amount of deadwood generated by the drought-induced dieback.

Concerning salvage logging, it caused stronger contrasts in spruce forests than in silver fir forests, where it generally had no significant impact. For example, in spruce forests, salvage logging reduced the density of large snags by 91% and large logs by 87% compared with unharvested declining plots. Most of the significant environmental effects on biodiversity associated with dieback were no longer significant after accounting for the salvaged plots in our study data.

Then, forest dieback and salvage logging induced much sharper and stronger effects on environmental and community metrics in the spruce than in the silver fir forests. The contrast between Bavaria and the French Pyrenees seems partly related to dieback severity. Finally, we invite forest managers to conserve biological and structural legacies through patches of deadwood-rich areas.

Keywords: Forest dieback; Salvage logging; Saproxylic beetles; Deadwood; Climate change; Drought; Bark beetles; Biological legacy; Early-successional forest

Résumé

Les perturbations naturelles sont des composantes majeures des dynamiques forestières. Cependant, dans le contexte actuel de réchauffement global anthropique, des changements importants des régimes de perturbation sont attendus. Les perturbations naturelles laissent généralement des héritages biologiques et structurelles qui sont cruciaux pour les espèces de début de succession. Néanmoins, ces héritages sont traditionnellement éliminés par les gestionnaires forestiers aux travers de coupes de récupération. Dans cette étude, nous avons étudié les conséquences des dépérissements forestiers et des coupes de récupération qui s'ensuivent sur les conditions d'habitat et les communautés de coléoptères saproxyliques.

Nous avons conduit notre étude dans deux types de forêts de montagne à dominance résineuse: les sapinières pyrénéennes (*Abies alba*) qui ont souffert de sécheresses, et les pessières bavaroises (*Picea abies*) qui ont souffert d'épidémies du scolyte typographe (*Ips typographus*).

Dans les deux contextes forestiers, le dépérissement a fourni des héritages biologiques sous la forme d'une augmentation des ressources en bois mort; cependant, cette augmentation était bien plus importante dans les forêts d'épicéas. Néanmoins, malgré cette augmentation de ressource, aucun des contextes forestiers n'avait gagné d'abondance totale ou de richesse spécifique après dépérissement, en comparaison des peuplements sains. En revanche, les compositions en espèces de coléoptères saproxyliques étaient significativement affectées par le dépérissement dans les peuplements d'épicéas, mais pas dans les peuplements de sapins pyrénéens. En pessière, les coléoptères saproxyliques ont répondu positivement à l'importante augmentation du bois mort dans les peuplements dépérissants, incluant une très forte réponse positive des espèces classées sur liste rouge. Les assemblages de coléoptères saproxyliques dans les peuplements d'épicéas étaient principalement déterminés par l'ouverture de la canopée et la quantité de bois mort. Dans les peuplements de sapins ; nous n'avons pas observé de réponses de la part des communautés de coléoptères saproxyliques, à l'augmentation de bois mort. Ce manque de réponse peut s'expliquer par la quantité relativement faible de bois mort généré par le dépérissement induit par la sécheresse.

Les coupes de récupération ont provoqué des contrastes plus forts dans les forêts d'épicéas que dans les forêts de sapins, où il n'a généralement pas eu d'impact significatif. Par exemple, dans les forêts d'épicéas, les coupes de récupération ont réduit les densités des chandelles de gros diamètre de 91% et des grosses pièces de bois mort au sol de 87%, en comparaison des peuplements dépérissants non-exploités. La plupart des effets environnementaux significatifs sur la biodiversité associée au dépérissement n'étaient plus significatifs après avoir pris en compte les coupes de récupération.

Par conséquent, le dépérissement forestier et les coupes de récupération ont induit des effets beaucoup plus marqués et forts sur les paramètres environnementaux et de communautés dans les peuplements d'épicéas que dans les peuplements de sapins. Le contraste entre la Bavière et les Pyrénées françaises semble en partie lié à la sévérité du dépérissement. Enfin, nous invitons les gestionnaires forestiers à conserver les héritages biologiques et structurels par le biais d'îlots riches en bois mort.

Mots clés: Dépérissement forestier; Coupe de récupération; Coléoptères saproxyliques; Bois mort; Changement climatique; Sécheresse; Scolytes; Héritage biologique; Forêt en début de succession

1 Introduction

Natural disturbances such as droughts, storms or pest outbreaks are major drivers of forest dynamics (Chapin et al., 2011; Pickett and White, 1985). However, in the current context of anthropogenic global warming, shifts in disturbance regimes are expected (Sallé et al., 2014; Samaniego et al., 2018). Droughts in Europe will increase in area, duration and frequency as a result of global warming (Samaniego et al., 2018). Higher temperatures are likely to have direct positive impacts on insect pest species through lower winter mortality and higher voltinism (Bale et al., 2002; Jönsson et al., 2009), and distribution ranges are shifting northward (Robinet et al., 2007). Since climate change is more rapid in mountain regions (twice as fast as in other terrestrial regions; Auer et al., 2007), upland forests are important sentinels for monitoring.

Though the consequences of disturbances are often deemed destructive in terms of habitat, leading to "biodiversity loss" (Lehnert et al., 2013), from a conservation perspective, natural disturbances could have a

positive impact on forest habitats and associated biodiversity (Kulakowski et al., 2017; Lindenmayer et al., 2006; Swanson et al., 2011; Thorn et al., 2017). Natural disturbances leave biological and/or structural legacies (i.e. "*the organisms, organic materials, and organically-generated environmental patterns that persist through a disturbance and are incorporated into the recovering ecosystem*"; Franklin et al., 2000), which depend both on the forest characteristics prior to the disturbance and on the disturbance itself. For example, the main biological legacies from bark beetle outbreaks and windstorms are respectively snags (standing dead trees) and logs (downed dead trees), both of which lead to an overall increase in deadwood amount and in stand structural heterogeneity on a large spatial scale (Swanson et al., 2011; Thorn et al., 2017).

Forest managers usually respond to such natural disturbances with salvage logging in order to recover the economic value that would otherwise be lost but also to control insect pests by removing infected trees (Lindenmayer et al., 2008; Müller et al., 2019; Thorn et al., 2018). Thus, natural disturbances could supply more resources (i.e. deadwood) for some organisms such as saproxylic insects, which are particularly at risk in heavily managed forests (Grove, 2002; Stokland et al., 2012), while salvage logging would affect them negatively (Thorn et al., 2018). Indeed, by avoiding the recruitment of biological legacies such as large dying trees, snags and logs, salvage logging reduces saproxylic habitat and connectivity, and homogenizes landscape configuration (Leverkus et al., 2020; Lindenmayer et al., 2008; Thorn et al., 2018).

Since biological and structural legacies appear to be very important for the recruitment of early-successional species (e.g. Fontaine et al., 2009; Kortmann et al., 2018 for birds; Wentzel et al., 2019 for bats; Thorn et al., 2016 for arthropods and Thom and Seidl, 2016 for a broader perspective), it seems very important to retain specific legacies after natural disturbances. However, the current lack of studies on how different sources of disturbance change habitat conditions and, as a result, biodiversity, does not allow us to identify important biological and structural legacies.

We investigated the effects of two types of forest dieback followed by salvage logging on both habitat conditions and saproxylic beetle communities, a group that we expected to respond to natural disturbances modifying the habitat (canopy opening, amount of deadwood; Bouget et al., 2014; Lassauce et al., 2011). We studied forest dieback caused by (i) warming-related drought stress in forests dominated by silver fir (*Abies alba* Mill.) in the French Pyrenees (Camarero et al., 2011), and by (ii) bark beetle outbreaks (following a windstorm in Bavarian Norway spruce forests (*Picea abies* (L.) H.Karst.); Müller et al., 2008, 2010; Thorn et al., 2014).

Firstly, we analysed the effects of the two types of natural disturbances plus the anthropogenic disturbance (i.e. salvage logging) on habitat conditions. Secondly, we studied the effect of the disturbance and salvage logging on the saproxylic beetle communities in the forest.

Finally, we proceeded to a broader ecological analysis by addressing three questions:

1. Do effects on saproxylic beetle community metrics relate to a change in habitat quantity or heterogeneity caused by disturbances?

2. Are the ecological relations between environmental conditions and saproxylic beetle community observed under forest dieback process still significant after salvage logging operations?

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3. Do saproxylic beetle communities react in the same way to the changing environments in both studied contexts of natural disturbance (drought stress and bark beetle outbreaks) ?

2 Materials and methods

2.1 Study area and study sites

The study was conducted in two types of conifer-dominated highland forests undergoing severe dieback: silver fir forests in the Pyrenees (southwestern France) and Norway spruce forests in Bavaria (southeastern Germany; Fig. 1).
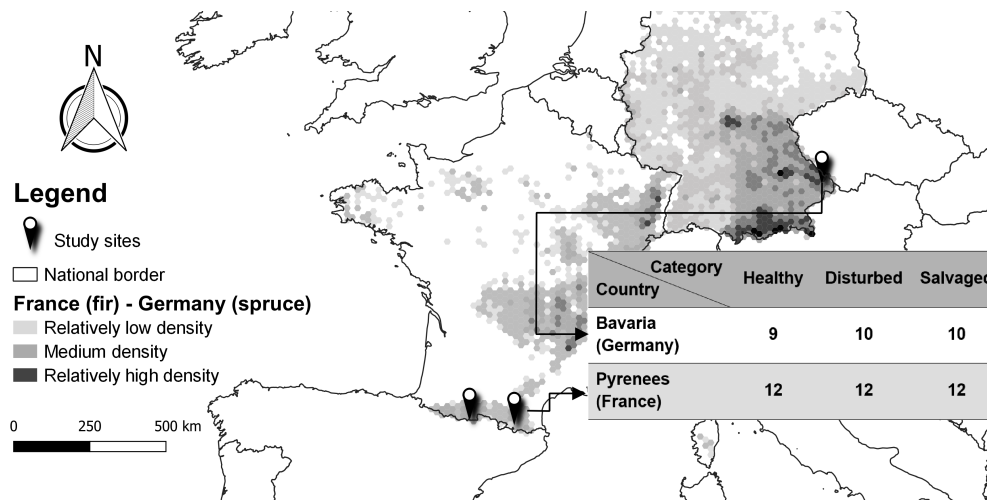

Figure 1: *Map showing the study sites in Germany (Bavaria) and in France (Pyrenees) and the number of plots for each country and each stand category. Mapping was performed in QGIS 3.10. Hexagonal binning was based on GBIF data for Abies alba in France and for Picea abies in Germany (GBIF.org, 2020).*

In France, the study plots were divided into two distinct zones (Fig. 1): 17 plots in the Aure Valley in Central Pyrenees (960—1481 m a.s.l., 1265 m on average), and 19 on the Sault Plateau in the Eastern Pyrenees (705—1557 m a.s.l., 1013 m on average). Forests cover 50% of the Aure Valley area and 73% of the Sault Plateau area. Silver fir stands occupy 50% and 75% of the two forest areas, respectively. In the study plots, dieback mainly occurred after the 2003 drought.

In Germany, 29 study plots were installed in the Bavarian Forest National Park (660 m to 1352 m above sea level, 1084 m on average). Forests cover about 98% of the Park area (Bässler et al., 2009). In hilly and higher montane sites, more than 80% of the forests are dominated by Norway spruce (*Picea abies* (L.) H. Karst), whereas in lower altitudes, forests are a mix of Norway spruce (58%) and three main secondary species: common beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Mill.) and mountain ash (*Sorbus aucuparia* L.). In the Bavarian plots, forest dieback was mainly caused by massive outbreaks of the bark beetle *Ips typographus* L. (Coleoptera, Curculionidae, Scolytinae), which occurred in 2001 (±5 years) in unharvested plots and in 2009 (±4 years) in salvaged plots.

In both countries, the plots were divided into three categories: undisturbed forests ("healthy"), unharvested disturbed forests ("disturbed") and harvested (salvage logging) disturbed forests ("salvaged"; Fig. 1).

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2.2   Beetle sampling and identification

We sampled saproxylic beetles with one (Bavaria) or two (Pyrenees) flight-interception traps per plot. The traps consisted of a crossed pair of transparent plastic shields (40 × 60 cm) above a funnel leading into a container with an unbaited preservative (50% propylene glycol and 50% salt water with detergent). The traps were hung roughly 1.5 m above the ground in the centre of each plot from April to October for one sampling year only, in 2016 in Bavaria and in 2017 in the French Pyrenees. All the saproxylic beetles collected were identified to the highest possible taxonomic level (French dataset: G.P. and external experts; German dataset: Alexander Szallies). For the sake of balance, we drew a random subset of one trap per plot in the Pyrenean dataset *a posteriori*.

2.3   Species traits

We used the FRISBEE database to characterise species ecological traits: feeding guilds (zoophagous, xylophagous, saproxylophagous) and substrate guilds (cavicolous, xylofungicolous, flower-visitor) (Bouget et al., 2019). To distinguish between rare and common species, we used the FRISBEE database for French data (rare species have a patrimonial value ≥ 3; Brustel, 2001) and the red list status for Bavarian data (species are classified as "rare" if above the "of least concern" IUCN category; Seibold et al., 2015; Tab. 1).
We extracted quantitative niche trait values from Gossner et al. (2013) and Janssen et al. (2017) for preferences in terms of deadwood diameter, deadwood decay stage and forest canopy openness. For each plot and each niche trait, we calculated two multidimensional indices: community-level weighted means (CWM), defined as the mean of the trait values weighted by the relative abundance of each species bearing each value; and functional dispersion (FD), i.e. the mean distance of each individual species from the weighted centroid of all species in the assemblage (dbFD function, FD R-package; Laliberté et al., 2014).

2.4   Environmental variables

Stand variables associated to living and microhabitat-bearing trees were measured according to standardized protocols, whereas deadwood metrics were assessed with slightly different methods in the two regions.

2.4 Environmental variables

Table 1: *Overview of the response variables used in our study (mean and range in Bavarian Norway spruce and Pyrenean silver fir datasets); CWM = Community-Weighted Means; FD = Functional Dispersion; rare species = patrimonial value ≥ 3 in France and red-listed in Germany.*

Variable name	Short description	Pyrenees (silver fir)		Bavaria (Norway spruce)	
		Mean ± se	Range (min - max)	Mean ± se	Range (min - max)
Total Ab.	Abundance of all saproxylic beetles	451 ± 46	74—1517	120 ± 15	19—304
Total SR	Species richness of all saproxylic beetles	58 ± 2	37—93	32 ± 2	10—57
Rare sp. Ab.	Abundance of rare saproxylic beetles	11.4 ± 3.1	0—104	8.2 ± 2	0—37
Rare sp. SR	Species richness of rare saproxylic beetles	3.8 ± 0.3	0—9	2.7 ± 0.5	0—9
CWM wood diameter	Mean trait value of deadwood diameter preference	2.24 ± 0.03	1.9—2.5	2.31 ± 0.05	1.26—2.58
FD wood diameter	Trait variance of deadwood diameter preference	0.53 ± 0.03	0.18—0.98	0.67 ± 0.03	0.3—1.13
CWM wood decay	Mean trait value of deadwood decay preference	2.53 ± 0.05	2.04—3.25	2.94 ± 0.06	2.04—3.25
FD wood decay	Trait variance of deadwood decay preference	0.71 ± 0.03	0.37—0.96	0.79 ± 0.04	0.32—1.19
CWM canopy	Mean trait value of canopy-openness preference	1.68 ± 0.02	1.37—1.88	1.84 ± 0.03	1.58—2.22
FD canopy	Trait variance of canopy-openness preference	0.74 ± 0.03	0.36—1.17	0.92 ± 0.05	0.32—1.47
Cavicol. Ab.	Abundance of strict cavicolous beetles	24.5 ± 2.9	3—76	8.7 ± 1.4	1—33
Cavicol. SR	Species richness of strict cavicolous beetle	7.2 ± 0.5	2—13	3.4 ± 0.4	1—9
Xylofungicol. Ab.	Abundance of strict xylofungicolous beetles (all the species living in fungi, whatever the trophic guild)	96 ± 9	25—245	34 ± 9	4—264
Xylofungicol. SR	Species richness of xylofungicolous beetle	21 ± 1	7—33	12.5 ± 1	4—27
Floricol. Ab.	Abundance of flower-visiting beetles	12.6 ± 1.7	3—57	35 ± 6.5	1—129
Floricol. SR	Species richness of flower-visiting beetles	6 ± 0.5	1—15	7 ± 0.7	1—15
Zoophag. Ab.	Abundance of zoophagous beetles	84 ± 10	19—227	42 ± 6.5	4—135
Zoophag. SR	Species richness of zoophagous beetles	21.6 ± 1.1	13—41	11.5 ± 1	3—24
Conif. Xyloph. Ab.	Abundance of conifer xylophagous beetles	105 ± 25	6—836	25 ± 6.8	1—175
Conif. Xyloph. SR	Species richness of conifer xylophagous beetles	6.4 ± 0.4	2—12	5 ± 0.6	1—16
Pest sp. Ab.	Abundance of pest species	42 ± 10	1—310	23 ± 7	1—174

Firstly, we applied a relascope sampling protocol in Bavaria and the Pyrenees to record living or dying trees (≥ 17.5 cm in DBH), dead trees, snags (> 4 m in height; DBH ≥ 7.5 cm), and high stumps (height < 4 m and > 1 m; DBH ≥ 7.5 cm). Relascopic sampling is characterized by a variable sampling radius and the use of a dendrometer linked to a basal area factor (one in the case of our study; Bitterlich, 1984; Piqué et al., 2011). In relascopic sampling, the probability that each tree is included in the plot is proportional to its diameter (Piqué et al., 2011). For each element, we recorded DBH, tree species, status (living tree, dying tree, snag, high stump, log), decay class for deadwood (4 categories from fresh deadwood to significantly decayed deadwood), and TreMs (tree-related microhabitats) borne on living trees and snags. All variables whose name ends with "0.3 ha" were evaluated with the relascope sampling protocol, 0.3 ha being the approximate area explored with the method (Tab. 2).

In addition, in both regions, we applied a protocol related to the Index of Biodiversity Potential (Gosselin and Larrieu, 2020; Larrieu and Gonin, 2008) to perform an exhaustive survey of tree-related microhabitats

2.4 *Environmental variables*

(TreMs; Larrieu et al., 2018), large deadwood pieces (snags and logs ≥ 37.5 cm in diameter 1 m from the largest end) and number of strata covering ≥ 20% of the area in a 1-ha circle centred on each plot. Canopy openness, defined as the total proportion of open area providing flower resources, was also assessed in this 1-ha plot. Variables whose name ends with "1ha" were assessed with this protocol (Tab. 2).

Table 2: *Overview of the environmental predictors used in our study (mean and range in Bavarian Norway spruce and Pyrenean silver fir datasets); DW = deadwood; TreM = Tree-related Microhabitat.*

Predictor name	Short description	Unit	Pyrenees (silver fir)		Bavaria (Norway spruce)	
			Mean ± se	Range (min - max)	Mean ± se	Range (min - max)
DW vol. 0.3 ha	Total volume of deadwood in a 0.3-ha plot	$m^3.ha^{-1}$	51 ± 9	3—220	125 ± 25	0.5—435
Snag vol. 0.3 ha	Volume of standing deadwood (> 7.5 cm in diameter) in a 0.3-ha plot	$m^3.ha^{-1}$	19 ± 4	0—106	60.5 ± 15	0—325
Snag density 1 ha	Number of large standing deadwood pieces (> 37.5 cm in diameter) in a 1-ha plot	$nb.ha^{-1}$	8.6 ± 1.3	0—34	34 ± 7.5	1—129
Log vol. 0.3 ha	Volume of downed deadwood (> 17.5 cm in diameter) in a 0.3-ha plot	$m^3.ha^{-1}$	32 ± 6	0—151	65 ± 13	0—220
Log density 1 ha	Number of large lying deadwood pieces (> 37.5 cm in diameter) in a 1-ha plot	$nb.ha^{-1}$	13.9 ± 1.4	3—36	25 ± 5	1—88
DW diversity 0.3 ha	Number of deadwood types (tree species*diameter*decay*position)	nb	7.6 ± 0.8	1—27	7.5 ± 0.7	1—15
Dead trees rel. BA 0.3 ha	Proportion of dead trees in total basal area in a 0.3-ha plot	%	6.2 ± 1.1	1.3—32.3	32 ± 7	1.7—98.3
Dead trees BA 0.3 ha	Basal area of dead trees (snags) in a 0.3-ha plot (> 10 cm in diameter)	$m^2.ha^{-1}$	3.6 ± 0.6	0—14	10.8 ± 2.4	0—46
Living trees BA 0.3 ha	Basal area of living trees in a 0.3-ha plot (≥17.5 cm in diameter)	$m^2.ha^{-1}$	30.4 ± 2	15—66	16.7 ± 3.6	0—61
Canopy openness 1 ha	Cumulative proportion of open areas (clearings, edges, areas with a well-developed herb layer composed of flowering plants) in a circular 1-ha plot	%	26 ± 4	1.8—79	52 ± 7	2.5—98
Sapro TreM density 1 ha	Total density of saproxylic microhabitat-bearing trees in a 1-ha plot	$nb.ha^{-1}$	3.7 ± 0.7	0—22	1.9 ± 0.45	0—8
Sapro TreM diversity 1 ha	Diversity of saproxylic microhabitat in a 1-ha plot	nb	3.3 ± 0.3	0—7	1.8 ± 0.3	0—5
Polypore density 0.3 ha	Density of fungus-bearing trees in a 1-ha plot (fruiting bodies of tough or pulpy saproxylic fungi)	$nb.ha^{-1}$	26 ± 8	0—249	39 ± 9	0—283
Cavity density 1 ha	Density of cavity-bearing trees in a 1-ha plot (woodpecker breeding and feeding holes, cavities with mould with an entrance above 10 cm in width)	$nb.ha^{-1}$	2 ± 0.5	0—14	1.3 ± 0.35	0—6

Among a list of 47 TreM types recorded (Larrieu et al., 2018), we selected a subset known to be important to saproxylic beetles (Stokland et al., 2012) and left out epiphytic structures (like mistletoe) and buttress-root concavities (Larrieu et al., 2018).

Downed log volume was based on the census from the relascope sampling method in the Pyrenees, and on data from the fixed-area plots (0.1 ha) in Bavaria. Fixed-area protocol is characterized by a fixed sampling radius and an equal probability that each tree is included in the plot (Piqué et al., 2011). We defined deadwood diversity as the number of combinations crossing the following deadwood features: status (lying or standing

deadwood, crown deadwood), decay stage, diameter class and tree species, as suggested by Siitonen et al. (2000).
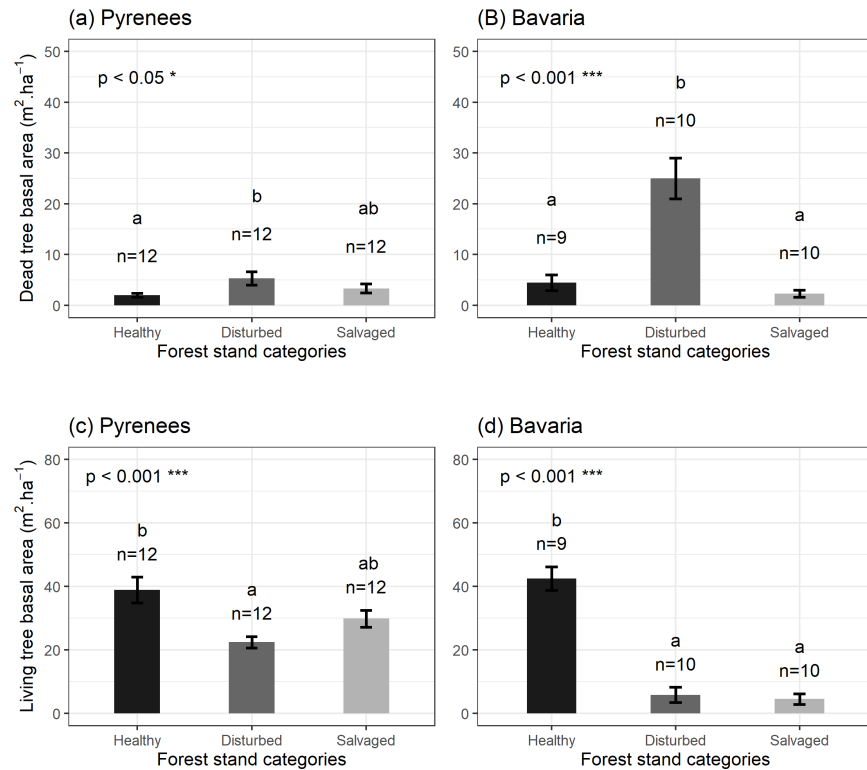

Figure 2: *Basal area (m^2.ha^{-1}) of dead trees (a, b) and living trees (c, d) in the 0.3-ha plots for each country and each stand category. Dead trees (snags) more than 7.5 cm in diameter are included. Letters indicate significant differences between each category (p value top-left). The letters result from post-hoc Tukey tests on generalized (negative binomial) linear mixed models.*

2.5 Statistical analysis

Data analysis was conducted with R software 4.0.0 (R Core Team, 2023). In each country, we split our dataset into two subsets to study two different processes and their effects on forest stand features and on saproxylic beetle communities (Fig. S.1): the "dieback" subset merging healthy and declining plots to assess the dieback effect, and the "salvage" subset merging declining and salvaged plots to test the effect of salvage logging operations.

For each response variable (abundance and species richness of feeding and substrate guilds, niche trait guilds, abundance and species richness of saproxylic beetles as a whole and of rare or red-listed species), we first selected the best fitting error structure with the fitdist function from the fitdistrplus R-package (Delignette-Muller et al., 2019). For the French data, we implemented generalized linear mixed models with "site" (Aure Valley or Sault Plateau) as a random variable (glmmTMB R package; Magnusson et al., 2020) to deal with "over-dispersion" for count variables (Bates et al., 2020). For the Bavarian dataset, as we only analysed a single geographical location, we used "glm" and "glm.nb" (MASS R package) in case of "over-dispersion"

(Ripley et al., 2020).

We explored the influence of forest stand features associated to dieback or salvage logging effects (Fig. S.1) on a subset of non-collinear variables (log of "Snag vol. 0.3 ha", "Lying dead wood diversity", "Log density 1 ha", "Canopy openness 1 ha", "Sapro TreM density 1 ha", "Sapro TreM density 0.3 ha", "Living trees BA 0.3 ha"; "check_collinearity" function, performance R-package; Lüdecke et al., 2020). We then selected the best model for each saproxylic beetle guild in the "dieback" subset ("dredge" function, MuMin R-package; Bartoń, 2020). In a second step, we ran each best model on data from the "salvage" subset only to check if the environmental effects related to dieback were still significant after salvage logging (Fig. S.1). We extracted parameter estimates and p-values ("model.avg" function, MuMin R package) and carried out a Holm p.value adjustment ("p.adjust" function).

To determine if the species composition of saproxylic beetle assemblages was influenced by dieback category (i.e. "healthy", "unsalvaged declining" and "salvaged declining" plots) and stand features, we performed NMDS (Nonmetric Multidimensional Scaling) and CAP (Canonical Analysis of Principal coordinates) ordinations and PERMANOVA analyses (Anderson and Walsh, 2013), based on between-plot Bray-Curtis distance matrices (vegan R-package; vegdist, metaMDS, capscale, adonis functions Oksanen et al., 2022). Through the CAP ranking of the environmental variables in line with their total contribution to inertia, including inertia co-explained with other variables, we evaluated the drivers of the variations in species composition in the "dieback" and "salvage" subsets. We also assessed the range of dissimilarity values within each dieback category in each country (vegan R-package, anosim function).

3   Results

Our final dataset comprised 16,075 specimens of 393 saproxylic beetle species belonging to 50 families in the Pyrenees and 3,470 specimens of 230 saproxylic beetle species belonging to 40 families in Bavaria.

3.1   Effects of forest dieback and salvage logging on stand metrics

Overall, forest dieback induced sharper environmental effects in Bavarian spruce than in Pyrenean silver fir forests, especially on the deadwood component but also on stand structure and TreMs. As expected, forest dieback led to a significant decrease in the basal area of living trees in both silver fir and spruce forests, and a parallel increase in various deadwood-related parameters: basal area of dead trees, lying deadwood volume (0.3-ha-scale), total deadwood volume and, to a lesser extent, deadwood diversity (0.3-ha-scale), and density of large snags and, to a lesser extent, of large logs (1-ha-scale; Fig. 3). In addition, declining spruce forests showed a significant increase in standing deadwood volume (0.3-ha-scale), relative basal area of dead trees, density of fungus-bearing trees and canopy openness, with a decrease in the density of saproxylic microhabitat-bearing trees and cavity-bearing trees, in particular (Fig. 3).

Salvage logging in Norway spruce declining stands had significant impacts on stand metrics. Even though it did not affect canopy openness, it did reduce total deadwood volume, lying deadwood volume (0.3-ha-scale) and the density of saproxylic microhabitat-bearing trees in both silver fir and spruce forests (Fig. 3). On the whole, salvage logging caused stronger differences with disturbed unharvested stands in spruce forests

than in silver fir forests, where it generally had no significant impact (Fig. 3). In spruce forests, salvage logging reduced the density of large snags by 91%, large logs by 87%, standing deadwood volume by 95%, deadwood diversity by 56%, density of fungus-bearing trees by 95% and relative basal area of dead trees by 91% compared with unharvested declining plots (Fig. 3).

3.2 Effect of forest dieback and salvage logging on species richness, abundance and traits

Saproxylic beetle community metrics responded to forest dieback more strongly in the Bavarian spruce plots than in the Pyrenean silver fir plots (Fig. 3). Moreover, significant responses were distinct, and sometimes, the effects were even opposite between the two regions. The only unequivocal response we observed in both spruce and silver fir dieback plots was the lack of significant variations in the abundance and richness of xylophagous and xylofungicolous beetles among dieback classes (Fig. 4). With spruce dieback, red-listed, cavicolous, flower-visiting or zoophagous species had a higher abundance and richness in declining than in healthy stands (Fig. 4). Conversely, forest dieback led to a decrease in the abundance and richness of zoophagous species in silver fir forests (Fig. 4).
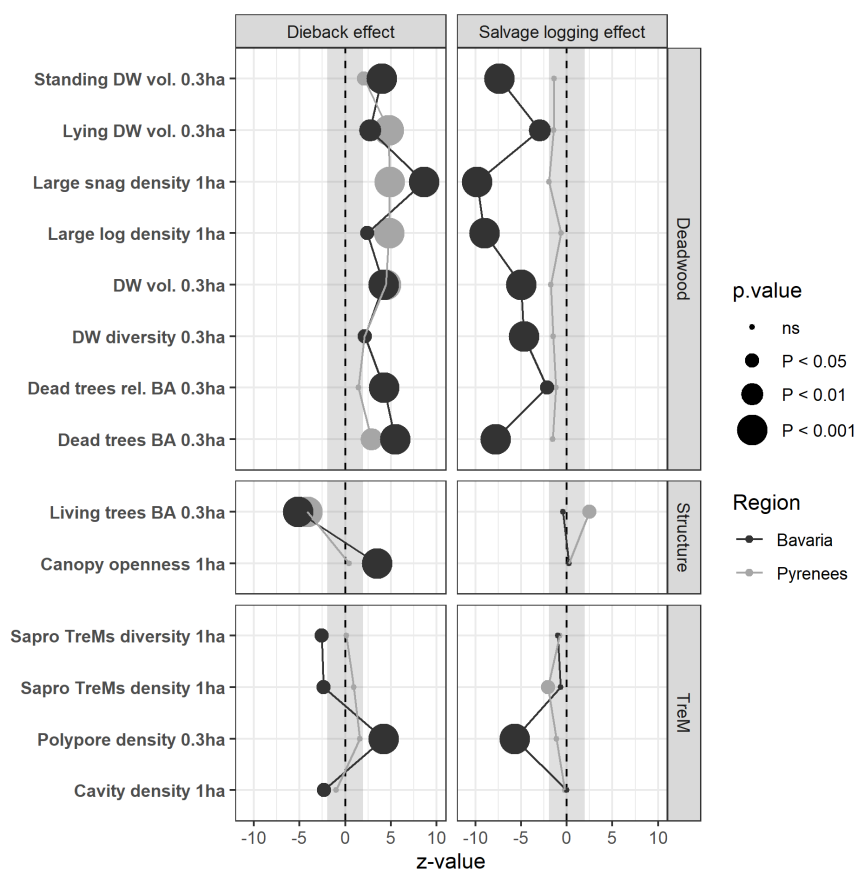

Figure 3: *Response of local forest stand features (deadwood, stand structure and tree-related microhabitats) to tree dieback (left panels) and salvage logging (right panels) in the Bavarian spruce forests (black) and in the Pyrenean silver fir forests (grey). Circles indicate effect significance and their diameter varies with p-value (lines between points are for visual purposes only); shaded areas indicate the range of non-significant values (z-values: ± 2.0).*

Regarding deadwood niche characteristics, declining spruce stands hosted assemblages with higher mean-diameter trait values than did healthy stands: beetle species assemblages sampled in declining spruce stands were on average associated to larger deadwood (Fig. 4). The increasing mean and decreasing dispersion of the decay trait in declining spruce stands indicate that beetle assemblages occurring on these declining plots were mostly composed of species associated to more fully decayed deadwood (Fig. 4). The increase in mean and dispersion of the canopy trait in declining spruce stands indicates that both open-canopy and closed-canopy preferring species occurred on more declining plots, but that assemblages were on average associated to more closed-canopy conditions (Fig. 4). The decrease in canopy trait diversity for silver fir stands means that a narrower range of species in terms of canopy preferences occurred on the declining plots (Fig. 4).

Overall, the effects of both dieback and salvage logging practices on community metrics were stronger in the spruce than in the silver fir plots (Fig. 4). Abundance and richness of cavicolous species, richness of red-listed species and of xylofungicolous species, and mean diameter trait decreased and abundance of flower-visiting or zoophagous species increased in the salvage-logged spruce plots (Fig. 4). Contrary to expectations, the abundance of conifer-associated xylophagous beetles did not significantly decrease in the salvaged-logged spruce plots compared to unharvested declining plots, and it even increased in the silver fir plots (Fig. 4). Finally, in the silver fir plots, the abundance of xylofungicolous species increased with salvage logging (Fig. 4).
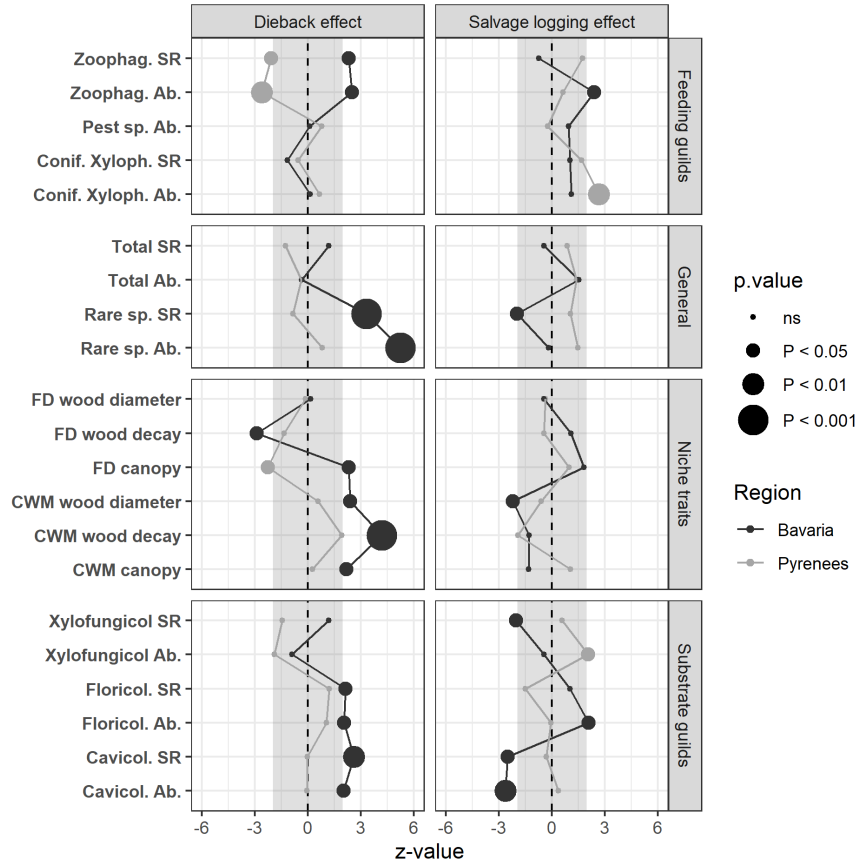
Figure 4: *Response of local saproxylic beetle community metrics (feeding guilds, niche trait guilds, substrate guilds and general diversity metrics) to tree dieback (left panels) and salvage logging (right panels) in Bavarian spruce forests (black) and in Pyrenean silver fir forests (grey). Circles indicate effect significance and their diameter varies with p-value (lines between points are for visual purposes only); shaded areas indicate the range of non-significant values (z-values: ± 2.0).*

3.3 Effects of forest dieback and salvage logging on assemblage composition

3.3.1 Effect of forest dieback on assemblage composition

Canonical Analysis of Principal coordinates (CAP) showed that the species composition of the saproxylic beetle assemblages was greatly modified by dieback in spruce (Fig. S.3) but not in silver fir stands (Fig. S.2). The silver fir CAP (Fig. 5) indicated that variations in species composition were only influenced by the dominant geographic site effect (Aure or Sault; Fig. 5 and S.2). However, significant environmental drivers associated to tree dieback were detected in the spruce dataset. Among the local forest stand features, basal area of living trees, but also openness and density of large snags contributed the most to inertia (Fig. 5). To a lesser extent, basal area of dead trees, TreM density, total volume of deadwood and density of large logs also significantly contributed to variations in assemblage composition. Within-class dissimilarity in unharvested declining plots was not (spruce forests) or only slightly and non-significantly (silver fir forests) higher than in healthy plots (Fig. 6).

3.3.2   Effect of salvage logging practices on assemblage composition

Saproxylic beetle species composition was significantly modified by salvage logging, though to a lesser extent than by dieback, in spruce (Fig. S.3) but not in silver fir forests (Fig. 5 and S.2). The environmental drivers of species composition associated to salvage logging were quite close to the variables related to dieback. Whereas variations in saproxylic beetle composition were only influenced by a strong geographic site effect in the silver fir forests, they were governed by the prevailing effect of canopy openness, and driven, to a lesser extent, by TreM density, deadwood diversity, basal area of living trees and density of large logs and large snags in the spruce forests (Fig. 5). Within-class dissimilarity in unharvested declining plots was significantly (silver fir forests) or slightly but non-significantly (spruce forests) higher than in the salvaged plots (Fig. 6).
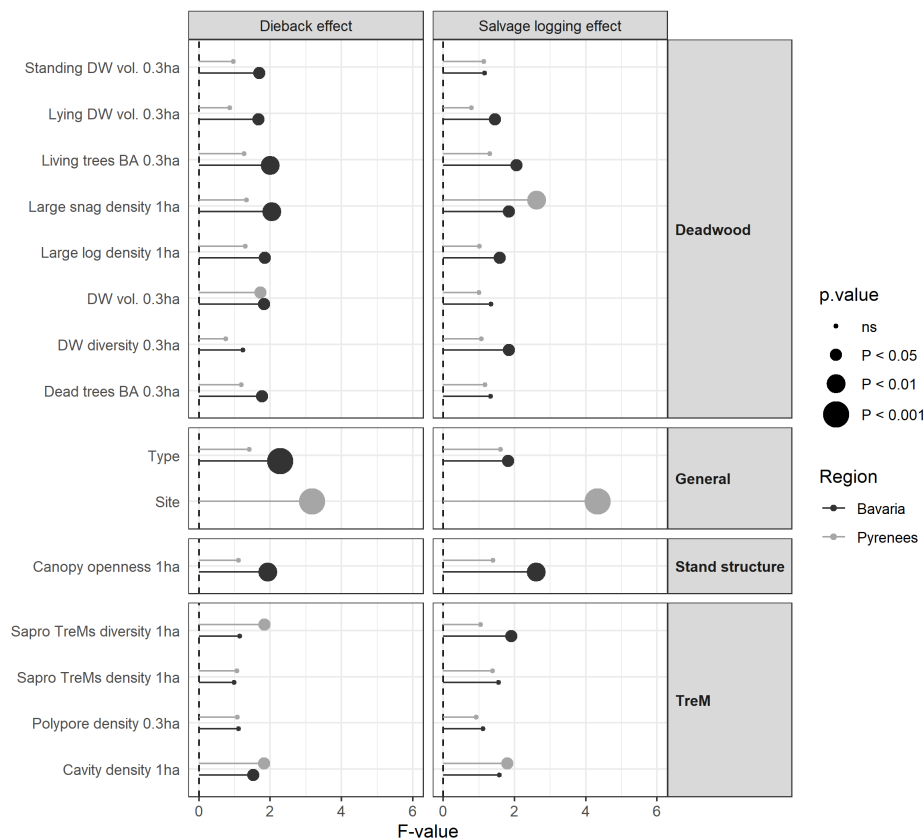

Figure 5: *Environmental drivers of variations in saproxylic beetle species composition, associated to tree dieback or salvage logging effects in Bavarian spruce forests (black) and in Pyrenean silver fir forests (grey). Effects of local stand features (deadwood, stand structure and tree-related microhabitats) tested with Canonical Analysis of Principal coordinates based on Bray-Curtis distance matrices: total inertia explained by each variable including inertia co-explained with other variables (bottom panel). Circles indicate effect significance and their diameter varies with p-value (100-run permutation tests).*
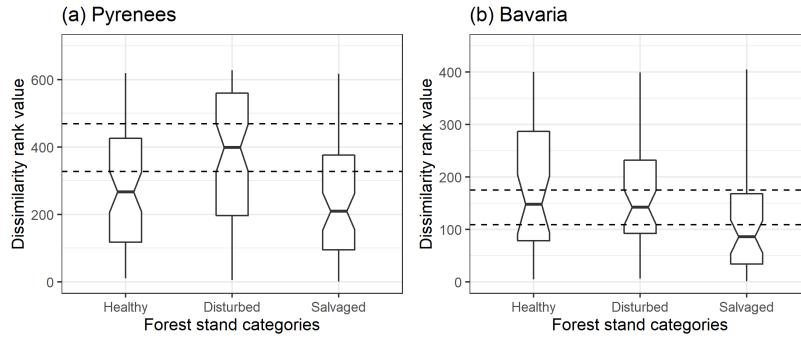
Figure 6: *ANOSIM plots showing the dissimilarity among beetle assemblages within the given forest stand categories in the Pyrenees (left) and in Bavaria (right). The bold horizontal bar in the box indicates the median; the bottom of the box indicates the 25th percentile; the top of the box indicates the 75th percentile and the extreme data points are marked by whiskers. Notches are used to differentiate group medians: if the notches for two boxes do not overlap, this is strong evidence that two medians differ (Chambers et al., 2018). Dotted lines indicate lower and upper notches from the disturbed category for comparison with the healthy and salvaged categories.*

3.4 Are the effects associated to forest dieback still significant after salvage logging operations?

Considering only the environmental variables that were both significant and included in the best models on community metrics, we detected many more effects of stand features associated to dieback effects (from healthy to declining) in the spruce than silver fir forests.

Overall, the metrics describing deadwood and stand structure had far stronger effects on saproxylic beetle assemblages than did TreMs (Tabs. 3 and 4).

In the spruce forests, the volume of standing deadwood was the most significant variable for saproxylic beetle communities with positive effects on abundance and species richness for all species, xylofungicolous, flower-visitor, zoophagous or red-listed species, but not for conifer-associated xylophagous species (Tab. 4). Cavicolous species positively responded to an increase in standing deadwood volume, both in abundance and richness (Tab. 4). Furthermore, the richness of all species and flower-visiting species increased with the density of large logs in the spruce forests (Tab. 4). In the silver fir stands, increasing canopy openness led to higher abundance for all species, as well as to higher abundance and richness for flower-visiting species (Tab. 3). The abundance of xylofungicolous species in the silver fir forests was positively affected by the basal area of living trees (Tab. 3).

Furthermore, several negative environmental effects associated to dieback were detected: there were slightly negative effects of lying deadwood diversity on the abundance of all species and xylofungicolous species in spruce forests (Tab. 4), and of zoophagous species in silver fir forests (Tab. 3); and a slight negative effect of the local density of TreMs on the abundance of red-listed species (in spruce forests; Tab. 4).

The vast majority (79% in the spruce stands, Tab. 4; 100% in the silver fir stands, Tab. 3) of these significant environmental effects associated to dieback were no longer significant after salvaged plots were included in the analysed data, i.e. in the subset merging salvaged and unharvested declining plots.

4 Discussion

4.1 Overall natural and anthropogenic disturbance effects

In both of the forest contexts in our study, dieback provided a biological legacy through an increase in deadwood resources (Fig. 3); however, the increase in deadwood resources was much greater in the spruce forests. In addition, in the spruce forests, dieback provided a structural legacy through an increase in canopy openness (Fig. 3). As a result, assemblage species composition was more strongly modified by dieback in the spruce than in the silver fir forests (Figs. 2, S.2 and S.3). Nonetheless, despite this increase in resources, and in contrast to other studies (Müller et al., 2010; Thom and Seidl, 2016), neither type of forest gained in total abundance or species richness after disturbance, compared to healthy stands. In our analyses, we did not take into account geographical features such as altitude or slope orientation, in addition to stand features. However lower altitudes or sun exposed slopes could significantly affect insect communities and their response to environmental changes. Nonetheless, all our study plots remain in the montane context (min: 660 m; max: 1560 m).

Table 3: *Effects of stand features (deadwood, stand structure and tree-related microhabitats) associated to dieback and salvage logging effects in* **Pyrenean silver fir forests** *on saproxylic beetle community metrics (feeding guilds, niche trait guilds, substrate guilds and general diversity metrics). Effects were tested with generalized linear mixed models (using "site" as a random variable). The variables involved in the best model of dieback effects (left panel) were assessed (direction and significance) in the models of salvage-logging effects (right panel). "Neg. binom." is the negative binomial probability distribution; "poisson" is the Poisson distribution"; "linear" is the Gaussian distribution.*

Response variable	Probability distribution	Disturbed + Healthy Best model	Estimate (β) ± se	Disturbed + Salvaged Estimate (β) ± se
General guilds				
Total Ab.	Neg. binom.	Canopy openness 1 ha	**0.28** ± 0.1	0.14^{ns} ± 0.14
Total SR	Neg. binom.	Null model		
Rare sp. Ab.	Neg. binom.	Large log density 1 ha	**0.34*** ± **0.16**	0.1^{ns} ± 0.35
Rare sp. SR	Poisson	Null model		
Substrate guilds				
Xylofungicol. Ab.	Neg. binom.	Living trees BA 0.3 ha	**0.31** ± 0.1	0.1^{ns} ± 0.11
Xylofungicol. SR	Neg. binom.	Null model		
Cavicol. Ab.	Neg. binom.	Null model		
Cavicol. SR	Poisson	Log standing DW vol. 0.3 ha	-0.15^{ns} ± 0.09	0.06^{ns} ± 0.08
Adult feeding guilds				
Floricol. Ab.	Neg. binom.	Canopy openness 1 ha	**0.27*** ± **0.1**	0.15^{ns} ± 0.13
Floricol. SR	Neg. binom.	Canopy openness 1 ha	**0.23*** ± **0.09**	0.18^{ns} ± 0.09
		Sapro TreM density 0.3 ha	0.14^{ns} ± 0.09	**0.17*** ± **0.08**
Larva feeding guilds				
Zoophag. Ab.	Neg. binom.	Lying DW diversity 0.3 ha	**-0.25*** ± **0.1**	-0.15^{ns} ± 0.11
Zoophag. SR	Neg. binom.	Log standing DW vol. 0.3 ha	-0.11^{ns} ± 0.07	0.11^{ns} ± 0.09
Conif. Xyloph. Ab.	Neg. binom.	Canopy openness 1 ha	0.41^{ns} ± 0.2	-0.08^{ns} ± 0.3
Conif. Xyloph. SR	Poisson	Canopy openness 1 ha	0.16^{ns} ± 0.08	0.14^{ns} ± 0.08
Pest sp. Ab.	Neg. binom.	Canopy openness 1 ha	**0.57*** ± **0.26**	0.38^{ns} ± 0.27

Salvage logging caused significant contrasts in dieback effects for stand and community metrics between the spruce and silver fir plots. Globally, salvage logging modified assemblage species composition in the spruce

forests only, not in the silver fir forests. This modification was less than for dieback. Unlike the overall negative impact of salvage logging on saproxylic beetle richness found in the meta-analysis by Thorn et al. (2018), in our study salvage logging had non-significant, or only slightly significant, effects on saproxylic beetles (Fig. 4).

4.2   Saproxylic beetles were affected by habitat/resource changes induced by forest dieback

4.2.1   Effects of changes in habitat/resource quantity

In the spruce plots, saproxylic beetles responded positively to the large increase in deadwood in the declining stands, as shown by an asymptotic concave function model (Fig. 7 a and b), in accordance with the "*Species-Resource Relationship*" (SRR) concept (Godeau et al., 2020). The "*species-energy hypothesis*" may be the underlying driver here (Seibold et al., 2016). Forest dieback resulted in higher amounts of large snags and logs, which are known to be key factors for saproxylic beetles (Bouget et al., 2014). The highly positive impact of increasing dieback on red-listed species, probably driven by the increase in volume of large deadwood and especially snags (Tab. 4), should be underlined. According to our trait database, the rare or red-listed species captured in our study were, on average, more closely associated to larger deadwood than were the common species (Fig. S.7); this confirms the importance of large deadwood pieces for insect diversity conservation. Accordingly, saproxylic species in declining spruce stands had a preference for larger deadwood than in healthy stands. Previous studies had already shown the importance of large deadwood for saproxylic beetles (Bouget et al., 2012, 2014; Brin et al., 2011). In addition, for degree of deadwood decay, the mean trait increased while the functional diversity decreased with dieback, indicating that increasing forest dieback favoured a specialist community associated to well-decayed deadwood pieces. These results for diameter and decay niche traits are in line with Gossner et al. (2013), who found beetle assemblages with a higher demand for large-diameter and highly-decayed deadwood in forests where large amounts of deadwood had accumulated.

4.2   *Saproxylic beetles were affected by habitat/resource changes induced by forest dieback*

Table 4: *Effects of stand features (deadwood, stand structure and tree-related microhabitats) associated to dieback and salvage logging effects in **Bavarian Norway spruce forests** on saproxylic beetle community metrics (feeding guilds, niche trait guilds, substrate guilds and general diversity metrics). Effects were tested with generalized and general linear models. The variables involved in the best model of dieback effects (left panel) were assessed (direction and significance) in the models of salvage-logging effects (right panel). "Neg. binom." is the negative binomial probability distribution; "linear" is the Gaussian distribution.*

Response variable	Probability distribution	Disturbed + Healthy Best model	Estimate (β) $\pm$ se	Disturbed + Salvaged Estimate (β) $\pm$ se
General guilds				
Total Ab.	Neg. binom.	Log standing DW vol. 0.3 ha	**0.49*** $\pm$ 0.13**	$-0.08^{ns} \pm 0.13$
		Lying DW diversity 0.3 ha	**-0.31* $\pm$ 0.12**	$0.19^{ns} \pm 0.12$
Total SR.	Neg. binom.	Log standing DW vol. 0.3 ha	**0.29** $\pm$ 0.10**	$0.06^{ns} \pm 0.08$
		Large log density 1 ha	**0.21* $\pm$ 0.09**	$0.12^{ns} \pm 0.07$
Red-listed sp. Ab.	Neg. binom.	Log standing DW vol. 0.3 ha	**1.43*** $\pm$ 0.42**	$-0.26^{ns} \pm 0.21$
		Sapro TreM density 0.3 ha	**-0.42* $\pm$ 0.16**	$0.09^{ns} \pm 0.23$
Red-listed sp. SR	Neg. binom.	Log standing DW vol. 0.3 ha	**0.96*** $\pm$ 0.25**	**0.48** $\pm$ 0.15**
Substrate guilds				
Xylofungicol. Ab.	Neg. binom.	Log standing DW vol. 0.3 ha	**0.7** $\pm$ 0.22**	$0.18^{ns} \pm 0.15$
		Lying DW diversity 0.3 ha	**-0.6** $\pm$ 0.19**	$-0.09^{ns} \pm 0.15$
Xylofungicol. SR	Neg. binom.	Log standing DW vol. 0.3 ha	**0.37** $\pm$ 0.13**	$0.08^{ns} \pm 0.14$
Cavicol. Ab.	Neg. binom.	Log standing DW vol. 0.3 ha	**0.69** $\pm$ 0.23**	**0.57** $\pm$ 0.17**
Cavicol. SR	Neg. binom.	Log standing DW vol. 0.3 ha	**0.41* $\pm$ 0.19**	$0.13^{ns} \pm 0.19$
Adult feeding guilds				
Floricol. Ab.	Neg. binom.	Log standing DW vol. 0.3 ha	**0.74** $\pm$ 0.23**	$-0.22^{ns} \pm 0.16$
Floricol. SR	Neg. binom.	Log standing DW vol. 0.3 ha	**0.46** $\pm$ 0.16**	$-0.07^{ns} \pm 0.08$
		Large log density 1 ha	**0.28* $\pm$ 0.13**	$-0.005^{ns} \pm 0.09$
Larva feeding guilds				
Zoophag. Ab.	Neg. binom.	Log standing DW vol. 0.3 ha	**0.66*** $\pm$ 0.13**	$-0.16^{ns} \pm 0.12$
		Lying DW diversity 0.3 ha	$0.2^{ns} \pm 0.1$	$0.08^{ns} \pm 0.15$
Zoophag. SR	Neg. binom.	Log standing DW vol. 0.3 ha	**0.42*** $\pm$ 0.11**	$0.11^{ns} \pm 0.09$
Conif. Xyloph. Ab.	Neg. binom.	Sapro TreM density 0.3 ha	**-0.56* $\pm$ 0.26**	**-0.73* $\pm$ 0.29**
Conif. Xyloph. SR	Neg. binom.	Null model		
Pest sp. Ab.	Neg. binom.	Sapro TreM density 1 ha	**-0.58* $\pm$ 0.27**	**-0.77* $\pm$ 0.3**

Unsurprisingly, among the environmental drivers associated to dieback effects, increasing snag density had a strong and significant influence on univariate community metrics (Tab. 4) and assemblage composition in spruce forests (Fig. 5). According to the literature, snags (and even more so, large snags) decline drastically in managed forests (Ekbom et al., 2006), even though they are essential for rare or red-listed species conservation (Bouget et al., 2012, 2014; Hammond et al., 2004; Kappes and Topp, 2004; Sverdrup-Thygeson and Ims, 2002).

The lack of response of the saproxylic beetle communities in the silver fir plots may be explained by the relatively low amount of deadwood generated by the drought-induced dieback, with levels remaining below critical threshold values (Müller and Bütler, 2010).
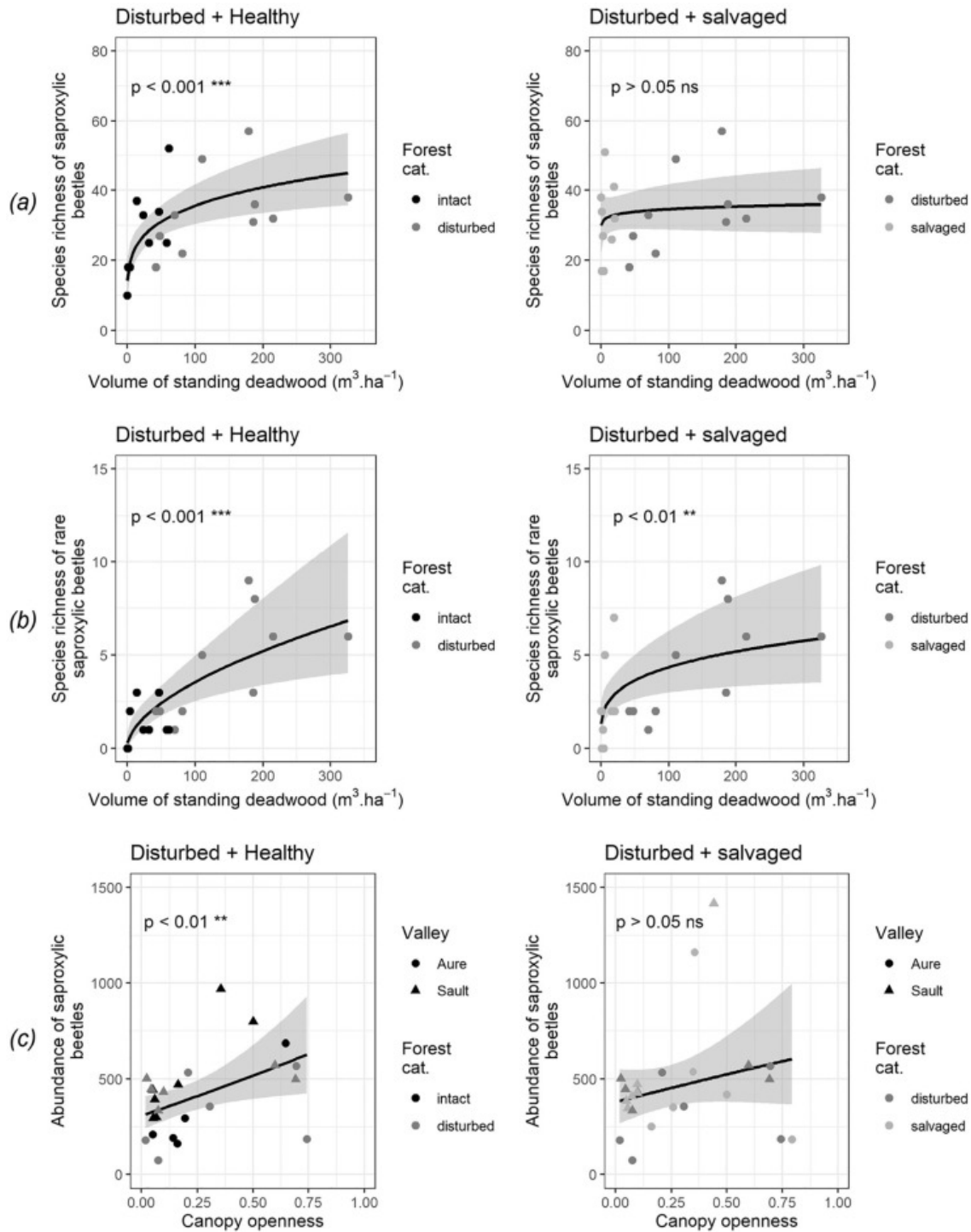
Figure 7: *Relationship between standing deadwood volume in Bavarian spruce forests and mean species richness of saproxylic beetles (a), or red-listed saproxylic beetles (b), and between canopy openness in Pyrenean silver fir forests and mean abundance of all saproxylic beetles (c). Left: disturbed and "intact" (or healthy) stands; Right: disturbed and salvaged stands. The black line is the regression curve from the negative binomial model (with a log-transformation of x) and the grey area indicates the 95% confident interval. "intact" = "healthy".*

4.2.2 Effects of changes in habitat/resource heterogeneity

Habitat heterogeneity has several dimensions at the local scale. Firstly, higher canopy-openness values indicates a finer-grain within-stand mosaic of closed-canopy and open-canopy patches. In our case study, canopy openness, which increased with stand dieback in the spruce stands, strongly drove assemblage composition and significantly fostered flower-visiting species (Fig. 5), and positively influenced several guilds of saproxylic beetles in the silver fir stands (Fig. 7 and Tab. 3). Similarly, Bouget et al. (2013) had already described potential interactions between an open-mosaic forest environment and saproxylic beetles. Secondly, substrate diversity, i.e. deadwood and TreM diversity, reflects the number of available niches. In our study, deadwood diversity increased in both declining spruce and silver fir stands, though less strongly than deadwood volume, whereas TreM diversity decreased (although not significantly in the silver fir context). In addition, deadwood diversity did not appear among the best variables influencing total species richness and abundance, as did deadwood volume. Nevertheless, (i) deadwood volume and diversity were highly correlated (Fig. S.8), and (ii) total saproxylic beetle species richness, taken independently, responded positively to deadwood diversity in the spruce stands (Fig. S.9). Therefore, habitat quantity and heterogeneity could possibly have had additive positive effects on saproxylic beetle species, in agreement with the "*habitat-heterogeneity hypothesis* underlying species coexistence (Seibold et al., 2016).

4.3 Salvage logging caused the loss of ecological relationships resulting from the dieback process

Most of the significant environmental effects on biodiversity associated with dieback were no longer significant after accounting for the salvaged plots in our study data (Tab. 3 and 4). Moreover, we measured a large depletion of deadwood resources in salvaged declining stands compared with declining unharvested stands in the spruce forests (an 86% decrease in total deadwood on average; Fig. 3). However, whereas saproxylic beetles positively responded to the additional dieback-induced deadwood in spruce stands (see 4.2; Fig. 7), they did not decrease in abundance or species richness subsequent to deadwood depletion (Fig. 4). Deadwood is one of the main biological legacies induced by forest dieback (Swanson et al., 2011) and we therefore expected its loss to affect the key group of saproxylic beetles. Extinction debt processes may explain the limited immediate deleterious effects of salvage harvests in our results (Kuussaari et al., 2009; Tilman et al., 1994). Indeed, saproxylic beetle species may initially survive the habitat loss following the harvesting, but then go extinct after a "*relaxation time*" determined by species life span and landscape mitigation processes related to neighbouring habitat patches and beetles dispersal abilities (Kuussaari et al., 2009).
Nevertheless, when comparing the declining unharvested plots to the salvaged declining plots, we measured several functionally consistent responses of the beetle community in the spruce forests:

  i we found a decrease in red-listed species richness parallel to a decreased mean diameter niche trait as a result of the decrease in large snags and large logs (Fig. 3 and 4);

  ii we found a decrease in the species richness of fungicolous beetles as a result of a decrease in the density of fungus-bearing trees (Fig. 3 and 4).

The negative consequences of salvage logging on red-listed species richness had already been highlighted by Thorn et al. (2014) in the same region, and was likely due to the decrease in snag density. Furthermore, on our spruce plots, cavicolous beetles declined in both abundance and richness parallel to the decrease in snag volume (Fig. 4 and Tab. 4). For zoophagous beetles, the significant increase in their abundance in our salvaged declining spruce stands was not consistent with a potential bottom-up effect of beetle decline on higher trophic levels within the saproxylic food web.

In line with a likely decrease in habitat heterogeneity caused by the salvage logging, as suggested by the consistently observed reduction in deadwood diversity in spruce stands, we detected an increase in within-class assemblage similarity in the salvaged declining plots compared to the unharvested declining plots (significant for silver fir but not for spruce stands; Fig. 6). Removing all of the biological legacies inherited from the forest dieback during salvage logging would likely simplify the forest structure compared to declining unharvested stands. In agreement with our results, this could lead to reduced variability in species composition, i.e. community homogenisation (Cobb et al., 2007). It should be remembered, however, that the positive relationship between within-stand heterogeneity and local forest biodiversity has been empirically challenged (see above; Schall et al., 2018, despite the strong theoretical background supporting this relationship; Wilson, 2000).

In the Bavarian context, response patterns to salvage were clearer but it should be noticed that unharvested declining plots and salvaged plots not only differed by harvesting practices but also by a different time lag from the dieback-inducing event. Indeed, massive bark beetle outbreaks occurred in 2001 (±5 years) in unharvested plots and in 2009 (±4 years) in harvested plots, which could have amplified short-term effects of salvage harvests studied in 2016.

4.4 Contrasting responses of saproxylic beetle communities according to forest dieback context

Forest dieback and salvage logging induced much sharper and stronger effects on environmental and community metrics in the spruce than in the silver fir forests (Tab. 5 and Fig. S.10). Whereas the species composition of saproxylic beetle assemblages was significantly affected by dieback and salvage logging in spruce stands, neither dieback nor salvage logging modified species composition in the silver fir forests. Potential limitations in our comparison of case studies should be reminded. The contrast between Bavaria and the French Pyrenees seems partly related to dieback "severity" (Figs. 2 and 7; Tab. 5). A simulation approach suggested that more severe disturbances have more positive impacts on biodiversity (Thom et al., 2017). In the spruce stands, pest-induced dieback recently caused massive tree mortality over large landscape (Thorn et al., 2014), while in the silver fir stands, drought-induced dieback generated only small patches of dead trees (Camarero et al., 2011), even if recurrent droughts can result in significant long-term delayed mortality (Bréda et al., 2006). The spruce forests in our study naturally have a higher baseline level of deadwood than the silver fir forests (Tab. 5); in addition, they showed a stronger dieback-induced increase in deadwood and in canopy openness (Tab. 5). Moreover, even though spruce and silver fir are valuable species-rich host trees (Lemperiere and Marage, 2010; Müller et al., 2015), the regional species-pool in the Bavarian National Park landscape was possibly more likely to be enhanced by improved habitat conditions.

Indeed, saproxylic beetles are known to respond to large-scale habitat effects (Gibb et al., 2006; Økland et al., 1996).

Table 5: *Some of the features characterising the two forest dieback processes in the study.*

Features	Bavaria	Pyrenees
Dieback agent	Storm + bark beetle outbreak	Droughts
Tree species	*Picea abies*	*Abies alba*
Studied species proportion	77%	62%
Dieback severity	High-severity	Moderate-severity
Disturbance scale	Large	Large
Size of deadwood patches	Landscape scale	Local scale
Year of onset 2001	(±5 years)	2003
Baseline deadwood level in healthy plots	60.2 $m^3.ha^{-1}$	23.4 $m^3.ha^{-1}$
Average deadwood accumulation caused by dieback	+212.3 $m^3.ha^{-1}$ (+353%)	+60.6 $m^3.ha^{-1}$ (+259%)
Decrease in living-tree basal area caused by dieback	-36.6 $m^2.ha^{-1}$ (−86%)	-16.4 $m^2.ha^{-1}$ (−42%)
Increase in canopy openness caused by dieback	+53%	+9.4%

5 Implications for forest management and future research

Saproxylic beetle species had contrasting responses to disturbance depending on the type of disturbance (drought-induced or pest-induced dieback and salvage logging). In Bavaria, they benefitted from the severe forest dieback caused by massive bark beetle outbreaks. Conversely, they did not significantly respond to the drought-induced forest dieback in the Pyrenees. Indeed, the local accumulation of deadwood in the French plots was insufficient to favour saproxylic biodiversity. Further research should consider the influence of (i) dieback level at the landscape scale on local and regional biodiversity, (ii) contrasting factors that trigger dieback, and (iii) dieback severity. Future investigations should also focus on the network design of retention patches of deadwood-rich areas in managed forest landscapes (Müller et al., 2010). Retaining biological legacies associated to forest dieback (such as large snags) could help to limit the negative impact of salvage logging on key habitat features and may therefore be a good addition to a biodiversity-friendly management approach.
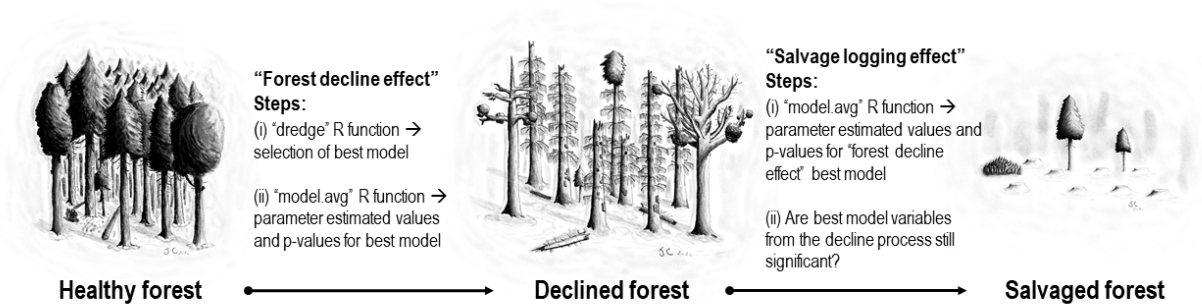
6 Supplementary material

Figure S.1: *"Process logic" of our data analysis. First: the natural forest dieback process – we assessed the best model (with the dredge function from the MuMin R package) to obtain beta estimates and p-values by "model averaging" with the MuMin R package. Second: the anthropogenic effect (salvage logging)– we carried out "model averaging" on the salvage logging dataset and then checked to see if the variables from the dieback-effect best models were still significant. The objective was to assess how salvage logging changed the ecological relationships between stand features and saproxylic beetle communities.*

Table S.1: *Table of stand feature effects (deadwood, stand structure and tree-related microhabitats) associated to dieback or salvage logging effects in* **Pyrenean silver fir** *forests on saproxylic beetle niche traits (CWM = "community weighted mean"; FD = "functional diversity"). Effects were tested through generalized linear mixed models (with "site" as a random variable). The variables involved in the best model for dieback effects (left panel) were assessed (direction and significance) in the models of salvage logging effects (right panel). "Linear" is a Gaussian distribution.*

Response variable	Probability distribution	Disturbed + Healthy		Disturbed + Salvaged
		Best model	Estimate (β) ± se	Estimate (β) ± se
Niche traits				
CWM wood diameter	Linear	Lying DW diversity 0.3ha	**-0.06* ± 0.03**	$0.004^{ns} \pm 0.02$
FD wood diameter	Linear	Lying DW diversity 0.3ha	$0.06^{ns} \pm 0.04$	$-0.006^{ns} \pm 0.04$
CWM wood decay	Linear	Living trees BA 0.3ha	**-0.11* ± 0.05**	$-0.08^{ns} \pm 0.05$
		Large log density 1ha	**0.11 ± 0.04**	$0.08^{ns} \pm 0.05$
FD wood decay	Linear	Canopy openness 1ha	**-0.06* ± 0.03**	$-0.04^{ns} \pm 0.03$
CWM canopy	Linear	Null model		
CWM wood decay	Linear	Canopy openness 1ha	**-0.09* ± 0.04**	$-0.04^{ns} \pm 0.04$
		Living trees BA 0.3ha	**0.08* ± 0.04**	$0.02^{ns} \pm 0.04$

Table S.2: *Table of stand-feature effects (deadwood, stand structure and tree-related microhabitats) associated to dieback or salvage logging effects in **Bavarian spruce forests** on saproxylic beetle niche traits (CWM = "community weighted mean"; FD = "functional diversity"). Effects were tested with generalized and general linear models. The variables involved in the best model for dieback effects (left panel) were assessed (direction and significance) in the models of salvage logging effects (right panel). "Linear" is a Gaussian distribution.*

Response variable	Probability distribution	Disturbed + Healthy		Disturbed + Salvaged
		Best model	Estimate (β) ± se	Estimate (β) ± se
Niche traits				
CWM wood diameter	Linear	Large log density 1ha	$0.12^{ns} \pm 0.07$	$0.05^{ns} \pm 0.04$
FD wood diameter	Linear	Log standing DW vol. 0.3ha	$\mathbf{0.09^* \pm 0.04}$	$-0.002^{ns} \pm 0.05$
CWM wood decay	Linear	Log DW vol. 0.3ha	$\mathbf{0.24^{**} \pm 0.08}$	$0.08^{ns} \pm 0.07$
FD wood decay	Linear	Living trees BA 0.3ha	$\mathbf{0.14^{**} \pm 0.05}$	$0.08^{ns} \pm 0.05$
CWM canopy	Linear	Lying DW diversity 0.3ha	$\mathbf{0.08^* \pm 0.04}$	$0.03^{ns} \pm 0.04$
FD canopy	Linear	Canopy openness 1ha	$0.12^{ns} \pm 0.06$	$0.11^{ns} \pm 0.06$
		Large log density 1ha	$\mathbf{0.12^* \pm 0.04}$	$-0.03^{ns} \pm 0.06$

Table S.3: *Analysis of between-class dissimilarity of saproxylic beetle assemblages based on Bray-Curtis distance matrices ("adonis" function from the vegan package, Oksanen et al., 2022). Comparison of species assemblage composition between healthy and unharvested disturbed stands (middle column) and between unharvested disturbed and salvaged stands (right column).*

Context	Healthy vs. Disturbed	Disturbed vs. Salaged
Pyrenees	$p = 0.25^{ns}$	$p = 0.12^{ns}$
Bavaria	$\mathbf{p < 0.001^{***}}$	$\mathbf{p = 0.029^*}$

P-values after a 999-run permutation test: *** $P < 0.001$; * $0.05 > P > 0.01$
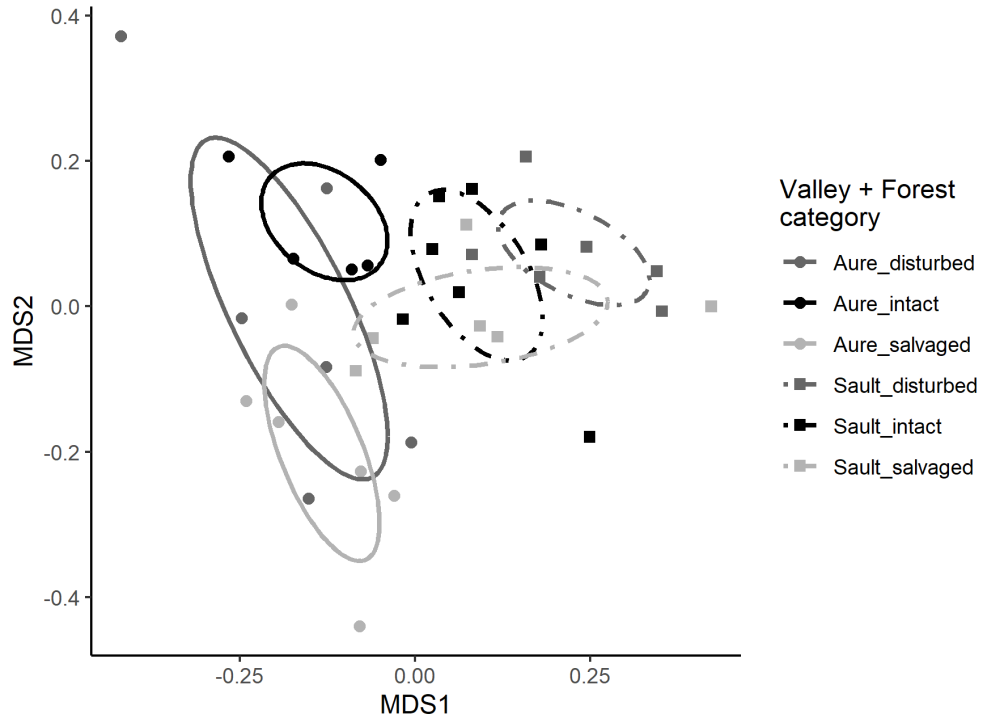
Figure S.2: *Results of the non-metric dimensional scaling (NMDS) analysis of communities in the Pyrenean Abies alba forests.*
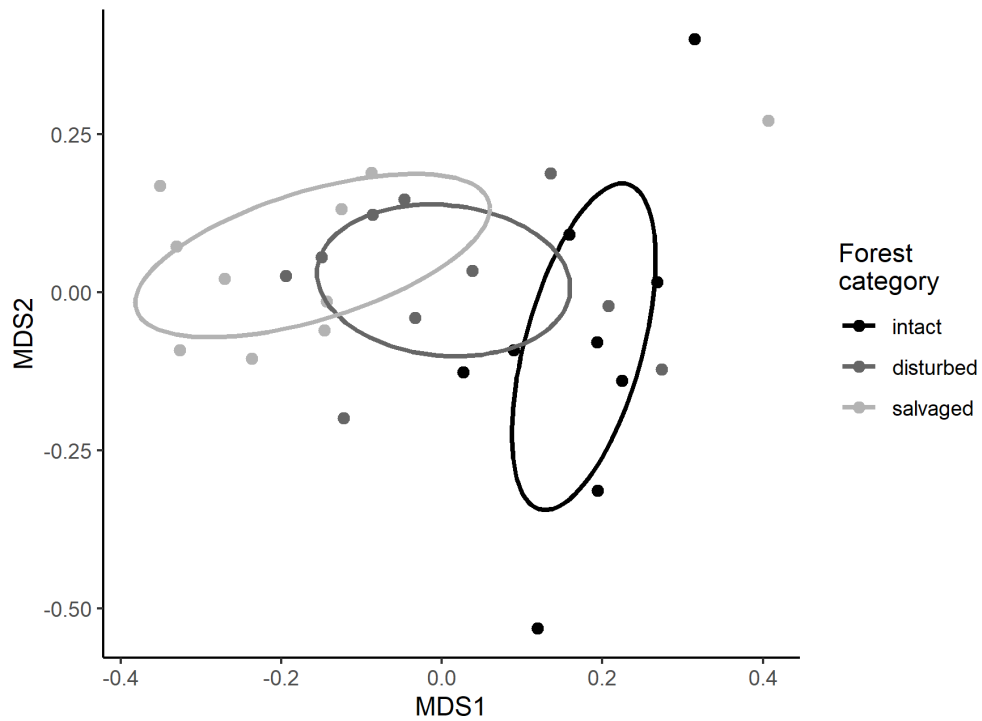

Figure S.3: *Results of the non-metric dimensional scaling (NMDS) analysis of communities in the Bavarian Picea abies forests.*
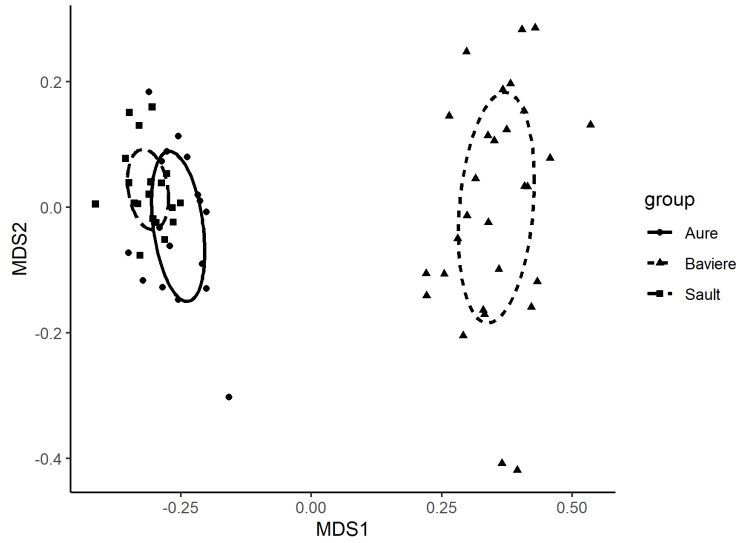
Figure S.4: *Results of the non-metric dimensional scaling (NMDS) analysis of communities at all study sites.*
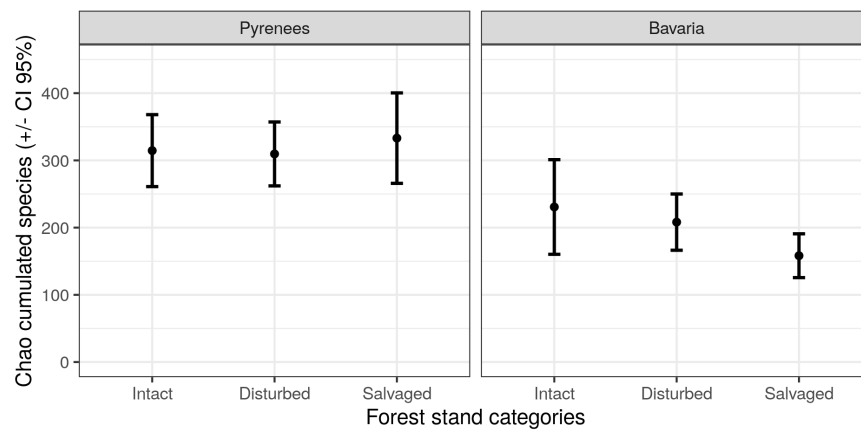

Figure S.5: *Extrapolated species richness using the Chao method for each country and each forest category. Points represent means and error bars the 95% confidence interval. "Intact" = "healthy"*
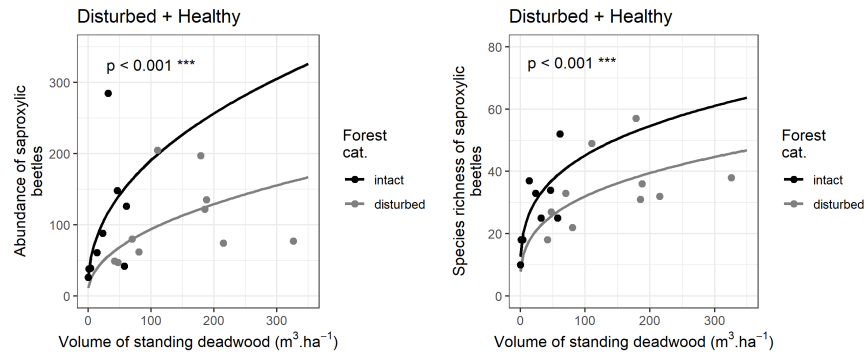
Figure S.6: *Relationship between volume of standing deadwood in Bavarian spruce forests and abundance of saproxylic beetles as a whole (left); and species richness of saproxylic beetles as a whole (right). Lines are the regression curves from a negative binomial model (with log-transformation of x on the right). "intact" = "healthy"*
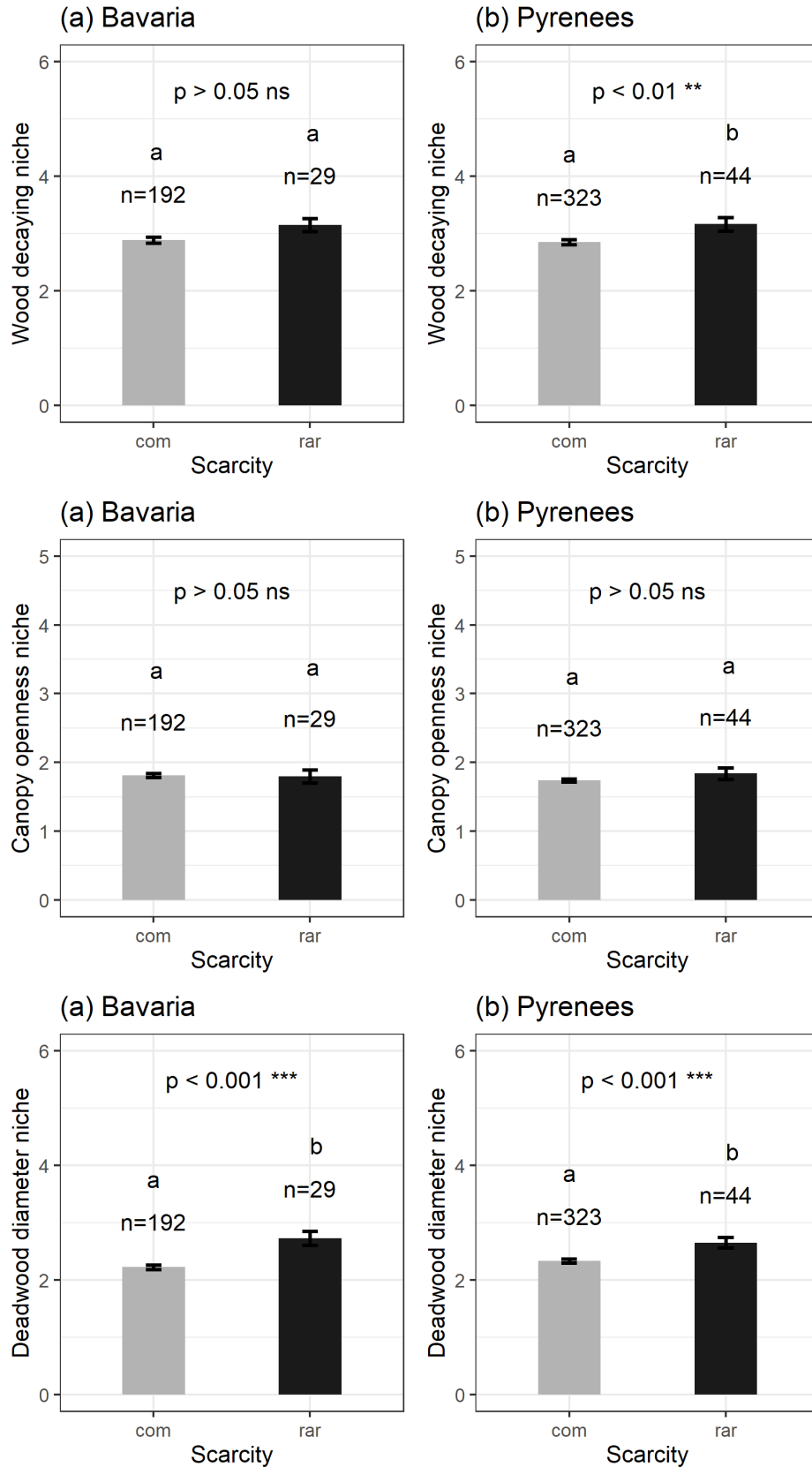
Figure S.7: *Mean niche occupied by common ("com") and rare ("rar") (red-listed in Bavaria) species captured in Bavaria (a) and the Pyrenees (b). Letters were assigned after a Student's test.*
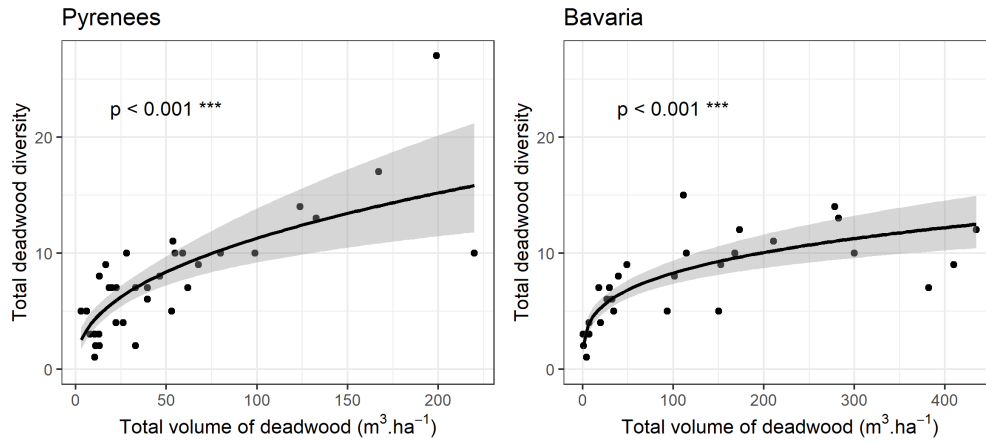
Figure S.8: *Relationship between deadwood volume and deadwood diversity in the Pyrenean silver fir forest (left) and the Bavarian spruce forest (right). The black line is the regression curve from a negative binomial model and the grey area indicates the 95% confident interval.*
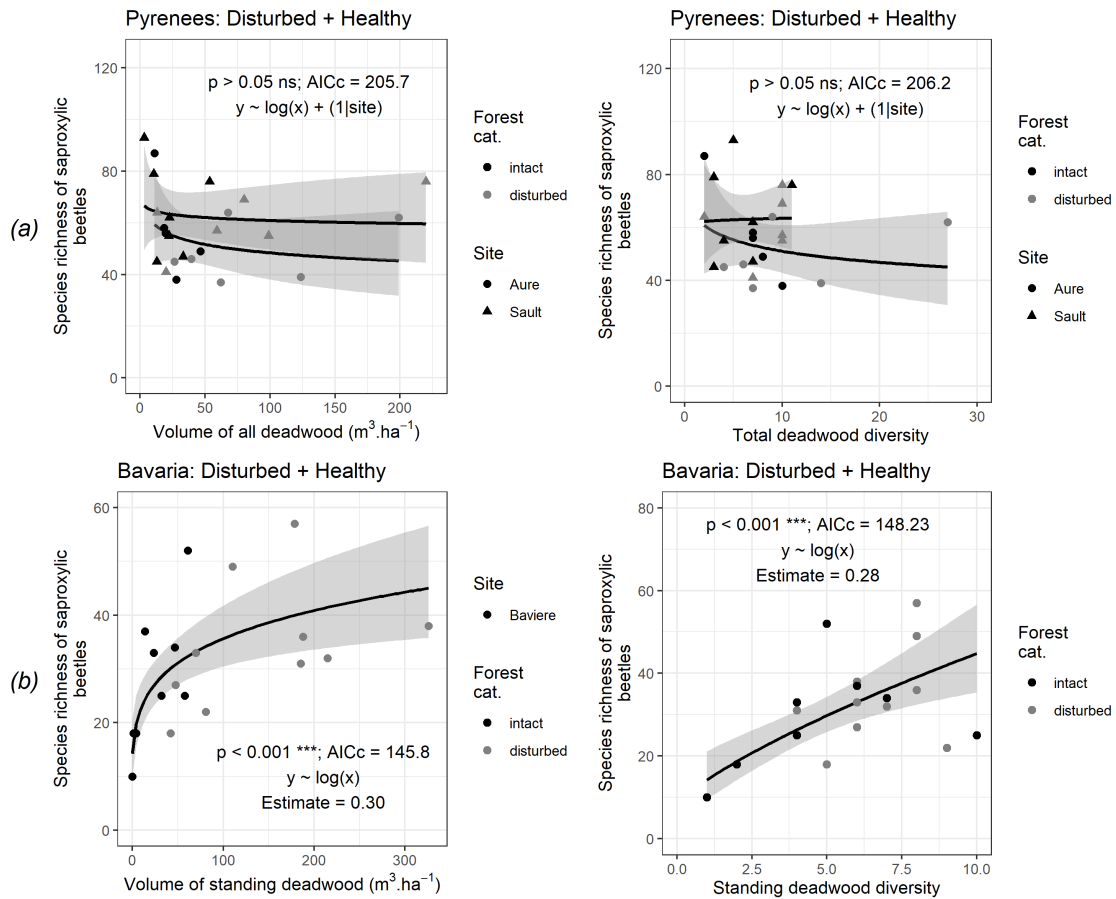
Figure S.9: *Model comparisons between total saproxylic beetle species richness in each region (Pyrenees = a; Bavaria = b) and (left panels) deadwood volume (reflecting resource quantity) and (right panels) deadwood diversity (reflecting resource diversity). We selected the variable associated with the lowest AICc for each resource quantity variable (all, standing and lying deadwood volume) and for each resource diversity variable (all, standing and lying deadwood diversity). The black line is the regression curve from the negative binomial model and the grey area indicates the 95% confident interval.*

(a) Bavaria spruce forest

(b) Pyrenean fir forest

Figure S.10: *Pictures of insect-induced forest dieback in Bavaria (left) and climate-induced forest dieback in the Pyrenees (right). The severity of the phenomenon is very different for each of the two cases: very severe in Bavaria, moderately severe in the Pyrenees.*

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